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THE STRUCTURE AND LIFE OF FOREST TREES

The Structure and Life of Forest Trees

By

Dr. M. BÜSGEN

PROFESSOR IN THE ROYAL PRUSSIAN FOREST ACADEMY IN HANN.-MÜNDEN

THIRD, REVISED AND ENLARGED EDITION

BY

Dr. E. MÜNCH

PROFESSOR IN THE FOREST ACADEMY AT THARANDT

ENGLISH TRANSLATION

BY

THOMAS THOMSON, M.Sc.

UNIVERSITY LECTURER IN FORESTRY, UNIVERSITY COLLEGE OF NORTH WALES, BANGOR



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PREFACE TO THE SECOND EDITION

In the following book it is sought to present to those wishing to make a close study of the life of trees an account of the principal questions with which science is now occupied in this field. The references to the literature, though owing to the plenitude of material they can make no claim to completeness, should enable the reader to go more deeply at need.

Research work in the sphere of tree-life has increased so greatly since the appearance of the first edition that a complete revision was necessary. Should the book be found of use in indicating open questions and facilitating their solution its purpose will be fulfilled.

M. BÜSGEN.

Hann.-Münden,
June, 1917.

PREFACE TO THE THIRD EDITION

Büsgen's work has fulfilled in a very high measure the purpose ascribed to it by him in the Second Edition ; namely, to indicate open questions and facilitate their solution. The effect of the book is to be traced over and over again in the literature and, not least to its influence, are due many of the scientific advances which leave no chapter of the subject matter untouched and now make its revision necessary.

Büsgen died on July 22, 1921.

Entrusted with the honourable task of preparing the new edition, I have endeavoured to carry on Büsgen's work in his spirit. Büsgen left some verbal alterations for the first chapter and a large number of short abstracts from the literature which I was able to use. Nevertheless, I alone must bear responsibility for the changes. When making additions and alterations I have adhered as far as possible to the text of the second edition, but many sections have had to be more drastically reconstructed or new ones inserted. I have only made abbreviations of the old text as considerations of space required.

The illustrations have been increased by forty-seven. A newly-compiled List of Authors, which became necessary owing to the multiplication of references, and the carefully enlarged index will facilitate reference. The popular plant names used in the text have their botanical names attached to them in a special index. I acknowledge with thanks the assistance rendered to me in the preparation of the index and the correction of proofs by Forstreferendar H. Lehmann, attached to the Botanical Institute of the Forest Academy.

The book should, in the future as in the past, form a bridge between Botany and Forestry, communicating to the forester the results of botanical research and to the botanist the valuable advances in forest botany contained in forestry literature, which, without such help, are often too easily lost to general botany.

E. MÜNCH.

THARANDT,
October, 1926.

TRANSLATOR'S PREFACE

DURING recent years many valuable works have appeared both in England and America on Silviculture, Forest Management, and other branches of Forestry, but there is, so far, no book dealing comprehensively with the structure and life of forest trees. It is true that there are important standard works such as Dallimore and Jackson's "Handbook of Coniferæ," which describe the various species, and that much information as to their structure and physiology is to be found in the various textbooks of Silviculture and Botany, but no work collects together in one volume the results of past researches in this field with references to the original papers. It is to fill this gap that I venture to put forward this translation of Büsgen's book.

A vast body of forestry literature has grown up which is of a botanical nature. The scientists attached to the various Forestry Schools and Government Forestry Research Institutions have contributed enormously to the advancement of our knowledge of trees, and their papers have largely appeared in the technical forestry periodicals or in the publications of the institutions themselves. The pure botanist has also found in the phenomena of tree growth a very fruitful field for research. The great size and long life of trees have confronted the plant physiologist with problems which have challenged his attention, whilst the importance and complexity of the forest as a plant formation have made it the subject of close investigation by the ecologist. There is therefore a great mass of material in botanical literature which deals with trees.

It was in order to bring together the results of research appearing in forestry and botanical literature that Büsgen wrote his book: "Bau und Leben unserer Waldbäume." The first edition appeared in 1897 and contained 225 pages with 100 figures. It not only gave a survey of what was known of the structure and physiology of trees, but also pointed out open questions and suggested lines of

research. The numerous references guided those who wished to pursue any part of the subject more deeply to the original sources.

The second edition appeared in 1917, and the progress made in all branches of the subject in the intervening years necessitated a considerable enlargement and revision of the book. Büsgen died in July, 1921. The present edition owes much to the editor, Dr. E. Münch. Whilst preserving the main lines of Büsgen's work, he has expended and rewritten many of the sections and has himself contributed in no small degree to the advances which have made the further revision and enlargement of the book necessary. In particular he has given in Chapter XII.2, the first account in forestry literature of his own theory of the circulation of sap and its mechanism, and has also added an entire new chapter on "Local Races," on which he is a recognised authority. This latter subject is one of particular importance to British forestry which is so largely concerned with afforestation with exotic species.

Owing to the length of the work and the already copious bibliography, I have not thought it advisable to attempt to introduce additional English references. A list of the more important German works available in English editions is given after the list of authors cited. I have checked the references with great care and trust that they will be found free from errors. I hope that the volume will prove a useful addition to our forest-botanical literature.

THOMAS THOMSON.

BANGOR, N. WALES.
June, 1929.

CONTENTS

CHAPTER I

PAGE

THE FORM OF THE TREE 1

1. The Tree in the Change of the Seasons 1
2. The Annual Shoot 2
3. Arrangement of the Buds on the Annual Shoot. Length of the Internodes 5
4. The Lammas Shoot 10
5. Length of the Annual Shoots. Height-Growth . . . 13
6. Long Shoots and Dwarf Shoots 21
7. Angle of Divergence 25
8. Tree and Shrub. Self-cleaning. Cladoptosis . . . 28
9. Alterations of the Original Arrangement of the Branches. Crown Forms 34
10. Tree Heights. Tree Girth. Tree Age 37
11. General Remarks on the Causes of the Form of Trees . . 38
12. Effect of the Force of Gravity on the Form of Trees . 43
13. Tree-Form and Light. Nature of Stimulus Phenomena . . 46
14. Change of Form according to the part of the Tree, Age, Environment, and Hereditary Disposition . . . 49

CHAPTER II

THE BUDS. 53

1. The Interior of the Bud 53
2. The Bud-Scales 55
3. The Origin and Perfecting of the Buds 59
4. The Resting of the Buds and its Cessation 61
5. The Unfolding of Buds 65
6. Dormant Buds and Epicormic Branches 70
7. Adventitious Buds and Shoots 73
8. Cause and Significance of the Formation of Epicormic Branches 75
9. Summary of Bud Characters of certain Trees. 79

CHAPTER III

PROPERTIES AND LIFE PROCESSES OF THE MERISTEM OF THE TREE 80

1. The Cell 80
2. The Origin of Cells at the Growing Point 88
3. The Epidermis 91
4. The Origin and Formation of the Conducting Channels. Secondary Thickening 92
5. Survey of the Tissues of the Mature Shoot 96
6. Growth in Length of the Cambium Cells. Torsion of the Fibres 97
7. The Seasonal Course of Cambium Activity in General . . 98
8. Causes of the Quiescence and Activity of the Cambium . . 104

CHAPTER IV

PAGE
THE ELEMENTS OF THE XYLEM 106
1. Lignification 106
2. The Living Constituents of the Xylem 110
3. The Dead Constituents of the Xylem 117
4. Change from Sapwood to Heartwood 121
5. The Pith 129
6. Summary of the Characteristics of Important Timbers . . 131

CHAPTER V

THE TREE RIND 133
1. The Bast 133
2. The Outer Rind and Epidermis 139
3. Cork and Bark 141
4. Substances contained in the Cells of the Rind . . . 147
5. Resin 149
6. The Lenticels 155

CHAPTER VI

THE ANNUAL RING 157
1. Survey 157
2. Breadth of the Annual Rings and Nutrition 161
3. Annual Ring Breadth and Growth Stimulus, Stem Form, Eccentricity, Pressure Wood 165
4. Causes of Annual Ring Formation 178

CHAPTER VII

ANATOMICAL BASIS OF THE TECHNICAL PROPERTIES OF TIMBERS 186
1. Relation between the Strength, Specific Gravity and Structure of Timber 186
2. Specific Gravity 192
3. Tensile Strength. Shrinkage. Fissibility 194
4. Hardness 195

CHAPTER VIII

THE LEAVES 198
1. General 198
2. The Size and Form of the Leaves 200
3. The Anatomical Structure of the Leaves 208
4. Operation of the Stomata 215
5. The Leaf Parenchyma 220
6. Shade-leaves and Sun-leaves 224
7. The Chlorophyll Granules 231
8. Assimilation and Respiration 233
9. Assimilation and Light 241
10. Assimilation and Carbonic Acid 244
11. Arrangement of Leaves in Regard to Light 247
12. Utilisation of Light by Plants. Photometry 250
13. Assimilation and Heat. 256
14. Energy of Assimilation 257
15. Death and Fall of the Leaves 260

CHAPTER IX

PAGE

THE ROOT 269
1. The Form of the Root System 269
2. Functions of the Root System and Structure of the Root Tip 281
3. Bleeding 287
4. The Growth of the Roots in Length and Thickness . . 292
5. Mycorrhiza 295

CHAPTER X

WATER ECONOMY OF THE TREE 301
1. The Water Consumption of Trees 301
2. The Water-Content of Trees. 307
3. The Movement of Water in the Tree 309

CHAPTER XI

THE MINERAL NUTRIENTS 325
1. General 325
2. The Time of Absorption of Mineral Substances . . . 327
3. Mineral Content of the Leaves 329
4. Mineral Content of the Rind 333
5. Mineral Content of the Wood 334
6. Mineral Content of Various Species 335
7. The Rôle of the Mineral Nutrients in Plant Life . . . 336
8. The Nitrogen Supply of Forest Trees. Vegetation of the Locality 342

CHAPTER XII

MOVEMENTS AND TRANSFORMATIONS OF SUBSTANCES IN THE BODY OF THE TREE 350
1. The Stem of the Tree as a Storehouse of Reserve Substances 350
2. The Descending Sap Stream and the Circulation of Sap . . 359

CHAPTER XIII

FLOWERS, FRUITS AND SEEDLINGS 367
1. Flower 367
2. Flowering and Fruiting Conditions 368
3. The Female Flowers and their Parts 371
4. The Male Flowers and their Parts. Sex Distribution . . 376
5. Pollination and Fertilisation 381
6. Distribution of Fruit and Seed 389
7. Germination 392
8. The Seedling 398

CHAPTER XIV

LOCAL RACES 403

INDEX 415

LIST OF AUTHORS CITED 426

COMMON NAMES OF PLANTS USED IN THE TEXT WITH THE CORRESPONDING SCIENTIFIC NAMES . 434

THE STRUCTURE AND LIFE OF FOREST TREES

CHAPTER I

THE FORM OF THE TREE

1. The Tree in the Change of the Seasons.—The most prominent feature of our plant world in winter is the complete predominance of woody structures among the remnants of vegetation that venture to defy the severity of the cold season of the year. Not that there is an entire absence of herbaceous parts of plants. Dead nettles (*Lamium* species), daisies (*Bellis perennis*), the leaves of the violet, groundsel (*Senecio vulgaris*), still persist alive above ground. They do not, however, rise much above the soil and are generally protected by a covering of snow during the most dangerous period. Up above, only the juiceless, leathery leaves of the ivy and the tough needles of the conifers recall the green mantle of summer foliage. The leaves of the broad-leaved trees and the tender needles of the larch have fallen. Winter is the time of drought in the plant world. Tender leaves, in the dry January air, would transpire more water than the roots in the frozen soil could absorb, would dry up and so burden the tree uselessly in winter. Not every tree is adapted to bear the weight of ice or snow which would be apt to accumulate on a full canopy of foliage. Life has retreated into the hardy twigs, branches and stems which expose to the desiccating winds only a small evaporating surface and are protected from loss of water by cork and bark. Their hardness provides in addition a certain amount of protection against animals, which, less fastidious in the snowy winter than in the abundance of summer time, seek out what they have previously passed by. Cold itself is the least of dangers to our winter trees. Their living cells are not sensitive to frost in winter. They are protected by changes in the substances within, among which the formation of sugar is the best known. They prevent the complete using up of the cell contents in the formation of ice, which partly through the withdrawal of water and partly through coagulation would be destructive of life.[1] Pojarkova [2] found a close correlation

[1] Maximow, Chemische Schutzmittel der Pflanzen gegen Erfrieren. Berichte der Deutschen Bot. Gesellschaft, XXX, 1912; the same: Experimentelle und kritische Untersuchungen über das Gefrieren und Erfrieren der Pflanzen. Jahrb. f. wissenschaftl. Bot. 53, 1914. Leipzig, Borntraeger.

[2] Pojarkova, A., Winterruhe, Reservestoffe und Kälteresistenz der Holzpflanzen. Ber d. Deutsch. Bot. Ges. 42, p. 420. Winckler, Einfluss der Aussenbedingungen auf die Kälteresistenz usw. Jahrb. f. wiss. Bot. 52, 1913 (Alteration of Osmotic Pressure by Cold). Further literature on still disputed questions of frost hardiness in: Neger, Die Krankheiten unserer Waldbäume. Stuttgart, 1924. Molisch, Pflanzenphysiologie als Theorie der Gärtnerei. Jena, 1922.

between the course of starch conversion and the profoundness of the winter rest. Species of trees in which a large quantity of starch is converted into sugar have a profounder winter rest and are, at least in part, less susceptible to winter cold than species in which this conversion is only insignificant. The frost hardiness of different varieties of wheat is associated with exactly similar processes.[1]

The broad-leaved trees and the larch are "**hygrophilous**" water spendthrifts in the summer and "**xerophilous**" water misers in the winter. Hence they have been called "**tropophilous**" or changing trees. In the perennially humid tropical regions there are trees which bear broad, rapidly-transpiring, leaves throughout the year and are thus exclusively hygrophilous. It is they which form the main constituents of the boundless forests of the Amazon region, the Cameroons and the Congo basin.

In regions where long dry periods occur, trees are found which are far better adapted to stand temporary dryness than our broad-leaved trees. Small, tough leaves, which transpire little during dry periods give them a xerophilous aspect throughout the year. However, the terms hygrophilous and xerophilous should be applied with caution. The adaptations of plants are far too many-sided to allow of a conclusion as to life conditions to be drawn from appearance alone. Thus our spruce, with its small, hard needles, has the outward appearance of a xerophilous tree. But everyone knows that it requires both soil moisture and atmospheric humidity and that it is apt to wither during the dry winter weeks on the frozen soil in sunny situations favourable to transpiration from the leaves. Physiologically the Scots pine can be more properly considered as a xerophyte as it endures prolonged dryness better than the spruce, though this is not particularly expressed in the structure of its needles. No one would judge, however, from the needle structure that the green Douglas fir stands summer drought remarkably well and that the yew is very sensitive to winter dryness. The water economy of plants does not, indeed, depend on the giving off of water alone, but just as much on the absorption and transport of it; as is explained in Chap. X, 1.

To the seeker for colour and movement the bare, rigid branches of the woody plants in winter are without charm, but they afford full satisfaction if the trees are considered as structures and their architectural organisation is examined. Unconcealed by the green covering, the relative size and arrangement of the individual structural parts stand out clearly and the laws on which the particular form of each individual tree depends are soon discovered.[2]

2. The Annual Shoot.—The way in which trees in our climate are built up seems, in the first place, to be conditioned by the alternation between summer and winter. On account of the low temperatures, poor light and the difficulty of providing water, the growth of our trees is interrupted every winter by a period of rest which divides their whole

[1] Schander u. Schaffnit, Auswintern des Getreides. Landwirtsch. Jahrb. 52, 1918.
[2] Wigand, Der Baum Braunschweig, 1854, Vieweg & Sohn. Rossmässler, Der Wald. Leipzig u. Heidelberg, 1881.

development into annual sections. Thus arise, as architectural units or structural parts, the annual shoots—leafy twigs, each of which originating in a bud, develops in the course of the summer and, after forming new buds, enters in the autumn into a resting condition. It is from the proper study of them that we must start if we wish to understand the form of our mid-European trees. In climates in which the influences which bring about an alternation between rest and growth are not connected with the yearly occurrence of a summer and a winter, rest and growth alternate according to other periods. Continuous, uninterrupted growth is comparatively rare. The formation of annual shoots is the characteristic of tree growth from which we have to start in this book, where we are dealing only with our native European trees.

The twigs of our woody plants increase in length by apical growth. Just as a wall rises by the setting of one stone on top of the others, so every year, to the end of the twig is joined a new shoot, which by the end of the summer is fully grown and retains for the rest of its life the length then reached.

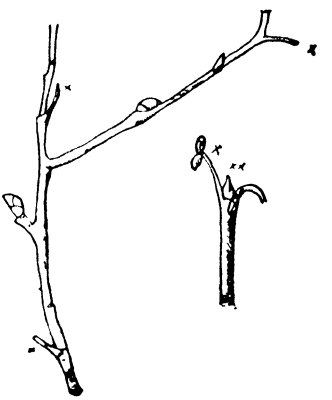


Fig. 1.—Shoot tip of birch. × withering apex of shoot; ×× the lateral bud replacing it, in the axil of the uppermost leaf stalk.

In most of our native woody plants every annual shoot possesses, in consequence of the nature of its junction with its predecessor, an identity so obvious that older botanists regarded the tree, not as an individual but as an aggregate of annual shoots; somewhat as a coral branch was regarded as a colony of animals. The growth of the shoot does not simply stand still in the autumn, to be again resumed in the same way the next year. Each one ends either in a terminal bud prepared during the summer and endowed with special arrangements for the winter, or the tip perishes and next year's continuation proceeds from the uppermost lateral bud.

A terminal bud capable of growth is formed by our conifers, the ashes, maples and, though not invariably, by beeches and oaks. It is noteworthy, however, that, in the case of most of our broad-leaved trees, the second condition obtains. It is so with the birches, elms, aspen, hazel, willows, lime, the *Prunus* species, hornbeam, and not seldom with beeches and oaks. The loss of the tip of the shoot in these trees takes place without any perceptible external cause. It ceases to elongate and thicken and finally dries up and falls off or remains for a time on the tree as a small woody point a few millimetres in length beside the substitute shoot from the uppermost lateral bud. In the following year it can hardly be detected that the substitute shoot did not originate in the terminal bud, because, as a rule, it places itself in a direct line with the mother shoot, so that the dead end, as at × in the birch in Fig. 1, appears as a lateral appendage. In the lime it only appears as a scar near the top lateral bud, which is bent towards the tip of the shoot. The death of the terminal bud is more important for the structure of

the whole in the case of those woody plants whose lateral buds stand opposite to each other in pairs, as in the lilac, buckthorn (*Rhamnus cathartica*), and the elder (*Sambucus*). Here the two uppermost side buds often develop simultaneously and equally, so as to produce a forking, whilst the main axis undergoes no direct extension. In the buckthorn the point of the mother axis remains for a long time as a short, hard thorn in the fork. The immediate cause of the death of the end of the twig is to be sought in the successful competition of the upper leaves with it for the water ascending from the older parts of the shoot. This follows from the fact that the removal of those leaves at the right time can prolong the life of the tip.[1]

Further development of the apex of the twig may also be induced by early removal of the uppermost lateral bud, for example in limes and lilacs. Finally [2] the shedding of the terminal shoot may be retarded or accelerated by suitable regulation of the evaporation from the leaves of the twig, as when, in the case of long continued rain, the starving shoot tip often survives. The actual shedding of the tip, just like the fall of the leaves, is brought about by the slow formation of a separation layer.[3] The most remarkable thing in the whole process is that the substitute shoot from the side bud, which, if the proper terminal shoot had been retained would certainly have grown in a lateral direction, now takes up the position of the terminal shoot. It is the same phenomenon as the erection of a lateral shoot into the position of a leader when the original leading shoot is destroyed accidentally by storm, snow-break or the biting of animals. One or more of the upper lateral shoots grow erect, to produce the bayonet or candelabrum-shaped tops found especially in conifers.

An annual shoot often ends with the formation of an inflorescence, such as, for example, the catkins of the amentaceæ (birch, hazel, alder and their varieties) and the cones of the conifers. In the amentaceæ the growth of the shoot is continued from a lateral bud below the inflorescence. In the larch the axis of the shoot, after forming the floral parts, may grow on again, thus forming the so-called proliferating cones.

Finally the annual shoot may be brought to a close by the frosts of late autumn. This happens in the robinia, mulberry, *Philadelphus*, *Prunus serotina*, etc., at least in our climate, which does not always allow these exotics, adapted to a longer growing season, to complete the ripening of their long shoots. It also occurs in willows when they are stimulated by cutting into a growth prolonged into the autumn and are prematurely surprised by frost. The renewal then takes place by means of a lateral bud. For the rest, the time of completion of shoot development is by no means determined by the season alone. Beeches, horse chestnuts, walnuts, pedunculate oaks close the majority of their terminal buds as early as May or June, the beeches in Vienna at the

[1] Berthold, Physiologie der pflanzlichen Organisation, Bd. II, p. 246. Leipzig, 1904, Engelmann.

[2] Wiesner, Der absteigender Wasserstrom und dessen physiologische Bedeutung. Bot. Ztg., 1889, 1.

[3] Tison, C. R., Paris, 1906, Tome CXLII, p. 222; Bull. de la soc. Linnéenne de Normandie, 5 sér., 9. vol. Caën, 1905.

beginning of May. Alders are in rapid growth until August, and it is the same with stool shoots of the oak, and with still other woody plants, especially in youth so long as the weather permits of growth. Moreover, all the shoots of a tree need not behave alike.

The boundaries between the single consecutive annual shoots of a shoot-series are usually marked by the groups of ring-like scars left by the bud scales. Where this is not the case, as in the guelder rose (*Viburnum opulus*), the character of the surface affords indications for distinguishing the different shoot generations, as it is subject to continuous alteration by the formation of cork and bark or the deposit of lichens or other surface impurities. The boundary between two annual shoots is called the " bud-trace." [1] The buds on the shoot at this point are usually very small and may, in part, perish in spr ng (*Acer pseudoplatanus*). Where they appear to be lacking they are probably there, though very much undeveloped. The scars of the bud scales are often still recognisable after many years on branches which have greatly increased in thickness, as they may originate folds in the bark. Dwarf shoots several years old are often completely covered with such traces of former bud-scales (Fig. 12). They are termed " **ringed spurs** " in fruit growing.

3. Arrangement of the Buds on the Annual Shoot. Length of the Internodes.—On comparing the annual shoots of different trees, apart from their varying length and thickness, the characteristic arrangement of the buds upon them is a striking feature. They are always found close to a leaf scar, either directly above it or above it but somewhat displaced laterally, so that the arrangement of the buds on the shoot corresponds very nearly to that of the leaves. The leaf and the shoot belonging to it (axillary shoot) arise as paired rudiments,[2] whose units are so far dependent on each other that, if the supporting leaf is removed while still young or its normal action hindered, the axillary bud starts into growth [3] and thus provides for the formation of new leaves. Later on each leaf supplies an important direct contribution to the nutrition of the adjoining section of the shoot. The removal of a leaf prematurely checks the growth of the next lower internode, so that by removing leaves it is possible to upset the normal proportional size of the internodes.[4]

If the buds of a twig all stand at different levels upon it (beech, hornbeam, lime, willow, alder), they are said to be " scattered," if two or more are found opposite to each other on the same part of the shoot, they are said to be " opposite " or " whorled " (maple, lilac, ash, horse chestnut, guelder rose, etc. *See* Table in Chap. II, 9). Scattered buds may be arranged either in a spiral line or in two longitudinal rows on opposite sides of the shoot: spiral or alternate (beech, hornbeam, lime) arrangements of buds. Opposite buds generally appear in four ranks, *i.e.* each consecutive pair of buds at right angles to the one below.

[1] Berthold, Bd. II, p. 32.
[2] Goebel, Flora, 1911, p. 248.
[3] Dostal, Berichte der Deutschen Bot. Gesellschaft, 1909, XXVII, p. 547.
[4] Tammes, Periodizität morphol. Erscheinungen bei den Pflanzen. Verh. Kon. Ac. Amsterdam, IX, No. 5. Ref. Bot. Zentralblatt, 1904, Bd 95, p. 247.

In the case of the alternately arranged buds of the beech, elm, lime, etc., it is striking that, on inclined shoots, they are displaced laterally from the associated leaf scars, so that an upper and a lower side of the shoot can be distinguished (*see* Fig. 2). Seedlings of the beech do not exhibit this phenomenon, however. Here the small buds stand in the axils of the cotyledons and the first, almost opposite leaves, exactly over the points of attachment or the scars of these organs. In the case of other trees, also, young plants show an anomalous arrangement of the buds. Thus the first year's leaves of the elm are in opposite decussate pairs, those of the second year arranged alternately. In the lime seedling the leaves form a spiral, later they form two ranks. In the gean and the common cherry the leaves in the first year are opposite, from the second year onwards, spirally arranged. In *Prunus padus* the spiral arrangement begins even in the first year, after the first two leaves, which are opposite.[1]



FIG. 2.—End of a long shoot of *Fagus sylvatica*. Upper side. The buds displaced with respect to the leaf scars towards the upper side of the twig. Reduced.

Kny[2] observed the twisting towards the zenith of the axillary buds on the lateral branches of a large number of woody plants, among which are *Carpinus betulus* and other *Carpinus* species, *Corylus avellana*, and *colurna*, several species of *Ulmus*, all the limes cultivated in Germany at the time (1877), many oaks, and the sweet chestnut (*Castanea sativa*, Mill.). Unlike previous investigators, however, he was unable to detect the phenomenon in *Juglans*. It is at any rate established that the arrangement of the buds is often among the most constant characteristics of different plants. This is true, for instance, of the opposite arrangement of the genus *Acer* and others, which never passes over into a spiral or alternate one whilst the two ranked arrangement of the buds, for example in beeches, birches and elms, may become a spiral one on upright shoots. *Salix purpurea* has its leaves and buds partly opposite and partly alternate. The opposite arrangement of the leaves and buds is also maintained only very inaccurately on vigorous shoots of the ash and often passes over into a spiral one. Modifications into a spiral are frequent also in the hornbeam, and erect hazel shoots quite commonly show such an arrangement. When Kny[3] removed all the buds but one from a hazel shoot in mid-March, this bud produced a shoot, which at first, as is the rule with lateral shoots of the hazel, had leaves arranged alternately. It then developed leaves in spiral succession and at the same time the distinction between the upper and lower side disappeared. Theoretically, of course, an extraordinary number of spiral arrangements of varying steepness are possible. In actual fact, however, only two are very common, which are described

[1] Goebel, Organography of Plants, Eng. Ed., 1900, Oxford, p. 70; Sylvén, Botaniska studier tillägnade F. R. Kjellmann, Upsala, 1906. Comp. German Ref. Bot. Zentralblatt, 1907, Bd. 104, p. 244 and 402; Vuillemin, Rev. générale d. Bot., Tome XIV (*Ulmus campestris*).

[2] Kny, Sitzber. d. Ges. naturf. Freunde, 1876. Bot. Ztg., 1877, p. 118.

[3] Kny, Ein Versuch zur Blattstellungslehre. Ber. d. Deutschen Bot. Gesellschaft, XVI, 1898, p. (60).

as the $\frac{2}{5}$ and $\frac{3}{8}$ arrangements. These fractions are arrived at when a line is drawn from any bud to the next above it, from this to the next but one and so on, until a bud is reached which stands vertically above the original one. The number of buds, excluding that standing directly above the first, which the line touches is taken as the denominator, the number of turns of the line round the shoot as the numerator. Bud arrangement $\frac{2}{5}$ therefore means that the buds are arranged in a spiral in such a manner that to pass from a given bud through all the intermediate buds to the next one standing directly above it, the stem must be encircled twice and five buds will be passed. One-third spirals are also not uncommon, sometimes changing into $\frac{2}{5}$ spirals on the same shoot. The arrangement of the scales on the silver fir cone is according to the fraction $_{2}^{8}/_{1}$. It implies a very shallow spiral, rising only very gradually, which does not correspond with the steep spirals in which the scales appear to the eye to be arranged. To discover the laws of leaf, and therewith bud-arrangement,[1] was an important aim of the botany of Darwin. Later Schwendener [2] succeeded in deriving leaf arrangements mathematically from certain assumptions as to the space conditions in the vegetative cone, *i.e.* the point of the shoot, the region of formation of new organs. It then appeared that these assumptions were not always realised in nature and a great dispute about the matter arose which is still going on. The most important recent work in this field has been done by Van Iterson [3] and Schoute.[4] The last-named work is well adapted as an introduction to the subject and puts forward a theory which I set out here to show the lines of thought in which the research moves.[5] Schoute assumes that in the growing point bud-forming materials or energies may be present which have a restricting influence on leaf-formation. Every part of the vegetative cone in which the influence of the bud-material ceases, forms, in so far as other influences do not prevent it, a leaf primordium (leaf centre), at first invisible to the eye. From these leaf-centres leaf-material or leaf-forming effects spread in the surrounding region in the form of a circle of diffusion, somewhat as an oil spot spreads on paper. On such an area no other leaf-centres can appear, bud-material can, however, which on its part hinders the formation of new leaf-centres on the same circle of diffusion. On this basis Schoute explains the mathematical regularity of leaf arrangements without, like Schwendener, making assumptions about the space conditions and mutual pressures of the primordia in the vegetative cone which are not always to be recognised in nature. Iterson deduces the most important leaf arrangements mathematically from assumptions based on observations of the conditions at the

[1] The biological importance of leaf arrangement for the illumination of plants. (*See* the chapter on Leaves.)

[2] Mechanische Theorie der Blattstellungen. Leipzig, 1878. Comp. also Winkler, Jahrb. f. w. Botanik, 1901, XXXVI, and Leisering, the same, 1902, XXXVII; Winkler, the same, 1903, XXXVIII, p. 501.

[3] Van Iterson, Mathematische und mikroskopische-anatomische Studien über Blattstellungen nebst Betrachtungen über den Schalenbau der Miliolinen, Jena, 1907.

[4] Schoute, J. C., Beiträge zur Blattstellungslehre, I. Die Theorie (Extrait du Rec. d. travaux bot. Néerlandais. Vol. X. Livr. 3 and 4, 1913).

[5] Mathematical treatment. (*See* also Church, On the Relation of Phyllotaxis to Mechanical Laws, Part I and II. London and Oxford, 1901 and 1902); Iterson's own abs. Bot. Zentralbl, 1908, Bd. 108, p. 49.

vegetative cone and on the position of the first leaves of seedlings and shoots and also explains the predominance of a certain series of spiral arrangements ($\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, etc.) by means of a justified mathematical assumption.

An example of the effect of mechanical pressure on phyllotaxis is given by the behaviour of the lateral buds of certain conifer twigs examined by Weise.[1] The first two leaflets of these buds stand like "bud cotyledons" opposite each other, right and left of the needle in whose axil the particular bud is situated. They are followed by other leaves or needles which are now arranged in decussate pairs, three-membered whorls or in spirals. Whether the spiral runs to the right or to the left round the shoot depends on the position of its first leaf, *i.e.* the third leaf of the shoot. This, unlike the bud cotyledons, is generally directed towards the stem. It is, however, diverted either to the right or to the left by the pressure of the neighbouring organs, and in this way the direction of the spiral is determined.

The buds of seedlings of Douglas fir and other Abietineæ, offer another example After the whorled cotyledons the succeeding needles are placed quite irregularly until, later on, a characteristic spiral arrangement is built up. According to Schwendener the initial absence of regularity in the arrangement of the needles is associated with the fact that, owing to the rapid growth in thickness of the stem of the seedling, the proportion between the size of the individual leaf rudiments and the circumference of the stem is altered irregularly. As growth proceeds this relationship gradually assumes a fixed magnitude and the leaf arrangement also becomes fixed.

The distances between the buds in the middle portion of an annual shoot are often quite uniform. As a general rule the lower buds follow each other very closely, then their distance increases, finally diminishing again towards the upper end of the shoot. In many plants—as in the pedunculate oak—the buds are markedly crowded towards the end of the shoot. This rule shows that the course of life (great period) of the whole tree is reproduced in the single annual shoot. It is an expression of the law valid for every twig as for every root, even for every individual cell, that the structure in question at first grows slowly then quickly reaches a maximum rate of elongation on which follows a rapid or more gradual diminution of the rate of growth. This is the reason why the lateral buds which are originally formed closely crowded together are later separated by different distances. At first, while the shoot is only elongating slowly they are only a small distance apart, in the period of maximum growth they are separated by longer intervals and towards autumn again by small ones. This growth in length will be further considered in Chap. I, 5.

The budless parts of the shoot between the places on which the buds are situated are called "**internodes,**" the parts on which buds and leaves are attached, "**nodes,**" a not unuitable term, because there is often a knotty swelling of the stem at such places. The following series of figures may serve as examples of the conditions observable. They give in millimetres the length of consecutive internodes of shoots of

[1] Weisse, Flora 58, 1891.

various woody plants. The very short lowest internodes are not always given.

Carpinus betulus	I.	2, 4, 10, 18, 25, 36, 40, **45, 45,** 35, 30, 34, 34, 30, 25, 15.
	II.	7, 29, 34, 34, 50, 56, **65,** 50, 55, 50, 50, 52, 42, 45, 40, 18, 45, 5.
Quercus sessiliflora	I.	1, 1, 1, 6, 9, **18,** 11, 8, 4.
	II.	0, 5, 1, 4, 7, 8, 12, 12, 12, **17,** 12, 12, 5, 12, 3.
Crataegus oxyacantha		1, 2, 5, 10, 15, **19,** 17, 15, 4.
Corylus Avellana		75, 55, 52, 45, 45, 40, 40, 35, 35, 13, 5.
Sambucus racemosa	I.	5, 10, 20, 60.
	II.	2, 5, 18, 78, **145,** 135, 125, 45.
	III.	3, 10, 35, 85, **120,** 95
Prunus padus		4, 5, 6, 6, 6, 6, **7, 5,** 6, 5, 6, 5.
Acer platanoides		4, 4, 5, 14, 5, **19,** 16, 15, 14, 5, 10, 5, **4, 2, 5,** 11, 5, **12,** 11, 5, 10, 8, 5, 2, 5.

Nachtigall has carried out a great number of internode measurements on the hazel, hornbeam and sweet chestnut.[1] Curves drawn for the mean lengths of the internodes show that the course of variation in those lengths is characteristic for each of the three plants. It ought to be investigated whether if very large numbers of measurements are made, only so-called "probability curves" are obtained. This is not unlikely, as many independent factors affect the length of the internodes, some of which like temperature, moisture, light and nutriment, belong to the environment and some lie in the internal mechanism of the plant. The greatest internode length occurs at the time when there is the most favorable combination of the factors that promote growth of the internodes, whilst before and after that period a shortening is observed. The position of the highest point and the steepness of the rise and fall of the curve are peculiar to each species of plant. Individual deviations are large, as is evident from the above series of figures.

In the broad-leaved trees the number of buds on the annual shoot is generally regulated by the number of leaves. As a rule a bud stands above each leaf. *Pterocarya fraxinifolia* has, above each leaf, two to three buds one above another and in quick growing shoots of the ash, lilac and other oleaceæ, two buds sometimes occur above each other in the leaf axil, the stronger being the uppermost. Even the bud scales often show axillary buds. An exception is afforded by the beech, for example, in which axillary buds are absent from the lowest or the two lowest leaves, and on dwarf shoots even from all the leaves, which, however are only two or three in number. In the hornbeam, lime and birch also, axillary buds are absent from the two lowest leaves of a shoot whilst they are always present elsewhere; while, on the other hand, two or three buds are found in one leaf axil not infrequently on strong shoots of the hornbeam, quite commonly on the bird cherry (*P. padus*). Such extra buds are called "**supplementary buds.**" They

[1] Büsgen, Cupuliferen, in Lebensgesch. der mitteleurop. Blütenpflanzen, II, 1. Ulmer, Stuttgart.

often remain in the condition of dormant eyes, growing out only in special circumstances, such as the destruction of the main axillary bud. In the alder the fourth is the first leaf to have a bud and in the barberries shoots develop only from the axils of the leaves on the long shoots, whilst the rosette leaves of the dwarf shoots remain budless.

The total number of leaves and so also of buds on an annual shoot is, in many trees, already determined in the bud from which the shoot originates. In other cases it depends on the growing season, especially in those plants which go on growing until frost kills the tip.

In the conifers many needles are generally without axillary buds. Spruce shoots, for instance, are free from buds in the whole of the lower part; whilst in the middle and upper part some six buds are found irregularly distributed among an enormously larger number of needles, and at the end of the shoot, two to five of them are crowded together almost in a whorl. The latter give rise to the whorls of branches which are so characteristic of the spruces as well as of the firs and pines. In the pines all the leaves have axillary buds, but these leaves—except in seedlings—develop only into small scales, and the buds become dwarf shoots with two, three or five needles according to the species. Only at the tip of the shoot occurs a false whorl of large buds which form long shoots. A year's shoot of *Taxus baccata* for example, bore a bud in the axil of the 13th, 14th, 21st, 22nd, 23rd, 32nd, 33rd, 37th, 41st, 46th, and 48th leaf—they were thus irregularly distributed. Peculiar cases are presented by the snake or monstrous forms [1] of the spruce and silver fir, whose twigs produce only terminal shoots and almost no lateral ones at all. Spruces are known which from the first develop only terminal shoots so that the whole tree takes the form of a simple column. On old branches of the common spruce, it is often only the terminal bud and two lateral buds just below it, one to the right and one to the left that develop. Burtt [2] has pointed out that confining the buds to the ends of the branches in conifers, ensures that all the young shoots are suitably lighted.

4. The Lammas Shoot.—The contraction of the length of the internodes of the Norway maple in the middle of the growing season in the series of figures on p. 9 is very striking. This is a phenomenon which occurs in many other woody plants and may be associated with the formation of a regular closing bud in the middle of the summer; intermediate structures between bud scales and ordinary foliage leaves may also appear (Fig. 3). The part of the annual shoot formed after the pause in such cases appears as a new growth to which the name of Lammas Shoot has been given in view of the approximate date of its appearance. The resting buds of beeches and oaks, formed in early summer, open after a short rest, which, in the oak, lasts about a month and in the beech, on the average, three weeks. The lammas shoots of the oak are very vigorous, longer, indeed than the spring shoots, the height-growth of young oaks often depending principally on the long

[1] Schröder, Die Vielgestaltaltigkeit der Fichte. Zürich, 1898 (Sep. fr. Vierteljahrsschrift d. naturf. Ges. Zürich, 1898, XLIII).

[2] Habitus der Coniferen. Tübingen, 1899.

lammas shoots. Three or four times repeated lammas shoot formation also occurs, on young oak coppice regularly, the lammas shoots themselves sometimes branching.

As a rule the tendency to lammas shoot formation is greater in youth than in later years. It also occurs in youth on the conifers, as on spruce and the green Douglas fir. In the case of the latter, the lammas shoots are often not ripened and die of frost, a characteristic which is of importance in their cultivation in our climate.

In the beech, normal lammas shoots only occur in youth and on stool shoots. They are distinguished by great hairiness and an unwonted number of buds, several often standing above each other in one leaf axil. Späth [1] found a resting period of only three days in lilacs (*Syringa Persica*). The condition in which the cessation of growth in the summer is not associated with the formation of a closing bud but only with a period of rest, sometimes accompanied by the formation of structures intermediate between bud-scales and normal leaves, Späth terms "**Concealed Lammas-shoot Formation.**" Such is found in the *Acers* (Fig. 3), ashes and *Prunus* species (*P. serotina*).[2] As with the true lammas shoot, by no means all the branches exhibit the phenomenon. In young alders, birches, hornbeams and many other species, also in conifers (*Larix*, *Picea* [3]) the lammas shoots branch so that the lateral twigs appear from buds without scales and without a resting period. These "**Accessory Shoots**" afterwards develop only weakly and, in the case of the alder, are prone to produce flowers and then perish (Berthold II).

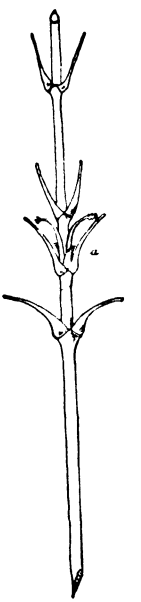


FIG. 3.—Lammas shoot formation in the Norway Maple (*Acer platanoides*). The Lammas shoot begins at *a*.

We are still without a complete insight into the cause of lammas shoot formation or rather the summer cessation of growth, though the recent work of Späth and Klebs [4] has contributed much to the solution of the problem. Nutrition, the accumulated reserve materials, water supply (summer pause in the growth of roots, *see* Roots) and the weather are involved. Summer rainfall especially promotes lammas shoot formation. Plants with and without lammas shoots are, however, often found together in the bed.

This at least is to be perceived without further investigation: that everything which provides a plentiful supply of water and soil nutrients relatively to the existing amount of foliage promotes lammas shoot formation—the proportionally greater root development of young plants, mutilation (coppice shoots, and water shoots), defoliation by

[1] Späth, Der Johannestrieb. Berlin, 1912, Parey.

[2] *See* also Burger, Unters. ü. d. Höhenwachstum der Bäume. Mitt. d. Schweiz. Zentralanst. f. d. forstl. Versuchswesen, XIV, Bd., 1. H., 1926.

[3] In young spruces in the autumn it is not uncommonly found that at the top, terminal and lateral buds have grown out, often only latteral ones, whose shoots are as a rule stronger than the new leader and turn very steeply upwards. Berthold, II, p. 42.

[4] Über das Treiben der einheimischen Bäume, speziell der Buche. Abh. d. Heidelberger Akad. d. Wiss., math.-naturw. Kl. 3. Abh. Heidelberg, 1914, C. Winter.

frost, drought or insect attack, heavy manuring, plentiful rainfall. Whatever appear to be the correlations involved between the amount of root and foliage, the amount of foliage places itself in balance with the state of the roots. Still, according to Späth's experiments, it would not be correct to trace to unusually favourable nutrition every opening of buds occurring in the summer of their formation when the foliage is undamaged, as a worstening of growth conditions does not suppress lammas shoot formation.

The causes which condition the alternation between rest and growth in our plants have been treated most thoroughly by Klebs. In the particular case of the oak and beech, Werner Magnus [1] has put forward the view that the two-fold growth in summer, broken by a resting period, is an inheritance of these trees from evergreen ancestors, which like many tropical woody plants [2] have had a "periodicity" in shoot formation unconnected with our mid-European seasons.

We may grant this much: that the power of passing into a resting condition during our summer may perhaps be inherited from ancestors in warmer regions. It is not to be assumed however, in the present state of our knowledge, that the alternation between rest and growth, even with its accompanying phenomena such as the formation of scaled buds, is independent of external conditions and is due only to the inherent qualities of the plant. Indeed, the circumstance that sweet chestnuts, limes, *Sorbus aucuparia* and fruit trees may be induced by the weather, injury or the like, to open before the winter resting period, the buds prepared for the following spring is an indication of this.

Späth makes a sharp distinction between such proleptic shoots, taken in a manner from the next year, and the true lammas shoots which he only recognises in beech and oak. It is, however, more correct to recognise here only differences in degree. In the hindering or complete stoppage of the process of shoot formation in the middle of the summer there may, for instance, be involved a relation between the mineral nutrition and the carbohydrates formed in the leaves, which is unsuitable for growth.[3] Wiesner[4] observed that the completion of the growth of twigs by the closing of the terminal bud set in earlier in shade shoots than in light shoots and came to the conclusion that the increased shade due to the production of foliage might also have an influence on the closing of summer buds. The same applies also to instances such as that quoted by Nobbe[5] in which three generations of a pear tree were characterised by flowering and fruiting several times a year.

The foliage of lammas shoots often differs from that of the first shoots.[6] Thus in many varieties of oaks the lammas shoots may exhibit the more deeply incised leaf forms. Colour varieties may bear normal green leaves on the first shoots and white flecked foliage on the lammas shoots. It is not always the lammas shoot that bears the

[1] Biol. Centralblatt. 1913, XXXIII.

[2] Simon, Studien über die Periodizität der in dauernd feuchten Tropen gebauten heimischen Bäume. Jahrb. fur wiss. Bot., 1914, LIV.

[3] Klebs, *loc. cit.*

[4] Photometrische Untersuchungen, II. Sitzungsber. d. Wiener Akad. d. Wiss., Bd. 104, I, 1895.

[5] Döbner-Nobbe, Forstbotanik, 4. Aufl., 1882.

[6] Späth, *loc. cit.*

abnormal form of leaf. It sometimes happens that the leaves of the first shoots establish the variety whilst in the lammas shoots a return to the normal form occurs (*e.g. Quercus sessiliflora var. mespilifolia*).

It is occasionally assumed that the growth of the lammas shoot goes hand in hand with the formation of a half-year's ring in the wood. According to Späth this is not the case with accessory shoots and his "true" and "concealed" lammas shoots. The formation of abnormal wood in the mother twig only takes place in the case of proleptic breaking of the buds, often brought about by external influences and, if the second growth occurs late in the year, may show a false ring boundary by reason

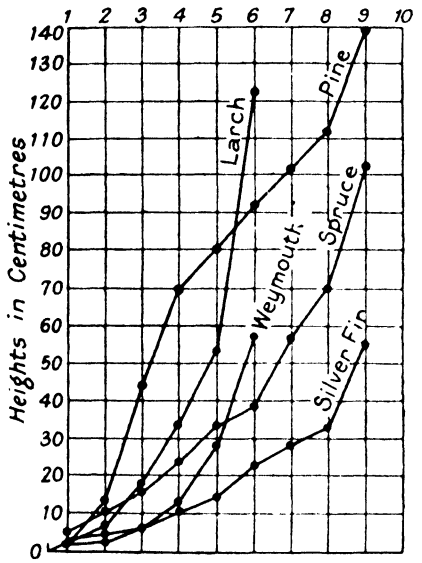


FIG. 4.—Height-growth of larch, Scots pine, spruce, silver fir, Weymouth pine, in the first ten years. From figures by Flury in the Mitteil d schweiz Zentralanstalt f. d. forstliche Versuchswesen, 1895, Bd. IV.

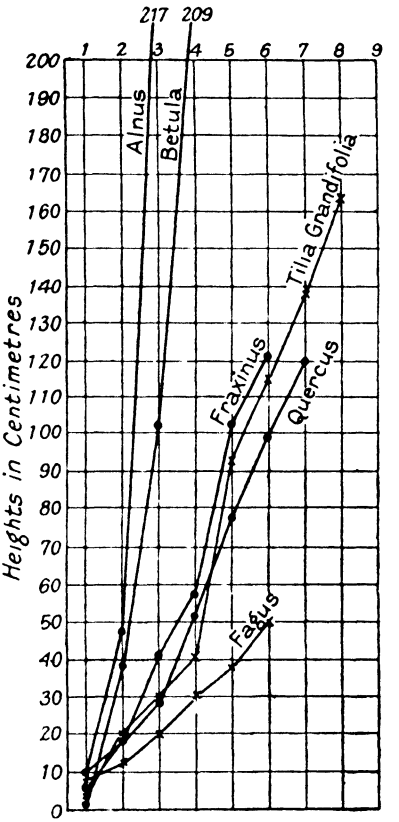


FIG. 5.—Height-growth of beech, oak, alder, ash, birch, elm in the first nine years. From figures by Flury in Mitteil. d. schweiz Zentralanstalt f. d. forstliche Versuchswesen, 1895, Bd. IV.

of wide water-conducting organs like those of spring, appearing anew among the narrow late-wood elements. If the second outgrowth occurs earlier in the year, wider wood elements are also produced but only result in an indistinct zone formation.[1]

5. Length of the Annual Shoots. Height-Growth.—The length of the annual shoot and the total height ultimately reached by the tree depend, like all manifestations of life, on internal disposition and external influences. That under equally favourable external conditions one species of tree produces longer annual shoots than another depends

[1] For further literature (*see* Späth, *loc. cit.*).

on internal disposition. Such differences become evident even in early youth. Poplars, birches, alders and larches are species with rapid growth in youth, while even under favourable circumstances the silver fir and yew are very slow growing. As a rule the shade-bearers are slow growing and the light-demanders fast growing when young. The ultimate height reached by a tree depends, however, less on the rapidity of growth in early years than on the length of time during which growth is maintained. Both quick growing species like larches and poplars and slow growing ones like silver fir may become trees of the first dimensions.

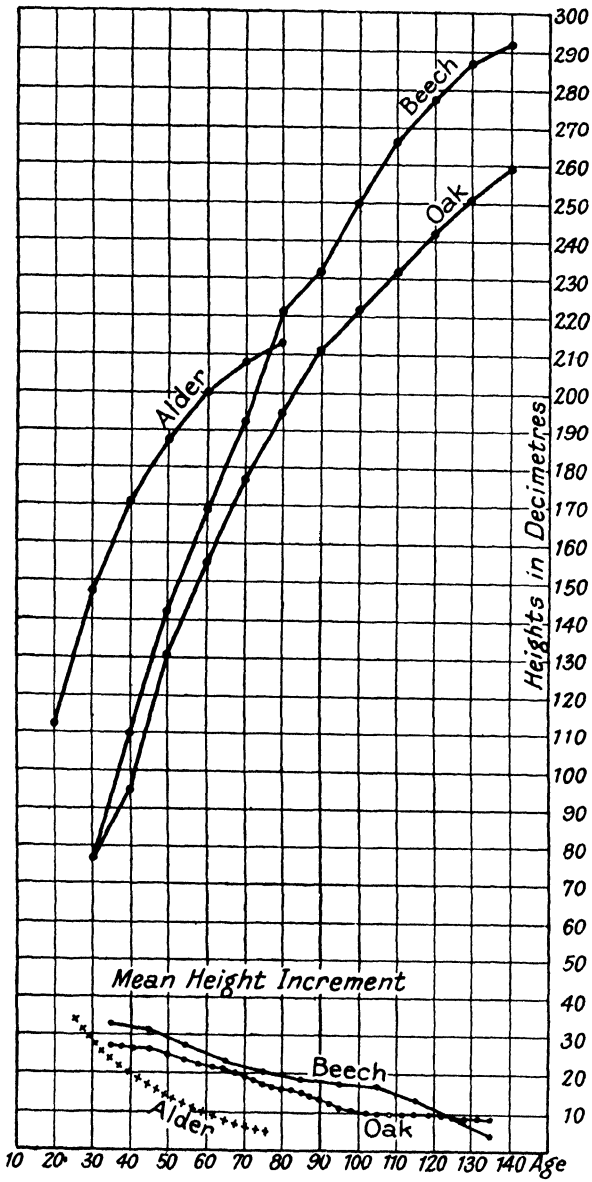


FIG. 6.—Mean heights of stands on the best soil. Broad-leaved trees. From forestry observations.

Under constant external conditions the annual height-growth increases for a number of years, at first as a rule only slowly, afterwards at a constantly increasing rate up to a maximum. It then falls off with the increasing height of the tree at first slowly and then more and more rapidly. In the case of the "quick growing" species the maximum rate of height-growth is reached earlier than in that of the "slow growing" ones. Thus the poplar, alder, ash and birch attain their maximum rate of growth even in the second to the fifth year, with shoots a metre long, while, on the other hand, the beech, spruce and silver fir only do so in their third or fourth decade. There is normally, however, a "great period of growth" (Sachs) which, in many species of trees, may

culminate very early. The height reached with increasing age may be represented by an S-shaped curve, the current annual height-growth by a curve with an ascending and a descending branch (Fig. 7).

To R. Weber [1] belongs the credit for having first analysed these growth-curves and brought them into mathematical form from a correct physiological point of view. Weber showed that, in the youthful stage, so long as the tree has still to take possession of its root space and to multiply its organs, growth in length increases by geometrical progression until a certain height is reached at which the resistances to the supply of water to the leader become obtrusive. The higher the terminal bud then rises above the ground so much the more difficult becomes the provision of water for the growing leader and the smaller the sap pressure, because a constantly increasing height of lift and filtration resistance have to be overcome. As the sap pressure falls the length of the annual shoot falls in about the same proportion, and the height h_x, reached by the tree at the age x, approaches a maximum value H_{max} from the end of the juvenile period, at first rapidly and then asymptotically more slowly, according to the equation $h_x = H_{max}\ (1 - e^{-cx})$. The constant c in this

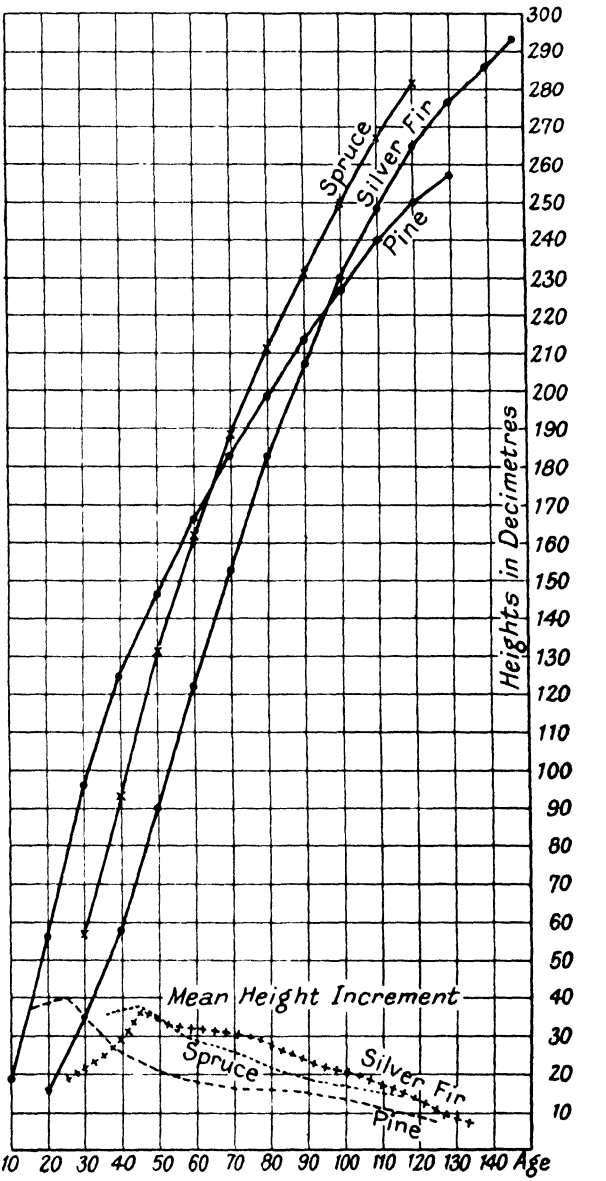


FIG. 7.—Mean heights of crops on the best soils. Conifers. From forestry tables.

[1] Weber, R., Lehrbuch der Forsteinrichtung mit bes. Berücksichtigung der Zuwachsgesetze der Waldbäume. Berlin, 1891, *comp.* also Tischendorf.

equation is the measure of the individual energy of growth. Weber writes this expression $H_{max}\left(1-\frac{1}{1{\cdot}0p^x}\right)$. The current height increment is proportional to the difference $H_{max}-h$, *i.e.* the amount by which the height attained falls short of the height attainable in the given locality. For pines of Class I Schubert [1] gives the current height increment as: $h'=\frac{1{\cdot}73}{100}(35-h)$. The exactly corresponding expression is valid for the volume increment of woods. It is this equation which always appears when a growth has to fight against a resistance which increases with the size reached by means of the growth. Similar regularities and mathematical relations were again found later by Robertson,[2] Mitscherlich [3] and others in other processes of growth in the animal and plant world.

The course of height growth is not governed by the species alone, but differs according to the individual and especially according to the climatic race. Trees from an unfavourable climate, especially from elevated or northerly situations, even when transplanted into a favourable climate grow more slowly from the first than trees of the same species from a better climate, as has been proved by comprehensive researches [4] by Cieslar, Engler, Schott, Schotte, Münch, and Burger.

These rates of height-growth, dependent on internal causes, are very greatly modified by the influences of the locality, so much so, that in forestry height-growth serves as the best measure of the quality of the locality. Height-growth depends in the first place on the quality of the soil and the climate, especially the heat, length of the growing season and the amount of precipitation. But the yearly weather during the growing season has also a great effect so that, as the curves in Figs. 4 to 7 show, the theoretical regularity of growth is seldom attained. The size of the leading shoot is mainly determined by the quantity of reserve materials accumulated during the previous year [5] and therefore by the weather of the preceding summer, at least in all species which unfold their annual shoots suddenly and in a brief period. In these the new shoot is for the most part, in the case of broad-leaved trees almost entirely, built up from reserve materials, and the number of the leaves, which regulates the length of the shoot, depends only on the nutrition at the time when the bud is being formed. In cool, moist climates, warm dry years,[6] and, on the other hand, in warm dry climates, wet years have a favourable effect on the height-growth of the following

[1] Schubert, J., Über das Wachstum von Kiefernbeständen. Ztschr. für Forst- u. Jagdwesen 1924, p. 473.

[2] Robertson, Th. Br., Archiv für Entwicklungsmechanik 25, p. 581, 1907.

[3] Mitscherlich, E. A., Das Gesetz des Pflanzenwachstums. Landwirtsch. Jahrb., Bd., 67, p. 167, 1919. *Comp.* also Rippel, A , Die Wachstumskurven. Ber. d. Deutsch. Bot. Ges. 37, p. 169, 1919. Schüepp, O., Üb. Form u. Darstellung der Wachstumskurven. *Ibid*, 38, p. 193, 1920.

[4] Literature given in Chap. XIV.

[5] Möller, Ztschr. f. Forst- u. Jagdwesen, 1905.

[6] Hesselman, H., Über den Höhenzuwachs u. d. Sprossbildung d. Kiefer in d. Sommern 1900–1913. Mitt. d. Forstl. Versuchsanst. Schwedens, 1. H., p. 42. Laitakari, E., Unters ü. d. Einw. d. Witterungsverh. auf d. Längen- u. Dickenwachstum d. Kiefer. Acta forestalia Fennica 17, 1922.

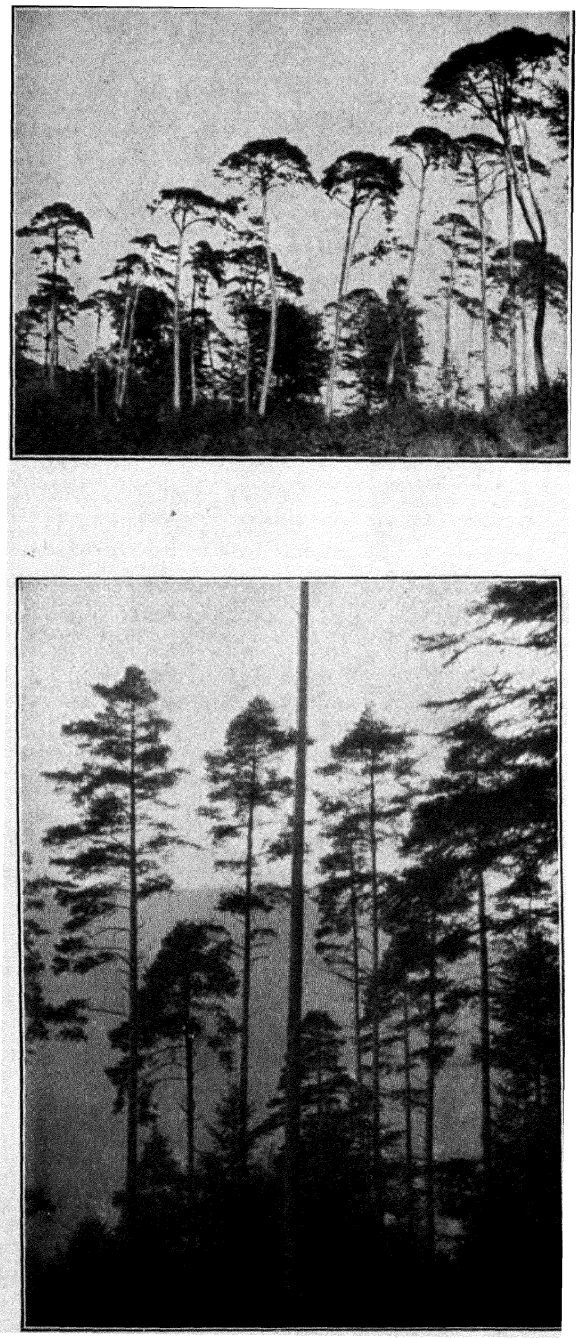


FIG. 8.—Pines of the same age in similar localities. Above: Pines of the Pfalz, crooked stemmed, coarse, flat-topped. Below: Black Forest Pines, straight, slender, fine branched, with pointed tops. (After Münch.)

[*To face p.* 17.

year.[1] In the middle and lower situations of Germany a summer drought of short duration may seriously injure the height-growth of the spruce and other species and when they occur repeatedly may throw it back for decades and so lead to enormous losses of increment.[2] The weather during the elongation of the shoots is of less influence, as it can no longer affect the number of leaves in the year's shoot which are already laid down in the bud, and can only draw the leaves further apart or crowd them closer together by elongating the shoot axis to a greater or less degree. If the needles in these cases stand very close on the shoot they are called "**brush shoots.**"

The length of the leading shoot is also influenced by the wind conditions. Strong wind greatly curtails the length of shoots so that exposed woods are generally much sloped off on the windward side [3] and on stormy sea-coasts and on mountain tops high tree growth becomes impossible.[4] Overcrowding of trees checks height-growth, especially in the spruce. The exclusion of light also acts as a check. All species of trees, even the shade bearers, grow more slowly in the shade than in full light, other conditions being the same. Shade bearing trees standing in lateral shade only, form an exception, especially the beech which in such circumstances may grow faster than when isolated.[5] For the rest, the proportion of height-growth to diameter growth is indeed raised by shading (the stems become more slender) because diameter growth is even more reduced than height-growth by the exclusion of light. Absolutely, however, height-growth under a canopy or in the side shade of higher trees falls behind as compared with that in a position with full lighting.[6] The diminution of longitudinal growth by strong light, well known in physiology, plays no part here because it is very soon outweighed by the increased growth consequent on greater assimilation. On measuring the height-growth of young plants[7] raised under different intensities of illumination the following series was obtained, beginning with the species least checked in growth by the poorness of the light: 1. *Abies pectinata*, 2. *Ulmus*, *Fagus*, *Acer pseudoplatanus*, 3. *Fraxinus*, *Quercus*, 4. *Alnus glutinosa*, 5. *Betula verrucosa*.

The diminution in the length of the shoots from a certain age of the tree onwards is of great importance for the form of the tree crown. So long as the formation of vigorous long shoots predominates the crown appears not properly closed. It breaks up into isolated stiff branches. When, later on, the formation of short shoots predominates the whole outline grows more regular and the gaps between the long main branches are closed. "Rounding off of the crown" sets in. This is especially striking in the ash which, when young, forms long shoots almost exclusively but when older rounds off its crown by the production of dwarf shoots. If we designate the different orders of branches on a tree,

[1] Cieslar, Einige Beziehungen zwischen Holzzuwachs und Witterung. Zentralbl. f. d. ges. Forstwesen, 1907.

[2] Wiedemann, E., Zuwachsrückgang und Wuchsstockungen der Fichte. Tharandt, 1925.

[3] Münch, E., Windschutz im Walde. Forstl. Wochenschr. Silva, 1923, p. 1.

[4] Bernbeck, O., Wind u. Pflanzenwachstum. Englers Bot. Jahrb., 45. Bd., 4. H.

[5] Engler, A., Unters ü. d. Blattausbruch u. d. sonstige Verhalten der Buche. Mitt. d. Schweiz. Zentralanst. f. d. forstl. Versuchswesen, X. Bd., 1913.

[6] Weidemann, E., Zeitschr. f. Forst- u. Jagdw., May, 1926.

[7] Boysen Jensen, Tidskrift f. Skovvaesen, Jan., 1910.

mother shoot, daughter shoot, grand-daughter shoot, etc., the rule is that the power of shoot production falls off with the later generations. Length and thickness are greater in the mother shoot than in the daughter shoot, greater in the latter than in the grand-daughter shoot. A comparison between the spruce and the silver fir shows how greatly these conditions influence the appearance of trees. The stems of the spruce form pointed pyramids because the mother shoots always retain the lead over those of later generations. The silver fir has a broad top, known as the "**Eagle's Eyrie**" because at a certain age the daughter shoots reach a greater length then the mother shoot.

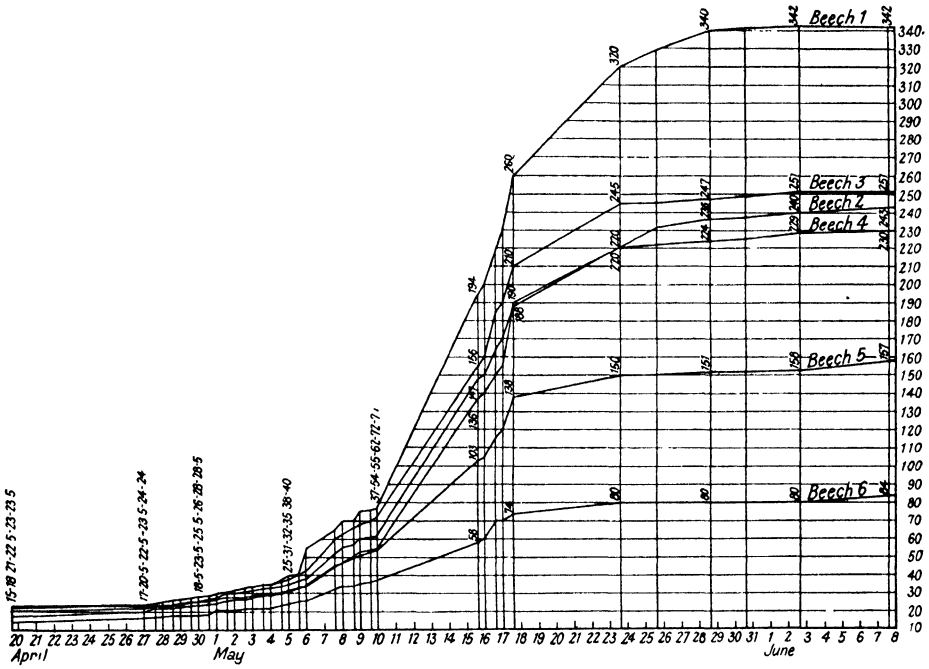


FIG. 9.—Development of the annual shoot of the Beech (*Fagus sylvatica*). Lengths of the shoots in millimetres. Growth begins about April 27, is most rapid between May 10 and 18, and ceases before the middle of June. (After Büsgen in Zeitschr. f. Forst- u. Jagdwesen, 1916, XLVIII.)

Similar variations among themselves are shown by various local races, especially of the Scots pine. The pine of the mountains and of the north has generally a pointed crown up to an advanced age, lowland pines from milder regions tend more to the rounding off and flattening of the crown in old age (*see* also Chap. XIV, Figs. 8 and 169).

The annual elongation of the shoot, like the course of height-growth throughout the life of the tree, has also its great period between a slow beginning and a gradual slackening off.[1] This is most striking in the case of those shoots which are already completely laid down in the bud and unfold all at once in the spring, as in the beech (Fig. 9). The regularity is less pronounced or even completely obliterated in twigs whose growth lasts over a longer time accompanied by the continuous

[1] Büsgen, Blütenentwicklung und Zweigwachstum der Rotbuche. Ztschr. f. Forst- u. Jagdwesen, 1916, p. 289. With increment curves of various broad-leaved trees.

formation of new leaves, as in young ash trees (Fig. 10). We have already pointed out in Chap. I, 3, that the great period of growth finds expression in the annual shoot in the unequal spacing of the leaves and buds.

In the new shoot a distinction is to be made between the formation of new cells which goes on at its tip (meristem), and the rapid growth in

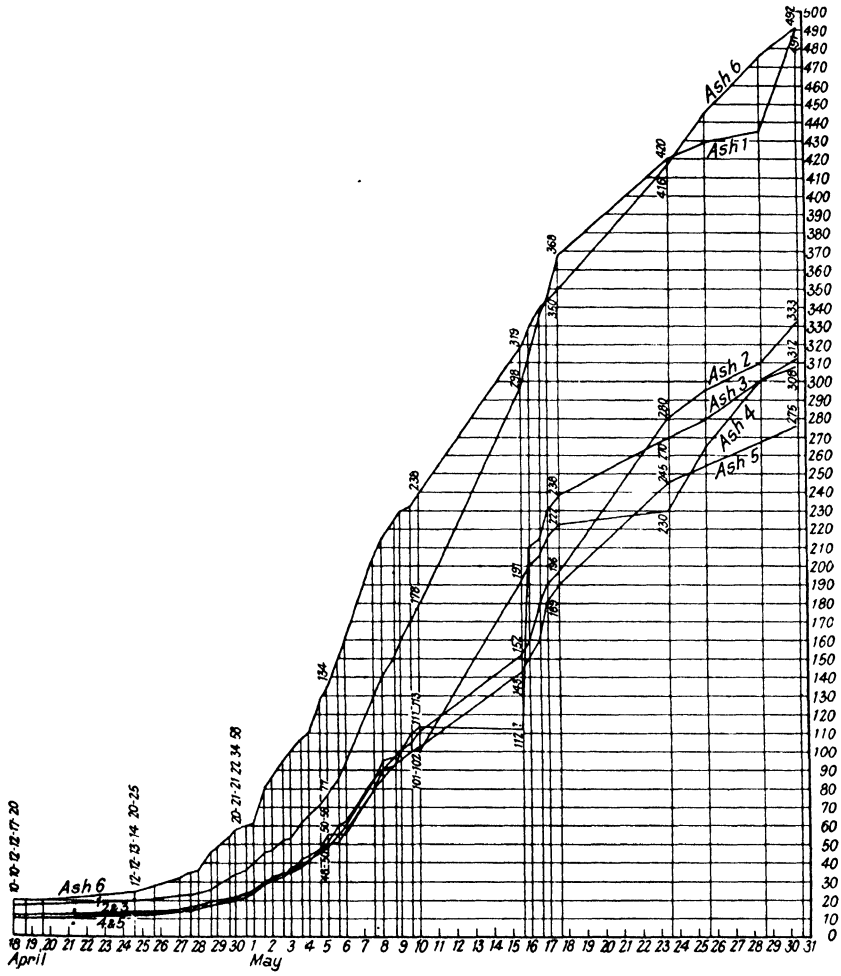


FIG. 10.—Shoot development of the Ash. At first the growth increases progressively, later it is almost constant.

length when the bud has opened, which is due principally to the lengthening of the cells (stage of elongation). In the spruce, for example, the young shoot at first grows equally throughout its length until it has reached about one-tenth of its final dimensions. Later on, a zone of maximum growth is formed in the spruce shoot, which at first lies at its base and then moves forward gradually towards the tip.[1] Little

[1] Rothert, Cohns Beitr. z. Biologie, 7, Heft 1, 1894; Jost, Vorlesungen über Pflanzenphysiol., 3. Aufl. p. 377. Jena, 1913, G. Fischer; Nachtigall, Forstwissenschaft. Centralbl., 38, 1916. Berlin, Parey.

is known of the distribution of growth in the annual shoot in the case of broad-leaved trees. Van Burkom [1] found in *Acer* a zone of strongest growth near the base of each internode which later moves towards its upper end. In other cases the annual shoot passes through the period of growth as a whole. With the perfecting of its internal structure, lignification, suberisation, storage of reserve materials, etc., as a third stage in its formation, the new annual shoot reaches maturity.

A glimpse into the chemical changes associated with the process of growth in the shoot is afforded by Berthold's description.[2] At the top of the growing shoot of the sycamore (*Acer pseudoplatanus*) are found in succession from above downwards, a starch containing, a tannin containing and a sugar containing zone. The last is followed first by a second tannin containing and then by a second starch forming zone which immediately adjoins the zone of the final form. As the perfecting of the tissues progresses up the shoot, the zones contract whilst the starch which is to be stored up as a reserve accumulates up till the autumn.

Previous to this, Sachs [3] had already found the nutrient substances in young, vigorously growing shoots invariably distributed as follows: in the meristem at the tip—protein; then in a region where main growth begins—starch only, below this a region with grape sugar only, whilst lower still carbohydrates were absent altogether from the cells. (*Compare* also Chap. III, 2.)

The elongation of the meristematic cells to their final size ensues on the osmotic absorption of water into the cell sap, in consequence of which the latter exerts a pressure, the turgor pressure, on the cell walls and stretches them. It was formerly thought that the concentration of the cell sap and consequently the turgor pressure, might be greatest in the zone of greatest elongation, and it was sought in this way to explain the increased elongation in that region. According to Ursprung and Blum,[4] however, the greater growth in the zone of elongation is not due to a higher osmotic pressure but to the resistance of the cell wall to stretching being less there than in other parts of the shoot.

The typical course of growth of shoots described above may be modified, and irregularised, but seldom completely obliterated by external influences. As Burger [5] has shown, temperature in particular exerts a great influence on the course of annual height-growth. A favourable influence of rainfall on the elongation of shoots could only be detected, in his numerous measurements, after prolonged drought; as a rule, in the cases under investigation, rain exerted a retarding influence on elongation, and, indeed, in a striking manner even when no considerable fall of temperature was associated with the rain. No direct influence of sunshine could be detected. Pines, spruces and larches from the lowlands commence their growth later, finish it much

[1] Burkom, Versl. K. Akad. Wet., Amsterdam, 1912, p. 766 and Diss., Utrecht, 1913.

[2] Untersuchungen zur Physiol. der pflanzlichen Organisation, II, 1, 218. Leipzig, 1904, Engelmann.

[3] Sachs, Vorlesungen über Pflanzenphysiologie, 1882.

[4] Ursprung und Blum, Eine Methode zur Messung des Wand- und Turgordruckes der Zelle. Jahrb. f. wiss. Botanik 63, 1924.

[5] Burger, H., Unters. üb. Höhenwachstum versch. Holzarten. Mitt. d. Schweiz. Zentralanst. f. d. forstl. Versuchswesen, XIV, Bd., 1 Heft, 1926.

later and attain a much greater length of shoot than those from higher elevations and from the far north.

Stool shoots and root suckers generally show their greatest height-growth in the first or in the first two years. Here the characteristics of the juvenile stage disappear because the young shoots enter at once into the possession of a fully developed root system and the stored materials of the stump and its roots, and so find themselves in the same position as regards nutrition as older shoots.

6. Long Shoots and Dwarf Shoots.—In many trees two kinds of shoots may be very clearly distinguished which are termed long shoots and dwarf shoots. If we examine in winter a several years old branch system of not too old a beech, we find its main branches ending with

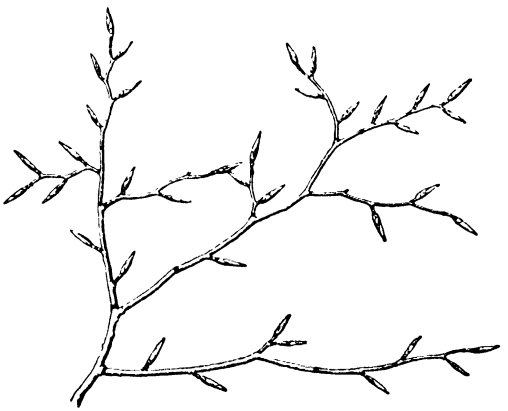


FIG. 11.—Branch system of Beech with long and dwarf shoots. The boundaries of the shoots indicated by transverse marks on the axis.



FIG. 12.—Ten-year-old dwarf shoot series of the Beech (*Fagus sylvatica*).

shoots of the current year, bearing sessile buds. On the older parts of the branches, however, we find structures which look like stalked buds, but are, in fact, dwarf shoots which may attain a considerable age (*see* Figs. 11 and 12). They grow only a few millimetres each year, producing a few leaves but usually only very small lateral buds or none at all, and end with a normal terminal bud. It is noteworthy that the terminal bud of a dwarf shoot may quite abruptly again produce a long shoot and *vice versa*. Thus I found a twig composed of six dwarf shoots, then one long shoot and then finally twelve dwarf shoots. Areschoug [1] terms long shoots of this kind which interrupt series of dwarf shoots, "**Regeneration Shoots,**" and is of opinion that every dwarf shoot series must die if it is not interrupted from time to time by regeneration shoots. The dwarf shoots of the hornbeam, though longer than those of the beech, are quite sharply differentiated from the long shoots. In the birch the dwarf shoots are wont to die off after a few years. They lose their terminal buds and then remain on the long twigs as short woody stumps, often furnished with small dormant lateral buds. A more gradual transition between long shoots and

[1] Beiträge zur Biologie der Holzgewächse. Lund Univ. Arsskrift XIII. Ludd, 1877.

dwarf shoots occurs in the lime, whose branch system is depicted in Fig. 13. It resembles that of the hornbeam and possesses a characteristic feature in the curving back of many short shoots. In both trees the branching appears much more free, lively and abundant than in the beech. The pines, larches, cedars and barberries have dwarf shoots which do not undergo any growth in length, so that their leaf structures appear crowded together in pairs or groups. These are, in the case of the conifers named, the needles standing in pairs (pine) or in tufts (larch, cedar) and a few membraneous scales preceding them which form the needle sheath, and in the barberries, the green foliage leaves. In the larches and cedars the long shoots bear scattered needles, in the barberries triple-pointed thorns which

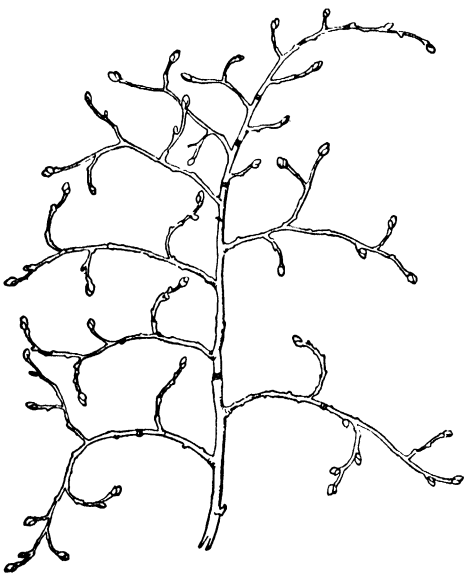


Fig. 13.—Branch spray of Lime.

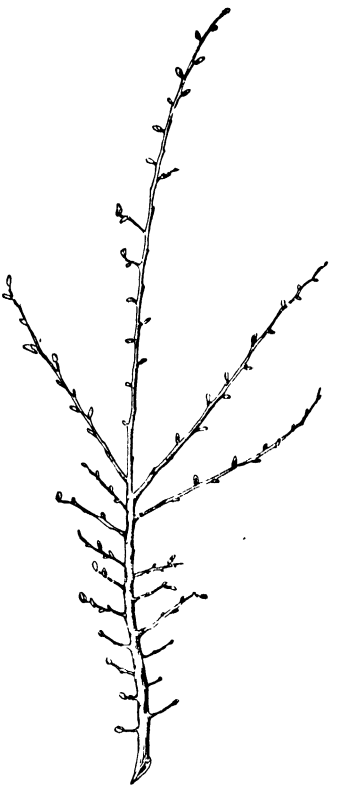


Fig. 14.—Two-year-old spray of the Elm.

are really leaves, as is proved by their arrangement and the presence of dwarf-shoot buds in their axils. In one- and two-year-old plants of the pine the leaves on the long shoots are green, with serrated edges, but later they are reduced to inconspicuous scales in whose axils the dwarf shoots arise. The dwarf shoots of the pine produce needles once only, whilst those of the larch form needles four to six years in succession and may even then grow into long shoots, which are, however, comparatively weak. The ordinary long shoots of the larch arise from the terminal bud and from a number of lateral buds in the upper portion of the long shoot of the previous year. In older larches they have, for the first four weeks after the opening of the buds, quite the character of dwarf shoots and it is only then that they grow out into long twigs. The dwarf shoots with tufted needles arise

from the other buds. Dwarf shoots, one to four years old produce secondary regeneration shoots which look as if they were standing on two to five-year-old long shoots.[1] Except for the group of buds at the end which produce long shoots, dwarf shoots alone are produced on the long shoots of the pine.

Apart from their somewhat different size, the buds show no kind of external indication as to whether they will give rise to a long shoot or a dwarf one, in fact all vegetative buds are exactly alike in their nature. In many cases it is entirely in the power of the cultivator to determine which of the two forms of shoot he will cause to grow from a given bud. Nevertheless, in the natural course of things, they do not appear to be irregularly mixed together but occur in a definite order whose regularity is not without importance for the life of the tree. This regularity consists in general, in the daughter twigs of a year's shoot becoming the longer the nearer they arise to the tip of the shoot. The terminal shoot is usually the longest. Thus the pronounced dwarf shoots of the beech, birch, barberry (*Berberis*) and pine are always found clothing the lowest parts of the annual shoot and also when, as in the elm and poplar, the transition between long and dwarf shoots is more gradual, the twigs grow larger towards the tip of the mother shoot (Fig. 14). In ashes and willows all the side twigs of an annual shoot are developed pretty equally. The field maple and others (alder, hazel, dogwood) form exceptions to the rule, in so far that whilst it is true the short shoots arise from the lowermost buds of a twig and shoots gradually increasing in length from the middle ones, those from the upper buds again fall off in length. Among accessory shoots the middle ones are always the longest though the lowest may be of considerable length (Berthold, II, 35).

It is on the dwarf shoots that the flowers are formed. The flowers therefore stand, as a rule, nearer the base of the twig whilst the foliage is placed more towards the tip and so develops in better light. In many willows, the flower buds, on the contrary, occupy the upper and the vegetative buds the lower part of the twig. This may be associated with the falling off in power of growth towards the end of the twig, which the willows exhibit in common with the shrubs rather than with the trees. The greater narrowness of the vessels in the dwarf shoot and, on the other hand, the greater formation of starch-storing cells at the expense of those having only a strengthening function, may favour the formation of flowers, which is promoted by gardeners by supplying water sparely.[2] In the beech, flower formation is not confined to the dwarf shoots, though these may also produce them. In the pine and spruce the female flowers take the place of long shoots at the tips of the twigs, while the male flowers arise from lateral buds which would otherwise give rise to dwarf shoots. Only exceptionally, in the so-called "**Cone-breeding**" of the pine does a female flower arise from every dwarf shoot rudiment.

[1] Lebensgeschichte der Blütenpflanzen Mitteleuropas, herausg. von. Kirchner, Loew und Schroeter. Stuttgart, E. Ulmer.

[2] Herrmann, A., Unterscheide in der Anatomie der Kurz-und Langtriebe einiger Holzpflanzen (*Fagus*, *Acer*, Pomaceæ, *Ginkgo*, *Berberis*) Österr. bot. Zeitschr., 1916, p. 34.

The foliage of its dwarf shoots contributes greatly to the enrichment of the leaf cover of the tree and to the full utilisation of the space exposed to the light as they produce new leaves for a number of years and so provide foliage also on the older parts of the branches (Fig. 15). In older trees dwarf shoot formation predominates; it is also promoted by unfavorable conditions of the locality. Thus in the shade of close woods young beeches are found which, on account of their small size, might be thought to be undergrowth two to three years old but which are actually ten or more years old and do not attain any height because they only develop series of dwarf shoots interrupted by very short long shoots. Old fruit trees and pruned street trees (*e.g.* red thorn, *Crataegus*) exhibit a peculiar confused form of crown as compared with forest trees in general. This is due to the regular arrangement of the shoots being disturbed by pruning and by frequent heavy fruit production. Two kinds of phenomena occur here; the shooting up of long erect shoots out of the usual order in all sorts of places in the crown and the vigorous development of those daughter twigs which arise on the upper side of the curve on branches which have been bent by the load of foliage or fruit. Vöchting[1] has set out in detail these conditions and also the peculiarities of weeping trees.

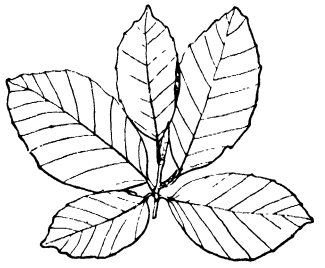


FIG. 15.—Dwarf shoot of the Beech; showing the enrichment of the leaf cover.

A particular form of dwarf shoot is that of the thorns of the sloe (*Prunus spinosa*), hawthorn, wild apple, wild pear and other pomaceæ. They are shoots which cease growth early without producing a terminal bud, but may, however, bear leaves with buds capable of development in their axils. The thorns of the purging buckthorn are the ends of long shoots (Fig. 16).

The prickles of the roses and brambles are of quite a different structural nature. Arranged entirely without reference to the leaves and buds they can only be compared with the hair structures of other plants which they resemble both in their mode of origin and their anatomical characteristics.

The occurrence of thorns is not independent of external conditions. In many blackthorns (*Prunus spinosa*) in shady situations they are entirely absent. Wiesner[2] points to the conversion into thorns of the twigs of many woody plants, as a consequence of the action of too strong illumination. The supply of water also plays a part, so that thorn formation may be diminished, for example, by decreasing the evaporation.

The thorn-like dwarf shoots, like other similar structures, act as a means of protection against damage by the higher animals. Their value as such, like that of all such means of defence, is limited, *i.e.* they

[1] Vöchting, Über Organbildung im Pflanzenreich. I. Bonn, 1878, Cohen & Sohn; II, Bonn, 1884, E. Strauss.

[2] Photometrische Untersuchungen II. Sitzungsber. d. Wien Akad. d. Wiss. 3, 104, 1895; Die Lichtgenuss der Pflanzen. Leipzig, 1907, Engelmann.

do not prevent every injury but they are effective in preventing it reaching such severity as to endanger the existence of the species. Thorns are also indirectly effective in this direction by providing protection to birds' nests whose inmates repay the service later by the destruction of caterpillars and the distribution of seed.[1]

It is obvious that the main function of the long shoots is to extend the tree crown in an upward and horizontal direction. The tree acquires thereby a greater total leaf-surface for utilising the sunlight and in addition obtains the means of producing an infinite amount of seed. Finally, a well developed crown protects the soil from the impoverishing effect of the sun's rays and the consolidating effect of heavy rain, as well as its own stem from the rays of the sun which may cause the death of the unprotected rind (bark-scorching). It likewise suppresses many unwelcome competitors by its shade and thus becomes an important, many-sided weapon to the long lived tree in the struggle for existence.

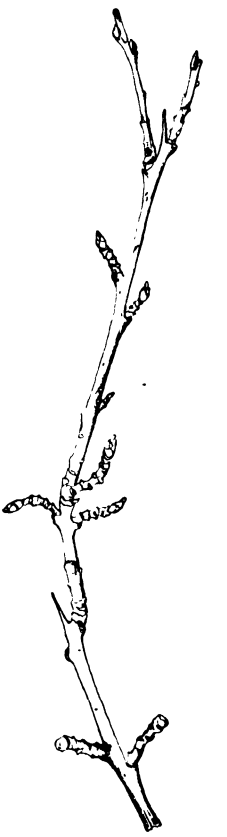


FIG. 16.—Shoot series of the Purging Buckthorn. The ends of long shoots form thorns.

Details in the form of the branches may also be understood through their significance in the life economy of the tree. The thickness of the branches and twigs of the broad-leaved trees in our climate—not always in the tropics—corresponds directly to the load they have to carry, including a not too excessive weight of snow in winter. In particular, the greater or less fineness of the ultimate twigs is an indication of the size of the load of foliage growing on them in the summer and often through this, of the size of the individual leaves. It is necessary, however, to make a distinction between erect shoots and hanging branches such as are seen on older spruces and birches. The pendulous branches do not require to be and are not so thick as the upright ones because they depend only on tensile strength. They, therefore, ultimately entirely cease to grow in thickness. The hanging twigs of the birch also act as an effective weapon against agressive neighbours whose foliage they injure by whipping.

7. Angle of Divergence.—Hand in hand with the variations in the nature and arrangement of the shoots, go variations in the angle at which they spring from their mother branch. As a general rule the upper, stronger shoots diverge at a more acute angle than the lower ones (*see* Fig. 17); it is especially small in the case of the fastigiate trees. The branches of the Lombardy poplar run almost parallel with the main stem and not uncommonly the tips are even bent towards it.

[1] Delbrouck, Stacheln und Dornen. Inaug-Diss. Bonn, 1873, and Bot. Ztg. Bd. XXXI, p. 777; see also Stahl, Pflanzen und Schnecken. Jena, 1888, G. Fischer.

Normal branch systems are occasionally to be seen on fastigiate trees, having arisen by mutation from single buds.[1]

The direction of the branches of a tree is not determined by the angle of divergence alone. Many a branch leaves the stem of the tree at an acute angle (angle of attachment) but bends down in its further course so that the angle becomes more obtuse. The tip of the branch may finally curve upwards. Thus almost every part of the branch makes a different angle with the stem. Burtt [2] has called the angle of the middle course of a branch with the vertical, its "**Angle of Inclination**" (Neigungswinkel), the angle formed by the turned up tip of the branch with the vertical the "**Geotropic Angle.**"

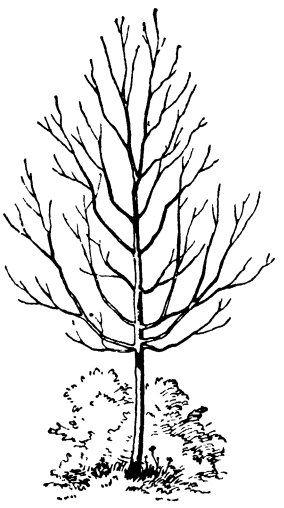


Fig. 18.—Maple.

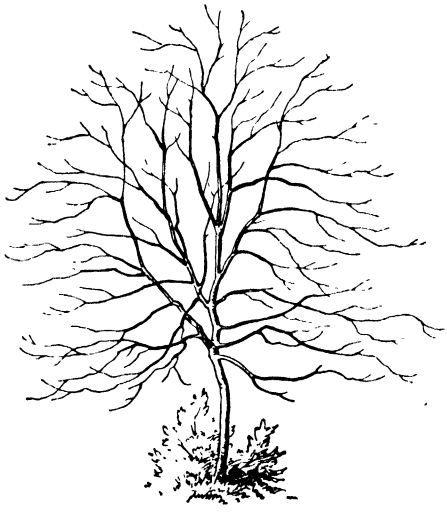


Fig. 19.—Wild Cherry.

How much the inclination of the branches influences the form of trees is shown by the illustrations, Figs. 17, 18 and 19, and here it is not so much the angles of attachment as the angles of inclination which are effective.

With regard to the economy of trees, it depends on the direction of the branches whether rain water falling on the tree is conducted towards the centre or the circumference of the crown. Erect branches favour the former course. Horizontal branches allow the water to fall directly downwards or, with the help of the leaves, towards the outside, just as it mainly drips off to the outside from branches that are bowed over. The running off of water towards the stem occurs especially in youth when regeneration has appeared by stool or root shoots, whilst the conducting of water outwards is found more in older trees and is especially striking, for example, in the lime. The water then falls to the benefit of the young absorbing roots which are more numerous under the outermost branches of the crown than close to the stem.

[1] Schenck, H., Mitt. d. Deutsch. Dendrol. Ges., 1916.
[2] Burtt, Über den Habitus der Coniferen. Inaug.-Dissert., Tübingen, 1899.

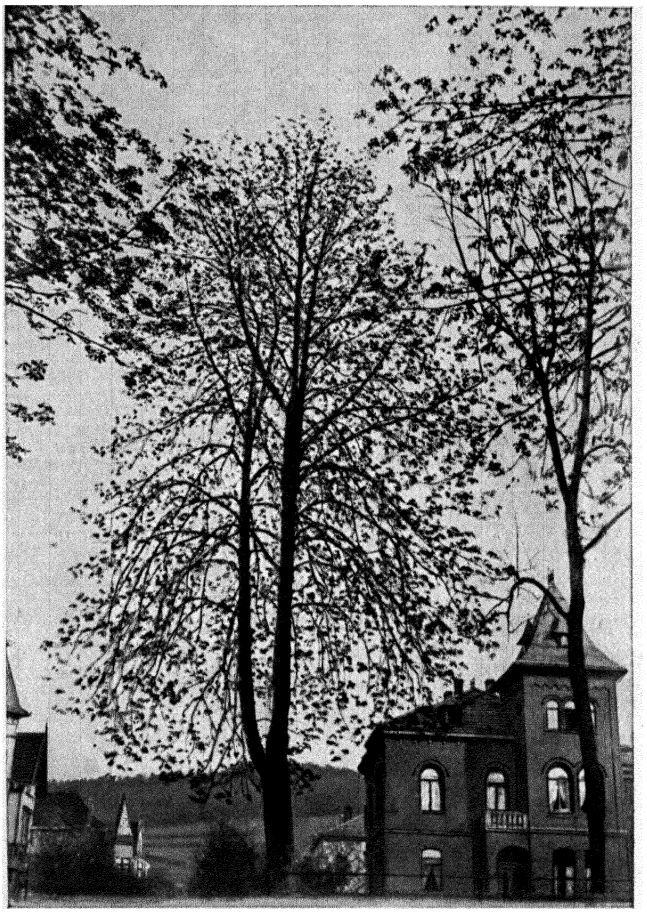


FIG. 17. Horse Chestnut in early spring. The upper branches running out at an acute angle, the lower ones becoming more and more pendant. The ends of the branches again erecting themselves (geotropic angle).

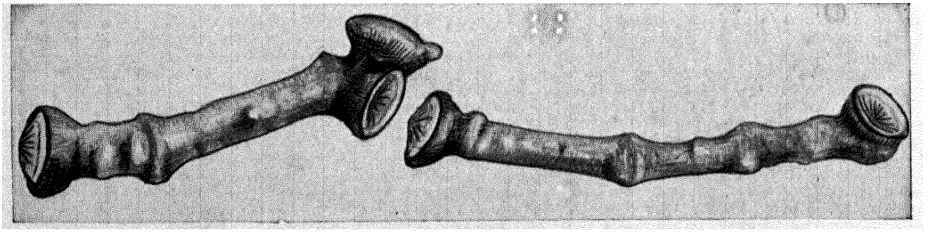


FIG. 21.—Abscissed branch of Oak dismembered into annual shoots by bowl-shaped separation layers. (Mch.)

[*To face p.* 27.

Riegler [1] found the following figures for a rainfall of 402.8 millimetres under the crowns of 55 year old trees.

Percentages of total precipitation:

Species	Reached the Soil [2] (4) and (5)	Evaporated from Crown	Ran down Stem	Fell through Crown	Intercepted by Crown (3) and (4)
(1)	(2)	(3)	(4)	(5)	(6)
	%	%	%	%	%
Beech	78.2	21.8	12.82	65.4	34.6
Oak	79.3	20.7	5.71	73.6	26.4
Maple	77.5	22.5	5.96	71.5	28.5
Spruce	41.2	58.8	1.37	39.8	60.2

The total rain falling on the crown in each case was as follows:

Beech	26,081 litres
Oak	24,273 ,,
Maple	36,901 ,,
Spruce	12,044 ,,

There are a whole number of causes which determine the direction of growth and the inclination of the branches of trees (*see* Chap. I, 12 and 13). Here it need only be stated that they are not unchanging. Rogers observed on a very cold morning that the branches of the lime in his garden had bent down to the ground and blocked up the path. He had already determined to cut them off, but in the course of the day, as it became warmer, the branches rose again. In 1865 and 66 Caspari studied the phenomenon in Königsberg and in 1872 Geleznow [3] was able to use fresh branches of the Weymouth pine (*Pinus strobus*) as a thermometer for low temperatures by fastening them by one end in a horizontal position and observing the bendings which followed changes of temperature. Willow branches [4] bend inwards in the winter and with falling temperature and outwards in the spring. Probably these movements are due to the same cause as the daily variations in the diameter of trees (*see* Chap. X, 3), namely withdrawal of imbibed water from the wood by the cohesion tension of the transpiration stream. Lighting also influences the direction of the branches.[5] Only in a few trees (spruce) are the branches of an unequally lighted crown equally inclined to the main stem on the lighted and shady sides. The branches directed towards the fore-light are generally more horizontal, whilst the weaker ones, facing the after-light are inclined steeply upwards. In this way the hinder branches shade themselves less and their leaves are better able to enjoy the strongest light that reaches them. In

[1] Mitteil. a. d. forstlichen Versuchswesen Österreichs. herausg. von Seckendorff, II. Wein, 1881; Hoppe, Regenmessung unter Baumkronen. The same, Bd. XXI. Wien, 1896.

[2] Not counting the amount dropped from the hanging branches.

[3] Melanges biol. du Bull. de l'acad. imp. d. St. Petersburg, Vol. IX, December, 1872. Reprinted in Ann. des sciences nat. sér. Bot., 1876, T. II.

[4] Ganong, Ann. of Bot., 1904, Vol. XVIII.

[5] Wiesner, Lichtwuchs der Holzgewächse. Centralbl. für das ges. Forstwesen. Wien, 1897.

many trees the branches which otherwise are directed upwards, practically hang down when the lighting is poor. In such cases some part is played by the weight of the foliage. Thus the deeply shaded branches of the horse chestnut (Fig. 17) hang almost vertically downwards because they become long and slender in consequence of the shade and so can offer no resistance to the weight of the foliage. The erection of the growing tip and the acute angle of divergence then give the whole branch an S-shaped curvature.

The influence of weight on the carriage of the branches of the pine and spruce is very striking in snowy situations. The winter load of snow bends the branches down beyond the elastic limit.

8. Tree and Shrub. Self-cleaning. Cladoptosis.—Several connected annual shoots form what is called a branch system and the aggregate branch systems are united into what is called a tree or shrub, though there are all sorts of intermediate forms leading over from the one to the other.

In the simplest case, what is understood by a tree is a woody plant which develops a single, upright stem which never, or only at a certain height, passes over into a number of branches of equal strength, or, if it is branched down to the ground, is distinguished from the branches by its stronger development, as in the case of spruces growing in the open. If several stems are formed, when they reach a height of more than about fifteen feet and a diameter of four inches, we speak of a many-stemmed tree, when smaller of a tree-bush, large shrub or ordinary shrub. In the case of single stemmed trees also a certain size is generally assumed. If it falls short of this we speak of a plant of tree-like form. Among these are included also woody and even herbaceous growths which produce, from creeping shoots, upright crown-bearing stems, such as the moss *Climacium dendroides*, scarcely five centimetres high, the banana, whose stem is almost entirely formed of the lower parts of the gigantic leaves, and the large kinds of bamboo whose stiff woody stems, though they resemble rather a grass-haulm in structure, may be termed trees on account of their appearance and are treated as such, for example in the judicial practice in the Dutch Indies.[1]

The tree-stem is formed either by the prolonged growth of a vertical axis with a continuously increasing terminal bud (palms) or by the arrangement in a straight line one after another of shoots possessing apical growth (conifers and broad-leaved trees) which emerge either from the terminal bud of the upright annual shoot or from the uppermost lateral bud. Such a chain of shoots, by going on growing in thickness as a whole, develops into the tree stem. This form of stem is most simply expressed in the fir, spruce and larch. Here we have a single main axis which runs from the root to the topmost point of the tree. Round it the lateral branches are grouped so regularly that Rossmässler could quite rightly call the conifers a mathematical race. Among broad-leaved trees, only the alder and, in certain cases, the sessile oak show a similar growth. With the other broad-leaved trees and the

[1] Ham, S. P., De in de Literatur voorkomende definities van het Begrip "Boom." Natuurkundig Tijdskr. v. Nederl. Indië. Deël. LXIII, 2.

Scots pine, the formation of a many branched crown begins sooner or later, since the rate of growth of what was hitherto the main shoot declines and even falls behind that of the lateral shoots.

This is connected with the fact that the twigs mutually influence each other with respect to their length and direction.[1] "As in a well ordered state every citizen is dependent on every other with regard to his freedom of action towards the outer world, so in the life of the tree, every neighbouring branch and the sum total of all the branches restricts the growth of the individual branch within definite limits. Removing or even checking the growth of the terminal shoot promotes the growth of the lateral shoots and *vice versa*. The whole branch system is in a condition of tension, which alters as soon as the growth, even of a single member, deviates from the normal path." Thus Mogk explains the broader and more compact form of isolated trees by the check which the leaders suffer by reason of the strong development of the side shoots due to the favorable lighting. In the forest the less well lighted side branches do not hinder the growth of the vertical shoots so much, so that a more slender form of tree is produced. The angle of divergence of the branches increases in the crown from above downwards because influencing by other branches increases in the same direction; and even the falling off in the length of shoots with the increase in the age of the tree is ascribed by Mogk to the increasing check exerted on the individual branch by the ever increasing number of the side branches. That there is, actually, no general senile condition present, he concludes from the fact that if the tree is pruned the new branch systems are exactly like those of a young tree. In this, however, we cannot entirely agree with him (*see* Chap. I, 14).

Specially significant for the production of an obvious distinction between stem and crown, is the phenomenon of self-cleaning, *i.e.* the dying off of the lower, more heavily shaded branches, by which the stem even becomes a smooth cylinder. On the death of branches of oaks, young spruces and silver firs,[2] a piece of the base of the branch a few centimetres long, still remains alive for some time so that it grows in thickness in connection with the stem and merges directly into it. Meanwhile the dead part of the branch has time to wither and drop off; the wound is covered over with callus without enclosing a dead piece of branch which might occasion disease phenomena later (Fig. 44, left). In conifers, especially spruce and silver fir, often also in pine, larger branches decay as a rule, too slowly. Their dense wood, impregnated after death with resin and brown masses, offers great resistance to destruction. Their dead stumps are enclosed by the growing stem, like foreign bodies, as "**Horny Knots.**" If boards are cut from such pieces of the stem the knots shrink on drying more than the stem-wood by reason of their greater richness in wood substances, and fall out, leaving a round knot hole.

As stems free from branches up to a great height are the most

[1] Mogk, Untersuchungen über die Korrelation von Knospen und Sprossen. Archiv für Entwicklungsmechanik der Organismen, herausg. von Roux, 1914, Bd. XXXVIII, 4.

[2] Hartig, R., Die Zersetzungserscheinungen des Holzes der Nadelholzbäume und der Eiche. Berlin, 1878, Springer.

valuable, it is the concern of the forester to prevent the occurrence of strong branches and to artificially encourage self-cleaning, which he does by raising the tree in as close a stand as possible during early years. Stems, the shade of whose own crown is not sufficient to induce self-cleaning, remain branched very low down, when in open positions, *e.g.* spruces in park land. Of forestry importance is the tree's power of spreading or extending,[1] *i.e.* the power of suppressing sister trees in crops of the same species and age. It depends mainly on the characteristics of the crown but also on the activity of the roots. It is great in beech, oak and Scots pine, small in the ash and spruce and is shown by the production, in the case of the first named trees, of comparatively few but large trees on a given area. Thick sowing does not therefore prevent the ascendancy of the best specimens, whilst in spruce thickets, with thick sowing, all the plants enter equally into competition and a great number of middle sized stems grow up together among which the forester by means of his thinnings, must provide space for the most promising trees of the future. With regard to the relations between crown and root, Hauch's work indicates that species with great power of spreading stand transplanting worse than others.

In conjunction with self-cleaning, the spontaneous shedding of twigs, "**Cladoptosis,**" should be considered. According to Hempel and Wilhelm [2] this occurs in the pine, oak, elm, walnut, ash, Norway maple and bird cherry. In the Cupressineæ of the genera *Thuya* and *Chamæcyparis*, etc., the organs of assimilation which become superfluous are cast off only in the form of twigs, the small scale-like leaves are firmly concrete with the twig and in general do not separate from it. It is a process which in its anatomical characters resembles the normal shedding of leaves and prevents the death of the twig on the tree. At the boundary of some one annual shoot all the cell walls, even the lignified ones, in a curved, bowl-shaped layer through rind, wood and pith, are dissolved (Fig. 20) so that the twig falls out as from a ball joint (Fig. 21). In the oak the separation is not confined to a single annual shoot boundary, rather in shed twigs of several years, the separation is shown in all shoot boundaries, so that the twig can be completely broken up into annual shoots. Shed twigs generally still carry the dry foliage when they fall. In many years, as after the hot summer of 1911, they bring a considerable part of the foliage of old oaks to the ground. They thus promote the opening of the crown to light and air and prevent the accumulation on the tree of dead branches which give a foothold to injurious enemies. By preference it is the dwarf shoots that are shed; in poplars, however, which shed twigs already dying from such causes, and in willows, it is long shoots. In many trees cladoptosis begins as early as July, in others later, increasing until the late autumn, and varying in extent according to the individual and the year. Abscissed branches 3 to 3½ feet long have been observed in *Populus Canadensis*, and 2½ feet long in *Quercus sessiliflora* (Röse, Botanische

[1] Hauch, Spredningsevene. Bot. Tidsskr., XXVI, Kjobenhavn, 1904, and XXX, Kjobenhavn, 1910, and Algemeine Foest-und Jagdzeitung, 1905.

[2] Bäume und Sträucher des Waldes. Wien, Hölzel; s. also V. Höhnel, Über den Ablösungsvorgang der Zweige einiger Holzgewächse. Mitteil. a.d. forstl. Versuchswesen Österreichs, Heft 3 and weitere Untersuchungen über den Ablösungsvorgang, etc., 1879.

Zeitung, 1865). As regards age, they are often one-year-old twigs in the poplars and willows, in other cases, however, often six or more years old. These represent in the oak for the most part weak side shoots; but according to Röse the terminal shoot also may break up, whereupon it is replaced by a lateral shoot erecting itself in the already familiar manner. The region of separation between the shed twig and the mother axis, lies, in the oak and poplar at the base of the twig, in the willows and the bird cherry, above the first undeveloped leaves. Drought, age, feeble growth, especially on poor soil, may increase the number of cast off branches, whereas they may be almost completely absent in young trees with plenty of nourishment. On the other hand, it was just in such trees that the dismembering of terminal branches in the oak and the lime was observed. According to Nördlinger,[1] branch abscission in the oak occurs mainly after hot summers, and since, as a rule beech and oak mast years follow a hot summer, the observation that plentiful twig shedding foretells seed years is explained. It is noteworthy that according to observations on the oak, no withdrawal of important structural substances precedes the separation of the shed branches. They carry with them to the ground considerable quantities of starch which is thus lost to the tree. The fallen shoots of spruces and firs are not to be classed with those spoken of so far. They are caused by squirrels, also by birds which peck at or through the twigs. Squirrels seek the spruce twigs in order to devour the young male flowers. In this way they bite many twigs right through which then fall off directly. Others, partly gnawed through, remain hanging until a strong wind brings them in large numbers simultaneously to the ground. As the appearance of large quantities of these, not in the true sense, abscissed shoots shows that many flowers were present to attract the squirrels, a good seed year may be quite properly deduced from them. In the pine the fall of twigs occurs in consequence of beetle attack and finally the mutual shading of them in the crown leads to the death of many. All these losses naturally influence the form of the crown. Thus Röse traces the "open structure" of the grey and black poplars and the "close rodlike structure" of willows and poplars to twig shedding, and the knotty, much broken, branchy growth of our oaks is due to the loss of twigs through shedding or shade (Fig. 22).

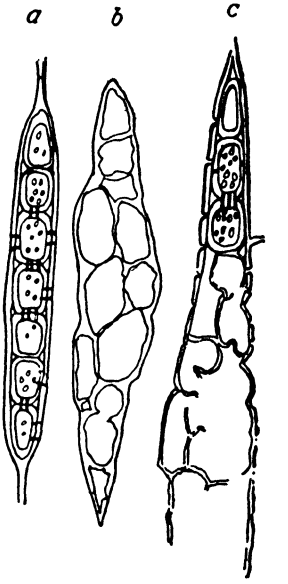


FIG 20.—From the tissues of the separation layer of an abscissed branch of the Oak. (*a*) Original medullary ray. (*b*) Medullary ray within the separation layer, the cell-walls are dissolved. (*c*) The lower end of the medullary ray reaching into the separation layer is dissolved. (MCH.)

It is hardly necessary to mention that the occurrence of inflorescences at the end of the annual shoot influences the branching.

[1] Nördlinger, Forstbotanik, 1874, I.

The difference between tree and shrub is due to the rapid falling off in growth of the main axis in shrubs—if one is formed at all. It consists, apart from the first juvenile stage of the plant, either of a single annual shoot which possesses no terminal bud capable of growth, or of a series of shoots each one weaker than the last. In the elder (*Sambucus nigra L.*, *see* Fig. 23), for example, the branches are bent down by their own weight and that of the leaves and inflorescences, perhaps also through a plagiotropous heliotropism, whereupon one of the twigs springing from the upper side of the branch generally takes over the further development, itself to meet the same fate later. The position which this continuation shoot occupies on its mother branch is no accidental one. It is the general experience that on convexly bent

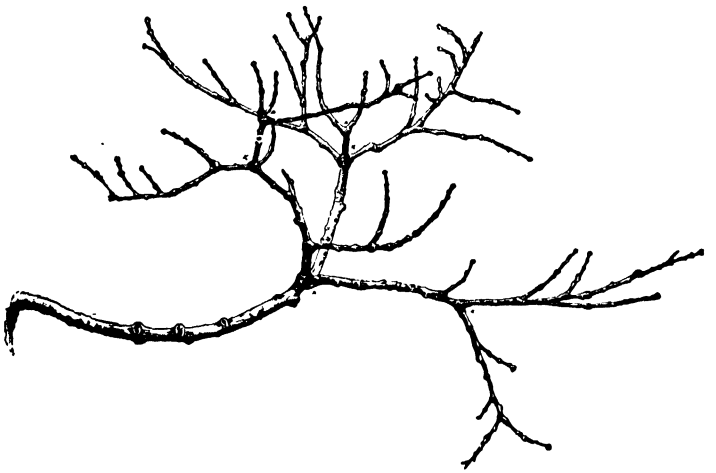


FIG. 22.—Branch system of the Oak. At × twigs have been lost. From Cupuliferen by Büsgen in Lebensgesch der m. Blütenflanzen. Stuttgart, E. Ulmer.

branches, in contradistinction to straight ones, the strongest twigs develop on the upright basal portions of the branch and with increasing vigour towards the summit of the curve, so that the leading shoot arises just before or at this point. This is a particular case of the general rule, laid down especially by Vöchting and applicable also to trees, that the highest point of a branch system is so much the more furthered in growth, the more direct and straight its connection with the main root. The nearer the direction of an axis lies to the vertical line over the middle of the main root, so much the more energetic is its whole growth; the further it deviates from it the slower is its development.

A similar condition to that of the elder determines the form of the hanging or weeping trees,[1] which arise as varieties of the willows, ashes, beeches, wych elms, etc.[2] The crowns of these trees merely consist of branches convex above and massed above and beside each

[1] Vöchting. *loc. cit.* on p. 24.

[2] In weeping oaks and weeping spruces the stem is straight. A weeping oak in the Forstrevier Lindau (Heinemanns Fleck) in the Dukedom of Anhalt, has, with a tall straight stem, the aspect of a birch with its hanging rod-like branches. Weeping spruces are illustrated: Forstlnaturwiss. Zeitschr., 1898, p. 149, in the abstract of: Conwenz' Beobachtungen über seltene Waldbäume in Preussen (Abh. z. Landesk. d. Prov. Westpr., Heft IX. Danzig, 1895.

other in the same way as in the elder, the ends of which hang down in so far as they are not pruned off by the gardener. Many weeping trees make an attempt to grow in height, by those portions of the different orders of branches lying before the curves, raising themselves and seeking to place themselves in a straight line and so producing an upright stem as in Fig. 23. They soon sink obliquely down again as they evidently do not possess sufficiently powerful geotropism and have weakly developed wood which cannot bear its own weight.[1]

In the beech, individuals occur which exhibit little or no tendency to grow upwards, much rather do their leader and branches grow irregularly hither and thither. Oppermann[2] terms them "**Rank Beeches**" (Renkbuchen). They are especially plentiful in Denmark and in the Baltic Islands, as well as in the Süntel, near Hanover (Süntelbuche), but are not absent, generally in a modified form, from any beech forest elsewhere, and cause difficulties in forestry by disfiguring the woods. Corresponding forms are found also in oak and Scots pine. The very instructive ecological and geneological causes of the occurrence and distribution of the rank forms, revealed by Oppermann, will be discussed in Chap. XIV.

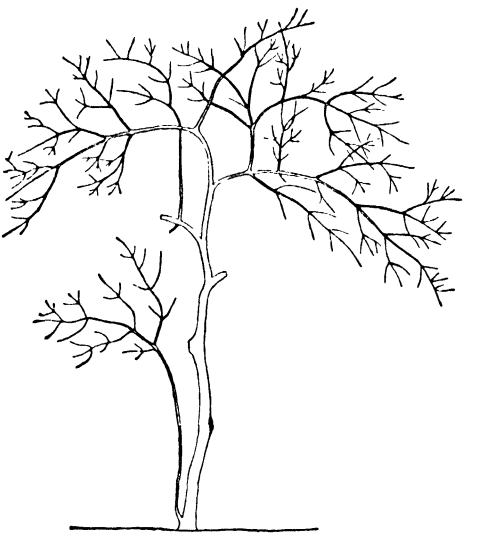


Fig. 23.—*Sambucus nigra*. The stem consists of the basal portions of branches which have soon bent downwards and ceased to grow.

The creeping posture of the stem of the mountain pine is produced by the oldest shoot of the upright leader taking a recumbent position each year.

Besides the decreasing power of growth of the main axis, there is a second condition which leads to the formation of a shrub, namely, that, in contradistinction to a tree, it is not the side shoots that spring from the uppermost but those from the lowermost leaf axils which develop most strongly and often surpass the mother shoot. Here again the gardener can evoke a tree-like form, *e.g.* in the gooseberry, by removing all the shoots but one, which then thickens into a stem. In nature the number of branches of equal importance tends to increase because the formation of shoots from the lowest leaf axils of the branches continues even after the upper portions of them have died off. Added to this is the formation of secondary buds, so that a mother stump gradually arises, half or entirely buried in the ground, whose structure

[1] Anatomischer Holzbau der Trauereschе: Jaccard, Mem. Soc. vaud. Sc. Nat., 1925, 2. Quoted from Bot. Zentralbl.

[2] Oppermann, Renkbuchen in Dänemark. Zentralbl. f. d. ges. Forstwesen, 35, 1909, p. 108. The same: Die Weisskiefer in Jutland. Das Forstl. Versuchswesen in Dänemark, 1923, 2.

may be still further complicated by the formation of stolons and root suckers.

The ultimate causes of shrub or tree formation are to be sought in the constitution of the plants in question. Tree formation is characteristic of the spruces and silver firs and also, as a rule, of oaks and beeches, shrub formation of other woody plants. Not infrequently, however, external circumstances decide whether the one form or the other appears. Trees become bushy when the main axis is continually destroyed, if in such cases there are buds capable of development present. It is thus in the far north, where twigs which project above the surface of the snow succumb to drying up by the winter storms. There birches and spruces form low, the latter almost turf-like brushwood.[1] In our climate the bushy growth of the beech in high altitudes is well known. Strong persistent winds and also oft-repeated browsing, may, like the hedge shears, make trees become bushy. Darwin tells in his "Origin of Species" (sixth edition, 1880, p. 56) of pines, which for twenty-six years were kept down to the height of the heather by the grazing of cattle, without dying. It has already been mentioned that the same species of tree may present in youth a bushy, later a treelike form.

9. Alterations of the Original Arrangement of the Branches. Crown Forms.—The branch system develops from the annual shoot by the buds growing into further annual shoots, the buds on these into shoots of the third order and so on, so that the form of the whole should depend in the first place on the arrangement given by the position of the buds, and then on the length of the individual members of the tree. But if we thought of trees and shrubs as built up by the said annual shoots in accordance with the arrangement of leaf and bud peculiar to each species and with the rules as to the sequence of long and dwarf shoots on a mother branch, we should, in most cases, obtain quite unnatural pictures. We should seek in vain in nature for a sycamore or a horse chestnut which resembled the plant of our imagination.

Vertically growing shoots of young trees present the original conditions in their complete regularity. An upright sycamore twig is always characterised by decussate pairs of shoots [2] and the outer twigs of the elm seen against the sky display in the completest manner the alternate arrangement of their side shoots (*see* Fig. 14, p. 22). On more or less horizontally growing branches of the sycamore, however (and other decussately branched trees behave in the same way), the daughter twigs situated on the upper and lower sides of the branch soon fall behind in growth and the further development of the branch system is undertaken by the twigs growing on the right and left flanks of the mother shoot. Ultimately the upper and lower shoots may die off completely, so that hardly any difference can be seen between the originally two ranked arrangement of the shoots of the elm and the originally four ranked one of the sycamore. In the horse chestnut the formation of the branch system is strongly influenced by the terminal inflorescences and the absence of side shoots in the axils of the middle

[1] Kihlmann, Pflanzenbiol. Studien aus Russisch-Lappland. Helsingfors, 1890.

[2] Occasionally the shoots stand in three-membered whorls.

leaves of each annual shoot. Whole branches may be made up of the basal portions of shoots, which in each case spring from leaf axils on the underside of their mother branch, whilst their own branching proceeds by means of the flank shoots (Fig. 24), indeed, also in the ash, horizontal spreading is not the rule.

The opposite phenomenon to the development of a fanlike disposition in spiral or decussate branch arrangements is found in trees with buds disposed in two ranks. If here the lateral twigs of the successive leading shoots forming the main axis remain in one plane, a flat, fanlike branch system must develop which can never build up a tree-crown spreading out on all sides. This does happen, in fact, with beeches which grow up in the shade of older neighbouring trees. Six or eight year old trees of this sort almost resemble the beech leaf in outline and even in trees several metres high in shady situations the disposition of the whole crown in one plane may be recognised. Such fans are never held vertical but bend over somewhat in elegant curves so that the side branches are oblique to horizontal. The form of the fan is then determined by the leaf surfaces placing themselves in a plane at right angles to the incidence of the light. The fan arrangement often does not occur at all or only in the second order of twigs. This is especially the case in open situations, *e.g.* in beech regeneration without standards.[1] There the main stem grows directly upwards and with it is associated a transition from the two-ranked arrangement into a spiral one. Where the latter is not complete the deviation from the plane of the buds on the mother axis is brought about by the planes of branching of the different orders of shoots not corresponding with one another. The angular bending of the branch from bud to bud produces further alterations in the direction of the twigs and finally, external influences working towards the same end are never absent.

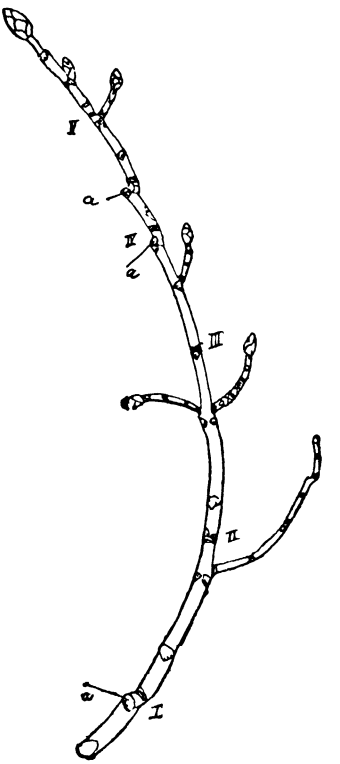


FIG. 24.—Shoot series of the Horse Chestnut; at *a* inflorescences have been situated.

It may sometimes happen in a bent over, fanlike branch system, that a shoot springing from the middle, still fairly vertical portion of the fan, places itself in an upright position and, thanks to its straight connection with the root, develops with special vigour. Two or more lateral buds may simultaneously develop into vertical shoots so that crowns arise formed of several upright branches of nearly equal strength growing together. In upright shoots of the elm a twisting of the plane

[1] Engler, A., Schatten-und Lichtflanzen der Buche und einiger anderer Laubhölzer. Mitteil. der Schweiz. Zentralanst. für das Forstliche Versuchswesen, X, 2. Zurich, 1911.

of branching of almost 90 degrees occurs, so that the lower side branches are at right angles to the upper ones. Lateral twigs of the second and third order also do not lie in the plane of branching of the mother shoot. Thus, in Fig. 14, p. 22 (elm branch system), shoots springing from the lateral buds would project behind and in front of the plane of the paper.

In consequence of the struggle of the twigs among themselves for light and watery sap, there appears instead of the original branch arrangement,anot her one which Wiesner[1] very suitably calls a "**Physiological Branch-arrangement.**" If all the annual shoots remained, a hundred-year-old oak would show ninety-nine orders of branches (generations) whereas actually only five or six can be counted. A fifty-year-old plane tree would possess forty-nine twig generations, whereas Wiesner could only find seven. This phenomenon comes to pass by part of the branches being entirely lost and others dying or withering up, at least at their upper ends, whilst their basal parts merge into a common axis, a false axis or sympodium. Thus, in Fig. 22, p. 32, the axis which slopes up from left to right, in the approximately twenty-year-old branch system of the sessile oak, is a false axis formed by the bases of a large number of shoots joined together, the terminal parts of which have apparently been situated at the places marked *x*. Instead of nineteen generations of branches there appear to be only four. The reduction of the generations in young trees of the pines is brought about by the loss of lateral twigs on the older parts of the branches. In this case Burtt [2] found the formation of false axes only in the circumference of the old crowns. A birch branch, ten years old, which produces only two side twigs a year, must have formed 19,683 leaf shoots. Wiesner could only count 238 on a ten-year-old birch branch exposed to the light and only 182 on a branch of similar age which was suppressed and in the shade. In each case, however, he found not nine but only five orders of branches. By examining stems and buds and counting a false axis as one generation, more than eight orders of branches are never found on our trees (*Carpinus betulus*, *Fagus sylvatica*, *Taxus baccata*), but as a rule only six or fewer. Wiesner[3] proved by a great number of photometric experiments that this regulation of the branching is produced not only by correlations but primarily by the lighting conditions. He measured the strength of the total daylight as well as that of the light inside the crowns of the trees by means of sensitive paper. It appeared that the multiplication of foliage shoots by the sprouting of buds proceeds until a certain minimum of illumination is reached, which possesses a constant value between certain limits for each species. From the limit given by this minimum onwards each new production of shoots has as a consequence the death of others. Whether the new production of shoots is itself influenced by the lighting is doubtful, at least in deciduous trees, which in their winter condition keep back so little light that every bud receives enough to enable it to

[1] Wiesner, Untersuchungen über den Lichtgenuss der Pflanzen usw. Sitzungsber. d. K. Ak. d. Wiss. Wien. Math-naturw. Kl. Bd. CIV, Abt. I, 1895.

[2] Habitus der Coniferen. Inaug-Dissert. Tubingen, 1899.

[3] *Loc. cit.* and also 1893, Bd. CII, Abt. I; Lichtgenuss der Pflanzen. Leipzig, 1907, Engelmann.

sprout. The proof by Jost and others that light is necessary for the complete unfolding of buds is therefore not relevant here.

The crowns of trees are very varied as to the general form of the branching and especially the arrangement, number and size of the branches and the comparative lengths of the different branch generation. If they are composed of two-ranked shoot systems, stratified crowns may arise, as in the beech, where branch systems themselves quite flat, appear disposed in layers one above another and the prolific formation of dwarf shoots contributes to the characteristic form. When the arrangement of the branches is spiral the crowns become more rounded, as in the oak. If the growth of the lower, oblique branches predominates over the height-growth of the middle parts of the crown, table like, flat crowns arise, such as are not uncommon in leguminous trees.[1] If the foliage is developed regularly on long shoots a uniform shade of the crown arises as in the sessile oak. If the leaves are arranged more in rosettes on dwarf shoots, irregularly scattered patches of sky can be seen through the canopy. This is the case with the pedunculate oak, which can, not infrequently, be distinguished from its sister species by this characteristic.

10. Tree Height. Tree Girth. Tree Age.—The function of the stem is in the first place to support the crown of the tree. It thrusts up the leaves into the light and makes the spreading of them in the open possible. Raised above the competition of grasses, mosses and other clump and turf forming plants, and the bushes, the crown obtains room to develop almost as it will, a limit being set only by its own energy of growth, the difficulty, increasing with the distance from the soil, of supplying it with water,[2] and the expenditure of building materials necessary for the maintenance and increase of the sustaining power of the stem and branches. It is true that even stem forming plants in their earliest years have to encounter the competition of the whole outer world. Once they have become strong, however, a considerable growth in height may raise them above their immediate surroundings even in the first few years.

Kannegiesser [3] has collected figures of the greatest age and greatest girth of trees (*see* Table, page 38).

The greatest heights attained by trees are shown by the following figures [4]: *Euchalyptus amygdalina*, 155 metres (Australia); *Sequoia gigantea*, 102 metres (California); *Pseudotsuga Douglasii*, 90 metres (California); *Ceiba pentandra* (Cameroons), 60 metres and over; *Altingia excelsa*, 56 metres and over (Java); *Abies pectinata*, 50 metres; *Picea excelsa*, 50 metres; Eucalypti on Lake Maggiore reach a height of 20 metres in 9 years.

[1] Not only in the tropical tree steppes where the tabular form is regarded as an adaptation to the climate.

[2] Weber, Forsteinrichtung, 1891, p. 151.

[3] Allgemeine Forst-und Jagdzeitung, 1906, and: Flora, hrsg. v. Goebel, 99, 1909, p. 414. G. Fischer, Jena. In *Taxus* a deceptive appearance of great age is given by the fusion of several stems into one false one (*comp.* Lebensgeschichte der Blütenpflanzen Mitteleuropas I, 1. *Taxus*, by Schroeter u. Kirchner Stuttgart, 1908, Ulmer).

[4] Faber, Bot. Zentralbl., Beihefte, Baumriesen, 1898, 158.

Species.	Greatest age.	Greatest girth metres.
Acer pseudoplatanus	600	9·70
Betula alba	—	2·50
„ *nana*	80	0·13
„ *odorata*	124	0·69
Carpinus betulus	151	—
„ (under pollarding)	240	5·90
Castanea vesca	700	15·20
Corylus avellana	100	1·50
Fagus sylvatica	630 /930	8·20
Populus nigra	150	5·65
Quercus pedunculata	1500	15·20
Tilia	800 /1000	17·00
Ulmus	500	13·20
Abies pectinata	300	6·90
Juniperus communis	544 /2000	0.5 /2.75 [1]
Larix	500	7·50
Picea excelsa	400	4·70
Taxus baccata	3000	> 15·00

11. General Remarks on the Causes of the Form of Trees.— Like every other plant, the tree possesses in a high degree the power of adapting its form to the conditions of the locality. Fixed in its habitat, it cannot, by changing its position, avoid unfavorable conditions and seek favorable ones. It therefore has the power of so disposing its organs towards the given external circumstances as to make the best of them. In many cases the influence of the factors of the locality on the form of the tree is at once recognisable or becomes clear on simple examination. Thus, light, gravity, and wind are seen to determine the direction of the tree branches. In other cases only close investigation shows that external influences co-operate in the formative processes and finally there are features in the form of trees in which we believe we must recognise peculiarities of their constitution which are more or less independent of external factors. Such are, for example, the order of the leaves and buds and the polarity of cuttings, examined by Vöchting,[2] by virtue of which, no matter in what position they are planted, they always produce by preference shoots from the end situated towards the apex of the branch and roots from the other end. External conditions may prevent this polarity being exhibited but they do not make it completely ineffective. A cutting stuck in the ground upside down may, by the darkness and moistness of the conditions, be enabled to root itself at the tip, but planting upright is always more favorable because in this position the external conditions for root formation and the internal properties of the cutting work in the same direction. Karzel

[1] Measured at the ground.

[2] Über Organbildung im Pflanzenreich I. Bonn, 1878, Choen u Sohn; the same, Bot. Ztg., LXIV, 1906, Abt. I, p. 101; Klebs, Willkürlische Entwicklungsänderungen bei Pflanzen. Jena, 1903; Karzel u. V. Portheim, Österr. bot. Zeitschr., LIX, 1910. Lundegardh,H., Physiol. Studien ü. d. Baumarchitektonik. Ref. in Zeitschr. f. Bot. 9, p. 590, 1917.

and V. Portheim, moreover, distinguish between the behaviour of cut and undamaged twigs.

If a shoot on a plant is girdled, numerous shoots appear below the place of girdling in spite of the extreme shortage of nutrients; above the place, if the rind is kept in the dark, for the most part roots appear. From this it is evident that the polarity is only operative by means of the conduction channels of the rind, not of the wood. Janse's [1] idea that the formation of young shoots on cut twigs does not take place only because the nourishment is taken from them by the previously appearing roots whose origin is nearer to the cambium, is hardly to be brought into accord with this observation.

How greatly polarity influences the growth of the cells is shown not only by Vöchting's comprehensive experiments, but also by the course of the fibres found in coalescing roots and in the occlusion of stumps. When two roots whose tips are directed in opposite directions, grow into each other, the fibres appearing in the new annual ring turn and twist in a wonderful manner so that they are ultimately directed in the same way and the formative sap can flow in the normal direction from the apical to the basal pole. (Neef.) [2]

"Internal conditions" are, at least partly, concealed external conditions; as for instance, the pressure conditions which exist in every part of the plant in consequence of the omnipresent attraction of gravity. When this attraction works in the opposite direction, in weeping trees for example, it influences the place of origin of new long shoots.[3] The apparent reversal of polarity by strong centrifugal force made to act in opposition to the attraction of gravity was due, however, to checking the development of buds which would otherwise have developed long shoots.[4] The existence of galls and deformities caused by insects shows that external influences are not without effect on formative conditions which are apparently entirely based on the individuality of the plant. The correlations already mentioned may be related to the water and food supply of the individual buds. Everywhere is seen the modelling influence of the outer world. There finally remains, as the sole inherent property, in the sense in which the words have always been previously used, the many sided power of the living portion of the plant body to respond in one way or another to changes in its environment, whether they be within or without the plant—the "**Reaction Norm**" (Woltereck). To determine the conditions under which a particular answer follows is the task of the investigator. As to how that power may have come into existence in the past under the influence of the environment, is a question which at present does not stand in the scientific orders of the day.

Berthold has found the following brief expression of the condition under consideration: "The whole external and internal structural condition of an organism and its whole course of development are in a high degree plastic. The normal is only a special case which arises when

[1] Janse, J. M., Ernährung, Adventivbildung und Polarität, Flora, 1925. Goebel-Festschrift, p. 257.

[2] Neef, F., Über polares Wachstum von Pflanzenzellen. Jahrb. f. wiss. Bot., 61, 1922, p. 205.

[3] Hering, Jahrb. f. wiss. Bot. XL, 1904.

[4] Küster, Ber. d. Deutschen bot. Ges., XXII, 1904, p. 167.

a whole number of factors act on it in a quite definite qualitative and quantitative combination from which, however, it will vary at once more or less widely if the surroundings become different."

The hereditary disposition to react in certain ways to the environment is termed by Johannsen [1]: "**Genotype,**" the external form of the product of the co-operation of this disposition with the influences of the environment: "**Phenotype,**" or almost the same thing by Baur [2]: "**Modification.**" The phenotypes or modifications which occur most frequently under ordinary circumstances are often given the designation "normal form," those forms which occur more rarely, "deviations from the normal form," "sub-species," "anomalies" or "abnormalities," &c. It must be remembered, however, that the original meanings of the expressions "regularity" and "irregularity" would be quite nonsensical here, for in nature there is no such thing as irregularity. Even the most uncommon "abnormalities" are regulated by just as strict natural laws as the normal forms.

Of the relations between the action of external forces and the form of trees, the most easily observed is the dependence of the direction of the members of the body of the plant on factors of this sort.

The erect or inclined position of the shoots, the position of the leaves are all determined in a high degree, by the two forces which display their activity in all plant habitats: light and gravity, and it can be described as an especially marvellous artifice in the constitution of plants, that their limited power of locomotion is replaced by their sensitiveness to these universally present forces. It is the first condition for the life of the tree that it should utilise the amount of light meted out to its habitat to the best advantage for its nutrition. For this it is not sufficient that it should produce food-forming leaves in the greatest possible quantity. They must be so arranged that they do not compete among themselves for the enjoyment of the light and the very directions, displacements, bendings and twistings of the twigs and leaves suitable for this requirement are induced by the light itself in conjunction with gravity.

This sensitiveness is in some cases peculiar to joint-like organs and is retained by them for a long time; it is, however, by no means confined to such special organs in the tree, rather is it possessed by other parts of the shoot. The directive effect of gravity and light is displayed most rapidly in growing root and shoot apices. If they are displaced they curve back again into the original position even within a few hours by growing at different rates on two opposite sides. But strong branches and stems may also carry out movements of this sort. If trees are displaced out of their upright position, even spruce stems 20-30 centimetres thick may be bent in a curve to bring the top into the vertical, as Arnold Engler [3] proved conclusively. In one of the spruces examined by him, which had been placed in an oblique position by movement of the soil, a piece of the stem 16.20 metres long and up to 23 centimetres thick

[1] Johannsen, W., Elemente d. ex. Erblichkeitslehre. Jena, 1913, G. Fischer.

[2] Baur, E., Einführung in die experimentelle Vererbungslehre, Berlin, 1919; the same, Die wissensch. Grundlagen d. Pflanzenzüchtung, 1921.

[3] Engler, A., Tropismen und exzentrisches Dickenwachstum der Bäume. Zurich, 1918.

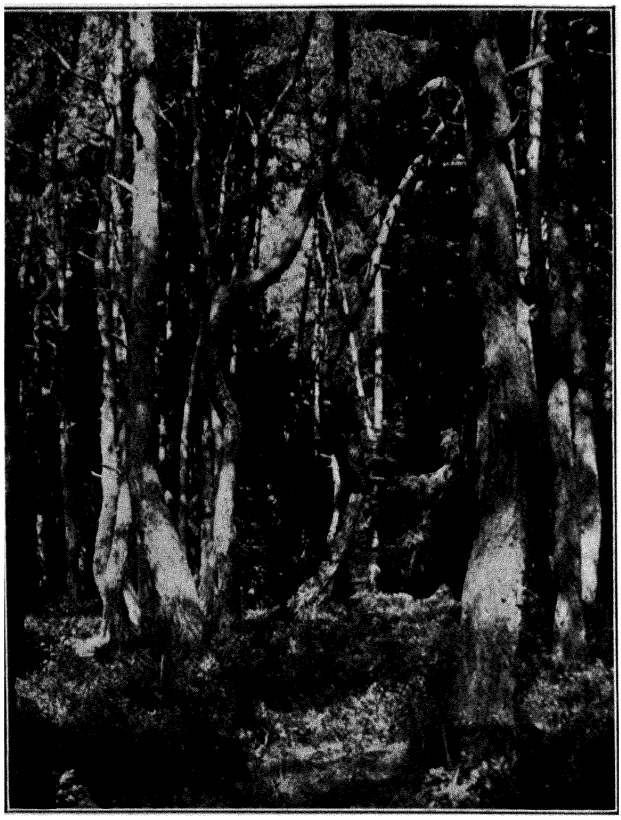


FIG. 25.—Bad form of growth of the South-west German lowland Pine on peat soil. After Münch.

had taken part in the geotropic erection of the tree (*see* also Figs. 88 and 89). Such a huge amount of work cannot possibly have been performed by the tender cambium layer not one-tenth of a millimetre thick. Engler therefore puts forward the assumption that the living cells of the mature wood take part in some, albeit still quite unexplained, way, in the work of curvature. Large stems of broad-leaved trees also carry out similar bendings when, after the conditions of illumination have been altered, they place themselves in a new position with respect to light. It is also an effect of gravity when the youngest branch tips in the pine (*see* p. 45), balsam poplar and other trees, turn upwards like the arms of a candelabrum, only to become horizontal later and leave the turning up to terminal shoots of the next year. The same phenomenon occurs in the prostrate stems of the mountain pine and here again gravity plays its part. Obviously we are not dealing here with phenomena which can be explained by the simple mechanical action of gravity. It is the same with regard to the action of light on plants.

The question of how far internal forces affect the external form of trees and in what manner the modifying effects of external factors are produced, is of great importance in forestry. It touches the methods of selecting seeds as well as the tending of crops. As Münch [1] has deduced, it is not the stem forms themselves that are hereditary but only the disposition to them, and external conditions determine how this disposition works out. The vertical and straight stem-form almost universally found in spruces and silver firs, depends upon their extremely energetic geotropism and the almost complete elasticity of their wood, by virtue of which, after mechanical bending, they immediately fly back again to the straight form or neutralise any bending they have undergone by rapid geotrophic erection of the stem or a substituting shoot. Broad-leaved trees are less fully geotropic and probably less elastic. The form and direction of their stems, in contrast to those of spruces and silver firs, are influenced and in certain circumstances bent by one-sided illumination. In the middle stand the pines. In power of resistance to permanent bending and in the energy of their geotropism the pines from high elevations and also of most of the northern races resemble rather the spruces, whilst certain lowland races from warmer climates resemble the broad-leaved trees. The matter is, however, complicated by the fact that these internal forces are influenced to a great extent by the environment. The better the locality the more decidedly geotropic are both the broad-leaved trees and the pine. It is possible practically to assess the quality of the locality by the energy of upward growth of their leaders. Oaks and beeches in the best localities may be straight and upright like spruces, on poor soils they are mostly crooked or oblique. Even the tops of old spruces may become so weakened in their geotropic energy, otherwise so marked, that they may lose for years their vertical growth and become bent by the wind. Such behaviour is to be observed as a result of repeated summer droughts. Correlations with root formation also seem to influence geotropic energy. If the downward penetration of the tap

[1] Münch, E., Beitr. z. Kenntn. der Keifernrassen Deutschlands. Allg. Forst. u. Jagdztg. 100 and 101, 1924–25.

root in the soil is hindered, the energy of upward growth seems to fall off. The strength of the wood and consequently its resistance to mechanical influences depends likewise on the locality. The same is true of the branching.

Pines of snowy regions, as was first pointed out by Kienitz, tend to form pointed, narrow, almost columnar crowns with short slender branches which offer only a small surface for the accumulation of snow

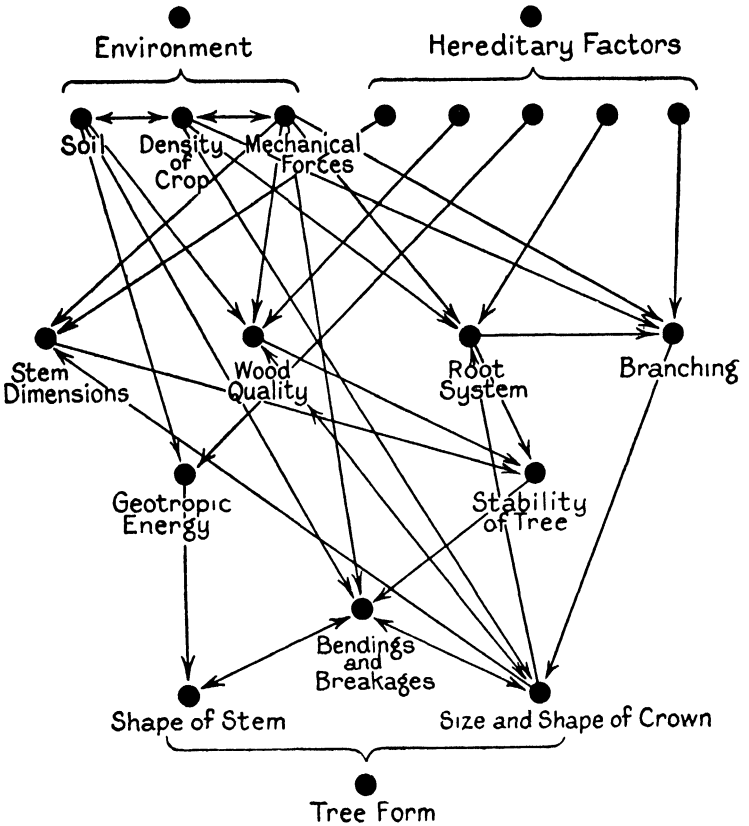


FIG. 26.—Scheme showing the dependence of tree-form on external and internal influences. After Münch.

and give elastically when loaded with it. Pines from the lowlands where there is little snow may form broad, thick branched crowns with impunity. This tendency to branchiness also changes with the locality and is correlated with root formation. The hereditary genotypic characteristic of the species and races is, in all these phenomena, not the tree form itself but only the disposition in certain conditions of the locality to display its geotropism, the strength of its timber, the length and form of its branches, etc., in a certain way. The power of modification of these characteristics on which the form of the tree is based, the limits within which the sum of them moves, is greater in the broad-leaved trees than in the stiff, to a certain extent fixed-charactered spruces and silver firs. As the conditions of the locality are also influenced by the

crop, complicated and invisible relationships between hereditary disposition, locality and tree form arise which Münch has sought to bring also into schematic form (Fig. 26).

12. Effect of the Force of Gravity on the Form of Trees.— There is of course no doubt that the individual members, the building stones of the plant body, are subject to the laws of gravity according to their mass. In the living being, however, the individual heavy particles and their effects are so linked up together that their weight is expressed not only in the weight of the plant members but also in other phenomena whose mechanical connection with the action of that force is still quite hidden from us. Botanists term effects on the living body, which are not directly discernable as of a mechanical nature: "**Stimulus Effects.**" It is an effect of this sort [1] when, for instance, branches in a reversed position, whether artificially reversed or as with the branches of weeping trees hanging down naturally, and in which therefore the attraction of gravity, instead of operating from tip to base does so in the opposite direction, grow more slowly and when their tips again erect themselves experience an acceleration in growth. We may further conclude that it is an effect of gravity when the root finds its way into the soil and, in spite of every diversion by stones or other obstacles, resumes its downward direction. It is the same force of gravity which prevents tree stems from deviating from their upward direction and keeps branches and twigs fast in their sloping or horizontal path of growth.

The nature of the influence of gravity on plants is perhaps made clearest by a comparison with man. To us the erect posture is natural. If we carry a burden with one arm which draws us to one side, we involuntarily raise the other arm to provide a counterweight to that burden; or if the light shines too brightly on our eyes we unconsciously contract the pupils. Such involuntary and unconscious movements correspond with the bendings which plant members carry out in order to retain their proper direction.

The importance of the directive effect of gravity is demonstrated most obviously in seedlings. How would the rootlet, emerging from the acorn or beech nut, find its way into the nourishing soil if its sensitiveness to gravity did not induce it to bend itself downwards, and how would the young plumule, buried in the rotting leaves, find its way to the light if that same sensitiveness did not show it the upward path? When germination begins, it is true, the seedling shoot of spruce and pine bends downwards, but it then thrusts upwards and only the apex remains bent down until it lifts up the cotyledons which at first stick in the seed shell [2] (*see* below under "Germination"). It is also important later on that, by virtue of this sensitiveness, after every accidental displacement, both the terminal shoot and the main root find their way back to the vertical position. The spruces on a steep mountain slope grow just as straight upwards as those on the mountain ridge because gravity directs them. This also applies to silver firs, but

[1] Hering, Jahrb. für wiss. Bot., XL. 1904, p. 499.

[2] Sperlich, Krümmungsursachen bei Keimstengeln, etc., Jahrb. f. wissenschaftl. Bot., 50, 1912.

not to broad-leaved trees, in which, as we shall see, the stimulus of light interferes as a co-determinant.

The power of shoots to grow straight upwards away from the centre of the earth in the direction of its radius, is termed "**Negative Geotropism.**" The main root, striving towards the centre of the earth is said to be "**positively geotropic.**" Thus "**Orthotropism,**" *i.e.* the straight upward and downward growth of the main shoot and the main root, is pronounced to be a consequence of the directive action of the force of gravitation.

Much less simple to understand are the conditions which determine the position of "**plagiotropic**" organs, *i.e.* those which grow inclined to the main axis. Among these are the branches and lateral roots of trees. At first it might be thought that their direction would be determined by that prescribed by their rudiments, thus in the case of shoots, by the buds out of which they emerge. This is, so far as we know, not directly affected by gravitation. It depends, like the arrangement of the buds, on conditions inside the plant body which are, in the meantime, not accessible to our investigation.

The sprouting of buds, however, does not always occur in the direction which appears marked out for them by their attitude as, for example, all buds adpressed to the mother shoot would lead in this way to impossible plant forms. All sorts of bending movements occur whose direction is quite independent of gravity (Figs. 41–43). The action of gravity on the permanent position of the twigs only becomes effective later.

The first unequivocal stimulus effect of gravity on the twigs emerging from the bud condition is shown in the fanlike spreading of the twig system found in the beech, hornbeam, elm and lime. Here all the twigs of the first, second and third order are in one plane and all turn their ventral surfaces upwards, whilst in their position in earliest youth they project sometimes above and sometimes below the plane of the fan and must therefore present their ventral surfaces to various parts of the heavens.[1]

Branches which, after the terminal shoot has been cut off, erect themselves out of the inclined position (become orthotropic) no longer form their subsequently growing members so as to produce a fan, but develop them all round or radially. In this way are produced the "false" leaders which are not uncommon, especially in spruces. The disturbance of the normal conditions (correlations) has altered the geotropism and the structure of the shoot. In the spruce, if the lateral shoots do not erect themselves, the secondary axes springing from their bases may do so and then grow on in the radial form.[2] It is in this way that the harp trees arise: fallen or oblique spruces out of whose leaning stem rises a row of upright, radially developed branches.

[1] In the opinion of Rosenvinge (Ref. to the Danish work in Bot. Jahresber, 1888, I, 99) the difference between ventral and dorsal sides (dorsiventrality) depends in the main on the attitude of the twig to the mother axis and is only to a small extent increased by the action of gravity. The inclined growth of the twig, determined by a whole number of conditions, develops in it the power of becoming dorsiventral in such a way that its ventral side takes up a definite position towards the mother branch.

[2] Goebel, Organography of Plants, Eng. Ed., p. 214, Oxford, 1900.

The twigs having emerged from the first juvenile condition, the stimulus of gravity displays itself in many cases in a curving upwards of their ends (*see* Fig. 44). Later they elongate and finally reach a condition of equilibrium which is determined in a complicated fashion [1] by their own weight, their greater or less stiffness—which is itself influenced by stimuli effecting eccentric growth in thickness (*q.v.*), by gravity and by reaction to light stimuli.

The behaviour of young pine branches offers a pretty example. At first, under the influence of their negative geotropism, they direct themselves straight upwards so that they stand on the mother branch

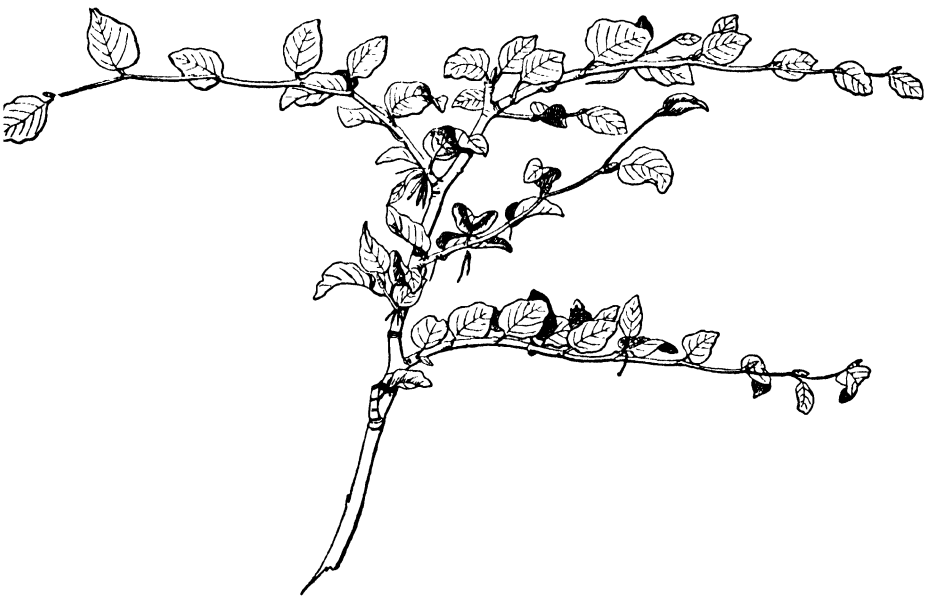


FIG. 27.—4–5 year-old shade-grown Beech. All shoots inclined (plagiotropic). From Büsgen, Cupuliferen.

like Christmas candles. On growing further they become somewhat limp and curve and droop down rather irregularly in consequence of their own weight. Finally, through the effects of geotropism and recurving they place themselves in the oblique position characteristic of them and only the end of the branch still appears somewhat curved upwards geotropically.

As a rule it is noticeable that sensitiveness to the stimulus of gravity falls off in successive orders of shoots and roots. Thus the upright main shoots and the lateral shoots of the first order show it decidedly, but it is often so little evident in the later orders of branches that the direction of their growth does not appear to stand in any relation to that of gravity. Nevertheless the yearly erection of the members of even the least important chains of dwarf shoots is noticeable,

[1] Baranetski, Uber die Ursachen, welche die Richtung der Äste der Baum-und Straucharten bedingen. Flora, 1901, Ergänzungsbd., Bd. 89; Kniep, Einfluss der Schwerkraft auf die Bewegungen der Laubblätter und die Frage der Epinastie. Jahrb. f. wiss. Bot., Bd. 48, 1910. Lundegardh, D. geotrop. Verh. d. Seitensprosse. Ref. in Biol. Zentralbl. 39, 1919. Wiesner, Sitzungsber. der Wiener Akad., Math.-naturw. Kl., CXI, Abt. I, 1902, p. 733.

e.g. in the beech, which leads to a fairly marked curvature. Epicormic branches (water shoots), *i.e.* shoots which emerge from dormant or adventitious buds, are often affected by gravity in the same way as the chief axis and grow vertically upwards so that they look as if they had been grafted on the inclined branches. This is often to be seen in silver firs whose branches are damaged by the shoot aphis and replace lost twigs by producing epicormic branches at their bases. They are reminiscent of strange parasites or of "witches' brooms," which are thick bunches of twigs which develop from still unknown causes by bud mutation or in consequence of infection by certain parasitic fungi. Such witches' brooms are independent of all tropistic correlations with other parts of the tree and always grow directly upwards no matter on what part of the tree they arise. The fungus has here robbed the growing shoot of the power of bringing its direction of growth into harmony with other parts of the tree. The epicormic branches on the stems of oaks also often look like alien growths on the tree by reason of their directing their growth in an arbitrary way which is not in keeping with the symmetry of the normal crown.

That the position of leaves (needles of the photometric Abietineæ) is also directed by gravity is shown at the end of Chap. VIII, 11.

Lateral roots, on emerging from the main root, strike into the soil in a slanting direction, to which they return if they are diverted by mechanical obstacles such as stones or hardened places in the ground. The directing forces are very complicated.[1] The lateral roots of higher order are little or not at all sensitive to the stimulus of gravity. Their direction in the soil is determined by other influences to be mentioned later.

If stems are displaced from the vertical by mechanical force of any kind, such as wind, weight of snow, the sliding of soil, or, in the case of young trees of snow, on slopes, by one-sided loading through unequal development of the crown, by light stimuli, etc., and then straighten up again by virtue of their geotropism, what is known as "**Scimitar Growth**" takes place.[2] Scimitar growth is to be seen most frequently in the larch, in which the curvature nearly always lies in the direction of the wind. The race of larches indigenous to the Südeten is less prone to scimitar growth than the alpine larch.[3] In broad-leaved trees scimitar growth occurs especially on steep slopes even in early youth as the result of earth slipping[4] and one-sided light stimulus.

13. Tree-Form and Light. Nature of Stimulus Phenomena.—The stimulus of the force of gravity, which determines the position of the shoot with respect to the surface of the earth, directs it also towards the open sky from which is radiated to it the light necessary for the life of the tree. But light also possesses a directive influence on shoots and leaves and works directly as well as by altering the

[1] Lundgardh, Ursachen d. Plagiotropie und Reizbewegung der Nebenwurzeln. Ref. in Biol. Zentralbl. 39, 1919.

[2] Hartmann, H., Ü. Säbelwüchsigkeit der Bäume. Zentralbl. f. d. ges. Forstwesen, 1925, p. 165.

[3] Cieslar, Zbl. f. d. ges. Forstwesen, 30, Jg. 1904.

[4] Schmid, J., Klima, Boden u. Baumgestalt. Neudamm, 1925.

sensitiveness of the plant members towards the stimulus of gravity. The parts played by the two directive forces in the disposition of a plant member in space are not always distinguishable with certainty.

For every plant and every part of a plant there is a certain strength of illumination with which they seek to supply themselves and which, we may infer therefore, is most suited to their requirements. The sensitiveness expressed in this way is called the " disposition for light " of the plant or plant member, and those of the latter which seek out a high degree of illumination are termed highly and others little disposed. This " seeking " takes place by bendings and twistings of special motile organs or of parts of the plant still in process of growth. The power of executing bending movements under the influence of a source of light is termed " **Heliotropism.**" Leading shoots of plants endowed with such a power of bending or heliotropic plants grow straight upwards when they are bathed in the amount of light which suits them, which for most of them is the diffused light of the clear summer sky. If they find themselves in light of too little strength, they bend towards the direction from which the strongest light comes, like our room plants which grow out from the dark interior of the room towards the light streaming to them from the sky. The main roots are " **heliophobic** " or light-shunning; under one-sided illumination they turn away from the light. It is by virtue of such " negative heliotropism " that the climbing tendrils of the Virginia creeper and the ivy cling to the wall and there develop anchoring roots. At maturity, however, then the ivy ceases to climb and turns to the formation of light disposed leaves and exchanges the indented juvenile form of leaf for the entire-margined, mature form, the shoots reverse their disposition, they become positively heliotropic and grow out from the wall towards the light. In bushes the heliotropic bending of normally upright branches is not infrequently to be recognised in gardens where they are growing under the shade of a tree or near a wall. It is always a sign that the situation is not sufficiently light for them. Fig. 28 shows a lilac branch stretching out towards the light. The original decussate arrangement of the twigs has completely disappeared through the turning of the shoots towards the light, and so much the more as the less favoured lateral shoots have entirely vanished.

Heliotropism is most strongly developed in the seedling stage—even spruce seedlings up to about three years of age exhibit sharp heliotropic bendings of the young stem under one sided illumination at the margins of woods. Later on no kind of heliotropic reaction of the stem is observable in our spruce; old stems, even under one-sided illumination invariably grow upright, whether it be that geotropism is strong enough to conceal heliotropism or that the latter altogether disappears later. The same holds for the silver fir ; in this case, indeed, no directing of the stem by light is observable, even in seedlings. The light disposition of the stems and branches is higher in the pines and larches than in the spruce and silver fir. Austrian pines often show striking heliotropic curvings of the branches and the sloping position of our pine and larch often observed in gaps and on the margins of

woods may also be caused by the one-sided lighting. According to the investigations of Arnold Engler, the heliotropism of broad-leaved trees, even up to old age, is far more marked than was formerly recognised. When gaps are formed in dense woods by the cutting out of single trees, the marginal trees bend into these gaps, even in the first year, to again rise upright under certain circumstances. Broad-leaved trees seldom stand upright on steep slopes, they generally grow with an inclination towards the valley—towards the stronger light—more markedly on sunny slopes, and poorly lighted and poorly crowned because crowded trees, more strongly than dominant ones. The oblique position is most marked in youth and middle age and in dense woods. The top is more strongly bent towards the light than the middle part of the stem. The butt ends often stand out from the hill side in scimitar growth so that an S-form of the tree arises. According to Engler's investigations, it is undoubtedly not simply a case of bending under load in consequence of one-sided branching, but of stimulus movements, in fact of the resultant effects of geotropic and heliotropic movements, in which, as may be once more mentioned, not only the growing tips of twigs but also thick axes down to the lower parts of the stem take part, with great expenditure of energy. The stimulus to such movements is taken up by the young twigs, exhibits itself there by bending movements and then invades the thicker parts of the stem. Engler traces back the manifold supplimentary bendings of tree branches also to light stimuli. The twigs which at first slope obliquely upwards, droop down later when they are overshadowed by higher branches so that they may better utilise the side light.

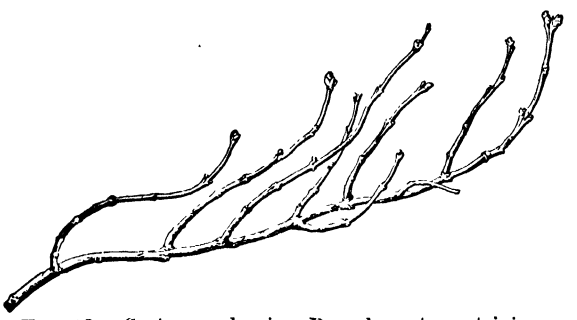


FIG. 28.—*Syringa vulgaris*. Branch system striving towards the light.

In spite of all this it is, however, to be noted that not every one-sided development of the crown or every curve of the stem towards the lighted side is due to light stimulus. A plentiful supply of light on one side leads to the greater nourishment of the illuminated side of the tree whilst the shade side is stunted. Wiesner speaks in these cases of "phototrophy." An example of this is shown in Fig. 29. In consequence of one-sided loading, the stem of trees branched on one side may curve quite passively towards the best lighted side by merely bending under the weight.

The sensitiveness of plants to the stimulus of gravity and light is a special case of the irritability of every living mass. Almost every alteration in the play of forces in the environment of a plant and also inside the plant body itself, may in fact, act as a stimulus and set up processes in the living substance which, in the cases here dealt with,

become visible as curvatures in growth. It is characteristic of all stimulus phenomena, to state it once again, that they do not stand in direct relation to the stimulus, like, for example, the movement of falling to the force of gravity. The stimulus only releases forces present in the internal mechanism of the living substance. These provide the necessary work or energy for carrying out the bendings or other stimulus movements. To avoid all misunderstanding the word "**stimulus**" might quite well be replaced by the word "**release.**" When gravity in an obliquely placed tree bends the stem upwards against its own direction and at the same time bends the tap root downwards, there is, indeed, no simple connection to be recognised between the expenditure of energy of the cause and the effect produced, but the process could also be imitated by suitable machinery. It would be wrong to conclude from the, at first sight paradoxical, process and from other peculiarities of stimulation phenomena, that stimulability is a fundamental speciality of living beings. It is only correct in so far that the term stimulus was originally confined to biological processes. Fundamentally the stimulation phenomena do not differ greatly from the corresponding processes in inanimate nature. The effect of the explosion of a charge of gunpowder is also not determined by the strength or the nature of the means by which the powder is ignited. With the progress of physiology it will be necessary to get away from the earlier idea which regarded stimulability as an exclusive prerogative of life. Stimulation effects reveal themselves more and more as chemical reactions and transmissions of stimuli as streamings of sap which most probably follow none other than the ordinary physical and chemical laws.

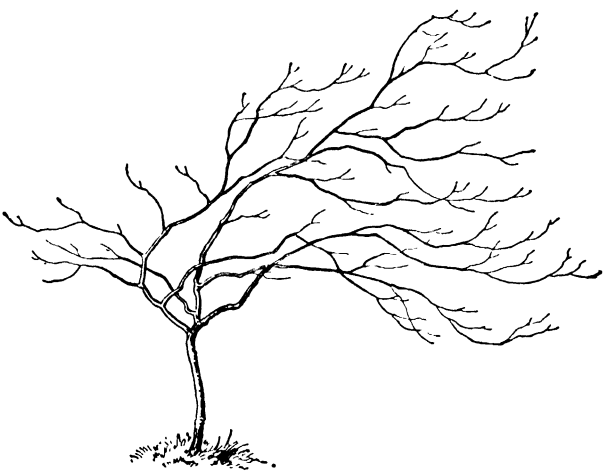


FIG. 29.—*Prunus domestica.* Apparent heliotropism (Phototrophy).

It would be outside the scope of this book to enter further into the details of theoretical stimulation physiology and its progress, philosophically so important. For these, works on general physiology must be consulted.

14. Change of Form according to part of the Tree, Age, Environment and Hereditary Disposition.—So far in our considerations we have looked upon the internal forces which prescribe the form of the tree as being generally constant for the species or the in-

dividual without regard as to whether all parts of the tree are animated by the same formative forces and whether these internal forces may not also change during the long life of the tree. We have, indeed, already referred incidentally to internal changes of disposition in the course of development. These ideas may now be pursued further.

It is quite a familiar phenomenon to the forester that the twigs and needles at the top of old spruces and silver firs look quite different from those of young trees of about man's height, so that they are not at once recognisable as belonging to the same species, and even experienced botanists allowed themselves to be deceived and constructed a separate variety *nigra* out of the top branches of the spruce. The upper branches of old silver firs are more densely covered with needles, and the needles stand erect and scimitar-shaped, in contrast to the parted, pectinate needles of younger plants. They are more thick-set, tougher, bear more stomata and exhibit also in their internal structure differences from young needles. It is further noticeable that the branches of older spruces generally stand out horizontally and their lateral twigs hang down limply like a fringe, which is never to be seen in young trees. If the leading shoot of an old spruce is grafted on a young spruce, a tree is obtained which resembles exactly in the structure of its branches and twigs and in the form of its needles the top of an old tree cut off and stuck in the ground. An artificially rejuvenated tree of this sort also bears cones more plentifully than a young one of the same age grown from seed. If, instead of a leading shoot or one of the youngest side branches, the end of an old horizontal branch has been taken, it is vain to expect it to develop into an erect tree. It retains for decades its horizontal growth.[1] Exactly similar practices have for long been carried out by gardeners. If an *Araucaria excelsa* is propagated by over grafting of pendent branches of the second order, the scion forms, instead of an erect tree a pendent branch which grows on feebly and remains unbranched. The gardener also knows that it is not a matter of indifference for fruit production from which part of the crown he selects his scions for propagation. If so-called water shoots (adventitious shoots) of apple tree, pear tree or the rose are used for grafting, trees are produced from them in which the nature of these shoots, their vigorous growth but small tendency to flowering is retained. Root suckers of the aspen when used as planting material behave differently from seedlings. They soon fall behind the latter in growth and become early affected by heart rot. Such differences in form and life activity are especially striking in the ivy. Young plants raised from seed have two-ranked, 3–5 lobed, leaves and creeping, light-avoiding, limp, shoots. Old fully lighted ivy stems differ from them by possessing pointed oval, spirally arranged, leaves on light-seeking, stiff shoots as well as by their annual production of flowers and fruit. If an old stem of this kind is multiplied by grafting, the mature form is retained in all its characteristics apart from rare throwbacks to the juvenile form. A non-creeping, entire margined, flowering form, falsely called var. *arborea* is obtained. An equally sharp distinction between the juvenile and the mature form is shown by the holly, *Ilex aquifolium*, which in

[1] According to specimens in the Tharandt Forest Nursery.

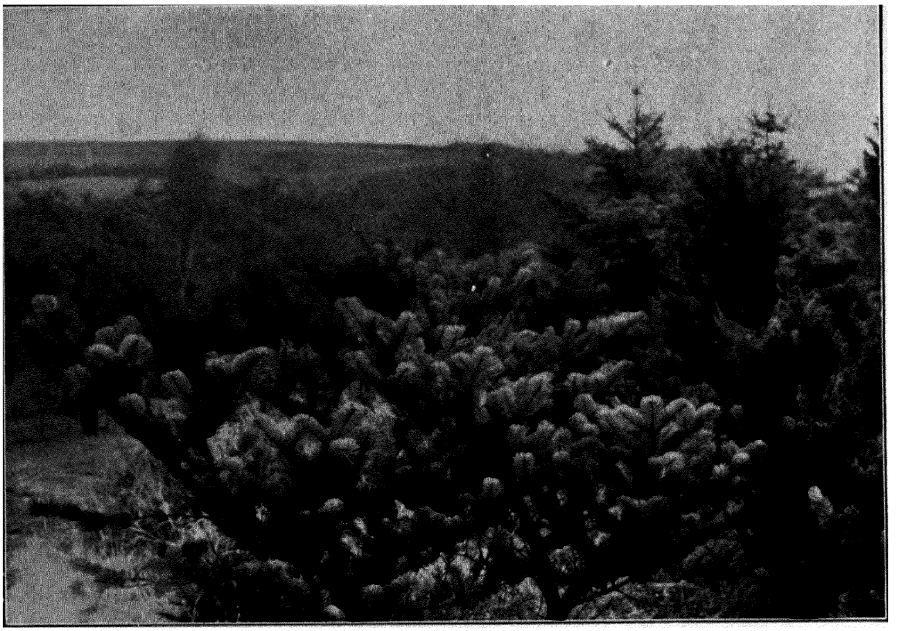


FIG. 30.—*Abies Reginae Amaliae*, from a lateral branch from the top of an old tree grafted 25 years previously on a 3-year-old Silver Fir. The tree retains the form of growth (eagle's eyrie) of the top branches and produces no leading shoot. From the Tharandt Forest Nursery. After Taubert.

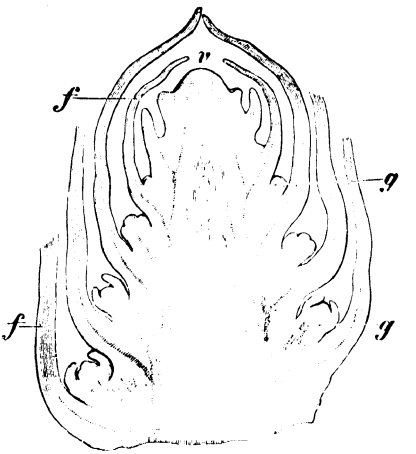


FIG. 31.—Apex of a shoot. (*v*) Growing point. (*f*) Leaf rudiments. (*g*) Bud rudiments for the next year. B.L.

[*To face p.* 51.

youth bears sharp prickly leaves and at maturity smooth margined leaves, and only then produces fruit. Not less great are the differences between the leaves of seedlings and older plants which will be discussed in the last section. Only the needle forms of the seedlings of the cupressineae, which can be perpetuated by the growth of cuttings, may be mentioned here. There is an important physiological difference between young spruce seedlings and older spruces. The former come into leaf in the spring, 4–6 weeks earlier than the latter. Throughout, we come across similar, though not always such marked, differences between the juvenile and mature form of leaves, the dependence of fertility on a certain age and other differences in form and life processes according to age and the part of the tree.

Thus internal readjustments take place with age, with the result that, under exactly similar external conditions, forms and other expressions of life change of themselves and similar changes are also produced by the position which the plant member occupies on the tree. Characteristics arise thereby which cannot be reversed at will by alterations in the life conditions, but are retained for a long time, in fact some of them permanently.

The characters of the parts of the tree which are determined by position are grouped by Molisch [1] under the term "**Topophysis**"; Seeliger [2] then introduced the term "**Cyclophysis**" for the characteristics determined by age or the course of life, two conceptions which in the future we shall not be able to do without.

Even superficial observation shows that the nature of the members of a plant is not completely determined by either topophysis or cyclophysis. All parts of plants are also very greatly modified by external influences. A silver fir at maturity forms the characteristic top needles we have described only when it grows in full light; in the shade of a light-demanding crop it retains the pectinate, juvenile leaves even up to an advanced age. It also remains smaller there than in full light. In a poor locality the tree becomes other than in a good one. Hardly a single characteristic is conceivable which would not be more or less altered by changing external circumstances.

Some of these properties induced by external conditions have also been proved to show a certain power of persisting, though they do not seem to be so permanent as many of the topophytic and cyclophytic characteristics. If a beech, raised in the shade, is transplanted into the light, it continues for several successive years to form shade-leaves and shade-buds prone to early sprouting. Aquatic plants accustomed to warmth react quite differently to high temperatures with the amount of their assimilation, from those of the same species grown in cold water (Harder). Perhaps also the phenomenon that badly nourished plants placed in better soil still remain stunted in growth for a long time may be traced to characteristics induced by the locality. The editor of this book would suggest the term "**Periphysis**" for characters induced by the influence of the environment, without necessarily

[1] Molisch, Pflanzenphysiologie als Theorie der Gärtnerei, 5 Aufl. Jena, 1922.

[2] Seeliger, Topophysis u. Zyklophysis pflanzlicher Organe u. ihre Bed. f. d. Pflanzenkultur Angewandte Botalik Bd. VI, H. 2, 1924 (Appelheft), p. 191. With further examples.

connecting with it the idea of the prolonged duration of induced characteristics.

The topo-, cyclo- and periphysis of the parts of plants are naturally different for different species, and indeed, for different individuals. Internal hereditary factors prescribe even in the fertilised egg cell of the incipient plant the characteristics for all its parts, for every age and for all possible external circumstances. We have already learnt of these internal forces passing over with the germ plasm under the conception "genotype." Genotype, environment, age and part of the plant together determine imperatively the characteristics of all plant members, and so the whole phenotype.

To return to our example; the previously described scimitar form of the spruce needle and the "arborea" form of the ivy are determined by cyclophysis and periphysis, but not by topophysis, because they occur only at maturity and only in full light, but on all parts of the old tree so far as they are fully lighted. The form of the primary leaves of seedlings is purely due to cyclophysis, because it occurs in the first stage of the life cycle, on the whole shoot and in every environment. The drooping form of the lateral shoots of the second order in *Araucaria excelsa* should be only of a topophytic character, because it is not confined to a particular age nor to a particular external condition.

We shall not be able to leave these concepts out of account if we wish to understand the form of the tree.

CHAPTER II

THE BUDS

1. The Interior of the Bud.—The rapid awakening of vegetation in the spring suggests that the rising temperature does not find the plant world unprepared. In fact during one growing season what is to be unfolded at the beginning of the next is already initiated and the true state of affairs is sometimes only hidden from the observer by the necessary winter covering of the young rudiments.

The wintering form of the young annual shoot is the bud. Like it, it is a leafy shoot, whose axis however remains very short and whose leaf organs are constructed in accordance with the requirements of winter.

If we make a median longitudinal section of the winter bud of a broad-leaved tree, we come upon the apex of the young shoot surrounded by the youngest leaf-rudiments (Fig. 31). The latter occur in acropetalous succession, *i.e.* so that the uppermost are always the youngest—as protuberances on the apex of the shoot (growing point) which they soon surpass in growth, bending towards each other over it so that its tender cells are always covered by the rudiments of the leaves. The acropetalous order of formation is characteristic of all leaf structures. It is constant from the lowermost bud scale to the uppermost and youngest leaf rudiment, so that no leaf occurs out of order and inserts itself, as it were, between already existing leaves. Between the young leaves are to be found their young axillary buds which sometimes originate earlier than the leaf to which they belong (Goebel *loc. cit.*). On breaking up beech buds, it is surprising to find what a small part of the whole is made up of the young annual shoot which forms its innermost part. It lies, a little pale coloured or green cone, in the middle of a thick covering formed by the bud scales with their hairs or glands, on a broad, firm, stock from which the outer bud-scales spring and which forms the termination of the shoot of the previous year. The boundary of the two shoots lies somewhere in the upper half of the " bud trace " (Berthold, II, p. 214), *i.e.* the part of the shoot marked by the places of attachment of the scales. This junction is often sharply defined, especially in the pith. In the maple and the ash (Fig. 32), for example, the pith ends in a dome, the **pith dome,** formed of stout-walled cells containing much starch. Above this, about where the bud-scales are situated outside, is often found a zone of tissue which is particularly

rich in crystals of calcium oxalate. This has been called the **oxalate nest.** This, again, is covered on the upper side by thick-walled cells which merge gradually into the tender tissue of the vegetative cone with the young leaf rudiments. The oxalate nest is absent in the ash bud; in the silver fir the green vegetative cone rests on a disc or shallow basin of thick-walled tissue, below which there is a conspicuous gap in the pith, filled with quite loose, not closely compacted, tissue. In the black alder (*Alnus glutinosa*) and the birch the tissue of the young shoot passes over into that of the previous year without the formation of distinct intermediate zones.

During the winter rest the vegetative cone itself is sometimes flat and broad, sometimes narrowly arched. In the silver fir Busse [1] depicts the winter vegetative cone of the terminal bud of the stem as flat, that of the long-shoot buds situated below the terminal bud of the leading shoot—the whorled buds—as long and slender. In the terminal bud of a long shoot in process of erection to replace the main shoot which had been removed, it had assumed an intermediate form. Further details of the inner structure of buds and of their physiology, in so far as it is expressed in the distribution and movement of starch, sugar and tannin, are to be found in the works of Berthold and Larkum [2] mentioned below. The tracing out of the physiological processes which to some extent follow the translocation of substances in the wood (*see* below) seems to be of special importance, because a further knowledge of them helps to smooth the way to an understanding of the alternation between the formation of buds and the growth of shoots. The period during which the formation of new tissues inside the bud takes place embraces in the main the summer in which the buds are formed, but it may begin a year earlier, when the annual shoot on which the buds are formed itself still lies in the bud. This period decides the number and the position of the leaves, flowers and axillary buds to be laid down in the bud, and their earliest stage of growth in which they are still formed of cells hardly differentiated from each other (embryonic growth). The elongation of the parts to reach their final size and internal development follows in the spring in which the bud opens.



FIG. 32.—Longitudinal section of the tip of an Ash shoot in winter with terminal bud and two lateral buds. The starch-containing tissue of the previous year's shoot, black. Above it, the rudiments of the new shoot surrounded by the thick bud-scales and hairs. Slightly enlarged.

In the narrow confines of the bud the young leaves are folded together in a manner which is characteristic for the individual plant and for whole related groups. Thus poplar leaves (Fig. 33) have their lateral margins rolled in towards the centre of the bud (involute vernation), while willow leaves are doubled in a simple boat-shaped form with the midrib as keel. The two halves of the leaves of the cherries and their allies lie folded at the midrib with their upper surfaces flat

[1] Beiträge zue Kenntnis der Morphologie und Jahresperiode der Weisstanne. Flora, 1893, p. 113.

[2] Larkum, Beitr. z. Kenntn. d. Jahresperiode uns. Holzgewächse. Diss. Göttingen, 1914. Braunscheidt, Z. Kenntn. d. Winterknospen unserer Laubhölzer. Diss. Göttingen. Wetzlar, 1917.

against each other. This folding together occurs also in the lime (Fig. 34), elms and hazel, but in these cases is combined with wrinkles and rather shallow folds following the course of the stronger lateral veins. The young leaves of the beech, hornbeam and our two species of *Acer* are closed up like a fan in folds which in the hornbeam are still somewhat noticeable in the mature leaves, but in the beech are almost completely smoothed out. Alder and birch (Fig. 35) resemble the beech. According to Arnoldi,[1] the arrangement of the leaves in the bud is determined mainly by their form and method of growth, but is also dependent upon space conditions in the bud. If the latter are altered, *e.g.* by the presence of flowers, the vernation of the leaves may undergo alterations.

The development of the young leaves on the vegetative cone exhibits, in spite of all subsequent variations, many common features. Thus, in the hump or pad-like first rudiment of a leaf, there may be



FIG. 33.—Cross section of a bud of the Black Poplar. The bud-scales, *k*, form an imbricate covering, the foliage leaves, *l*, have involute vernation. To each leaf belong two stipules, *ss*.

FIG. 34. FIG. 35.



FIG. 34.—Cross section of the inner parts of a bud of the Lime. The stipules between the doubled leaves. After N. J. C. Müller.

FIG. 35.—Cross section of a bud of the Beech. After N. J. C. Müller.

distinguished a lower part—the **hypophyll**—from which the leaf base and the stipules develop, whilst the whole of the blade and leaf-stalk arise from the upper part of the rudiment—the **epiphyll.** The leaf-stalk develops last, after the blade has already been partially formed. The lobes or leaflets of incised or compound leaves (ash) arise as branchings of the epiphyll, and similarly, teeth which on the fully grown leaf may only appear as inconspicuous incisions on the margin, may represent comparatively large branchings of the rudiment. The prominences on the leaf margins of *Quercus pedunculata* are produced by a strip of cell-forming tissue (meristem) on the leaf margin.[2]

2. The Bud-Scales.—In nearly all trees the tender embryonic shoot is wrapped in bud-scales.[3] They protect the young shoot they

[1] Über die Ursache der Knospenlage der Blätter. Flora, 1900, Bd. LXXXVII.

[2] Prantl, Berichte der Deutsche bot. Ges. I, 1883, p. 283. Further details of leaf development in the bud *see*: Deinega, Beiträge zur Kenntnis der Entwicklungsgeschichte des Blattes und der Anlage der Gefässbündel. Flora, 1898, Bd. LXXXV, p. 439. Goebel, Vergl. Entwicklungsgesch. der Pflanzenorgane. Breslau, 1884, Trewendt.

[3] *See* Büsgen, Cupuliferen in: Lebensgesch. d. Mitteleurop. Blütenpflanzen, II, and Neese, Zur Kenntnis der Struktur der Niederblätter und Hochblätter einiger Laubhölzer. Flora, 1916. (Comparison of vegetative and flower buds and the anatomy of transition forms.)

enclose through the winter, from drying out and from the attacks of hungry animals, and when the young shoot elongates they grow with it for a time, so that it is not exposed too soon or too suddenly to the influences of the environment. The bud-scales cannot be regarded as a protection against low winter temperatures; firstly, because our forest trees are frost hardy in winter, and secondly, because so small a body as a bud, whatever its internal structure, certainly immediately assumes the same temperature as its surroundings. The surface of the buds of our beech and oaks is easily wetted and able to absorb water. The scales are traversed by vascular bundles and contain, especially in the brown, hard parts exposed to the air, thick-walled, narrow, small cells in which stone-hard crystals of calcium oxalate are often present. Towards the base of the scales wider cells with living contents appear, which contain oil and starch and at the time the buds open, increase in size and multiply at the expense of these materials and effect a two-fold or three-fold elongation of the scale.



FIG. 36. — Cross section of a bud of the Plane. The tubular stipules appear as rings. After N. J. C. Müller.

Very widely distributed, both on the outside and in the interior of buds, are hairs of various kinds. They are sometimes silky, shining and stiff, sometimes softer hairs, sometimes glands which exude gummy or resinous substances. These last are found, for instance, in the buds of the birch, in fact on all their internal surfaces and also on the inside of the bud-covers. They are multicellular structures, each originating in one epidermal cell, whose secretion makes the buds hardly less distasteful to animals than do stiff hairs, and may act even better as a protection against drying up. In the beech the young leaves in the bud bear long silky hairs which soon disappear after expansion. The high polish of the lacquered buds of the aspen (*Populus tremula*), the polish and subsequent stickiness of those of the horse chestnut, the resinous covering of those of many conifers, especially of the balsam fir, are due to such secretions. The hairs on ash buds are the cause of their black colour. They are short-stalked structures with blackish brown contents. Stomata, which in the leaves are the outlets for the evaporation of water from the interior, are not altogether absent from the bud-scales, where they serve as passages for the exchange of gases between the cells at the base of the scale which are capable of growth and the outer air. The epidermis is strengthened by cork cells in the silver fir, birch, lime, horse chestnut and others.

The distastefulness of the buds to many animals (due to hard scales, hairs, crystals and resin) is still further enhanced by the bitterness of the cell contents, mucilage (the lime) or latex (Norway maple). In the bud-scales of the grape vine the calcium oxalate takes the form of sharp needles, the so-called raphides, which, as Stahl [1] pointed out, form a splendid defence against the attacks of slugs. Against certain enemies, which occasionally appear in great numbers in the winter or early spring, bud coverings provide no defence—particularly gall wasps and gall midges. Game also do not allow themselves to be prevented from

[1] Stahl, Pflanzen und Schnecken. Jena, 1888.

devouring the highly nutritious buds of many trees in winter, especially the silver fir, aspen, beech and hornbeam, by such protective arrangements.

Morphologically, the bud-scales are to be regarded as leaf structures. In a completely formed leaf we are accustomed to distinguish three parts: the often somewhat broadened leaf base, the leaf stalk and the actual leaf area or blade. In addition, in most of our broad-leaved trees (beech, hornbeam, ash, birch, hazel, alder, elm, willow, lime and wild cherry) there are small leaf structures, green in the willow but generally pale or reddish in colour, which are found on each side of the leaf base. These are the stipules, organs which have a function during the unfolding of the bud, but often, though not always, perish afterwards.

During the summer the blades of the leaves play the most important part, while the other portions, especially the leaf base and the stipules, recede from notice. The last leaves produced by the annual shoot towards the autumn, however, not only remain smaller than the earlier ones but undergo a complete alteration in the relative sizes of their individual parts. Whilst the blades get smaller and smaller the leaf bases and stipules increase in size until ultimately they appear to be the principal objects. From them, in most cases the bud-scales originate. Those bud-scales which are produced by the special development of the leaf-base occasionally bear on their tips an undeveloped blade in the form of a point or a minute leaf-like appendage, whilst the nature of stipules transformed into scales can be determined mainly by their situation on both sides of a main leaf which remains very small and indeed is often completely absent. Examples of leaf-base scales are those on the buds of the sycamore, walnut, horse chestnut, ash (*see* Fig. 38), black elder, laburnum and bird cherry (*P. padus*). The buds of the alder, oak, beech, lime, hornbeam, hazel, buckthorn, and the rose and apple species are covered by scalelike stipules. In the alder, between the two outer bud-scales is to be found the main leaf by which their stipular nature is established. An oak bud shows on the outside scales formed of pairs of stipules without a main leaf. Then follow more pairs of stipules which enclose leaf blades at first incompletely developed but becoming more and more completely so towards the interior.[1] The leaf blade also is not always unconcerned in the formation of bud-scales. The bud-scales of the privet, honeysuckle (*Lonicera*), mezereon, pine, silver fir, *Taxus* and juniper are leaf blades which sometimes

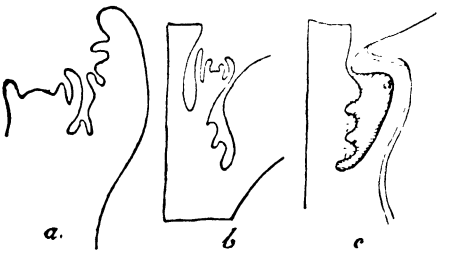


FIG. 37—*Robinia pseudacacia*. Leaf axils with buds. (*a*) Right, young pinnate leaf; in front of it a sharp bud rudiment. (*b*) Three superposed bud rudiments, the uppermost with leaf rudiments; on the right, the base of the covering leaf. (*c*) Three bud rudiments already almost enclosed by the base of the covering leaf. After Feist.

[1] For bud analyses of other trees *see* A. Henry, Knospenbilder I, Nova acta acad. Leopoldino-Carolinae, etc., XXII, 1847; Döll, Zur Erklärung der Laubknospen der Amentaceen. Frankfurt a. M., 1848, L. Brönner.

differ from the blades of foliage leaves only by their smaller size. The scales of the lilac may be regarded as leaf blades that remain small and in the wayfaring tree (*Viburnum lantana*) and alder buckthorn (*Rhamnus frangula*) the buds are enclosed by normally formed leaves covered with a thick felting of hair. These pass the winter in a juvenile folded condition and grow out into true foliage leaves at the time when the bud unfolds, though they may also fall off like bud-scales. Buds covered by such leaf structures not developed into the form of actual scales are called **Open Buds.** Buds in which the scales do not completely cover the inner parts, as for instance in *Sambucus nigra*, may be termed **Half Open.** Here we have an outer pair of dry-skinned, grey, scales and an inner one of juicy, violet, ones, both overtopped by young leaves, apparently quite unprotected. The epidermis of the latter, often together with the underlying layer of cells, forms folds as if it were too wide for the rest of the tissue. Actually there is between it and the latter a hollow space into which groups of green cells protrude in the form of papillae. The buds of *Sambucus racemosa* are closed.

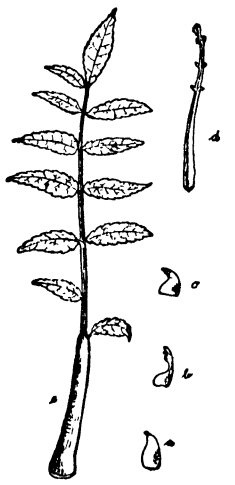


FIG. 38. — Ash leaf. Transition into the bud-scale. In (*e*) the leaf blade appears already reduced and the leaf base enlarged. In (*d*) the leaflets of the blade have almost completely disappeared. (*a*), (*b*), and (*c*) are ordinary bud-scales with an inconspicuous remnant of the blade at their tips.

The number of scales in a bud, as well as that of the leaves already laid down in its interior varies from plant to plant. A beech bud, for example, contained the following leaf structures: (1) Two bud cotyledons (*see* below), (2) 7–8 pairs of bud scales (stipules without main leaf), (3) four pairs of stipules with gradually increasing main leaf.

In the spruce, according to Schumann,[1] 90 bud-scales may be counted, in the Scots pine over 100 and in the Austrian pine over 350; an extraordinarily large number which is explained by the whole of the leaf structures of the long shoot contained in the bud being scale-like in form and being already completely fashioned in the bud. The needle-bearing dwarf shoots situated in their axils are at this time still in an embryonic condition. The number of scales visible on the outside of the bud is a significant characteristic for identification. There are 2–3 in the lime, 2 in the alder, a number in the beech, elm, oak and only one in the willow. (*See* the table at the end of the chapter.)

What has been said above as to the correspondence of the bud-scales to certain parts of the vegetative leaf does not rest on an arbitrary assumption. Observation and experiment alike teach that bud-scales and leaves actually originate in essentially similar rudiments, whose later development is decided by their surroundings, *i.e.* their relationship to other parts of the whole shoot competing with them in growth and nutrition and to the climatic conditions. By the early

[1] Antatomische Studien über die Knospenschuppen von Koniferen und dikotylen Holzgewächsen. Bibliotheca botanica, 15. Kassel, 1889. The older literature cited.

removal of the leaves or the tip of a shoot the buds actually destined for development the following year can be made to unfold in the year of their formation.[1] Real leaves are then formed from the primordia which in the ordinary course of things would have become scales. The not uncommon transition structures between normal leaves and bud-scales lead to the same conclusion.

An exceptional condition among bud-scales is presented by the so-called **bud cotyledons**—not on account of their nature, they are leaf structures like the rest—but on account of their arrangement. In most dicotyledonous trees, the cupuliferae, pomaceae, amygdalaceae and also in conifers—particularly, for example, in the beech, lime and wild cherry, not however in the alder—the lateral buds of the annual shoot begin with two small scales which differ from the succeeding bud-scales by always standing practically opposite each other, even when the latter are scattered. Because they thus separate themselves from the succession of other leaves like the real cotyledons which also are almost always opposite, they have been called the " cotyledons " of the shoot present in the bud ; a term which is reminiscent of the time when botanists disputed as to whether the tree was to be regarded as an individual or as a colony of individuals, the annual shoots.

Like the form and position of the leaves, the form and position of the bud-scales is characteristic for the individual woody plants and a valuable means of identification in the winter condition, as may be seen from the table at the end of the chapter.

Bud coverings of a peculiar sort are possessed by the planes, magnolias and the tulip tree. In the first the bud covering consists of a brown cap placed on top of the bud. It represents, like the bud coverings of the other two genera, a somewhat exceptional stipular structure.

Fig. 37 shows how, in the robinia, several buds are quite regularly placed one above another in each leaf axil and are then however all (*c*) or in part (*b*) covered over by the base of the leaf.

3. The Origin and Perfecting of the Buds.—The buds originate very early. Of fifteen trees which bear scaled buds, Albert [2] found in the leaf axils, of the birch in May, the guelder rose (*Viburnum opulus*), the ash and the Japanese quince in the beginning of June, the buds already present which were destined to pass through the winter, and in their interior the first of the leaves, to be opened in the following spring; were even in process of formation. Other woody plants like the two elders, the beech, the hazel, the Norway maple, etc., were equally far advanced at the beginning of July and two, the virginia creeper and the hawthorn, at the beginning of August. Woody plants with scaleless buds (*see* below) produced some of the first leaves of the bud even two years before the unfolding, thus doing so at a time when the shoot bearing those buds was itself sleeping in the bud. This remarkable behaviour was shown by the dogwood (*Cornus sanguinea*). The robinia resembles the first named plants.

[1] Goebel, Beiträge zur Morphologie des Blattes. Bot. Ztg., 1880. The same, Organography of Plants (Eng. Ed.), p. 216, Oxford, 1900.

[2] Albert, Entwicklungsgeschichte der Knospen einiger Laubhölzer. Forstl. naturw. Zeitschr., III, 1894.

Busse [1] found in the growing point of the silver fir, the development of the bud-scales for the coming winter in progress even by the end of April. On July 10th it was complete and the laying down of the needles destined to unfold the following year begun. In general the whole development of the winter bud [2] might be completed by the beginning of September, though inception and growth in the interior also often last into October and in isolated cases even into December. Larkum [3] has proved that in *Taxus*, *Populus*, *Prunus*, *Acer*, *Syringa* and *Fraxinus* the origination of bud scales is completed by the beginning of June, and in July the leaf primordia appear on the vegetative cone.

In most cases no more leaves are originated on the annual shoot in the summer than reach development the following summer; as on weak shoots of maple and horse chestnut and in the beech. On strong shoots leaves were, however, produced of which nothing was to be seen in the bud and the same occurred in the beech when Klebs caused them to sprout by subjecting them to electric light. The dwarf shoots of the pine, the needles of the silver fir, the leaves of the poplar, alder and ash were all found by Küster [4] present in the bud, whilst Sambucus, for example, forms in the summer numerous entirely new leaves. The rapid growth activity which begins in trees in the spring is prepared the previous year. Reserve materials are stored up in the bark and wood of root, stem and branches, of which a part is set in movement and is concerned with the building up of the new shoot and also with supporting the respiration which increases with the awakening into active life.



FIG. 39.— Unfolding of a bud of the Bird Cherry.

Möller [5] has shown, in particular for the pine, that the development of the spring shoot depends on the nutrition of the plant in the previous year. In the spruce also, all the needles that are to appear the following year are to be seen with a magnifying glass on the growing point in winter as tiny, regularly arranged tubercles, so that it is possible to foretell the length of the shoots of the following year, assuming that normal weather occurs at the time of the opening of the buds. According to Wiedemann [6] the number of needle primordia in the bud is determined entirely by the weather of the summer in which the buds are formed. In dry summers far fewer needles are prepared than in wet ones so that the shoots in the year following a dry year have usually few needles and remain very short (*compare* VIII, 2). A very remarkable correlation exists between the reserve material stored up in the summer and the number of needle primordia. The needle primordia themselves would require a vanishingly small quantity of material. The spruce "calculates"—to speak anthropomorphically—how many needles and how

[1] Morphologie und Jahresperiode der Weisstanne. Flora, 1893, p. 113.

[2] Berthold, *loc. cit.*

[3] Larkum, Beitrage z. Kenntnis d. Jahresperiode unserer Holzgewächse. Inaug.-diss. Göttingen, 1914.

[4] Beitr. z. wiss. Bot., hrsg. v. Fünfstück, II, 1898.

[5] Möller, Zeitschr. f. Forst-u. Jagdwesen, 1905.

[6] Wiedemann, E., Zuwacksrückgang und Wuchsstockungen der Fichte. Tharandt Kommissionsverlag Laux. 2 Aufl., 1925.

great a mass of shoots it will be able to build with the reserve materials available and regulates the number of needle primordia accordingly.

The flowers are also laid down very early in the bud. In the beech Büsgen [1] found the beginnings of the flowers of the following year even at the end of May. Th. Hartig [2] found the male flowers in August progressed as far as the rudiments of the anthers.

Whether flowers or only leaves will be laid down in the bud depends mainly on the weather that prevails at the time when the buds are formed. According to forest and garden experience, a plentiful flower year follows every hot, dry summer in many fruit and forest trees, especially in the beech. It is therefore possible, from the weather of the season in which the flowers for the following year are originated, to foretell whether a mast year is in prospect and to take measures accordingly. It would also be of practical value to determine more precisely the time and the external conditions of the origin of flowers in order to be able to foretell seed years as early and as surely as possible.

The buds are thus shoots which are produced at the same time as the leafy annual shoot and in its leaf axils, but while the shoot that bears them grows they show almost no growth and only develop some scales and leaf rudiments. Also during the winter resting period of their mother shoot they undergo only small changes. In the buds of the pine [3] even in November the future needles are visible as two pustules on every young dwarf shoot, between which the small, sharp, growing point appears. In February of the following year the condition is the same. The sole change which has taken place in the winter is a small increase in length. Askenasy [4] has investigated these conditions by measurements on the flower buds of the cherry. The flower primordia were first visible as such in the course of the July of the year preceding their unfolding. During August they increased daily by about 0.023 gram. In winter no complete rest occurred but only an exceedingly insignificant further development of the buds so that at the beginning of February their weight and size were only a little greater than in October, even after a particularly mild winter.

4. The Resting of the Buds and its Cessation.—It has been proved by experiment that the persistence of the buds almost without growth in the year of their origin is due to a constraint which proceeds from the growing mother shoot, whether it be that the latter competes for the mineral substances necessary for growth or that the carbohydrates produced by its leaves influence the nutrition of the buds in a manner unfavourable to growth (*see* below). Thus a connection or correlation between bud and mother shoot would be explained by causes inside the plant body but which, in relation to the protoplasm capable of growth, are really external influences.

The winter resting of buds appears in the light of these deductions

[1] Büsgen, Blütenentwicklung und Zweigwachstum d. Rotbuche. Zeitschr. f. Forst-u. Jagdwesen, 1916, p. 289.

[2] Hartig, Th., Vollst. Naturgesch. d. forstl. Kulturpfl., Berlin, 1852.

[3] Küster, Wachstum der Knospen während des Winters. Fünfstück's Beitr. z. wiss. Bot., II, 1898.

[4] Über die jährliche Periode der Knospen. Bot. Ztg., 1877.

merely as an extension, essentially produced by our climate, of the almost complete cessation of growth which characterises young buds even in the summer of their formation.

The regular alternation between rest and growth which we perceive in our native woody plants is evidently only a special case of a general phenomenon. All plants have the faculty of entering into rest under particular external conditions, and of awakening from it under others. What conditions bring about the change from the one state to the other in each particular species, depends just as much on their individuality as do the formative processes (bud formation) which, in individual cases, are associated with the passage from the one condition to the other. Klebs has done great service by demonstrating—albeit not without contradiction (*see* Kuhn u. Weber *loc. cit.*)—the incorrectness of the view that a periodical rest occurs " of itself " or, using the term in another sense than here, " from internal causes," and showing the way to a more correct apprehension of the phenomena encountered.

Horticultural experiments on the forcing of lilac have shown that the rest in August is easily broken by the artificial forcing methods to be mentioned later.[1] The period from the time when the buds begin to close to the end of August has been called the "**fore rest.**" On this there follows until the end of October the very profound "**middle rest,**" which can hardly be broken. November and December, finally, comprise the "**after rest,**" which is again a favourable period for horticultural forcing. Cherry branches brought into a room at the end of October do not flower, whilst they are induced to flower by warmth, slowly from the beginning of December, more quickly during January. Similarly, A. Fischer could not force a lime branch brought into the room in October to sprout, but succeeded with one brought in in the middle of November. In general, from January onwards the internal checks on growth of a plant have disappeared and the low temperature alone keeps the buds inactive. During February and March the osmotic pressure in the buds is already increasing, because substances in solution are carried to them or substances already there pass into solution.[2] The transformation of starch described by A. Fischer [3] is concerned with this. In October, after leaf fall, the buds hold large quantities of starch in the scales and in their bases, while the growing point with its leaf primordia is free from starch. During the winter, fatty oil and other substances appear instead of part of the starch, whilst another part of it migrates into the upper parts of the young shoot. Only when these processes have proceeded to a certain extent is it possible for the bud to sprout on the application of suitable warmth. Moreover, the nutrient substances stored in the bud itself do not go very far. A. Fischer found that after a considerable swelling of the bud they were already consumed, so that the additional food substances necessary have to be provided by the young leaves themselves or brought there from the twig.

[1] Johannsen, Ätherverfahren beim Frühtreiben, 2 Aufl. Jena, 1906, G. Fischer.

[2] Dixon and Atkins, Changes in the osmotic pressure of the Sap. (*Syringa vulgaris*) Sc. Proc. Roy. Dublin Soc., 1912, XIII, p. 219.

[3] Beiträge zur Physiologie der Holzgewächse Jahrb. f. wiss. Bot. XXII, 1890.

Wide differences occur in individual cases with regard to the time of the beginning and the end of the bud resting period and the boundaries between the fore, middle, and after periods. Finally the local conditions, the weather, the peculiarities of the individual plant, and even of the individual bud, determine when the rest is to end.

When the internal checks on the unfolding of the buds are removed the winter rest may nevertheless be prolonged if the other requisites for sprouting are absent—particularly the necessary warmth. We speak in this case of an " involuntary " winter rest, in contradistinction to the " voluntary " one produced by internal inhibitions.

The regular cessation of the winter rest towards the spring which prepares the buds for sprouting is not independent of external influences ; winter frost co-operates materially. Should the gardener wish to raise cuttings of conifer twigs, he must bring them into the frost-free glass house in the late summer before the first frost and protect them from frost during the winter. Only thus is it possible to ensure that the buds are retarded long enough for the cuttings to become sufficiently rooted. When woody plants are taken into the frost-free greenhouse in winter the longer they were previously exposed to low temperatures the sooner do they break into leaf (Molisch),[1] (Weber).[2] The roots also, according to Weber, seem to pass through a voluntary rest which can be brought to an end by frost. According to Engler,[3] sharp changes of temperature in the spring promote the termination of the voluntary winter rest in the beech. Frost therefore hastens the ending of the winter rest but it is not indispensable for it, as plants kept free from frost also finally sprout, though much later than those which have been subjected to it.

In nature frost appears to be the only means of curtailing the winter rest. Even more effective, however, are the artificial forcing methods first worked out by the gardening profession [4] and expanded into a long series [5] by physiologists in an attempt in this way finally to get on the track of the secret of winter rest. Prolonged bathing of the plants in warm water, treatment with ether vapour, alcohol, tartaric acid, potassium cyanide, prussic acid, tobacco smoke, acetylene, concentrated sulphuric acid, concentrated potash lye, galvanic current,[6] electric sparks, pricking or squeezing of the buds, break the fore and after rests, but scarcely the middle rest. The buds of the beech (*Fagus sylvatica*) resisted such experiments with peculiar stubborness until Klebs [7] finally induced them to open at the most diverse times by powerful electrical illumination.

The common characteristic of most of these forcing methods is

[1] Molisch, Sitzber. Akad. Wiss. Wien 118, 1909 ; 126, 1917.

[2] Weber, F., Ber. Dtsch. Bot. Ges. 39, p. 152, 1921.

[3] Engler, A., Unters. ü. Blattausbruch u. d. sonst. Verh. von Schatten-u. Lichtpflanzen der Buche. Mitt. d. Schweiz. Zentralanstalt f. d. forstl. Versuchswesen. X Bd., 1913.

[4] Molisch, Pflanzenphysiologie als Grundlage der Gärtnerei. Jena, 1922.

[5] Weber, F., Methoden des Frühtreibens der Pflanzen. In Abderhaldens Handbuch der biologischen Arbeitsmethoden, Abt. XI, H. 2. (There the new literature.)

[6] Bos, Biol. Zentralbl., XXVII, 1907.

[7] Klebs, Über das Treiben der einhimische Bäume speziell der Buche. Abh. d. Heidelberger Akad. d. Wiss. mathnat. Kl., 3. Abh. Heidelberg, 1914. C. Winter. Here the whole scientific literature ; Burgerstein, Fortschritte der Technik des Treibens der Pflanzen. Progressus rei botanicae, IV, 1911, Heft I ; Kühn, Austreiben der Holzgewächse und äussere Faktoren. Jahrb. f. wiss. Bot., 57, 1916 ; Weber, Treiben der Buche. Ber. d. D. bot. Ges. 34, 1916.

that the buds are brought near to the point of death or at least of injury. The effective chemical agents are all poisonous and would by excessive action kill the buds. Warm water promotes sprouting only when the temperature is near the threshold of injuriousness. Perhaps all these processes are only examples of the general biological phenomenon that poisons in small doses only act as stimulants. In the effective bud woundings isolated groups of cells at least are damaged. Weber [1] suggests an action by wound hormones (Haberlandt), that is, decomposition products of dead cells, which according to common experience stimulate local cell division. Still, this wound hormone theory is, according to Weber,[2] not universally applicable. It has been proved in certain cases that an increase in respiration [3] is associated with sprouting. Hand in hand with this goes an accumulation of sugar such as also takes place in the normal closing of the rest period. Frost also effects a transformation of starch into sugar (*see* Chap. XII, 1) and, according to Simon, also results in increased respiration. It is conceivable, according to Coville [4] and others, that the sugar-forming enzymes are generally separated from the starch by plasma membranes, but come into contact with it through frost and the mechanical effect of freezing, or that the permeability of the dividing plasma is increased. However, the respiration of twigs in the winter condition is, according to Simon, only about $\frac{1}{3}$ to $\frac{1}{4}$ less than at the time of the most vigorous vegetation, if the winter twigs are kept at 22 degrees. It was remarkable that in Simon's experiments, a great lowering of the respiration set in, at least in one-year-old twigs, just before diameter growth began. Perhaps, also, variations in the permeability of the plasma play a part in winter rest and its cessation; in resting plants the permeability of the plasma membrane is diminished or almost completely stopped (*comp.* Chap .III, 1). It is increased by potassium cyanide, which induces early sprouting. Tröndle,[5] especially,[6] shows that the permeability of the plasma is altered by wound stimuli. By means of cultural experiments with tropical woody plants Klebs [7] has shown that insufficient supply of mineral nutrients can bring about the occurrence of a resting period; whilst Berthold [8] had, in 1904, already indicated shortage of nourishment as a possible cause of the winter buds of our native trees becoming dormant. In Kleb's experiments the supply of fresh soil brought about the resumption of growth in young tree plants which had entered the resting condition. The application of food materials could even annul the effect of insufficient lighting which causes

[1] Weber, F., Frühtreiben durch Quetchen. Ber. d. D. Bot. Ges. 40, p. 148, 1922.

[2] Weber, F., Ruheperiode durch Frühtreiben, *b*, c. 42, p. 109, 1924.

[3] Müller-Thurgau u. Schneider-Orelli, Flora, 1912. CIV, 387. Traklionow, Ref. Bot. Zentralbl., Bd., 122, 1913, p. 423; Simon, Jahrb. f. wiss. Bot. Bd., 43, 1906; Bd. 54, 1914. (Periodicity in tropical trees.)

[4] Coville, T. W., The influence of cold in stimulating the growth of plants. Ann. Rept. Smithson. Inst., 1919-(1921).

[5] Weber, F., Studien ü. d. Ruhe d. Holzgewächse II. Sitzber. d. K. Akad. Wien, math.-naturw. Kl. I, Bd. 127, Wien, 1918.

[6] Tröndle, A., Ü. d. Einfluss der Verwundungen auf die Permiabilität. Beih. z. Bot. Zentralbl. 38, II, 1921.

[7] Über Wachstum und Ruhe tropische Baumarten. Jahrb f. wiss. Bot., Bd. 56. Leipzig, 1915.

[8] Untersuchungen zur Physiologie der pflanzlichen Organisation, II. Leipzig, 1904.

the setting in of the resting condition. A fixed proportion between the concentration of carbohydrates and mineral substances is a condition for growth. Excess of carbohydrates checks growth. The reduction of the excess by respiration or by the slow development of ferments re-establishes the concentration proportions necessary for growth and leads to the cessation of the rest. With *Pithekolobium Saman* (a tropical leguminous plant) Klebs was able to bring about the periodic alternation of rest and growth several times, by withdrawing and supplying nutrient materials.

5. The Unfolding of Buds.—The voluntary winter rest of most of our trees appears to cease so early in the year that the buds, ready to sprout, have generally to wait a considerable time for the occurrence of higher temperature before they are able to unfold. On the one hand it depends on the temperature when the forest becomes green and on the other hand it is the specific heat requirements and the specific reaction velocity of the buds which determine which trees appear green first. Larch, birch and alder often sprout in March in favorable weather, while oaks, ashes, spruces, beeches and many other species always do so much later, and it is hard to determine if the delay is due to a higher heat requirement or to a tardier removal of internal inhibitions—whether, in fact, it is a question of an involuntary or of a voluntary rest. The time of leafing in a series of years may vary very greatly, according to the early or late appearance of warm weather. Observations made at Giessen over about twenty years showed the variations in time of leaf unfolding to amount, in the horse chestnut, to 39 days; the beech, to 36 days; the pedunculate oak, to 24 days.

Birch, alder and mountain ash break into leaf early; ash, pine, and especially the acacia, late. The pedunculate oak in rare extreme cases, comes into leaf some 10–14 days before the sessile oak. In the beech, the time lies, according to the local climate, between April 18 (Baden-Baden) and May 17 (Karlsberg in Upper Silesia). In most districts in mid-Germany,[1] the beech foliage develops between April 20 and the middle of May. The first appearance of the beech leaf corresponds with the mean date of the early spring,[2] *i.e.* the arithmetical mean of the dates of the first flowers of the Norway maple and the gean (wild cherry) as well as the leaf break of larch, birch, hornbeam, pedunculate and sessile oaks. In an arrangement of most of the trees in the order of their breaking into leaf the beech stands in the fourth place, after the larch, birch and hornbeam. It is followed by the pedunculate and sessile oaks, silver fir, spruce (or spruce, silver fir). The leaf formation of the oaks, occupying 10–14 days, corresponds, on the whole, with the middle date of spring of Ihne's chart. The average date of the beginning of leaf formation in the pedunculate oak is also the time of

[1] Wimmenauer, Hauptergebnisse 10-jähriger forstlich-phänologischer Beobachtungen in Deutschland, 1885-1894. Berlin, 1897; Danckelmann, Phänologie der Holzarten im deutschen Walde. Zeitschr. f. Forst-u. Jagdwesen, XXX, 1898, p. 263.

[2] Ihne, Phänologische Karte des Frühlingseinzugs in Mitteleuropa. Petermanns Geograph. Mitteilungen, 1905, Tafel 9, and Phänologische Karte des Frühlingseinzugs in Grossherzogtum Hessen. Further phenological observations and phenological literature are to be found in the 33 yearly vols. of Phänol. Mitteilungen. (Darmstadt, Verlag der Landwirtschaftskammer f. d. Grossherzogtum Hessen, Jahrg., 1915, hrsg. von Ihne).

blossoming of the earlier varieties of apples. In Switzerland, the greening of the beech has been observed to ascend a mountain slope at the rate of 100 metres in 4.1 days, the autumn colouring to descend the same distance in 3.3 days.

According to the normal curves constructed by Burger, the pine sprouts first among the species examined, and this, indeed, independent of climatic race; six weeks later follow oak, hornbeam, black alder and larch, practically together, then mountain spruce, and finally lowland spruce. Here a measurable increase in the length of the shoot is taken as the indicator of the beginning of the breaking of the buds. If, on the contrary, visible greening by the production of new leaves is so considered, the larch is decidedly to be put in the first place and the pine in the last.

Cieslar [1] found that the spruces, larches and pines grown in the far north or at considerable elevations, brought into southerly localities started into growth much earlier than the native races because they originated where they enjoyed less heat. Nevertheless, this is not a universal rule for, according to Cieslar,[2] it is reversed in the oak; oaks from a warmer climate put forth their leaves sooner with us than those from a cooler one. At Eberswalde, pines raised from St. Petersburg seed unfolded their buds eight days sooner and ceased growth four days sooner in summer than native pines, but nevertheless remained behind them in height-growth and length of needle.

Beech buds that have been formed in the shade nearly always sprout earlier than those which have grown in full daylight. This is due, as Engler [3] showed, to the former possessing thinner and less tightly closed scale coverings and being therefore more sensitive to the effects of the external stimuli which promote the unfolding of buds. Moreover, these characteristics, developed under particular lighting conditions, persist under other conditions, at least for a time. Shade-grown beeches brought into the light, for many years sprouted earlier than light-grown beeches standing beside them, and conversely beeches raised in the light, when brought under a canopy for years remained backward in sprouting every spring. From these phenomena Engler explained the greening of the wood from below upwards. In species with heavily foliaged crowns the adventitious shoots and the buds on the lower and inner parts of the crown which are generally most shaded sprout first. For the same reason, according to Engler the beech forest in Switzerland clothes itself with leaves on an average eight days earlier on northern slopes than on southern ones.

In the spruce [4] the lateral buds of the twig awaken sooner than the terminal one, but as the terminal shoot also ceases its growth later in the summer it retains the lead. Where spring frosts are frequent this behaviour of the leading shoot is important for the maintenance of the species. The leader, in consequence of its unfolding later, escapes

[1] Zentralbl. f. d. ges. Forstwesen. Wien, 1898, p. 273.

[2] Cieslar, Zentralbl. f. d. ges. Forstwesen, 1923, p. 97.

[3] Engler, A., Untersuchungen über den Blattausbruch und das sonstige Verhalten von Schatten-und Lichtpflanzen der Buche und einiger anderer Laubhölzer. Mitt. d. Schweiz. Zentralanstalt f. d. forstlich. Versuchswesen. Bd. X, Zurich, 1911.

[4] Mogk, *loc. cit.*

frost more frequently than the lateral shoots and thus raises the plant above the layer of the atmosphere near the ground, in which danger from frost is greatest.

According to the Eberswalde[1] records, differences of 7 to 27 days have been observed in the time of greening of our native trees. In the beech a hastening or holding back of individual trees and branches is well known. Such individual differences—as much as six weeks in one plantation—are especially prominent in the spruce and have been more closely investigated by Münch[2] (Fig. 40). They play an important part in silviculture because on the time of opening of the buds depends the liability to damage by frost.[3] Only the young shoots are sensitive to frost and for this reason late spruces regularly escape late frosts even in the worst frost localities, whilst the early spruces in such situations are so often damaged by May frosts that they become crippled and are suppressed by the late spruces. In the end the entire crop consists only of late spruces; and as the tendency to start into growth early or late, according to Raunkiaer's[4] observations, is hereditary, a local race, hardy against late frosts is established by natural selection and descent in frost localities. Green-coned spruces sprout on the average somewhat later than red-coned ones.

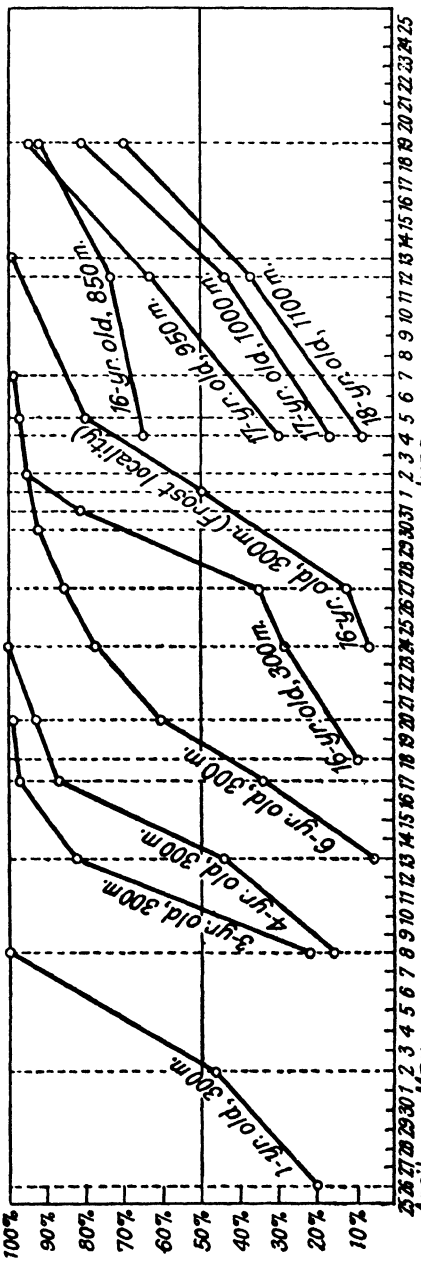


Fig. 40.—Time of opening of buds of Spruce woods of various ages and localities. On the ordinates the plants with opened terminal buds in percentages of the total number of plants. After Münch and Liske.

[1] Zeitschrift. f. Forst-und Jagdwesen, 1898, p. 265. More on Phenology, see above.

[2] Münch, E., Die Knospenentfaltung der Fichte und die Spätfrostgefahr. Allg. Forst-und Jagdzeitung, 1923.

[3] Münch und Liske, Die Frostgefährdung der Fichte in Sachsen. Tharandter Forstl. Jahb., Bd. 77, 1926.

[4] Raunkiaer, On leaf time in the descendants from beeches with different leaf times. Botank Tidskrift Bd. 36, p. 201, 1919.

In the spruce, according to Münch, the date of leafing is very much dependent on age (Fig. 40). Young plants, one or two years old, start first. Sprouting is retarded with increasing age year by year until about the 16–25th years up to at least four weeks. Old trees again sprout somewhat earlier than oldish thickets. For this reason young spruces require shelter from late frosts in all frost localities. Engler (*loc. cit.*) did not find such differences between young and old plants in the beech and other hardwoods; he found, in fact, young plants generally later to start into growth than old trees, because they have, as a rule, proportionally more fully lighted leaves and therefore more late-sprouting buds than old ones.

When the cells of the young shoot begin to grow there is a plentiful influx to them of water, which may in fact, be squeezed out in drops into the air spaces in the interior of the buds. Young, undeveloped leaves evaporate[1] more strongly than leaves whose internal structure is already approaching its final condition. It is therefore important that when the buds are breaking they should continue to have for a time the protection of the scales. Hence these also grow with them, the cells at their base multiplying greatly at the expense of their starch and their oil, which perhaps also fall to the benefit of other parts of the shoot. The complete emptying of the scales and their bending outwards is noticeable in the conifers. The inner scales form a cap over the young shoot and even when this is burst open, the stipules, which grow into long ribbons, still provide protection. Experiments by Grüss[2] with *Betula alba* and species of spruce, showed that young shoots without this cap, brought into a room after having been exposed to a temperature of −5 degrees, which they otherwise withstood, did in fact die.

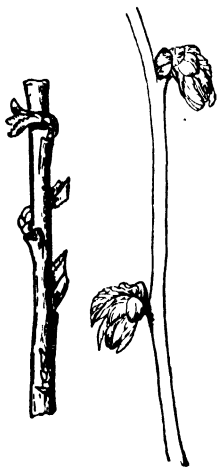


Fig. 41—Left: Twig of the Gooseberry with opening buds showing bending movements. Right: Hazel twig with opening buds.

In Askenasy's cherry tree (*see* page 61) in spring a growth of the flower buds began, at first slow, then continuously increasing and finally astonishingly rapid. In the last 6/10 days before they unfolded they doubled their green weight and showed, in the period from March 22 to April 2, a daily increase of 1.10 grammes, and from April 2 to 8 one of 3.359 grammes. The increase in dry weight showed a similar course. A quarter of the dry weight was built up during the summer before the year of flowering, three-quarters appeared in the spring in which they unfolded. The total weight, which includes the water supplied to the opening bud, increased even more quickly than the dry weight. The dry weight amounted to 50 per cent. of the total weight in the summer of the previous year, to 55 per cent.

[1] Schechner, Zur Kenntnis des absteigenden Wasserstroms. Anzeiger d. k. k. Akad. d. Wiss. Wien, XLVI, 1909, p. 272. Seeliger, Transpiration in den verschiedenen Altersstadien der Blätter. Inaug-Diss. Göttingen, 1911.

[2] Biologie der Knospe. Jahrb. f. wiss. Bot. XXIII, 1892.

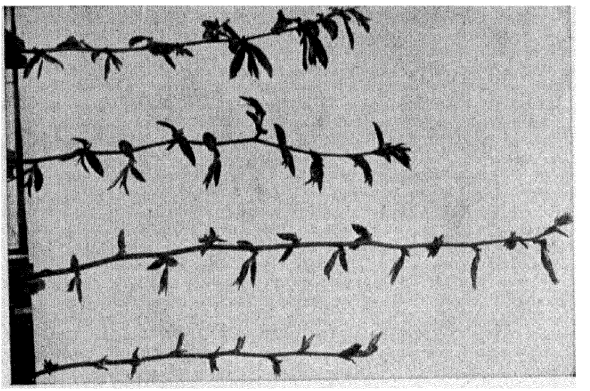


FIG. 42—*Carpinus betulus*. Movements of the buds during unfolding. Order of the age of twigs from below upwards.

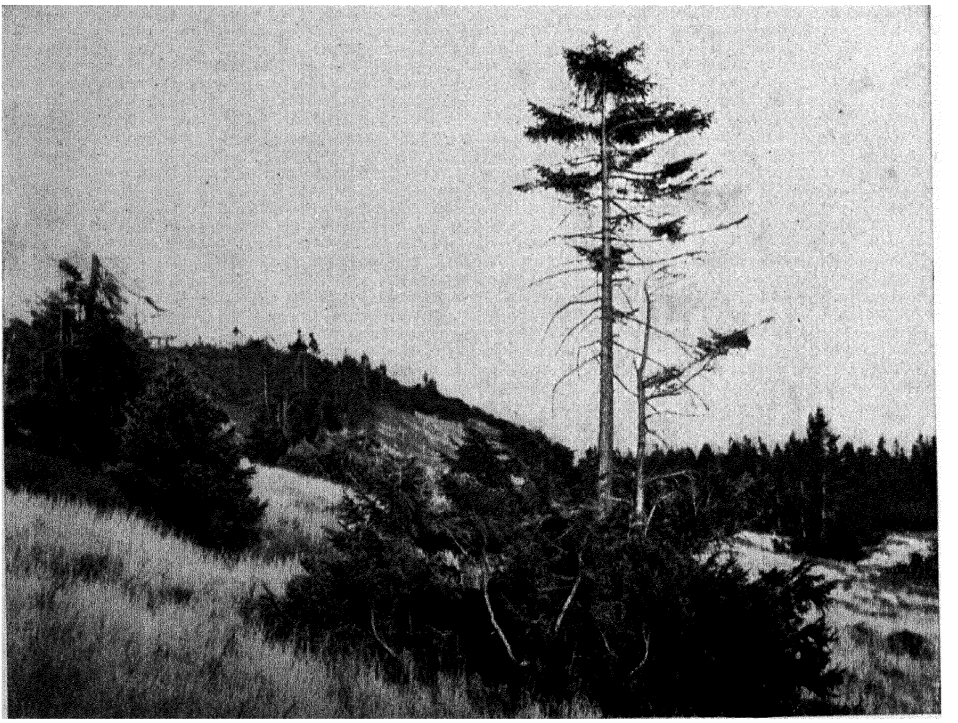


FIG. 45.—Group of Spruces at the tree limit in the Riesengebirge which have arisen from the rooted branches of the spruce in the centre. Phot. Zückert. (Mch.)

[*To face p.* 69.

in the autumn and sank to 20 per cent. at the time of unfolding. In spite of this Askenasy estimated the quantity of starch necessary for the formation of the approximately 200,000 flowers on the tree at 12 kilograms. This does not include what is consumed in respiration during the energetic formative activity. As the cherry blooms before the leaves appear, the whole of this quantity of starch must have been stored up in the stem and branches in the previous year. The temperatures of the previous year have no effect on the time of opening of flower buds. The growth of buds in spring depends only on the warmth of the early part of the year and varies with it, but set-backs in temperature are not able entirely to prevent its continuous increase. What Askenasy has proved for the cherry holds, without doubt, for vegetative buds and for the flower buds of other trees.

The movements which the buds undergo at the time of opening have already been slightly touched upon in Chap. I (p. 44). Many buds, when in a closed condition are more or less closely adpressed to the twig that bears them. During opening, the young shoot emerging from the bud then bends laterally as in willows, poplars and gooseberry bushes (*see* Fig. 41), or it turns away from the mother twig almost at right angles or even inclines towards the base of the twig. In these movements, which are especially striking in the hornbeam (Figs. 42 and 43), the apparent terminal bud (*see* page 3) also takes part. The initial conditions occur in twigs set in a reversed position as well as in a normal position. The direction of movement is thus determined, not by gravity, but by the relationship of the bud to the twig that bears it. Gravity, however, partly as a stimulus and partly in a simple mechanical way, does indeed bring about the continuous hanging down of the tip of the growing shoot after the period of bud opening, which is to be seen in the hornbeam and hazel. On the lateral twigs of the alder the opening buds and the young shoots bend outwards under the stimulus of light and gravity and in the bird cherry (*Prunus padus*) also, the twigs in process of development are directed outwards at the opening of the buds (Fig. 39).



FIG. 43. — Hornbeam twig during unfolding of the buds. The internodes shortened.

The unfolding of the leaf blade may proceed in various ways. In the simplest case (*Fagus*) it begins at the top of the leaf and proceeds regularly towards the base. Irregular growth leads to all sorts of bendings of the stalk and blade which Hinze [1] has collated. Movements of this sort whose direction is not dependent on stimuli in the environment have been called " nastic " movements (from the Greek).

Besides this many young twigs remain for a long time in the spring with their leaves in a half developed condition, even without any particu-

[1] Über die Blattentfaltung bei dikotylen Holzgewächsen. Beihefte z. bot. Zentralbl. X, 1901. Kassel, Gotthelft. Detailed accounts of the distribution and quantity of starch in unfolding leaves have been given among others by Berthold (Untersuchungen zur Physiologie der Pflanzlichen Organisation, I, Leipzig, 1818) and his pupils (Glatzel, Verhalten der Stärke in sich entwickelnden Blättern. Inaug.-Diss. Göttingen, 1912).

lar protective provision, and sustain no noticeable damage. In the lilac, for example, the buds open very early; the leaves which emerge from them remain for many days only half unfolded, until the nights become warmer, the soil temperature rises and the roots supply more water. According to Stahl's experiments (Bot. Ztg., 1894), the undeveloped structures in these cases lose much less water by evaporation than the fully formed leaves, which explains their hardiness at a time when the water supply is scanty.

One phenomenon which is very often very striking when buds are dissected may be considered to have a bearing on the discussion of the behaviour of young twigs towards late frosts. This phenomenon is the splitting of the bud-scales into two lamellae, which is due to their tissues being permeated by large empty spaces so that their internal cohesion is only small. After late frosts, these hollows in already opened buds, *e.g.* of the hazel and Norway maple, are found filled with large particles of ice. They thus serve to receive the water which is frozen out of the cells of the young shoot and preserve it from evaporation until it is reabsorbed on thawing. Grüss gives a similar explanation of the hollows which occur in the interior of the supporting shoot under the buds in many plants, *e.g.* the larch. The first mentioned air spaces are widely distributed in green juicy bud-scales.

6. Dormant Buds and Epicormic Branches.—We have seen, that what will become of a bud depends, in the first place, on its position on the mother shoot. In the ordinary course of things, nothing whatever becomes of many of the buds. These are, as a rule, those which are situated furthest from the apex of the shoot. They continue to "sleep" as in winter while the rest develop. To awaken them it is only necessary to remove the part of the shoot that lies above them or at least its buds, as is done in nature for example by spring frosts or the biting of animals. In such cases the buds, hitherto dormant, produce substitute shoots; a faculty which they still possess when the shoots that bear them have already ceased their summer growth. If the dormant buds do not produce shoots they often die off but they may also persist for many years and then be the originators of water shoots. These are also, like the adventitious shoots to be described in the following section, termed "adherent branches" (klebasten), because, at first they have no firm connection with the wood of the stem, but stick loosely in the bark out of which they can be easily torn. With the increasing diameter growth of the stem they become incorporated in the wood. In this way they may reduce the timber value of a stem and are therefore very important in forestry in the case of the finer timber trees, especially the oak, which is the most prone of all our trees to form epicormic branches.

The shoots newly originated on the stem arise mostly from such dormant buds which have developed in the axils of the bud-scales of their mother shoot. They are accordingly found on the bark folds which are wont to envelop from below upwards the places of attachment of former branches on the stem. Whilst the annual shoot, on which the dormant buds once developed, branched and grew in length and thickness, the stem which bore it also thickened and so enveloped its base higher and

higher (*see* Fig. 44). Thus these buds were transferred from the branch to the stem itself, there to outlive their mother shoot by many years. If they are to retain their power of growth it is essential that their connection with the xylem of the stem should not be lost. On splitting a branch or stem bearing a dormant bud a tract of water-conducting tissue is observed running from the interior of the bud right through the bark of the stem into the wood, which elongates concurrently with the increase in thickness of the stem. Jost [1] describes the process of this elongation in the lime and other broad-leaved trees. From the pith of the shoot, at the inception of the bud, an outrunner of the medullary tissue surrounded by woody elements and a cambium of its own, turns out in a radial direction into the bud. Parenchyma cells of this pith tube, which remain unlignified, elongate and divide with the progressive thickening of the shoot and thus prolong the "bud-stem." The vascular elements of the bud-stem, likewise running radially in the shoot, are ruptured thereby, but are replaced by new formations by the cambium in the region where the cambium of the shoot bends out into the bud stem. Connection with the xylem is retained in a similar way also in the dwarf shoots of the pine and in evergreen leaves. By this intercalary growth preventitious buds and dwarf shoots are distinguished from ordinary buds and long shoots which only show apical growth.

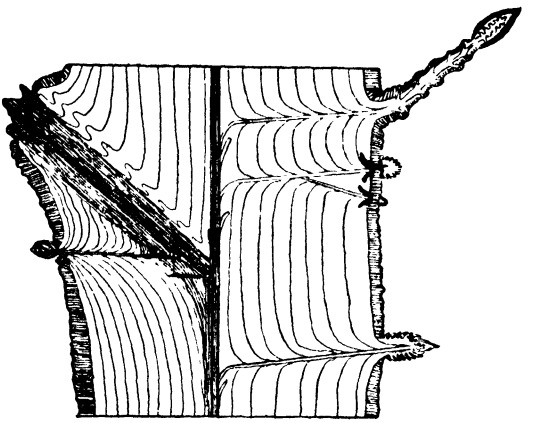


FIG. 44.—Longitudinal section of a piece of stem with Dormant Buds and Spheroblasts (the middle buds on the right). After Th. Hartig.

If the connection between the dormant bud and the wood of the shoot is for any cause interrupted, the dormant bud is no longer capable of producing a shoot. It may, however, in many species develop into a sphere the size of a pea, hazel nut or walnut, which can be easily prised out of the stem (beech, mountain ash, etc.) often by the hand alone (globular shoot, spheroblast).

According to Hamm (Ausschlagwald, 1896) the oak, elm, hornbeam, black and Lombardy poplars are particularly prone to cover themselves with epicormic shoots while the following show little tendency to do so : pine, birch and silver fir, the larch a little more. On strong epicormic shoots which develop after mutilation or cutting back the occurrence of accessory shoots is common. In general the tendency to epicormic branch formation is less in conifers than in broad-leaved trees. Our Scots pine opens dormant buds only in extremity, after complete defoliation by caterpillars.[2] A few dwarf shoots with ordinary double needles

[1] Jost, L., Über schlafende Knospen. Flora N.F. (Goebel Festschrift), p. 289, 1925.

[2] Liese, Wiederbegrünnug der Kiefer nach Foreulenfrass. Zeitschr. f. Forst-und Jadgwesen, 1926.

may then be formed from dormant whorl buds, and the dormant eyes between the destroyed needles of the dwarf shoots may become " rosette shoots " which consist of a bunch of primary needles with toothed margins like those of seedlings. In the axils of such primary needles dwarf shoots with ordinary double needles may also arise in the following year. As a rule, however, the rosette shoots have no permanence; they foreshadow the death of the tree. The North American *Pinus rigida*, not infrequently cultivated in Germany, on the other hand, develops preventitious shoots very readily even on old stems. Spruces of which the branches have been sawn back to the stump, as happens in alpine districts for the collection of branch litter, clothe themselves with new preventitious shoots; pruned larches do this even more readily.

Silver firs throw out epicormic shoots in abundance when they have lost their original branches through the attacks of the shoot *Chermes* or when they are set free after growing in close formation. On the twigs of the willows, strangely enough, according to Vöchting,[1] dormant root buds also occur; they are ready to grow out into roots as soon as the twig, in the absence of light, is placed in water or even in air saturated with water vapour. They facilitate the rooting of cuttings and are the reason why the stems of willows, subject to occasional flooding, are frequently covered with a fur of roots.

The formation of epicormic shoots decreases with advancing age, partly because of the hardening of the rind which makes the breaking through of the dormant buds more difficult and also because of the connection of the xylem of the stem with that of the bud being more often destroyed.

The clothing of the stem with green and the replacement of lost shoots, besides being brought about by dormant buds produced normally on the young annual shoot (preventitious buds), may be effected through so-called secondary buds, i.e. buds formed from quite inconspicuous rudiments, only as the result of mutilation, in the axils of leaves or bud scales in which no perfected bud would normally have developed. The power of producing such secondary buds is possessed especially by the spruce and on this to a great extent depends the inexhaustible power of recovery after cutting or grazing which makes it so suitable a hedge plant. The yew, hawthorn, privet, etc., are also good hedge plants which stand cutting and readily clothe themselves with leaves from ordinary and dormant buds. Corresponding forms often arise in nature through the repeated browsing of game or cattle.[2] Beeches, hornbeams and spruces which are repeatedly browsed assume the form of densely branched, almost spherical bushes or low pyramids out of whose centre a regular stem finally arises when the bush has become so broad that the animals can no longer reach the middle bud. A similar effect is produced on the spruce by late frosts. They destroy the young spring shoots, especially on the side branches, the leading bud escaping more easily as it is the last on the tree to open.

[1] Vöchting, Organbildung im Pflangenreich, Bonn, 1878.

[2] Klein, L., Charakterbilder mitteleuropäischer Waldbäume. In Vegetationsbilder hrsg. von Karsten u. Schenck, II. Reihe, Heft, 5–7. Jena, G. Fischer.

If the middle shoot has been fortunate enough to grow above the frost level it shoots up rapidly out of the dense cone.

7. Adventitious Buds and Shoots.—An important part in the life of trees is played by their power of producing buds in other places besides the vegetative cone. To it they owe their power of replacing lost twigs. Buds of this sort, arising, as it were, out of order, are called **Adventitious Buds.** They must not be confused with the dormant buds mentioned above, which while they may indeed produce shoots out of proper order, were nevertheless originally formed in due order with the rest in the growing point. Adventitious buds may be developed from cells whose active formation has already ceased. This is the case, for example, with begonia leaves which the gardener cuts off and places in moist sand for propagation purposes. On trees adventitious branches occur as a rule at wounds.

If the stem of a tree which is prone to adventitious shoot formation is cut down, buds arise at once in a circle immediately round the wound area, immediately below the wound or out of the healing tissue which begins to cover it, some of which at least grow out into new shoots which may make themselves independent of the decaying stump by rooting themselves. In this way arise "**coppice shoots,**" which therefore consist of adventitious shoots with which, however, shoots sprung from dormant buds may be intermingled. Certain replacing structures may be even regarded as essentially transition forms between normal and adventitious buds. Kerner, in his "Plant Life," gave this name, for example, to the secondary buds which appeared in the immediate neighbourhood of the place of separation of shed branches of willows and poplars. If adventitious buds occur in large numbers close together they may bring about the formation of burrs. As a rule adventitious buds are not formed superficially like the buds on the growing point, but originate from groups of cells further in the interior of the wound tissue and then break through it. This is explained by the superficial cells of the wound tissue soon beginning to form cork, whereupon they become incapable of any further manifestation of life.

The adventitious buds appearing on roots give rise to the so-called root-suckers which are found in such numbers in the poplars. All the young plants which spring up in a wide circle round an old poplar arise from the horizontally spreading roots. Root-suckers also originate in the interior of the tissues, in the deeper layers of the root cortex and especially in the dividing tissue from which the cork covering of the roots proceeds. They are sometimes scattered over the surface of the root, but in other cases they exhibit the same arrangement as the lateral roots and perhaps generally arise from dormant lateral root rudiments.

How varied is the tendency to produce coppice or root suckers in different species is evident from the following comparison which I have taken from J. Hamm's work on the "Ausschlagwald" (Coppice Forest) (Berlin, Parey) which appeared in 1896.

Root-suckers are formed :—

(1) On isolating the healthy complete stem or even in diffused light, in the case of: Balsam poplar, blackthorn, whitethorn, black poplar,

grey poplar, white poplar, Lombardy poplar, aspen, mountain ash, spindle tree, privet, dogwood, acacia, tulip tree, tree of heaven.

(2) From unhealthy or fallen trees with uninjured roots: Wych elm, white alder (according to Danckelmann also in vigorous woods), cherry, bird cherry, *Populus canadensis*, pear and field maple.

(3) The same with injured roots: Cork elm, field elm, wych elm, horse chestnut, sweet chestnut, hazel, plane, apple, lime, white beam, wild service trees, walnut, birch.

(4) Very little tendency to produce root-suckers, even by fallen trees with damaged roots, is shown by oak, beech, hornbeam, ash, sycamore, maple, common alder and tree willows.

With regard to the power of production of stool shoots, Hamm constructed the following list in which the respective trees are arranged according to the length and stoutness of the strong coppice shoots in normal localities: On the margin of the cut, even when cut high, coppice shoots are produced by:—all species of poplar—except the aspen, which produces only feeble shoots that generally soon die off—the willows—especially the tree willows—the acacia, the elms, hornbeam, lime, horse chestnut, the feeblest the beech, which shoots moderately well from the stump only up to the 30th year and on favorable sites (on which, indeed, it retains its power longer) but in certain circumstances, however, may produce numerous strong shoots. Thus, in the forest district Neuhausel, near Ehrenbreitstein on the Rhine, beech stools with about 80 strong coppice shoots have been reported.

In the hornbeam the supplementary buds described earlier increase the power of coppicing. Even when no injury has taken place the lower supplementary buds, especially on the lower shoots of older plants, may unfold though such twigs often dry up. Preventitious buds with undiminished power of development are still to be found on stems eighty years old and it is noteworthy that when pollarded the stumps are apparently much longer lived than the tree growing uninjured.[1]

A kind of "layering" has also been observed in the hornbeam in which small coppice shoots or lower branches buried under the leaf litter, root themselves. The same phenomenon is known in spruces which sometimes surround themselves, in this way, with a whole circle of offspring. At the upper forest limit on mountains and in the far north where the short growing season only permits of the formation of ripe seed very rarely, vegetative propagation of the spruce is even the rule.

The following produce coppice shoots at the root collar even with a stump height of 1 decimetre: alder, which according to Borggreve (Holzzucht, 1885, page 63) possesses "almost everlasting power of coppicing, albeit only above the water table," ash, *Acer* sp., sweet chestnut, white alder, bird cherry, wild cherry, birch (from the root swelling), oak, hazel, spindle tree, pear, apple, white beam, and others. The tenacity of life and power of reproduction of the root stock enables the hazel to survive in all close thickets.

With the power of sprouting from the stump there generally corresponds the power of shoot production in the upper part of the stem on which the "**pollarding**" of limes and willows is based.

[1] Hartig, Th., Vollständige Naturgeschichte der forstliche Kulturpflanzen. Berlin, 1852.

Stool- and root-shoots have the advantage over seedlings of the ample supplies of nourishment and water from the mother stool and its root system, so that they show from the first a very vigorous growth. In the balsam poplar, birch, hazel, maple, etc., a growth in length of 1.5 metres in the first year has been observed in coppice shoots. Oaks, hornbeam and *Pyrus* species show a growth of 0.60 metres and more, and the beech of over 0.40 metres. Later, when the reserves in the root stock are used up and a balance has been established between the coppice shoot and the remaining roots the striking growth in length of the shoots falls off.

8. Cause and Significance of the Formation of Epicormic Branches.—About epicormic branches (under which are included both preventitious and adventitious shoots) and their production there exists an abundance of material from observations both in the hardwood forest and on fruit trees, and because of their importance in forestry and horticulture a great deal of thought and experiment have been devoted to them. Their causes have, however, not yet been fully made clear, and it seems as if the solution of these problems is not yet altogether within reach, because observations are very soon encountered, which must be referred to fundamentally unexplained phenomena, of correlation and polarity.

Epicormic branches are produced in the most varied circumstances, which seem at first sight to have little in common with one another. They appear most luxuriantly as substitutes for the regular branches when these are damaged or lost; but also without such loss when the tree, previously grown in a close crop, is suddenly set free, so that, on account of the greater root space and better illumination, it at once becomes better nourished than in the crowded stand and increases the breadth of its annual rings, often by many times. (Light increment.)

In such cases it appears as if the superfluous sap seeks an outlet and so brings about the sprouting of dormant buds or as if the dormant buds were enabled to sprout by the more plentiful nourishment. How erroneous such anthropomorphic conceptions are is strikingly evident [1] from the fact that the same excess of preventitious shoots appears when the buds and sap are placed in exactly the opposite conditions. If a stem is ringed there immediately arises an extreme shortness of building materials and at the same time the activity of the roots is hindered because they are no longer nourished. In spite of this the dormant buds sprout just on the part where the shortage is greatest, immediately under the ring and not above it where nutrition at least as regards building materials, is ample. Suppressed beeches, before they die from overshading, cover themselves over and over again with epicormic branches, sometimes called "Agony shoots," because they give the impression that the tree in its death agony seeks to save itself by means of such substitute shoots. Dormant buds sprout when the shoot is placed out of its natural position, *e.g.* a stem or branch is bent down or a spruce is overturned or leans over (*see* also under Polarity). In such cases also superfluity of sap is not obvious as a cause of sprouting.

[1] Vöchting, Organbildung im Pflanzenreich, Bonn, 1878.

The great production of epicormic branches on oaks and beeches that have been recently isolated has also been ascribed to the increased light. That light does, in fact, promote the sprouting of buds,[1] may be adduced in favour of this. But on closer investigation it is found that in the absence of any such change, in densely grown woods, numerous epicormic branches are formed on many oaks and also on beech poles, which, on account of paucity of light alone, soon disappear again and are constantly replaced by new ones. Even the heavy shading of the oak stem by a beech underwood cannot prevent this. The formation of epicormic branches is greatest where crown development is inadequate in consequence of a close stand ; but it is also not absent in stems with a free crown. Many stems are very prone to form epicormic branches whilst others are not.

In many cases the causes of epicormic branch formation are certainly none other than the general conditions which also result in the production of lammas shoots and favour the growth of certain buds and shoots as against others. Between all the parts of the tree there exists a condition of balance, not only in their quantity but also in their mutual distribution on the tree and the position which the organs assume. Leaf and root, conducting channels, mechanical tissue, and stem-form all stand in a balanced proportion when development is unchecked. We may speak of correlations but can only recognise the fact but not furnish an explanation of the cause. If the correlation is destroyed by the loss of organs, substitution is at once effected and upsetting of the balance by altering the natural position of parts of the tree has similar consequences. If the regular buds are not sufficient for the rapid formation of substitutes, dormant buds also sprout or adventitious shoots are brought to their assistance. This applies equally to shoots and roots. The results of the ringing experiment described above indicate that the stimulus which regulates the correlation is transmitted only through the bast and, in fact, through the youngest layer of the bast. If this is broken in a certain place by girdling the shoot, the lower part of the stem is in the same condition as if the whole of the part of the tree above the ring did not exist. It sends out its substitute shoots as if the stem were cut through at this point.

Epicormic branches often possess such vigour of growth that they may reduce neighbouring parts of the crown to starvation by withdrawing nourishment. It appears as if they have a special drawing power for water and soil nutrients, though it is difficult to distinguish in many cases if their better growth is not due to their being better supplied with nourishment from the beginning, as substitute shoots for parts of the crown which are perishing from some other cause. In oaks that have been isolated the old crown opens out or dies in the same measure as the epicormic branches on the stem develop more strongly. If the epicormic branches are removed the failing crown may again revive. From this it is concluded that the epicormic branches draw away the water from the crown as they stand nearer to the source of supply. The position is not so simple however, for spruces and pines, without epicormic branches, often become dry topped in open stand, even when

[1] Jost, Berichte der Deutschen bot. Ges., 1894 ; Klebs *loc. cit.*, p. 26.

the lower part of the crown has not unduly developed. In many cases top drying precedes the formation of epicormic branches; these then develop so strongly only because more nourishment is left for them after the death of the crown. As R. Hartig describes the process in isolated oaks, the isolation increases the activity of the soil and enables the roots to spread, and the admission of plenty of light promotes the activity of the leaves so that the epicormic branches that are present and those which then arise, as well as the crown all thrive splendidly. Later on the activity of the soil falls off (overgrowing with grass, consumption of supplies of nutrients in the humus, etc.), the roots can no longer feed the excessive quantity of leaves and the shortage most strongly affects the crown, the water supply for which is most difficult. It dies from above downwards while the lowest epicormic shoots remain alive.

In consonance with his theory of tree structure according to static laws (*see* Chap. VI. 3), Metzger gives an original and illuminating representation of epicormic branch formation and top drying in isolated oaks but one that is also difficult to prove. Wind pressure on the crown is greater in open stand than in close. The increased wind pressure acts as a stimulus to bring about the strengthening of the lower parts of the tree by augmented diameter growth and at the same time the tree displaces its crown in a downward direction by the death of the old crown and its replacement by water shoots on the stem. Thus the leverage of the wind is reduced and the safety of the tree from wind break increased; the tree adapts itself in this way to the mechanical requirements of the new environment.

Coppice shoots arise in circumstances similar to those which lead to the formation of epicormic branches on the stem. Wounds in the roots through the dragging out of felled material, also cause their appearance as well as injuries in the upper part of the tree, crowding of the crown, disease of the stem, and over maturity.

Whilst the basic causes of the occurance of epicormic branches of all kinds are not clearly understandable, their biological significance is in most cases obvious. They serve for the replacement of lost or damaged parts, also, however, for the renewal of the whole individual and even for propagation.

Epicormic branches, especially in youth, live a certain life of their own on the tree. They are not only independent of other parts of the tree in their geotropism (*q.v.*) as already stated, but they also grow as a rule much more vigorously than regular shoots, although at first they have only a slender connection with the water conducting elements of the stem. During their first years of growth they bear only juvenile leaves (shade leaves *q.v.*) even when the regular twigs on similar parts of the tree bear light-leaves. Their leaves are also mostly larger than the normal ones and often differently shaped, as in the aspen, in which the leaves of coppice shoots are not only much larger than the regular ones but are also characterised by their hairiness and pointed oval form. Epicormic branches have also much less tendency to flower and, according to observations of the editor, are, in the beech, much more readily attacked by canker fungus than the ordinary shoots.

Several of these characteristics indicate that the epicormic shoots represent reversions to the juvenile form. The buds from which they originate have, in a manner, slept through the whole time between their inception and their sprouting and thus preserved their youth, whilst the part of the tree on which they stand has grown old through its life activity. We speak quite rightly of the rejuvenescence of the crown (Molisch) by water shoots in fruit cultivation, and roses and other bushes rejuvenate themselves every year by such shoots whilst the branches of higher order grow visibly old, exhaust themselves in fruit bearing and finally disappear. However, the epicormic branches on trees apparently grow old more quickly than the whole young plant, so that an oak crown formed of epicormic shoots may soon flower like the original crown and after a few decades presents the appearance of an ordinary, old tree-crown. Water shoots of fruit trees may flower and fruit even after a few years, but they are for a long time inferior in this to the regular shoots. Root suckers and stool shoots mature especially quickly. They soon fall off in growth and come prematurely into flower. Experience has shown that stool shoots of beech do not produce fully grown high forest, neither do stool shoots of oak if they have been cut back to the stump several times. Such phenomena have not indeed been fully explained; fungoid infection through the large wounds in the stool and other things may possibly be involved. In the case of coppice shoots of the aspen, however, there is no doubt that they behave more unfavourably than seedlings, irrespective of whether they remain connected with the mother root or are transplanted.[1] Root shoots of the plum when transplanted, have, according to Molisch,[2] a greater tendency to the production of root suckers than seedling plants (*see* also Chap. I, 14).

[1] Hofmann, E, Zur Anzucht der Aspe. Forstwiss. Zentralbl, 1902, p. 360, holds, to some extent, another view.

[2] Molisch, Pflanzenphysiologie.

9. Summary of Bud Characters of certain Trees.

I. Buds concealed.
  1. Opposite. *Philadelphus.*
  2. Spirally arranged. *Robinia.*

II. Buds not concealed.
  1. Buds stalked.
    (*a*) 1 or 2 scales visible. *Alnus, Viburnum opulus* (opposite).
    (*b*) More scales visible. *Ribes.*
  2. Buds not stalked.
    A. Open. *Viburnum lantana, Rhamnus frangula, Cotoneaster, Sambucus nigra.*
    B. Closed.
      (1) 1 scale visible. *Salix, Platanus* (cap scale).
      (2) 2 scales visible. *Tilia, Fraxinus.*
      (3) More than 2 scales visible.
        (*i*) Buds scattered.
          (*a*) Buds arranged in two ranks, alternate.
            1. Buds pointed.
              (*aa*) Scales two-ranked. *Ulmus.*
              (*bb*) Scales in more than two ranks. *Fagus, Carpinus.*
            2. Buds rounded. *Corylus, Castanea.*
          (*b*) Buds spirally arranged.
            1. Twigs without thorns or prickles.
              (*aa*) Scales green or brown bordered. *Daphne, Sorbus torminalis, aria.*
              (*bb*) Black. *Sorbus aucaparia, Juglans regia* (terminal bud grey-felted, pith chambered).
              (*cc*) Lacquered. *Populus.*
              (*dd*) Brown, not lacquered. *Prunus, Quercus, Pyrus, Betula* (buds somewhat hairy, twigs strikingly slender).
            2. Twigs with thorns or prickles.
              (*aa*) Leaf-thorns. *Berberis, Ribes grossularia, Caragana, Robinia.*
              (*bb*) Shoot-thorns. *Hippophae* (bronze-coloured scales), *Crataegus, Prunus spinosa, Pyrus communis, Pyrus malus, Rhamnus cathartica.*
              (*cc*) Prickles. *Rosa, Rubus.*
        (*ii*) Buds opposite. *Clematis, Lonicera, Fraxinus, Aesculus, Acer, Sambucus racemosa, Syringa, Evonymus, Ligustrum, Rhamnus cathartica, Cornus.*

CHAPTER III

PROPERTIES AND LIFE PROCESSES OF THE MERISTEM OF THE TREE

1. The Cell.[1]—From the external appearance of the tree we recognised the annual shoots as its constituent members. We saw how, independently and also in subordination to the requirements of the whole, they built up the wonderful structure. In just the same way an examination of the internal constitution of the tree shows us fundamental members (elementary organs) which independently and collectively work towards its development. These are the **Cells** (Fig. 46), simple structures and yet so infinitely complicated, on which, since their closer investigation by Schleiden, Naegeli and Mohl, the attention of all who study the life processes of animals and plants has more and more focused itself. Robert Hooke (1667) applied the term cell (cellula) to the small chambers of which a piece of bottle cork appeared under the microscope to be composed. We find the living tissue of all higher plants divided into such chambers, sometimes more rounded, sometimes angular, differing considerably among themselves and with a diameter of about 0.02 to 0.2 millimetres. Life is bound up with the contents enclosed within their walls, the **Protoplasm,** each of them representing a small portion of the total living mass of the plant. Almost all these portions are connected together by very delicate protoplasmic threads [2] which pass though the cell walls so that we may speak of a total protoplasm of every plant, a "**symplast,**" the separation of which into units by the formation of cells has assisted the division of labour between the various plant members and provided a rigid framework which makes the erection of the plant above the soil possible. For the rest the conception **cell** is now generally rightly applied to the living protoplast and not to the rigid chamber which may happen to enclose it. Thus, for example, a protoplasmic unit without a firm integument, such as occurs in the swimming swarm cells of many algae and in male reproductive bodies, and which is the rule in animal tissues, is called a membraneless or naked cell.

[1] Meyer, A., Morphologische und physiologische Analyse der Zelle der Pflanzen und Tiere. Jena, 1920. Verlag G. Fischer. Lundegardh, H., Zelle und Cytoplasma, in Linsbauer, Handbuch der Pflanzenanatomie, Abt. I, 1, Tl. Berlin, 1924.

[2] Kienitz-Gerloff, Bot. Ztg., 1891; Kuhla, Bot. Ztg., 1901, Abt. 1, Bd. LVIII, p. 30. Hill and Gardiner, Phil. Trans of the Roy. Soc. of London. Ser. B. Vol. CXIV, 1901. Strasburger, Jahrb. wiss. Bot. 36, p. 493, 1901.

To get an idea of the external characteristics of protoplasm we may picture it as a semi-fluid mass similar to white of egg, capable of being drawn out into threads and filled with a varying number of microscopically minute drops and grains and belonging, so far as its physical nature is concerned, to the emulsions.[1] These are mixtures in different proportions of liquids which are not mutually soluble. The simplest example is a mixture of minute oil drops with water produced by prolonged shaking. According to the number and size of the droplets, such a mixture may be mobile, like a liquid or immobile like a solid, though light body; sometimes it appears as a coherent liquid mass with enclosed droplets, sometimes chambered, *i.e.* consisting of minute particles, which, like the bubbles in beer froth, are bounded by stable walls which are nevertheless formed of thin, liquid films. Now protoplasm is formed, not of two substances only, but of many, of which the majority are colloids, *i.e.* swellable bodies like clay or gelatine, which may assume all intermediate conditions from the liquid to the solid state according to their water content. When one considers further that in the liquid particles of the emulsion chemical processes may go on isolated from each other and that stimuli alter their fluidity (viscosity [2]), the many sidedness which is characteristic of protoplasm may be realised and it is unnecessary to assign to it a definite structure beyond the clearly definable emulsionlike constitution. As to the chemical characteristics of the mass it may be said that in a dead condition it always gives the reactions of protein and other nitrogenous compounds, but may contain, in addition, carbohydrates and fats. Bodies of the protein class in the widest sense are never absent where life has manifested itself and they are a necessary concomitant of it. Among inorganic substances there is always water, which forms on the average over 50 per cent. of its substance, also, dissolved in this water, or in combination with organic substances, chlorine compounds, carbonic, phosphoric and sulphuric acids, and salts of the alkalis and alkaline earths. The chemical constitution of the cells is far from being exhausted with the substances named. They serve only as a general picture of the con-

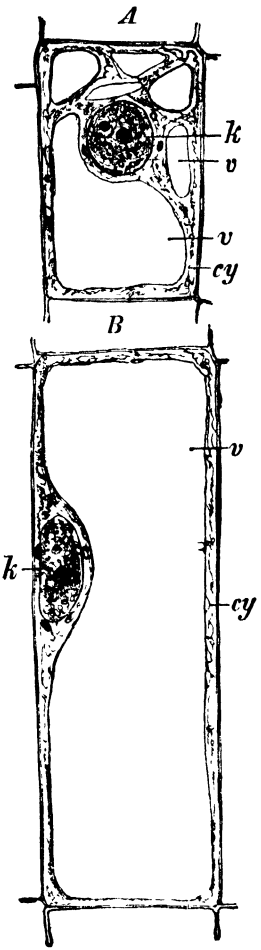


FIG. 46—A. a young, B. a mature cell. In the living protoplasm may be recognised: the nucleus (*k*), the cytoplasm (*cy.*); (*v*) spaces filled with cell sap (vacuoles). Highly magnified. BL.

[1] Rhumbler, Das Protoplasma als physikalisches System. Wiesbaden, 1914, Bergmann. (Sep. from Ergebnisse d. Physiologie, hrsg. von Asher u. Spiro, XIV, Jahrg.)

[2] Weber, Jahrb. f. wiss. Bot. 57, 1916. Ber. Dtsch. Bot. Ges. 39 and 40. Heilbronn, A. Jahrb. wiss. Bot. 61, 1922 and others.

stitution of the mass in which we must recognise the bearer of all plant and animal life. We find an almost infinite number of substances present in individual cases, some of which will be referred to later.[1]

A number of distinct structural parts are to be observed in the protoplasm of the individual cells, with which definite life processes are associated. There is first the bounding layer of the protoplasm towards the water-filled spaces in its own interior or towards its surroundings, whether it be water (as in the wall-less, free swimming, reproductive cells of many algae) or the water-permeated solid wall of the cells of the higher plants. This limiting layer, the **Plasma Membrane,** is characterised by its preventing the entrance of many substances into the cell and in this way placing the latter in a position to make a certain choice between the different substances offered to it. It lets water through freely, but is more or less impermeable to dissolved substances, especially those of high molecular weight. Like a delicate oil sheet on the surface of water, the plasma membrane envelops every plasma body as an infinitely thin film—Pfeffer[2] speaks of possibly one to two layers of molecules—and always reappears as a complete covering of the protoplasm when this is cut up into small pieces.

This restriction of the exchange of substances between the protoplasm and its environment by the " semi-permeable " plasma membrane is one of the most important preconditions of all life processes, and as it is lost at death, is often the only means of recognising whether a cell is alive or not. To make this important property clear by a simple example, a red beetroot may be cut up and the pieces, after rinsing, placed in fresh water. The red colouring matter contained in the vacuoles of the cells which are undamaged is unable to pass through the protoplasm and get out into the water. The water does not become red. If the pieces of beet be killed by heating the colouring matter immediately mingles with the water. Conversely, if colourless cells are placed in water in which certain harmless dye stuffs are dissolved, the latter do not penetrate the protoplasm so long as it is alive and its bounding layer is undamaged.

The complete permeability of the plasma membrane for water is demonstrated if slices of radish or tomato are sprinkled with salt. The salt immediately absorbs water out of the cells.

These examples demonstrate the fundamental processes on which the activity of tree roots and the exchange of substances between the living cells and the dead water-conducting tracts of the wood depend. They are examples of **Osmosis,** the interchange of substances through a semi-permeable membrane. As such the whole protoplasmic body behaves, but particularly the before mentioned plasma membrane. Its properties are to some extent those of the so-called superficial membrane which is present, for purely physical reasons, on the boundaries of every liquid. On the other hand it also shows chemical peculiarities,[3] *e.g.* besides protein substances[4] it is especially rich in

[1] Wehmer, C., Die Pflanzenstoffe, Phanerogamen. Jena, 1911, G. Fischer.
[2] Pfeffer, W., Pflanzenphysiologie. Leipzig, 1897.
[3] Czapek, Biochemie der Pflanzen, 2 Aufl. Bd. I. Jena, 1913, G. Fischer.
[4] Lepeschkin, Ber. der D. bot. Ges. XXVIII, 1910.

fatty bodies (lipoids), and the passage of substances through its layer does not proceed so simply as that of water through the pores of a filter made of blotting paper.[1] In this passage the chemical and physical relations of the substances in contact with the membrane to the bodies present in the membrane itself and their solubility or insolubility in them play a part.[2] The membrane itself is not unchangeable. Tröndle[3] found its permeability to be higher on sunny days than in dull weather, higher by day than by night, increasing from December to July, decreasing again from then onwards. Fitting found permeability to salts to vary and to be great in summer and small in winter; according to Lepeschkin[4] changes in illumination altered the permeability of the membrane.[5]

The complete permeability of the plasma membrane to water makes possible the easy absorption of water by the roots, and water interchanges in the interior of the plant. The osmotic penetration of water can develop forces which were for a long time considered impossible, but which are of the greatest importance for the transport of materials, especially in our forest trees, in which water and nutrient substances have to traverse great distances and overcome great resistances. It is therefore necessary to consider these osmotic forces more closely here.[6]

Animal membranes, such as pigs' bladders, are sufficiently permeable to water and sufficiently impermeable to dissolved substances to demonstrate the osmotic processes. If a pig's bladder, through the opening of which an upright glass tube is fixed, is filled with a solution of sugar and placed in a vessel of water, the sugar solution absorbs water through the walls of the bladder, the wall is placed in a state of tension and the sugar solution rises in the glass tube until, at a certain height, a static equilibrium is reached. The sugar solution thus produces simultaneously in the bladder an osmotic suction force and an osmotic pressure of equal magnitude, whose value can be measured by the hydrostatic pressure of the column of liquid in the upright tube and can be expressed in atmospheres. In a completely closed cell in the condition of equilibrium, the pressure on the cell wall and its opposite pressure on the cell sap is just so great that it nullifies the osmotic pressure of the sugar solution and checks any further absorption of water. The absorptive power of the cell as a whole is then nil, whilst previously, so long as the cell wall was still flaccid and not stretched, it was equal to the osmotic sucking force of the sugar solution. In

[1] The most complete account of the permeability of the plasma *see* Stiles, Permeability, London, 1924.

[2] On Adsorption effects *see* Czapek, Jahrb. f. wiss. Bot., Bd. 56, 1915; Pantanelli, Über Ionenaufnahme. The same.

[3] Berichte d. D. bot. Ges., XXVII, 1909, and Jahrb. f. wiss. Bot., Bd. 48, 1910.

[4] Beihefte zum Bot. Zentralbl., XXIV, 1909.

[5] Recent researches, also on the rate of absorption of substances into the cells, critique and the whole literature are given by Fitting, Untersuchungen und Aufnahme von Salzen in die lebende Zelle. Jahrb. f. wiss. Bot., Bd. 56, 1915; Pantanelli, Ionenaufnahme. The same, p. 689. *Comp.* also Tröndle, Beih. z. Bot. Zentralbl, 38, II, 1921.

[6] Fundamental works: Pfeffer, Osmotische Untersuchungen, 1877. Studien zur Energetik Abh. d. mathem. physic. Kl. d. Kgl. Säc hs. Ges. d. Wiss., Bd. 18, Nr. 3, 1892; Pflanzenphysiologie, 2 Aufl., Bd. I. Leipzig, 1891; Höber, R., Physikalische Chemie der Zelle u. d. Gewebe, 5 Aufl. Leipzig, 1922.

osmotic processes in the plant one has therefore to distinguish [1] an "**osmotic value,**" *i.e.* the power of a solution to develop in the interior of a cell an absorptive force and a pressure of a certain magnitude, an "**absorptive force of the cell contents**" equal to this, an "**osmotic pressure**" which the cell contents exert on the cell wall, and a "**wall pressure**" of the wall on the cell contents which is equal to the osmotic pressure for the time being exercised. The osmotic forces of the cell sap are assisted in the absorption and emission of water by the energy of swelling of the plasma.[2] The total pressure of the cell contents on the wall is also called the "**Turgor Pressure.**"

The osmotic value of a given solution increases more or less in proportion to its concentration. Generally solutions have the higher osmotic value the greater the number of molecules of the dissolved substances they contain; dissociation of dissolved molecules also increases the osmotic value. Substances with small, light molecules thus have, with equal concentrations by weight, a higher osmotic value than those with heavy molecules, and a dilute solution of a substance with low molecular weight may have the same osmotic value as a highly concentrated solution of a substance with heavy molecules; the two solutions are then "**isosmotic**" or "**isotonic.**"

If a cell filled with solution is placed in a solution of higher osmotic value, water flows out of the cell into the surrounding solution, the volume of the cell is reduced and the contained solution becomes more concentrated until it becomes isosmotic with the surrounding solution. The cell wall can only take part in this shrinkage to a limited extent, owing to its rigidity. If the withdrawal of water proceeds further, the plasma layer (utricle) continues to draw back still further so that it loosens itself from the cell wall (**Plasmolysis**). The osmotic value for threshold plasmolysis—where plasmolysis is only just visible—can be determined by placing sections of the tissue to be examined in solutions of different concentrations. The cell content has then at threshold plasmolysis the same osmotic value as the outside solution in which threshold plasmolysis is detected.

If the plasma of living cells were in all cases equally permeable to dissolved substances, and if every cell had a chance of saturating itself with water to the extent corresponding to the osmotic force of its content, the osmotic processes would be quite easy to interpret. But actually, in most cases, neither condition obtains. The varying permeability of the plasma make the critical examination of the osmotic forces difficult and the loss of water which the plant suffers from evaporation operates so that the cells are not saturated with water and turgid to the degree corresponding to their osmotic force. The wall pressure is then smaller than that which corresponds with the osmotic value of the cell sap and the cell as a whole has still a certain suction power for taking up a further quantity of water. It is this positive suction power of cells that brings about water absorption.

The osmotic forces in plants, especially in trees, may reach extra-

[1] Ursprung und Blum, Ber. Dtsch. Bot. Ges. 34, 1916, p. 88, 525. Höfler K., The same 38 1920, p. 288.

[2] Walter, H., Plasmaquellung und Wachstum. Zeitschr. f. Bot. 16, 1924.

ordinarily high values. Osmotic values of twenty atmospheres in the leaves are common, and those of forty and more atmospheres have often been proved also in the wood parenchyma. Such forces are necessary to maintain the sap streams in motion in the long, narrow conducting channels of large trees, to draw water from the soil and pump it up to the top. Only the division of the tissues into cells of microscopic smallness makes it possible for such great forces of pressure and suction to be sustained even in the tenderest tissues, because the pressure is exerted in each cell only on a very small wall surface. Under certain conditions, the cell, without carrying out any movement, acts simultaneously as a force-pump and a suction-pump, or as a power press of astonishing working capacity. One would hardly expect of such a delicate structure as the cell, that it would be able to thrust upwards and sustain a column of water several hundred metres high, and in the tissues of the root, to penetrate the solid ground and even to widen cracks in the rock.

Great importance in the transportation of materials is attributed by most physiologists to the beforementioned fine plasma connections (**Plasma Bridges, Plasmodesms**) which, in large numbers, lead through the cell wall from each cell to its neighbours (Pfeffer,[1] Kienitz-Gerloff, Strasburger,[2] Jost and Benecke [3]). They must, like every plasma body in contact with non-living surroundings, be enclosed in a semi-permeable plasma membrane along the dead cell-wall which they penetrate. Whether the plasmodesms generally have in their interior also a tubular space filled only with cell sap as has been proved for certain special cases (Sieve plates) cannot be directly determined by the microscope, on account of their exceeding fineness (their diameter measures generally a fraction of a micro-millimetre), though nuclei and apparently also small starch grains have been seen to pass through them. Where, however, such open connections of the sap spaces of the cells with each other do exist, the migration of substances from cell to cell by simple streaming results as soon as mechanical pressure differences are set up between the cells sufficient to overcome the friction in the narrow pores. It happens thus as soon as a cell has enriched itself with osmotically active substances more strongly than a neighbouring one, or if in one cell osmotic dissolved substances are converted into an osmotically less active form or are precipitated as solid substances such as starch, crystals or cell-wall. Such cells press out water by reason of their still existing wall pressure, their turgor diminishes so that room and falls of pressure are provided for the streaming in of solution through the plasmodesms.[4] The osmotic transfer of substances through the non-permeable or only difficulty permeable plasma membrane need not then be involved in the movement of material. Only to the surface of the plant and to the lifeless water conducting organs of the wood do plasmodesms never lead; in these directions the movements of substances are thus only possible by way of true osmosis.

[1] Pflanzenphysiologie. *loc. cit.* p. 92–93.
[2] *Loc. cit.*, 1901.
[3] Bennecke-Jost, Pflanzenphysiologie, I Bd., p. 287, 4 Aufl., 1924.
[4] Münch, Ber. Deutsch. Bot. Ges. 44, p. 68 ff., *comp.* Chap. XII, 2.

It is, perhaps, of importance for the understanding of the directive influence of external forces (light, gravity) on the tree, described in Chap. I, that the bounding layer does not take part in the movements which are detected in the interior of the protoplasm. These movements are either streamings which proceed side by side in different directions, or a united circulation of the whole protoplasm except the bounding layer, in one direction. In the latter case especially it would be hard, if not impossible, to conceive how the directing stimulus would come into existence unless the bounding layer, by reason of its immobility, were in a position to take up the direction of the stimulus. The protoplasmic movements, which in many plant leaves (*Elodea, Vallisneria*) occur only after wounding, and in other cases normally, accelerate the transport of substances taken up by the plants from place to place within the individual cell and so also from one cell to another.[1] With higher temperature the fluidity of the protoplasm, and with it the rate of streaming increases. It is also accelerated by dilute anæsthetics, but retarded by stronger ones and, in green cells, by strong light.[2] Such effects of temperature and anæsthetics may play a part in bringing the resting period to an end (*see* Chap. II, 4).

The plasma membrane, by reason of its activities, is thus seen to be a part of the protoplasm very important for the plant body as a whole. It should hardly be called one of its individual organs as it is not sharply delimited from the rest of the protoplasm. Such is, however, the case with the **plastids** and the **nucleus** (Fig. 47). The former are, in the higher plants, lens shaped or almost spherical structures which, in contradistinction to the nucleus, are present in numbers in each single cell. With such plastids is associated the green chlorophyll colouring matter which colours the leaves of trees ; others carry yellow or yellow-red colouring matters in flowers and fruits and others again are colourless. Many colourless plastids have the power of turning green in the light and, moreover, green ones may become yellow—colour changes which are familiar in the turning green of seedlings just emerging into the light, the turning green of leaves which are, at the opening of the buds, yellowish (Robinia and often beech), reddish (*Acer negundo*), or even reddish brown (*Amelanchier Botryapium*) and, on the other hand, the yellowing or reddening of leaves and fruits which are green in the immature state. The red and blue colouring matters are dissolved in the cell sap and combine their effects with that of the yellow or green plastids of the same or neighbouring cells. The orange red of the hip is due to the combined effect of the carmine red sap in the cells of the epidermis and the yellow spindle-shaped plastids in the underlying layer of cells. The best known function of the green and of many colourless plastids in the plant is the production of starch. In the green plastids the formation of this important plastic substance takes place in all parts of the tree exposed to the light, especially in the leaves and the living rind, whilst colourless plastids are the seats of

[1] Bierberg, Flora, IC, 1908 ; Kretzschmar, Jahrb. f. wiss. Bot., 1903.

[2] Ewart, Proc. Roy. Soc., Vol. LXIX, 1902, p. 466; Illumination by sunlight and concentrated gaslight induce streaming in *Elodea*; Nothmann-Zuckerkandl, Ber. d. D. Bot. Ges., 1915, 301.

starch formation in the parts not fully illuminated—the roots, the wood of the twigs and stems and in the seed. The greatest advantage of the green plastids over the colourless ones is that to form starch they require only a supply of carbon dioxide. The colourless plastids can only convert already existing organic compounds into starch. They play a part in the movement of materials in the tree and in the filling up of the storage organs.

The **Nucleus** is usually a lens-shaped body which, of all the constituents of the protoplasm, was the first to draw to itself the attention of researchers and to which has, as a result, been ascribed a specially important role in the life of the cell. The protoplasm can, however, carry out many life processes without a nucleus, even the formation of the solid cell wall.[1] In actual fact, however, in those parts of the plant in which the formation of new cells is going on, the nuclei form a very large part of the mass as compared with the other constitutents of the protoplasm (Fig. 47), and in the male sexual cells, apart from the nucleus, only very little other protoplasm is present. In the process of fertilisation, therefore, almost everything of the male parental character which is transmitted must be, at least originally, enclosed in the nucleus. Researches devoted for many decades to the peculiarities of structure and behaviour of the nucleus have led to the discovery of short fibres in the nucleus, which are present in a fixed number in all the nuclei of one species of plant. Before the formation of the cells destined for union in fertilisation the number of fibres in the nuclei falls to one-half, and in fertilisation itself, the full number is again restored by the fusion of the male and female nuclei. Because of their power of storing up colouring matters in themselves, the fibres have been called **Chromosomes.** The course of life of every higher plant falls into stages with simple and with double numbers of Chromosomes (*e.g.* in *Acer negundo*,[2] 12) (Alternation of generations). Every nucleus contains besides one, more rarely several, round nuclear corpuscles (**nucleoli**) which are also easily dyed. They are apparently protein reserve materials which are laid down in the nucleus like the starch grains in the chlorophyll granules.

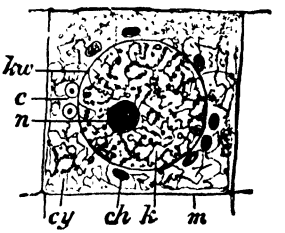


FIG. 47.—Young cell with nucleus (*k*) in which the nucleolus (*n*) may be seen. Cytoplasm (*cy*), plastids (*ch*) and centrosomes (*c*); (*m*) cell wall; (*kw*) boundary of the nucleus. BL.

The word protoplasm, or protoplast or shortly plasma (which has been translated first moulded or first moulder), indicates that the said protoplasm forms the origin of every organism, and that from it all life activities proceed. Excluding the nucleus and plastids, what remains of the protoplasm is called the **Cytoplasm.**

The solid wall [3] by which the cells of the higher plants are enclosed, consists in young cells of a very thin, elastically extensible but still

[1] Acqua 1901, Wisselingh 1907; *see* Czapek, 2 Aufl., Bd. I, p. 707.
[2] Mottier, Ann. Bot., XXVIII, 1914, p. 115.
[3] Van Wisselingh, C., Die Zellmembran, in Linsbauer's Handbuch d. Pflanzenanatomie, Bd. III, 2, Berlin, 1924.

rather fragile membrane which permits of the passage of water and solutions. It is not a simple chemical substance, but, in unlignified parenchyma cells, consists to the extent of more than 90 per cent., of cellulose. In addition there are other carbohydrates (hemi-celluloses), which are more easily decomposed, and gelatine-forming pectin substances. Fatty bodies may also be present in the walls of living cells. The walls of living cells may, as colloids, take part in the exchange of substances between the cells and their surroundings.[1] As the cells grow older the walls become thicker and undergo many chemical changes which affect their mechanical properties and their behaviour towards water. The protoplast often perishes at the same time so that the greater part of the plant, especially of a woody plant, finally consists only of the dead walls or membranes. Somewhat thicker, mature walls, such as are found in the tissue of the living part of the bark and the pith and in the wood, are usually stratified. Notably a middle layer is often conspicuous by reason of its strong refraction of light. It is called the **Middle Lamella,** contains calcium pectate and is more easily dissolved than the other portions of the cell wall. We are, therefore, for this reason able to break up a cellular tissue into its constituents by chemical means, *e.g.* by treating it with nitric acid and potassium chlorate or by allowing it to rot in water. As a rule, in the natural order of things, slits and narrow passages also occur in the middle lamella. Especially in living tissue, there is to be found a continuous labyrinth of very narow passages running between the cells, the "**intercellular spaces**" which open to the outside in the stomata and lenticels and make possible the access of air to the interior of the tree.

2. The Origin of Cells at the Growing Point.—Cells originate, without exception, by the division of previously existing cells. The same is true of the organs of the protoplasm. Nuclei always originate by the division of already existing nuclei, and any origin for the plastids, other than through division, has not been convincingly demonstrated, in spite of some assertions to that effect.[2] Never in the whole vegetable and animal world has a cell been observed to arise from structureless "sap."

In trees, cell division occurs wherever growth is taking place, such as at the tips of all shoots and roots, in the region between rind and wood and also in the layers of the cortex which bring about the formation of cork and bark, and finally in the neighbourhood of wounds, which the plant strives to cover up by the formation of new tissue.

The formative tissue or meristem of the tip of a shoot or root occupies the top of the sometimes slightly domed, sometimes conical, end of the axis which is called the **Growing Point** or **Vegetative Cone** (Fig. 31). In the roots it is covered by a peculiar cap. It consists

[1] Hansteen-Cranner, Beitr. zur Biochemie und Physiologie der Zellwand lebender Zellen. Jahrb. f. wiss. Bot., XLVII, 1910, and LIII, 1914. Rippel, A., Semipermeable Zellmembranen bei Pflanzen. Ber. Dtsch. Bot. Ges., 36, p. 202.

[2] Literature on Chondriosomes, etc., *see* Czapek, Biochemie, 2 Aufl. Bd. 1, p. 551, 552; Scherrer, Flora, CVII, 1914; Cavers, New Phytol., XIII, 1914; V. Derschau, Archiv. f. Zellforschung, XIV, 2, Leipzig, 1915. Lewitzky, G., Ber. Dtsch. Bot. Ges. 29, p. 538; 29, p. 685.

of nothing but small cells whose protoplasts contain no vacuoles, but have each a nucleus which is very large compared with the remainder of their substance. As the nuclei are characterised by containing nucleins —compounds of proteins with phosphoric acid and organic bases— herein lies a difference in chemical constitution between the formative tissue and the other parts of the plant.

The multiplication of the protoplasm in the growing point of flowering plants proceeds simultaneously in many individual cells since each increases somewhat in size and then, by forming a solid dividing wall of cellulose, divides into two approximately equal cells which again grow to the size of their mother cell and then undergo similar division on their own account.

In the lower plants (Algae) it appears that cell division takes place particularly at night, and so at the time when the formation of starch by the help of daylight is not taking place. According to Karsten's researches [1] on maize, this is also the case in the growing points of the shoots of higher plants, and the greater number of nuclear divisions in the tips of the shoots of seedlings of the Corsican pine took place between 2 to 4 a.m.[2] Probably the same behaviour might be detected in our forest trees, in so far as the enclosing of the growing point by stipules and young leaves does not prevent light reaching the embryonic cells of the vegetative cone. The diameter growth of the stem also goes on principally at night.[3] In roots, which live in darkness, cell division proceeds equally by day and by night.

In the growing point there can be observed a more or less obvious stratification parallel to its surface. Its epidermis especially is noticeable as a mantle enclosing the whole and consisting of a single layer of cells which is continually enlarging by cell multiplication. No such epidermis is formed on the roots of conifers—their surface consists of ordinary cortical cells. The layers of cells lying immediately under the epidermis behave in the same way, and the youngest leaf rudiments appear as folds which are formed in consequence of the great growth in area of the layers. Only that part of the growing point which lies above these primordia is able to restore itself again after an injury.[4] The direction of growth of the layers and consequently the position of the new cell walls is determined, within the limits of the individuality of the protoplasm in question, by the behaviour of the cells towards stimuli which act on the surface of the growing point and which result from the pressure and tension conditions prevailing in the interior.[5] There is also involved the fact that the position of the new cell walls is influenced by the same physical laws as the position of the thin walls of the cavities in a foam.[6] The placing of the incipient dividing walls in the direction of a tension and at right angles to a pressure was also

[1] Karsten, Über embryonales Wachstum und seine Tagesperiode. Ztschr. f. Bot., Bd. VII, 1915.

[2] Karsten, Ztschr. f. Bot. 10, H. 1.

[3] Friedrich, Ü. d. Einfl. d. Witterung auf den Baumzuwachs. Mitt. a. d. forstl. Versuchsw. Österreichs, 22, 1897.

[4] Linsbauer, Die physiol. Arten der Meristeme. Biol. Zentralbl., 26, 1916, p. 117.

[5] Schüepp, Wachstum und Formwechsel von Vegetationspunkten. Jahrb. f. wiss. Bot. LVII, 1916.

[6] Giesenhagen, Bot. Zentrbl., Bd. XCVIII, 1905, p. 333.

observed.[1] According to Douliot and Dingler,[2] growth in the vegetative cone in the conifers occurs by means of a single apical cell, as is the case elsewhere only in cryptogams, where the whole structure may be traced to one single cell.

The enlargement of the cells associated with the multiplication of the protoplasm in the growing point is only small. It soon sets in, however, in a second stage of life—that of elongation. Somewhat below the actual growing point cell division becomes more rare, cell cavities appear in the protoplasts and the whole cell rapidly enlarges to several times its original dimensions, so that its protoplast is stretched into a thin film which lies close to the cell wall (Fig. 46). The growth of the plant consists of the above described increase of substance and the elongation of the individual cells. An individual cell only grows when it finds itself in a condition of tension (turgor) like a bladder filled with water under pressure. This explains the great influence shown by the dryness and humidity of the air and of the soil on the growth of trees. The expansion of the cells is favored by the reduction of the elasticity of the cell wall and thence its resistance to constant stretching.

The final form and size of individual cells vary very much. Sierp [3] was able to determine hereditary mean values for the size of cells of every tissue of a species of plant, but also found that external causes have a great influence on the size of cells. The differences in size of the individuals of a species and their individual parts may be due to differences in the number and in the size of the cells.

Dwarf strains with a smaller number of cells may have larger cells than the normal form. For our purpose it is sufficient to distinguish two kinds: the roundish, shortly cylindrical or four-cornered parenchymatous form of cell—the common form in living plant tissues (Parenchyma)—and the elongated prosenchymatous form of cell pointed at both ends. The former are widespread in the growing points, the cortex of shoots and roots, the leaves and the pith, while the latter are found especially in the bast and wood fibres.

Growth by elongation, like the process of cell division, in the shoot, is greater at night than in the daytime, increases from evening till morning even when the temperature falls 8 degrees or more at night, and rapidly diminishes after sunrise in spite of rising temperature.[4] During the formative processes at the tip of the shoot (cell multiplication and growth) there are present in its interior, zones of different chemical condition [5] and therefore of different absorptive power and tensions in the tissues [6] (*see* also section on Growth in Length). Below the apex of the growing point there is found, at the time of the growth of the shoot, first a zone filled with fine-grained starch, a collecting place of building materials for the requirements of the growing point itself and the

[1] Kny, Jahrb. f. wiss. Bot. XXXVII, 1902, p. 55.

[2] Douliot, Annales d. sc. nat. Bot., sér. VII, T. XI, p. 283, and Dingler, Ber. d. D. bot. Ges., IV, 1886.

[3] Individuengrösse, Organgrösse and Zellengrösse mit besonderer Berücksichtigung des Zwergwuchses. Jahrb. f. wiss. Bot., LIII, 1913.

[4] Karsten, *loc. cit.* Gives literature.

[5] Berthold, Untersuchungen zur Physiologie der pflanzlichen Organisation, I, 1898, II, 1, 1904, Leipzig, Engelmann.

[6] Ursprung und Blum, Jahrb. f. wiss. Bot., 63, 1924.

completion of the cell walls. Beneath this starch zone, and thus in the somewhat older tissue, there is usually an abundance of so-called tannins which are important chemically as transition products of chemical reactions, physically as a means of increasing the pressure in the cells, and finally, ecologically as a protection against the attacks of animals. In the next, again somewhat older, zone are to be found quantities of reducing sugars together with amides, salts and organic acids. From here the sugar migrates to that collecting place from which the growing point can take more or less according to the rate of growth at the moment, without being affected by fluctuation in the transport from more remote tissues. The zone rich in sugar belongs to the fully grown portion of the shoot. When the internal formation of its cells is completed they fill themselves with starch, the material for forming which comes from the chlorophyll granules which have meanwhile come into action. The perfecting of the internal structure of the young shoot begins in *Acer* in the second half of April or in May. It starts in the first internode of the twig or in the second and proceeds from there upwards and downwards. In September and October, the time of the greatest accumulation of starch in the shoot, all parts of the bud which crowns it are also flooded with starch, as Berthold puts it, and perhaps it is in consequence of this that it now enters into a state of rest and for some time becomes incapable, under normal circumstances, of sprouting. Numerous other details of the distribution of substances in the shoot and in the developing bud are given by Berthold (*compare* also Chap. I, 5).

3. The Epidermis.—In the formation of the permanent tissue from the meristem, the earliest to appear, immediately behind the growing point, is the **Epidermis,** which is a single layer of platelike cells covering the whole of the young shoot, including its appendages. The external walls of the epidermal cells are very early distinguished by a chemical peculiarity. They are formed superficially of a substance only very difficulty permeable by water and water-vapour, which consequently forms the external covering of every plant. It consists, according to Van Wisselingh,[1] of a mixture of fatty, saponifiable substances and other bodies, from which, however, phellonic acid, always present in cork, is absent. In the young shoots of the ash-leaved maple (*Acer negundo L.*), in *Salix daphnoides* (Villars) and the needles of many conifers the action of the covering (Cutin or Suberin [2]), the " cuticle," in checking evaporation is further increased by deposits of wax, which form the easily-rubbed-off, bluish bloom on such twigs.

From the epidermis arise the hair structures which shoots and leaves of many trees exhibit in youth, from the bronze coloured and shining silvery scales of the sea buckthorn (*Hippophae rhamnoides*) and *Eleagnus*, to the branched, whorled hairs of the young plane shoot, which are troublesome to the mucous membrane of the respiratory organs and the eyes at the time they are shed in spring, and also the brown down which

[1] Van Wisselingh, Archives neerlandaises, T, XXVI, 1893. Ref. Bot. Zentralbl., III,1893, p. 109. The same, Die Zellmembran. In Linsbauer's Handbuch der Pflanzenanatomie. Bd. III/2, Berlin, 1924.

[2] Czapek, Biochemie.

distinguishes the current year's shoot of the Cembran pine from that of the Weymouth pine. It has already been explained that the coverings of resin and sticky substances which we found on buds are formed in hairs or epidermal cells. In particular the resinous exudations of young long shoots—especially stool shoots—of the common birch, which have given it the name *verrucosa*, originate in the interior of the cell walls of shield-shaped glandular hairs and also of epidermal cells without hairs. In other cases also the secretion of the hairs accumulates in the cell wall under the cuticle so that the latter is raised like a blister and ultimately bursts.

As the cells in the interior of the plant require the admission of air for respiration and of carbonic acid for nutrition, openings occur between particular cells of the epidermis which effect the necessary exchange of gases. They and kindred structures will be fully discussed in the chapter on Leaves.

4. The Origin and Formation of the Conducting Channels. Secondary Thickening.—A few millimetres behind the growing point of the shoot there is found, between the pith and the cortex, a layer of dividing tissue, the procambium, which is to be the originator of the greater bulk of the future stem.

The arrangement of the procambium and the further development of its products have, until recently, been generally wrongly represented. As Kostytschew[1] showed, there do indeed exist among dicotyledonous plants great differences, often not easily interpreted, in the origin and formation of the secondary elements of the shoot, but for our forest trees the process is uniform and simple.

In all perennial dicotyledonous woody plants with a closed xylem, the Procambium arises as a closed hollow cylinder surrounding the pith, consisting of soft-walled, elongated cells, rich in protoplasm, arranged irregularly in the cross section of the shoot. The elongation of the procambium cells, according to Th. Hartig, occurs by the almost cubical embryonic cells of the primary tissue dividing by inclined walls, after which the daughter cells grow into long fibre-like prosenchyma cells, pushing past each other by sliding growth in the manner shown in Fig. 48. Soon, still within the zone of elongation, the procambium sheath separates into three quite different kinds of tissue. On the pith side, generally in isolated strands, some procambium cells become primary wood elements, which are called **Protoxylem elements.** They strengthen themselves by ring-shaped and spiral lignified ridges whilst the remaining parts of the wall remain thin and extensible. The protoxylem elements follow the elongation of the shoot which at that stage is still proceeding; in this way the annular ridges are drawn apart and the course of the spirals becomes steeper. In the same way out of the cells on the cortex side of the procambium arise the first elements of the bast, the elements of the **Protophloem.**

[1] Kostytschew, S., Der Bau und das Dickenwachstum der Dikotylenstämme. Beihefte z. Botan. Zentralbl. 40, 1924, p. 295. *See* also Meyer, F. J., Bau und Ontogonie der Wasserleitungsbahnen. Progressus rei Botanicae, 5, 1917. Eames, On the Origin of the herbaceous types in the Angiosperms. Ann. d. Bot. XXV, 1911.

Between the protoxylem and the protophloem there remains a closed, hollow cylindrical sheath of procambium cells, which in cross section form a circle of cells generally in a single row, permanently capable of division—the **Cambium.** In many dicotyledons the cambium proceeds from several original cells. These cells continually divide in such a manner that they constantly cut off new daughter cells, now inwards towards the pith, now outwards towards the cortex ; in this way forming radially disposed rows of cells which sharply distinguish this permanent meristem, also called " row cambium " or " secondary cambium," from the procambium with its irregularly arranged cells. The daughter cells of the cambium mother cells may, however, also divide. Ultimately all the cambium cells cut off towards the inside become organs of the wood and all formed on the outside, elements of the bast. This cell division in the cambium proceeds, in the tree, for years and even centuries, the shoot becomes, as a branch or stem, continually thicker (secondary thickening), so that the cambium is naturally pushed farther outwards. Far more cells and generally wider ones are cut off as wood than, towards the outside, as bast, so that the xylem finally comprises the main bulk of the stem, about ten times as much as the bast and cortex. This being the construction of the shoot of out forest trees, true vascular bundles, such as are very conspicuous as separate strands in the parenchymatous mass of the ground tissue in monocotyledons, do not generally occur. Such vascular bundles or groups of vascular bundles (called leaf-trace bundles) do, however, extend out of the leaves through the leaf-stalk and the cortex to unite with the " tubular bundle " of the shoot. Where they run into it, the formation of the wood and bast parts of the tubular bundle proceeds more strongly in strands, so that in the young shoot, vascular-bundlelike strands may be recognised round the pith. These and the protoxylem project like the spikes of a crown into the pith tube. (Medullary sheath.)

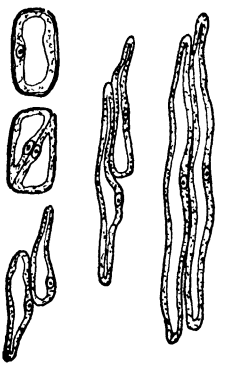


FIG. 48.—The production of prosenchymatous procambium cells from the parenchyma of the Meristem by sliding growth. After Th. Hartig.

Variations and deviations from this procedure occur in other plants, as distinct from trees and shrubs, albeit in a small minority of cases, of which we need only consider the type occurring in woody lianes. In the birthwort, *Aristolochia Sipho*, separate, almost cylindrical, vascular bundles are formed in the parenchymatous ground tissue in the course of the leaf traces, which are arranged in limited numbers round the pith. By the action of their cambium these bundles are, in section, extended in a radial direction. The parenchyma which lies between these bundles, uniting the pith with the cortex, called the " pith connection " (in contradistinction to the medullary rays of the wood to be discussed later) must, in order to keep pace with this growth, also divide in the same way in a radial direction. This is brought about by the establishment of an " interfascicular cambium " by a layer of parenchymatous cells of the pith connections in periferal continuation of the " fascicular

cambium " of the vascular bundles, dividing by cell walls which lie parallel to the surface of the shoot. From these are formed new cells, inwards and outwards, which, however, in this case, consist, not of wood and bast, but always only of wide-meshed parenchyma which extends the pith connection in a radial direction. Isolated strips of parenchyma of this kind are also formed later from the cambium inside the vascular bundles which, however, do not reach inwards as far as the pith (Figs. 49, 50). This method of growth was until recently regarded as the fundamental type of secondary thickening, but, according to Kostytschew, it is a rare exception and is absent in all trees and shrubs which form a closed xylem.

In the pine the procambium is interrupted by the bud stems (*q.v.*) leading from the pith into the dwarf shoots. The strands of the leaf traces of evergreen needles and the bud stems of the pine must every year extend outwards to follow the thickening of the stem. This is done in the way described for dormant buds on page 71 by their lignified elements rupturing and being again replaced by new structures from their own meristem.[1]

The development of the tissues in the root proceeds quite differently from that in the epicotyledonary shoot. Here as a rule no pith is formed. More often, two or more radially arranged ridges of woody elements arise which as a rule merge together in the middle, forming a star-shaped woody mass (Fig. 51). The bast is originally arranged not in a peripheral ring, but in isolated groups between the bundles of the protoxylem. The cambium forms a layer winding in and out between the wood and the masses of bast. It then divides as in the shoot, always producing bast to the outside and wood to the inside. The original arrangement of the three kinds of tissue thus soon disappears completely, so that a root which has undergone secondary thickening for several years is constructed practically like the stem. An important peculiarity in the primary structure of the root is that wood, cambium and bast are surrounded, as a central cylinder,[2] by a closed sheath formed of one layer of cells—the " **Endodermis** "—under which still another special layer of cells, the " **Pericycle,**" lies. In our trees the endodermis is also clearly formed as a sheath round the inner column in the nerves of leaves and the central cylinder of needles, where it is called the " **Bundle Sheath** " (Figs. 97–101, 105–107).

The form of the cells of the cambium sheath is in general that of rectangular prisms with upper and lower ends wedge shaped or sharp only at one side, the edge running in the direction from the pith to the cortex. Their greatest length lies parallel to the length of the shoot. Their size increases with age, in many plants over a series of years, and then remains constant ; in others it remains the same from the beginning to the end of diameter growth.

The duration of cell division in the cambium varies according to external conditions. According to Raatz's observations on the pine,

[1] Markfeldt, O., Ü. d. Verhalten der Blattspurstränge immergrüner Pflanzen beim Dickenwachstum des Stammes oder Zweiges. Flora. Bd. 68, p. 33.

[2] Schoute, Die Stelärtheorie. Groningen, 1902, P. Noordhoff; F. J. Meyer, Stelärtheorie und die neuen Nomenklatur zur Beschreibung der Wasserleitungsbahnen. Beihefte z. Bot. Zentrbl. XXIII, 1916, Abt. 1. Dresden-N, Heinrich.

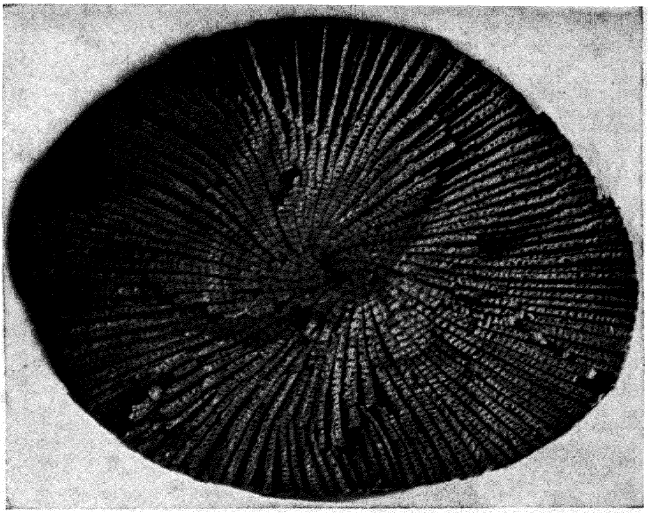


FIG. 49.—As Fig. 50, in cross section. The primary and secondary, shorter pith connections are arranged like the lamellae of a mushroom. The large vessels are visible as points. (Mch.)



FIG. 50.—Old shoot of *Aristolochia Sipho*. The pith connections have weathered away, the xylem between them appearing as radial bands. (Mch.)

[*To face p.* 94.

six cambium divisions occupied 42 days. He found 105 to 110 xylem elements and only 10–11 bast elements completed at the end of September.

The increase in the circumference of the xylem with diameter growth is accompanied by an enlargement of the cambium sheath which is brought about by the growth of cambium cells and their division in the direction of the radius of the tree.[1] This can be easily followed in conifers. There the wood elements in cross section are arranged in regular rows in the direction of the stem radius. The cell divisions which produce these radial rows are brought about by walls which lie parallel to the surface of the shoot (tangential walls). On the other hand the doubling of such a row, easily seen under the microscope, is effected, not by radial longitudinal division of the cambium cell but by a transverse division of such a cell, whereupon the ends of the daughter cells elongate by sliding apical growth similar to that in Fig. 48. This method of division is carried out, not only in conifers, but, as Klinken [2] states, also in broad-leaved trees.[3] Other changes in the cambium occur at the base of branches and twigs.[2] The cambium extends over from the stem on to the branch like the sleeve of a coat over the arm. During the thickening of the branches, if no formation of folds occurs at the point of attachment, either a shortening or a lateral displacement of the cambium cells must take place. All three phenomena occur. The displacement of growing cells with respect to each other is called "**Sliding Growth.**" [2] It has been thoroughly investigated, for example in the sliding growth on each other of the radial walls of the cambium cells of *Taxus* which are developing into fibres (Klinken, *loc. cit.*).

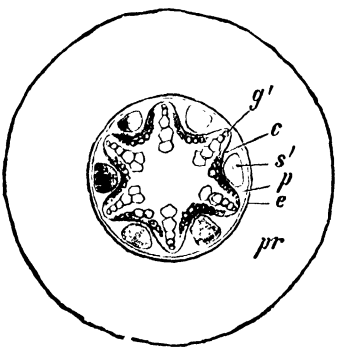


FIG. 51.—Cross section of a young root. *g'* xylem plate, *c* cambium, *s'* sieve-tubes, *p* pericycle, *e* endodermis, *pr* parenchyma of the root cortex. BL.

The walls of the cambium cells present a different appearance in autumn and winter, when growth and cell division cease, from that shown during the growing season [4] (Fig. 52 *a* and *b*). The winter cambium consists of comparatively few, in the spruce about eight,

[1] Details of the method and manner of cell formation in the cambium *see* Schoute, Über Zellteilungsvorgänge im Kambium. Verh. d. Koninkl. Acad. v. Wetenschappen te Amsterdam, II. Sect. Deel IX, No. 4. Amsterdam, 1902, Joh. Müller. (Written in German.) There further literature. C. Müller, Über die Balken in den Holzelementen der Koniferen. Ber. d. D. bot. Ges., 1890.

[2] Jost, Über einige Eigentümlichkeiten des Kambiums der Bäume. Bot. Ztg., 59, Jahrg., 1901. The difficulty presented by bordered pits to a comprehension of sliding growth appears reduced when it is observed that pits bordered on one side only are found, the second border being added only after half a year (*see* Strasburger, Leitungsbahnen, 1891, p. 12); pits may also be formed on walls which have united by sliding. Klinken. Über das gleitende Wachstum der Initialen im Kambium der Koniferen und den Markstrahlenverlauf in ihrer sekundären Rinde. Bibl. bot. LXXXIV, IX. Stuttgart, 1914, Schweitzerbart; Neef, Zeitschrift f. Bot. VI, 1914, p. 465 (gleitendes Wachstum).

[3] Neef, F., Ü. Umlagerung der Kambialzellen beim Dickenwachstum. Ztschr. f. Bot. 12, 1920.

[4] Knudson, Obser. on the inception, season and duration of cambium development in the American Larch (*Larix laricina*, Koch). Bull Torrey. bot. Club, 40, 1913.

layers of cells, and the cell walls running in the direction from the pith to the bark are conspicuous by reason of their thickness. Only small areas of the cell walls, the so-called pits, are not thickened. When growth in thickness begins, these walls, at least the majority of them, become (according to Kruger,[1] through stretching) as thin as the others.

5. Survey of the Tissues of the Mature Shoot.—We have recognised in the tissue of the young shoot as it appears after the formation of the cambium and a brief period of its activity, the following parts: pith, xylem, cambium, bast, outer cortex, epidermis. The nomenclature of these parts of the tissue shows little uniformity in Botany, it varies in fact with the standpoint of the authors, according as to whether they consider the tissue from the point of view of pure morphology and developmental history, or of physiology. Scientific anatomy has,

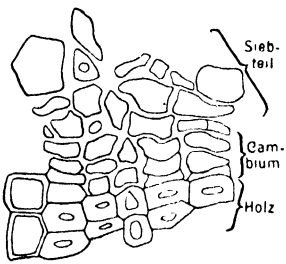


FIG. 52a.—Cambium of the Beech in winter. The radial walls of the cambium cells thickened; a few delicate tangential walls. Highly magnified (Zeiss-imm. 2, Apochr. Oc. 4. Tl. 150).

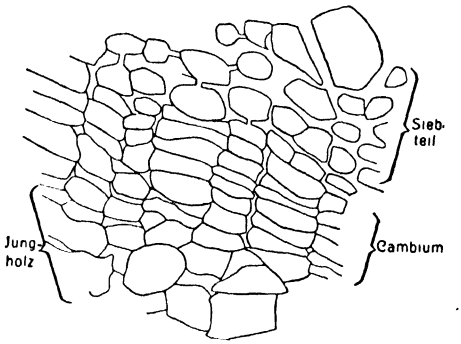


FIG. 52b.—Cambium of the Beech in summer. The radial walls mostly thin; numerous very delicate tangential walls. Magnified as Fig. 52a.

indeed, not altered the popular expression "pith." For the wood mass the terms **Xylem** and **Hadrome** are used, which it is true are not quite synonymous. Where the conducting tissues are separated in space from the mechanical tissues, as in the vascular bundles of the monocotyledons, Haberlandt's differentiation into "hadrome" (for conducting and storage tissues of the wood), "leptome" (for similar organs of the bast), and "stereome" (for the mechanical tissue) is suggested. They are however hardly applicable to the anatomy of the tree stem. The portion lying outside the cambium ring, which may be stripped off the growing tree in a continuous sheet, is called, in popular speech, simply "**Rind.**" To this comprehensive term we must adhere so as not to cause perplexity to the unlearned naturalist. In the rind we distinguish as "**Bast**" the generally long-fibred part which originated from the procambium and then from the cambium (inner bark, phloem) in which again "**Hard Bast**" and "**Soft Bast**" or, what is practically the same thing, the "**Stereome**" and "**Leptome**" of the rind are to be differentiated. From this is sharply distinguished the, mainly parenchymatous, "**Periderm**" which arose from the ground tissue. It is also called "**Primary Cortex**" on account of its origin; the elements of the primary

[1] Bot. Ztg., 1892. Wandverdickung der Kambiumzellen.

phloem are also sometimes included in it. We must, however, assign them to the bast as being in no way primary and being physiologically quite different. The term " bast " as commonly used, denotes only the well known strong, thick-walled, bast fibres. When we use it for the whole of the tissue derived from the cambium on the outer side, we must, to avoid misunderstanding as before said, distinguish in a given case, hard bast and soft bast. The whole is completely surrounded by the epidermis.

Secondary thickening brings about, as described above, an enlargement of the wood and bast and thereby of the circumference of the stem. The primary cortex enlarges by peripheral growth through the intercalation of new secondary elements which are in part also of a different kind. In an older shoot the parenchymatous outer cortex can therefore be no longer described as " primary." The greatest changes, however, occur in most trees through the subsequent formation of cork and bark which cause the death and ultimate shedding of the whole of the epidermis, the outer cortex and the older parts of the bast, so that the living rind of most trees in old age consists of bast alone.

6. Growth in Length of the Cambium Cells. Torsion of the Fibres.—The chief life processes of the cambium cells consist of the tangential and radial diameter growth described above and the divisions associated with it. An expansion of the cambium cells, however, in the direction of the long axis of the branches and stem is not completely absent and the transverse division of the cells may be associated with it. It is true that this longitudinal extension of the cambium cells cannot also lead to a growth in length of the whole part of the tree because every portion of the several years old twig consists for the most part of dead elements which would offer a strong resistance to an appreciable elongation. It has, however, sometimes a very striking result in the torsion of the fibres in trees, treated of by Alexander Braun [1] and Robert Hartig.[2] The phenomenon has been long familiar to the practical man as it influences in many cases the usefulness of the timber. It consists of the fibres of the wood running, not straight up and down, *i.e.* parallel to the axis, but in a sloping direction of varying steepness. Such timber splits badly or obliquely. The torsion of the fibres may be visible on the outside when the bark shows longitudinal fissures which then run spirally round the stem (juniper, lime, *Thuya, Arbor vitae*, elder) or when, as often at the root swelling, the stem forms prominent ridges which then likewise do not run straight upwards (hornbeam, Lombardy poplar). In other cases the torsion of the fibres is only recognisable after the removal of the bark, often only in the oblique course of splits and seasoning cracks. On looking at telegraph and fencing posts one may be convinced that slight torsion is almost the rule in pine and spruce. The greatest torsion was found by Braun in the pomegranate, where the direction of the fibres made an angle of 45 degrees with the vertical. Considerable torsion also occurs in the rowan, sweet and horse chestnuts and lilac (syringa), whilst in the Lombardy poplar and birch it

[1] Ber. über die Verh. der Berliner Akademie, 1854, 432. Bot. Ztg., 1869 and 1870.
[2] Forstlich-naturwiss. Zeitschr, IV, 1895, 313.

is generally very slight, with an angle of at the most 3–4 degrees. The direction of the torsion is generally ascending from right to left from the standpoint of the observer. But while the same direction of torsion often occurs in genera of the same family (the *Thuyas* and their varieties are, for example, all twisted to the right, the Abietineae, at least at first, all to the left, the Amentaceae to the right, except the sweet chestnut, which is twisted sometimes to the right, sometimes to the left, the willows to the left) it often changes, not only from tree to tree but even in the same stem with age. The latter is the case, for example, with the pine and spruce, while the torsion to the right in the horse chestnut and to the left in the Lombardy poplar remains constant. The distribution of fibre torsion is so widespread that Braun could detect it in 111 out of 167 species examined by him. It is connected, as already indicated, with the development of long-pointed wood fibres from the cells derived from the cambium. While such a growth of a cambium cell is taking place it pushes itself with its pointed ends between the rows of cells lying above and below it, forcing them to move aside. If this movement and insinuation occurs always in the same direction, if, for instance, the lower cell always grows past to the right of its upper neighbour and the displacement of the latter is always to the left, then all the fibres will be directed obliquely to one side; the wood shows torsional growth. If, on the other hand the cells push between sometimes to the right and sometimes to the left, no general oblique direction of the fibres can arise. The direction of the pushing past is determined by the direction of the dividing walls appearing in the cambium cells. According as these are directed upwards to the right or to the left, right or left torsion is set up. The pines examined by R. Hartig twisted, during the first ten years, all more or less to the left and the cross walls appearing in the cambium ascended to the left. In older, straight-fibred pines the direction of these cross walls varied with the part of the tree and with the annual ring.

Hartig's explanation of the torsion of fibres certainly goes back to a link in the chain of causation, but leaves unexplained the deeper cause of the one-sided growth of cells. So much appears certain, that torsion of the fibres occurs strongly and frequently in windy localities.[1] Whether or not torsion of the fibres increases the resistance of the stem to bending, as Neger assumes, is still to be proved. It may be that it is a question of a selective action of the wind favoring trees prone to torsional growth, for torsion of the fibres is congenital, as is shown by a small experiment in the Tharandt Nursery; descendants of a pine with pronounced torsion of the fibres, both seedlings and grafts, again showed torsional growth. Lang's explanation, whereby the mechanical effect of the wind striking on one side of the crown would bring about torsional growth [2] has also still to be proved.

7. The Seasonal Course of Cambium Activity in General.—The beginning of cambium activity is brought to the notice of the practical man as that period of the life of the tree during which the bark

[1] Neger, F., Flora. CIV, 1912, Note.

[2] Lang, Das Holz als Baustoff. Wiesbaden, 1915; *comp.* also Baumert, P., Knick-und Drehwuchs. Mitt. Dtsch. dendrol. Ges., 1925, p. 132.

may be easily stripped from the wood. The delicate walls of the newly formed cells are more easily torn apart than the thicker ones of the winter cambium. An exact determination of the limits of that activity naturally cannot be obtained by observations of this sort, they have, however, been made known by the labours of Theodor and Robert Hartig and other investigators. The annual commencement of diameter growth is governed, like the breaking of the buds, by the general life conditions, especially the temperature, but also depends on the particular nature of the species and individual.

Whilst in certain cases relationships of a nature not yet fully known, do exist between the development of the leaves and the beginning of cambium activity,[1] no such connection is recognisable in our forest trees under ordinary circumstances. In the spruce the bark can be stripped off the wood some time before the buds unfold. According to observations by Romell [2] diameter growth in the pine began, in some years, almost at the same time as, and in another year two or three weeks later than, height-growth. The duration of diameter growth varied very greatly—between 46 and 113 days as against 41–47 days for the duration of height-growth. The breadth of the annual ring does not depend on the duration of growth. Willows also, some time before the breaking of the buds, may be peeled, which indicates active growth of the cambium. In the oak and the ash, the appearance of the first vessels, the most certain proof that the cambium has begun to work, occurs long before any visible alteration in the buds ; in the elm their appearance coincides with the breaking of the buds or the commencement of flowering, and in the bird cherry it is first noticeable when the leaves have reached more than half their ultimate size. Walter [3] found that at Giessen, the formation of the annual ring in beech standards began on May 21, the first indication of the unfolding of the buds having appeared on April 24, the trees being in full foliage on April 28. Also in the oak and beech, which cease forming new leaves very early, diameter growth lasts longer than leaf formation, and in trees in which the growth of the leaves is prolonged the formation of wood may have already ceased at the base of the twig whilst new leaves are still unfolding at the apex. Strasburger[4] stated that in *Robinia pseudacacia* the cambium was in equally advanced activity all over the tree on April 30, whilst the leaves were just beginning to grow. Trees completely deprived of buds [5] nevertheless show diameter growth. Jost found a promotion of diameter growth going hand in hand with the formation of Lammas shoots, whilst, according to Späth,[6] the latter produce variations in wood structure just as little as do accessory shoots (*see* page 71). The formation of a false annual ring may be associated with the formation of proleptic shoots, *i.e.* such as would properly only unfold in the following year, especially when they appear late.

[1] Jost, Über die Beziehungen zwischen der Blattentwicklung und der Gefässbildung in der Pflanze. Bot. Ztg., 1893. Russow, Bot. Zentralbl., 1883, I.
[2] Romell, Mitt. d. forstl. Versuchsanst. Schwedens, H. 22.
[3] Forstlich-naturwiss. Zeitschr., 1898.
[4] Leitungsbahnen, p. 296.
[5] Hartig u. Wieler (quoted by Klebs, p. 84).
[6] Einwirkung des Johannistriebs auf die Bildung von Jahresringen. Mittiel. d. D. dendrolog. Ges., 1913.

In Central Germany, cambium activity usually begins in the second half of April or the first half of May. The kind of differences which however do occur, is brought out by the fact that Robert Hartig [1] found a spruce at the foot of a north slope still without growth on May 26, whilst some 100 paces away trees of the same species standing on sunny soil had already completed a quarter of the whole annual ring. In fifty-year-old beech pole forest, in consequence, Hartig thinks, of close stand and heavy leaf canopy, growth had not yet begun on May 25, whilst in a fifty-year oak, the first large vessels were already fully formed even by May 2 [2] In the pines of a close crop he found growth beginning later than in open stand, while cambium activity begins very late especially in slow growing, suppressed and overshaded trees. According to Mer [3] the first elements of a new annual ring appear 10–15 days later in underwood than in the held-over standards in consequence of the twigs of the former being warmed up later by the sun. Jaccard [4] distinguishes four periods of diameter growth in the conifers :

April-May : Beginning of vegetation, unfolding of the buds, development of the young shoots, comparatively small diameter growth.

June : Height of formation of spring wood.

July : Apparent height of formation of summer wood. Beginning of storage of reserve materials.

August-September : Formation of late wood, completion of the buds, storage of reserve materials.

The recognition of these periods is important for the determination of the influence of the weather on the formation of annual rings. Great variations occur in individual cases. Thus Wieler [5] found, in spite of similarity in external conditions (age, climate, soil), that the diameter growth of three spruces began on May 16, June 16, and July 7. A young tree of *Pinus strobus* exhibited diameter growth on April 24, two older ones only on May 26. *Pinus sylvestris* behaves similarly. *Abies pectinata* began between May 5 and 11, *Quercus rubra* already showed the formation of vessels on April 24, in *Quercus pedunculata* the new ring had breadths of 0.38 and 0.69 millimetres on May 6 and 10 and *Populus nigra* produced a ring 0.53 millimetres broad between May 13 and June 3. According to Wieler the beginning of wood formation in beeches varied from the end of April to the third week in May.

The cessation of diameter growth among Wieler's trees took place, in the spruces in the first half of September, in two old Weymouth pines (*Pinus strobus*) in August, in a younger one only in September.

[1] Hartig, Holz der deutschen Nadelwaldbäume. Berlin, 1885 ; the same and R. Weber, Holz der Rotbuche. Berlin, 1888 ; the same, Lehrbuch der Anatomie und Physiologie der Pflanzen, etc. Berlin, 1891. Mer, E., Réveil et extinction de l'activité cambiale dans les arbres. Comptes rend. de l'acad francaise, T. CXIV, 1892, 242, 501. Reuss, H., Beiträge zur Wachstumstätigkeit des Baumes nach praktischen Beobachtungsdaten des laufenden Stärkenzuwachsganges an der Sommerlinde. Forstl-naturwiss. Zeitschr. II, 1893, 145. *Comp.* also v. Mohl, H., Bot. Ztg., 1844, and Jost, Ber. d. D. bot. Ges., 1892 ; the same, Bot. Ztg., 1893.

[2] Untersuchungen über die Entstehung und die Eigenschaften des Eichenholzes. Forstl.-naturwiss. Zeitschr., III, 1884, p. 1.

[3] Sur les causes de variation de la densité des bois. Bull. de la soc. bot. de France, T., XXXIX, 1892.

[4] Accroissement en épaisseur de quelques conifères en 1911 et 1912. Journ. forest. suisse, 1913.

[5] Tharandter forstliches Jahrbuch, XLVIII, 1898, p. 39.

In *Pinus sylvestris* and *Quercus rubra* he found the ring not yet completed on September 8, but in the silver fir, completed on the same date. *Quercus pedunculata* finished diameter growth in August, *Populus nigra* between September 16 and 26, the beech in the latter half of August.

As is seen, the course and the end of cambium activity do not agree with the terminology which calls the first formed wood-elements "spring wood" and the later formed ones "autumn wood." The fact is that the first elements of the annual ring are usually more wide-lumened than the last; but the latter are already formed in the summer and in only a few cases is it known to what extent the tissue lying between these initial and final elements belongs to the spring or to the later season. The following examples may serve as proofs of the above.

According to R. Hartig, in beeches 50–150 years old, by the middle of June the increment was one-third, by the beginning of July a half, the end of July three-quarters, and by mid-August about completely formed. The whole activity of the cambium thus lasted 2½ months from about four weeks before the longest day till six weeks after it. A 50–69 year old oak, according to Hartig, had, on May 2, already formed the first vessels in all parts of the tree above ground. On June 21 on similar trees, growth was about half completed, but not to the same extent in the different parts of the tree. Expressed in fractions of the ring of the previous year the following breadths were found:

At 1.4 m.	0.45	At 7.9 m.	0.72
At 3.5 m.	0.45	At 12.3 m.	0.57
At 5.7 m.	0.45	At 14.5 m.	0.56 (3-4 yr. shoots.)

On August 19 growth in the lower part of the stem had ceased up to a height of 5.7 metres; at 7.9 metres and 10.1 metres the last portions were already laid down but still incomplete, *i.e.* thin walled and not lignified. In the 1–6 year old twigs growth was still going on. On September 5, however, growth had entirely ceased in all parts above ground. In this case growth lasted four months; two months before and two months after the longest day. For pine, spruce and larch Hartig places the period of growth activity in the leader in May, June and July; at breast height in June, July and August. In the silver fir he found three-quarters of the breadth of the ring completed on the average for the whole bole on June 29, and that cell division in the cambium at breast height in numerous older spruces near Berchtesgaden had nearly ended in mid-August. Mer places the time of formation of that part of the annual ring commonly called autumn wood, in conifers at about August 15 onwards, in the oak from as early as mid-June, and the time of change from spring to autumn wood in the silver fir at June 15. In general Mer found the autumn wood completed by about September 15, except for the large roots and the stem in which its formation was prolonged until towards the end of that month.

Variations are observed in regard to parts of one and the same tree according to age, locality and species. Cambium activity on the south side of trees is often hastened in consequence of the sunshine and the time of its cessation may also differ by over a week on different sides of the same tree.[1]

[1] Wieler, *loc. cit.*

In oaks, beeches, hornbeams, limes, poplars and silver firs, 25 years and less in age, in various localities and age classes, cambium activity begins, according to Mer, in the youngest shoots, and in older trees also simultaneously in the root swelling and the thicker parts often present at the base of branches. From the tips of the twigs it then proceeds to the older parts of the middle branches and lastly into the lower part of the stem. In this Mer's observations agree with the old account by Th. Hartig, quoted by Nördlinger in his Forstbotanik (1874, I, 155), according to which wood formation starts first in the tips of the twigs and slowly descends. The interval between the commencement of growth in the shoot tips and in the lower parts of the stem is there given as four weeks for the larch and sycamore and as imperceptible even at the beginning of May in oak and pine. Knudson [1] found the diameter increment in the American larch beginning in the middle twigs of the crown and then in the upper and lower ones. The diameter growth of the stem was ahead of that of the crown and apparently began in the middle of the stem or towards the base. During the resting period the cambium consisted of six layers of cells, in which, on April 19, the first alterations of form were visible and the formation of the bast had already begun in the middle of the stem. The formation of new wood began somewhat later and practically simultaneously on the whole stem, to attain its greatest activity, together with the formation of bast, after May 25. Wood growth was already nearly completed in one specimen on July 6. Brown [2] has investigated the beginning of cambium activity in *Pinus rigida* at Ithaca (U.S.A.) and found variations according to age and that, in older trees, cambium activity progressed from above downwards without there being, however, any variations in time between branch and stem.

Cambium activity ceases soonest, in a close stand, in the basal and middle regions of the weaker lower branches and only afterwards in their upper twigs. In strong branches of isolated trees it ceases first in the tip, then in the middle portion and last in the basal swelling. In stems it generally dies out from above downwards but, in more feebly growing individuals, it does so in the lower part first. It lasts longer in the lower parts of the root swelling, where the broadest annual rings are also found.

The thickening of the roots, according to Mer, begins 10–15 days later than that of the sub-aerial parts ; first in the oldest parts of the roots from which it extends to the youngest. According to Th. Hartig it begins in the half-inch lateral roots of the maple in mid-June, in the oak at the beginning of August—even later in the fibrous roots (Bot. Ztg., 1858). According to Mer diameter growth in the roots only goes on fourteen days later than in the stem and ceases first in the rootlets. The whole formation of wood in the roots would consequently last only about two months, as Hartig also supposed (for conifers only). On the other hand, according to Russow, the growth of wood in the root, in oak, ash, pine and larch begins only a few days after it starts in the stem. The formation of vessels commences, according to his investi-

[1] Bull. Torrey Bot. Club, 40, 1913, p. 271.
[2] Growth studies in Forest Trees. I. Bot. Gaz. LIV, 1912.

gations, in the bird cherry and the lime, almost simultaneously in both parts of the plant—in the lime even earlier in the root than in the stem. Gulbe [1] agrees with Mer that the activity of the cambium proceeds from the base of the stem into the thick roots and lastly into the thinner roots and allows a period of four to five weeks from the beginning of growth in the youngest shoots till it reaches the rootlets. According to his observations, extending over seventeen broad-leaved and coniferous species, the activity of the cambium of the roots only completely stops in the latter half of October, after having, in the course of two months ceased successively, first in the young shoots, then in the branches, the stem, and the thick roots and lastly the thin rootlets, that is—apart from the time of the year—in the same way as the awakening of cambium activity proceeded.

H. v. Mohl [1] found wood formation in the roots lasting over the whole winter and only ceasing after the commencement of diameter growth in the twigs in spring. This, however, according to other observations, must have been dependent on very specially favourable conditions.

Measurements of the course of growth by means of calipers or by self-recording measuring tapes have to reckon with the error due to the changes in girth of the stem with the amount of transpiration (dependent on atmospheric humidity) and the cohesion tension in the wood. Friedrich[2] utilised a steel tape which was passed round the stem and connected with an indicating mechanism. He obtained ascending curves rising in undulating lines whose variations within the general ascending direction ran quite parallel with the daily fluctuations in atmospheric humidity. A shower about mid-day may make itself evident in an increase in the circumference of the stem of the tree. The broad-leaved trees, which transpire rapidly only when in leaf, undergo these variations in diameter only so long as they bear foliage, while the evergreens do so also in winter on frost-free days. Frost produces in broad-leaved trees a rapid, in conifers a slower reduction in the tree's girth, which in long-continued frost may reach the dimensions of a complete annual ring.[2] Friedrich took the readings of his instruments at 7 a.m. as indicative of the actual growth of the trees. The permanent increase in size appears, as a rule, actually to proceed at night, at the time of maximum water content, maximum turgor of the cells and maximum swelling of their walls, and in the day-time only when the conditions in the interior of the stem are similar, by reason of evaporation from the leaves being checked. The daily rates of growth vary with the species in the same way as the annual rates, and are favorably affected by atmospheric humidity and by precipitations. The growth of the tree observed at 7 a.m. was the greater, the greater the humidity of the air during the preceding period of

[1] The literature which is not exhaustively given here is collected in Strasburger, "Über den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen." Jena, 1891, G. Fischer, p. 37. Additional full bibliography in Antevs, E., Die Jahresringe der Holzgewächse und die Bedeutung derselben als klimatischer Indikator. Eine Literaturzusammenstellung, Progr. rei botan., 5 Bd., 1917.

[2] Über den Einfluss der Witterung auf den Baumzuwachs. Mitteil. a. d. forstl. Versuchswesen Österreichs, hrsg. von der k. k. forstlichen Versuchsanstalt in Mariabrunn, Heft XXII; Zentralbl. f. d. ges. Forstwesen. Wien, 1897.

12–24 hours. In general the rate of growth increased rapidly to the end of May, then sank slightly until towards mid-June, reached a second maximum in mid-July, then decreased fairly rapidly and apparently ceased altogether by the middle of August. The maximum occurring in the middle of July was more easily recognised than that of the end of May. The forest trees observed were: spruce, *Pinus sylvestris*, and *P. Austriaca*, lime, beech and Norway maple. Caliper measurements [1] of whole woods gave for the ash at 1.3 metres height on the stem, an increment in stem area for (April) May 57.6 per cent., for June 32.9 per cent., for July to autumn 9.5 per cent. of the total year's growth. For beeches, according to the grade of thinning, the increment given for 1 ha. was: up to June 1 40.1–40.3 per cent., in June 39.6–41.7 per cent., for July to September 3.3–18.0 per cent. Early unfolding of the leaves did not go hand in hand with great diameter increment. Friedrich's investigations have since been repeated and confirmed by MacDougal.[2]

8. Causes of the Quiescence and Activity of the Cambium.—The question of the causes of the periodic alternation between quiescence and activity of the cambium was dealt with by Klebs [3] in connection with his work on the resting of beech buds. Klebs, with whom I agree, differing from many other investigators, is of opinion that the cambium of itself does not require a period of rest. In a severed cutting it becomes active at all times of the year, in order to participate in the formation of wound tissue. Just as in such cases it is stirred into activity by the wound stimulus, it would work in other cases, under favorable conditions, in winter as in summer. It is only necessary to set the stored reserve materials in movement, which Klebs, for example, succeeded in doing in the beech by electric lighting. His three-year-old experimental twigs which sprouted in the autumn had formed a distinct ring of growth in January. "Thus," Klebs conjectures, "the generally held view of the hereditary resting of the cambium is erroneous for the beech and most probably for all trees" (*see* above Chap. II, 4).

The causes which force the cambium into winter rest and awaken it from it, appear to be just as complicated as those which produce the resting of buds and their unfolding. Certain stimulants seem to be necessary to bring about cell division. Beyerinck speaks of "growth enzymes," Haberlandt [4] of "cell-division hormones." These stimulating substances are normally contained in the leptome; they can, however, be produced by wounding, from the decomposition products of damaged cells and then by "wound stimulation," set up cell division in the formation of wound cork, occluding callus, tyloses, local accelerations of growth,[5] regenerations, etc. Such local new formations take

[1] Heck, Jahreszeit und Zuwachs. Forstwissenschaftl. Zentralbl. 27 Jahrg., June, 1905. Berlin, Parey.

[2] MacDougal, D. T., Reversible Variations in Volume, Pressure and Movements of Sap in Trees. Carnegie Inst., Washington, 1925. Pub. 365.

[3] Klebs Abh. der Heidelberger Akad d Wiss., Mathem.-Naturw. Kl. Abh. 3. Heidelberg, 1914. C Winter.

[4] Haberlandt, Biol. Zentralbl. 42, p. 145, 1922.

[5] Münch, E., Versuche über Baumkrankheiten. Naturw. Zeitschr. f. Forst. u. Landwirtsch. 8. p. 425, 1910.

place as the result of wounding, also during the vegetative resting period. According to Haberlandt's [1] researches, no such new formations after injuries take place if the contents of the damaged cells are removed by washing and when injured pieces (of potato, kohl rabi, etc.) contain no leptome. Kastens [2] deduces from these and other observations, particularly from the results of ringing experiments, that the stimulating substances which set up cambium growth are formed in the leaves and transported to the cambium through the sieve tubes; an assumption which has still to be more fully proved and brought into harmony with opposing facts. For instance, cambium growth occurs, as we see, in spring, often even in the leafless stem as well as on felled stems, far from wounds and also on trees after defoliation by caterpillar attack, etc., even to such an extent as to exhaust the reserve materials.

[1] Haberlandt, Biol. Zentralbl. 42, p. 145, 1922.
[2] Kastens, Beirtr. z. Kenntnis d. Funktion d. Siebröhren. Diss. Hamburg, 1924.

CHAPTER IV

THE ELEMENTS OF THE XYLEM

1. Lignification.[1]—The mass of material to which the cambium gives rise on the side towards the pith, in twigs, stems and roots, together with the unimportant groups of wood elements already present in the young shoot before the cambium appears, form the **Xylem** or **Wood** of the tree; the part which, next to the vegetable foods, is the most important plant product of our climate. The greater bulk of it, the product of the cambium, is called the "**Secondary Wood,**" and those elements which were originated first, the "**Primary Wood,**" which, otherwise hardly visible to the naked eye, protrudes like tines or teeth from the massive cylinder of the secondary wood into the pith.

Common to all the elements of the xylem of the tree is the chemical constitution of their solid walls. A cell shed off by the cambium towards the pith hardly begins to differ from its sisters by its growth when there also begins a chemical change of its cellulose membrane, "**Lignification,**" which is finished in the same growing season but, nevertheless, sometimes remains incomplete, as often in the Weymouth pine and occasionally in the Scots pine, where, according to R. Hartig,[2] the membrane in question exhibits the reactions of cellulose to an advance age.

Lignified cell walls are generally more or less strongly thickened and stratified; as, for instance, in the true wood fibres (*see* below), the internal cavity of which not infrequently almost vanishes in comparison with the thick wall. In a cross section of a group of such fibres the middle lamella, common to cells in contact with each other laterally, is easily distinguished from the thickening layers proper to each fibre by reason of its great power of refracting light. The middle lamella is usually the most strongly lignified, whilst the thickening layers, at least in the parts next to the cell cavity, not infrequently exhibit the colour reactions of cellulose. Such inner wall-layers in the oak, beech, hazel, alder, birch and ash[3] may consist of hemi-celluloses which dissolve on boiling in 3 per cent. sulphuric acid, and in cases where the fibres remain alive for a long time, disappear again in the spring following their formation (Robinia). They then serve as reserve material like

[1] Van Wisselingh, C., Die Zellmembran, in Linsbauer's Handbuch der Pflanzenanatomie, Bd. III, 2. Berlin, 1924.

[2] Hartig, R., Flora, 1882.

[3] Schellenberg, Ber. Dtsch. Bot. Ges., Bd. XXIII, 1905.

starch does elsewhere. A very thin limiting layer, which is characterised by greater resistance to sulphuric acid, forms the boundary of the lignified cell walls towards the interior of the cell. Besides lignin the middle lamella contains pectin substances which have been thoroughly investigated, especially in fruits. They contain carbon, hydrogen and oxygen in different proportions to the carbohydrates and often, *e.g.* in the cherries, much mineral matter and very little or no nitrogen.[1] They gelatinise easily and are more rapidly decomposed by bacteria than the cellulose; a circumstance which is of importance in the extraction of hemp fibres. Warming with nitric acid and potassium chlorate brings about a rapid destruction of the middle lamellae. The cells and vessels of the wood may in this way be easily isolated for examination. (Maceration process.)

On lignification the cell walls lose the property shown by cellulose of colouring blue with iodine and sulphuric acid, become more or quite indigestible by animals (horses and cattle) [2] and also change their physical properties.[3] Lignified cell walls,[4] are less extensible and harder than cellulose cell membranes even when they are thinner. They do not, however, lose the power of still growing and dividing under certain circumstances.[5] Tubes with lignified walls, such as are distributed in the wood of trees (vessels), are therefore not easily bent in or crushed although they are exposed to great pressure by the surrounding tissues. According to technical experience, increasing content of lignifying matter (lignin—*see* below) makes the wood harder, more brittle and more resistant to bending, whilst reducing its resistance to tension—the latter increasing with the cellulose content of the wood. (Bauschinger, *loc. cit.*). No general connection exists between tensile and crushing strength and lignification, because unlignified fibres may be just as resistant to tensile strain as those whose walls are lignified. Ductility or pliability, *i.e.* the power of giving to forces exceeding the elastic limit, is also not, as was previously supposed,[6] generally increased by lignification. The power of swelling of the cell walls is also reduced by lignification. How great it is, in spite of this, appears from an investigation by F. Roth,[7] according to which in summer wood of *Pinus strobus* and *Pinus sylvestris* a shrinkage of the cell walls of 15–31 per cent., most often of 20-26 per cent., occurs on drying. Such a reduction of volume of individual cell walls on drying is, however, not to be confused with the shrinkage of the whole piece of wood in such circumstances. This

[1] For the chemistry of the pectins *see* Ehrlich, Pektinstoffe, Chemiker Zeitung, 1917, 41, p. 197. Rev. Ztschr. f. Bot., 1918.

[2] Haberlandt. Nährwert des Holzes und Verdaulichkeit der Zellwände des Holzes. Sitzungsber. der Kgl. preuss. Akad. d. Wiss., XIV und XLI, 1915.

[3] Kamerling. Zur Biologie und Physiologie der Zellmembran. Vorlaufige Mitteilung. Bot. Zentralbl., Bd. LXXI, 1897; Sonntag, Jahrb. f. wiss. Bot., Bd. XXXIX, 1903; Rothert in the article "Gewebe" in the Handwörterbuch der Naturwissenschaften IV, p. 1153. Jena. G. Fischer.

[4] Czapek, Biochemie der Pflanzen. I, 2. Aufl. Jena, 1913. G. Fischer. Here full bibliography. Technologically important: Handbuch der Forstwirtschaft, compiled by Lorey, 3 Aufl. hrsg. v. Wagner up to III, 1912.

[5] Schilling, E., Ein Beitrag z. Physiol. d. Verholzung u. d. Wundreizes. Jahrb. f. wiss. Bot. Bd. 62, 1923.

[6] Sonntag. Landwirtschaftl. Jahrbuch., Bd. 21, 1892, 839.

[7] Über das Verhalten der verholzten Zellwand während des Schwindens. Bot. Ztg., 1894, I, 218.

" shrinkage," important in the technical use if timbers, amounts only to about 0.1 per cent. in the direction of the fibres, 6–10 per cent. in the tangential direction and 3–5 per cent. in the direction of the radius. This deviation from the percentage of shrinking of the walls of the wood cells is explained by the piece of wood not consisting only of cell walls but also containing cellular spaces filled with air and other substances. On the drying of wood, breaks and fissures may occur in the thickening layers which do not, however, influence the passage of gases and heavy oils through the walls of the constituents of the wood, such as is involved in impregnation.[1] Lignification occurs during the life of the cells and is completed with the cessation of their growth, without its being possible to say that it is the cause of that cessation. If thickened, spirally winding ridges are deposited in the cell walls they are the first to be lignified, while the remaining portions of the walls continue to be of cellulose.[2]

With lignification the carbon content of the cell walls is increased and they show, chemically, a whole series of characteristic colorations, among which I select only a few. Van Wisselingh (1924) mentions over fifty of them. Aqueous or alcoholic cherry wood extract (phloroglucin) with hydrochloric acid colours lignified cell walls violet red ; aniline sulphate with a drop of sulphuric acid colours them yellow. A colour reaction given by Von Mäule [3] is also recommended : potassium permanganate colours the wood membranes yellow to brown ; decolorised by hydrochloric acid and washed, on the application of ammonia they assume a deep red colour. These colour reactions can be employed to recognise wood paper as such and to detect wood fibres in other papers.

By treatment with sodium acetate lye, sulphurous acid and other reagents, cellulose, such as is used in paper manufacture, is produced industrially from wood, and similarly, in preparations suitable for microscopic examination, the membranes of the wood elements may be altered by such lyes and acids so as to exhibit again the reactions of cellulose. Their microscopic structure remains unaltered.[4] It is therefore thought that lignification consists of an " incrustation " of the cellulose membranes with substances which can again be withdrawn from it by these means. The incrusting substances have received the name " **Lignin.**" To them is ascribed the increased carbon content exhibited by lignified membranes as compared with cellulose.

Pure cellulose contains : 44.4 per cent. carbon, 6.2 per cent. hydrogen, 43.4 per cent. oxygen. Lignified membranes contain : 48-50 per cent. carbon, 6 per cent. hydrogen and 43-45 per cent. oxygen. The lignin content is greater in hard and heavy woods than in softer ones ; but is rather variable in individual cases.[5] F. Schulze found in pine wood 41.99 per cent., hornbeam wood 51.59 per cent., alder wood

[1] Bailey, Forestry Quarterly, a Prof. Journal. Ithaca, 1913, Vol. XI.

[2] Nathansohn, Wachstum der trachealen Elemente. Jahrb. f. wiss. Bot. Bd. 32, 1898.

[3] Faber. Ber. Dtsch. Bot. Ges. Bd. XXII, 1904, p. 177. Mäule, Verhalten verholzter Membranen zu $KMnO_4$. Habilitations Schrift. Stuttgart, 1901.

[4] Braun, Technische Gewinnung von Zellulose aus Holz, etc. Inaug.-Diss. Hamburg, 1913.

[5] Cieslar, Mitteil, aus dem forstl. Versuchswesen Österreichs, hrsg. von der k. k. forstl. Versuchsanstalt in Mariabrunn b. Wien, Heft XXIII, 1897.

52.03 per cent., oak wood 54.12 per cent. lignin; it thus forms in hardwood timbers about half the mass of the cell walls.

Quickly grown timber of spruce and silver fir contains less lignin in the same volume than slow grown wood. Heartwood and old wood are richer in lignin than sapwood from the same height in the stem; late wood is richer in lignin than early wood, and in the spruce, silver fir and Austrian pine the lignin content at the base of the stem is greater than at two-thirds up. Cieslar concludes from this that wood rich in lignin is formed just where the mechanical requirements of the shaft of the tree are greatest. Good nutrition and favorable lighting, according to him, promote the production of lignin.

Since Payen's work on "Incrusting Substances" (1838-1839) there has been no lack of attempts to explain the chemical nature of lignin and the way in which it is combined with the cellulose. It is, at any rate, not a simple substance, but an aggregate of substances out of which carbohydrates and aromatic bodies have been separated.[1] Xylan, formerly called wood gum, a substance of the same percentage composition as cellulose (isomer) which dissolves in boiling water and is easily converted into wood sugar or xylose, may be extracted from wood by 5 per cent. soda solution. The following are the amounts of xylan in percentage of dry weight in various woods (Czapek, *loc. cit.* 687).

Spruce .	. 8·83– 9·20%	Oak .	. 19·69%
Beech .	. 33·12–23·18%	Birch .	. 26·21%

In the coniferous woods, which are poor in xylan, mannan appears to be present instead. Lignin acid, insoluble in water, has been obtained from woods rich in xylan (beech wood 12 per cent., oak wood 14 per cent.) The phloroglucin reaction has been traced by Czapek to a substance, called by him hadromal, belonging to the aromatic group of bodies, which is to be obtained to the extent of 1–2 per cent. from wood and is related to coniferyl alcohol. Grafe,[2] however, does not consider hadromal a simple substance and ascribes the reaction in question to vanillin. Coniferin, discovered by Th. Hartig in 1861 in the sap of the larch cambium, has not been identified with certainty in wood; though wood extracts smell of vanilla whose active principle, vanillin, can be obtained from coniferin. The sap of a spruce tree of medium size gave, according to Ebermayer [3] (1882), a quantity of vanillin whose value was 80 M. Formaldehyde is reported in the cambium sap of conifers.[4]

The combination of the incrusting substances with the cellulose will vary according to the part in question. Many substances may be combined with it chemically as esters, others, as Wislicenus suggests,[5] as colloids condensed by adsorption from the cambium sap on the cellulose skeleton of the wood elements. Wislicenus, by means of an adsorption analysis, found the cambium sap at the time of wood formation, very rich in such substances, which then greatly diminished towards the

[1] Grüss, J., Über die Ligninsubstanz. Ber. d. D. Bot. Ges., Bd. XLI, p. 48 und 53, 1923.
[2] Sitzungsbericht. d. Wiener Akad d. Wiss. math.-naturw. Kl., CXIII, Abt. 1, 1904, p. 253.
[3] Physiol. Chemie der Pflanzen, I. Berlin, 1882, Springer.
[4] Kleinstück, Berichte d. chem. Ges., XLV, 1912, p. 2902.
[5] Zeitschrift. f. Chemie u. Industrie der Kolloide, Bd. VI, 1910; Tharandter forstl. Jahrbuch, LX, 1909, p. 313.

end of the year's growth, in August of the normal climatic year 1912. In the climatically abnormal growing season of 1921 Wislicenus and Baerthel found the correlation of the colloid content of the " cambium sap " or " elaborated sap " and wood formation characteristically adjusted to the climatic irregularities of the year. After a very cold spring, active vegetation began in the middle of May in rainy weather, this was followed by almost winter cold in June, gradually warmer weather till mid-July and from then till mid-August hot dry weeks, cool summer weather beginning in August, which lasted until the end of September. The content of the cambium sap in colloid building-substances varied absolutely with these climatic conditions. The activity (colloid formation) of an alder standing in a watercourse, conspicuously reflected in the curve of its colloid content its independence of the drought.[1] The connection between colloid content of the " formative sap " and wood production may be considered proved. An important advantage to the plant of the chemical nature of lignin is to be found in the preservative properties of the aromatic compounds. They make the lignified cell walls which, as we have seen, form for the most part a dead framework, more resistant to decay-producing organisms, to which dead plant constituents succumb more easily than do living ones.

It is noteworthy that wood, especially coniferous wood, acts on photographic plates. The spring wood of the pine gives darker, the late wood, lighter rings in the print. Among broad-leaved tree woods: oak, beech and robinia act strongly, ash, elm, horse chestnut and plane only feebly. Resins are active, but gums, bark and pith are not.

2. The Living Constituents of the Xylem.—The most important seats of life in tree stems are the cambium and the rind. Living constituents extend from there only into the sap wood and their bulk is small compared with that of the dead membranes which form the conducting tissues and the fibres which serve for the rigidity of the whole structure. The living cells of the wood act as stores for that part of the food materials formed in the leaves which does not find immediate use in the growing points or in the cambium. These building materials are collected in the form of starch or fatty oil; substances whose presence, in addition to plasmolysis, is a means of determining if a wood cell is still living or not. It is known that starch, which is always easily identified by its blue coloration with aqueous solution of iodine, is formed only by the reactions of living cells and disappears from them on their death. The living wood cells form together a continuous network throughout the whole of the wood, of which one constituent—the **Wood Parenchyma**—forms lines running parallel to the boundaries of the annual rings (tangential) and is often only visible under the microscope or a strong lens, while the other—the radially directed **Medullary Rays**—is easily seen in many kinds of wood. In the wood of the silver firs the uniting of the medullary ray parenchyma by longitudinal parenchyma is very slight and in places absent altogether. The respiration of the living wood cells takes place by means of very narrow intercellular spaces which invariably adjoin them, and in young shoots communicate with

[1] Wislicenus, Zellulosechemie, VI, 51, 1925.

the outer air through the stomata of the epidermis and later on through the lenticels which will be described later.

Of our native trees the beech and the oak have the most conspicuous medullary rays (Fig. 53 *ms.*). They appear on the transverse section of the wood as glossy lines which run in the direction of the radius of the stem out of the xylem into the rind. The original rays which begin in the pith are called " primary " or " great " medullary rays. During the enlargement of the wood cylinder others are added which originate in the wood through cambium cells which have hitherto produced other elements, beginning to form medullary ray cells. These are called " secondary " or " small " medullary rays. Viewed as a whole the medullary rays are bands of varying width and thickness which, standing on edge, stretch from the pith to the rind. The thickness of the bands is best recognised in cross (transverse) sections, in which it is easy to determine under the microscope if a medullary ray is only one (simple ray) or several rows of cells thick. It is to be noted, however, that the band is often formed out of more rows of cells in the middle than in the upper and lower edges. Sections of the wood in the direction of the radius of the stem show the breadth of the often very lustrous bands (mirror or mirror grain) (Fig. 53 *ms.'*) and tangential sections show their thickness and breadth, also called " height," at the same time (Fig. 53 *ms.'''*). Here the cross sections of the medullary rays appear, according to their height and thickness, as extremely fine or thicker lines which run parallel to the length of the stem. They differ somewhat in colour from the wood fibres, being rather darker, and it is they that cause the colour of many woods to alter so much according to the direction in which it is viewed. The medullary rays are sometimes irregularly distributed over the surface of the tangential section, and sometimes arranged in rows above one another like the windows in a house of many stories. The true American mahogany is a good example of this.

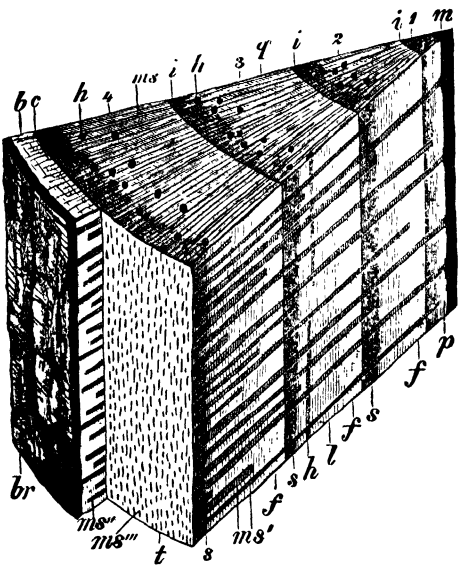


FIG. 53.—Segment from the stem of a Conifer. (*br*), bark, (*b*) inner rind, (*c*) cambium, (*f*) early wood, (*s*) late wood, (*h*) resin canal, (*i*) boundary of annual ring, (*ms'*) medullary ray in surface view, (*ms''*) the same in the rind, (*ms'''*) medullary ray seen in cross section, (*ms*) medullary ray seen from the edge, (*l*), (*t*), (*q*) indicate radial, tangential and traverse sections. 1–4 numbers of annual rings. BL.

Jaccard found the number of medullary rays in spruces and silver firs to be least in the lower third of the stem and to increase from there towards the top of the tree and towards its base where the maximum was reached at about 10–15 centimetres above the

ground.[1] Their number was smaller in the stem than in the same annual ring in the branches and very variable in different branches. Generally the rays were shorter and more numerous in the parts with the narrowest tracheids.

The medullary rays are chiefly formed of cells whose shape is best compared with that of a somewhat elongated brick with its long edges rounded or with a cylinder. In accordance with their function of transporting materials from the rind into the wood, these cells are so arranged that their long sides run in the direction of the rays, *i.e.* from the pith to the bark.

Associated with the parenchyma cells in many conifers are tracheids (*see* below) which, following the direction of the medullary rays, run along their upper and lower edges and are connected together by bordered pits. These transverse tracheids originate from cambium cells which produce normal tracheids and not through the transformation of young medullary ray parenchyma. In very high medullary rays, trains of tracheids appear also within the ray.[2] Among conifers,[3] medullary rays consisting only of living cells occur most frequently in silver firs, cupressaceae, and taxaceae, while rays consisting of tracheids alone or of tracheids and parenchyma cells are characteristic of the other abietaceae. The cross tracheids which accompany the medullary rays appear between the 1st and 30th years of life, according to the species. In many broad-leaved trees, the transverse tracheids on the edges of the medullary rays of conifers are replaced by peculiarly formed, high cells, which, like the trasverse tracheids, appear to carry on water transport in a radial direction.[4]

The walls of the medullary ray parenchyma cells are stout and in broad-leaved trees are, as a rule, provided with simple pits—at least where ray cell abuts on ray cell. Where ray cells abut on pitted vessels or tracheids (*see* below) pits are found bordered on one side. In many timbers, especially in the beech, it is observed that, on rupturing, the walls of the ray cells tear apart in spiral bands and Tuszon [5] sees in this, evidence of a spiral structure which tends to increase the rigidity of the individual cell and the whole xylem. Many medullary rays are more resistant to decay than the rest of the wood. When, for example, in rotten oak wood everything else has become a brown, crumbly mass, the medullary rays may still remain as solid bands. Kny [6] and others have determined the osmotic value of the medullary ray cells and have found it much higher during the period of winter rest than in the summer, smaller in young than in older wood, and different in differently constructed cells of rays of the willows, poplars and horse chestnuts. It is remarkable for its great magnitude in the winter, generally over 20 atmospheres and may even reach 40 atmospheres.

[1] Ber. Dtsch. Bot. Ges., XXIII, 1915.

[2] Thomson, Origin of the Ray Tracheids of Coniferae, Bot. Gaz., L, 1910.

[3] Ber. Dtsch. Bot. Ges., XXIV, 1906 (Burgerstein). Kny, Wandtafeln mit erläuterndem Text, VI, Berlin, 1884, Parey.

[4] Strasburger, Leitungsbahnen.

[5] Ber. Dtsch. Bot. Ges., XXI, 1903, p. 276.

[6] Landwirtschaftl. Jahrbücher, XXXVIII, 1909, p. 375. Here in the three genera investigated, three different medullary ray cell forms were distinguished : unmeshed palisades, merenchyma and meshed palisades.

The elongation of the medullary rays during diameter growth is, like the inception of secondary rays, effected by cambium cells inserted in their course where they pass from the wood into the bast.

The height of the medullary rays is greatest in the first annual ring and diminishes, at first rapidly and later more slowly until a lasting condition is reached. It again increases in old age. The cedar of Lebanon and the balsam fir have rays up to 40 rows of cells high, whilst in ginkgo they only reach 1 to 3 rows. For the rest, the number and height of the rays and also the size and number of their cells is not the same everywhere even in the same tree.[1]

The conifers (Fig. 54) possess medullary rays which are only one row of cells thick and, apart from the higher primary rays, are only 1–12 layers of cells high. Pines, spruces, larches and the Douglas fir have, in addition, broader rays, each of which contains in the middle a horizontal resin duct. In the silver fir, however, only the above simple rays are found. Among the broad-leaved trees the oak and beech, for example, have two kinds of rays: simple narrow ones, hardly or not at all visible to the naked eye and also broad, conspicuous rays built up of many sheets of cells. Single sheeted or single rowed rays are widely distributed. Two and three rowed rays are also not uncommon. They are termed in the literature multiseriate medullary rays. The still broader so-called compound medullary rays are less common. To them belong the broad rays of the beech (Figs. 56 and 68) and our oaks. The "false rays" of the alder, birch, hornbeam and hazel are also remarkable for their breadth. They are strips of the wood running from the pith to the rind which, in the alder and birch, besides the ordinary single rowed medullary rays, include other woody tissue without vessels, and in the hornbeam (Fig. 57) and hazel consist of medullary ray tissue which is penetrated by wood fibres and wood parenchyma.

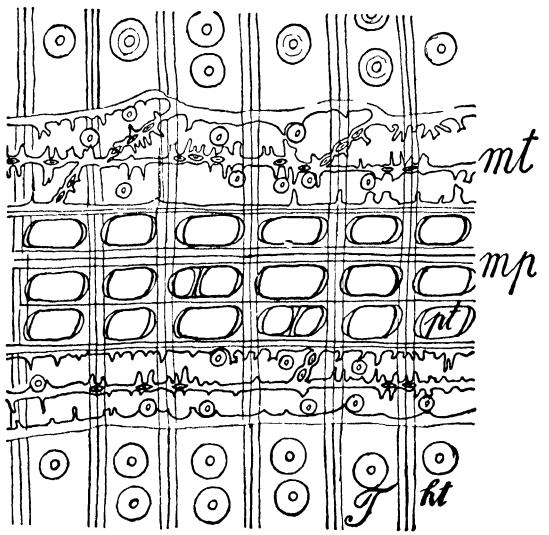


FIG. 54—Wood of *Pinus sylvestris*, radial longitudial section. (*T*) tracheids with (*ht*) bordered pits, (*mt*) medullary ray tracheids with small bordered pits, (*mp*) medullary ray parenchymae with large, rhomboidal, slightly bordered pits. (MCH.)

A penetration of fibres into the rays also occurs in the large medullary rays of the beech. In this case the height of the rays in the first years is, as Jost [2] showed, equal to the interval between two

[1] Esser, Abh. d. naturw. Ges. zu Halle, XVI, 1886; also Jaccard, *loc. cit.*
[2] Bot. Ztg., 1901.

leaves, *i.e.* to the length of an internode. In the succeeding years other wood elements appear in the medullary rays and divide them into several bands of lesser height whose original connection is still recognisable in their grouping. The changes in structure of medullary rays in the cupuliferae may be brought about [1] by a cambium cell, which previously produced medullary ray cells, beginning to form other wood constituents. It is also possible that from parts of the cambium which hitherto have produced wood fibres, such fibres may be thrust in between the neighbouring ray tissues by sliding growth. This may be the more common case. In the beech and oak, broad medullary rays may break up into narrower rays,[2] and, on the other hand, in *Fagus* the secondary rays may increase in height in their course towards the cambium by amalgamation with others. On the medullary rays of miocene oaks, etc., *compare* Eames.[3]

A few characteristics of medullary rays of particular plants: In the vine, plane, barberry and rose, all the medullary rays are very broad, in the ash, sweet chestnut, purging buckthorn, alder buckthorn (*Rhamnus frangula* L.) and the lilac, hardly visible.

Nördlinger, in his fine book on the technical characteristics of timber (Stuttgart, 1860), gives the following data, as regards which it is noted that the height and breadth of the mirror or medullary rays increases towards the rind.

Medullary rays over a hand high, *i.e.* over 160 millimetres high, often a foot high: wild clematis; about 160 millimetres, *i.e.* half a hand high: common alder; about 50 millimetres high: pedunculate oak; about 5 millimetres high: beech; about 2 millimetres high: plum (Fig. 58); about 1 millimetre high: Norway maple; about 0.5 millimetre high: ash; about 0.2 millimetre high, hardly visible: box. Medullary rays 1 millimetre broad are said to be very broad. They are found in the remarkable South African Casuarinas. In our trees the broader medullary rays of the oak measure 0.6 millimetre, those of the common maple 0.05 millimetre, the service tree 0.025 millimetre, and the willows [4] 0.015 millimetre.

The second form in which living elements of the wood occur is that of wood parenchyma. It consists of cells which often look like those of the medullary rays, but are arranged, not in the direction of the stem radius, but rather somewhat elongated in the longitudinal direction of the stem and sometimes have the form of short, wide, often transversely divided fibres (substitute fibres). The wood parenchmya cells are often arranged in bands, which extend from one medullary ray through the other wood to the neighbouring ray (metatracheal parenchyma [5]), they often surround the vessels (paratracheal parenchyma), spreading outwards somewhat from there in the direction of the ring boundaries. The bands of wood parenchyma appear to the naked eye, or under the

[1] Jost, Bot. Ztg., 1901.

[2] Zeijlstra, Recueil d. travaux bot. Néerlandais, Vol. V, 1908.

[3] Eames, On the Origin of the Herbaceous Type of the Angiosperms. Bailey Thompson, On the origin of the Multiseriate Ray of Dicotyledons, and the critique by P. Groom in Annals of Botany, XXV (1911), and XXVI (1912). Also Bot. Gaz., 1910.

[4] Burgerstein, Markstrahlen von *Populus* und *Salix*. Ber. d. Bot. Ges. XXIX, 1911.

[5] Gerry, Thyllen, Journ. of Agricult. Dep. of Agricult., Washington, 1914.

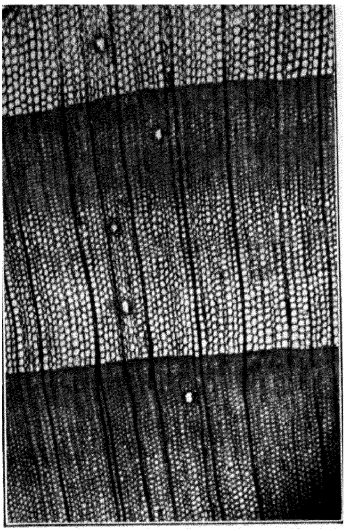


FIG. 55.—Transverse section of Larch wood (magnified 25 times). Medullary rays appear as dark lines. Bark side above, pith side below.

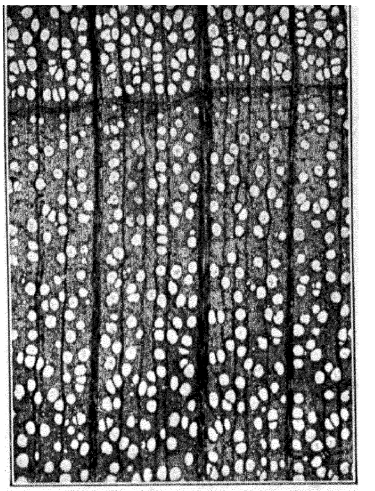


FIG. 56.—Transverse section of Beech wood (magnified 25 times), with broad and narrow medullary rays.

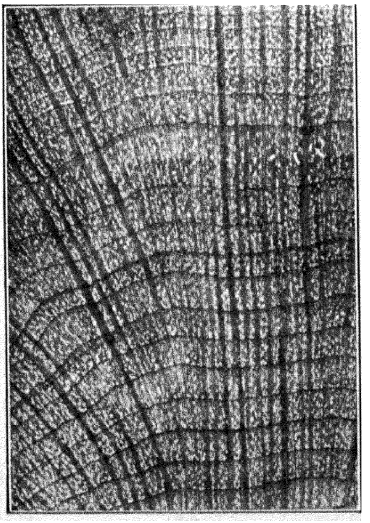


FIG. 57.—Transverse section of Hornbeam wood (magnified 2½ times). Shows the indistinct, false medullary rays.

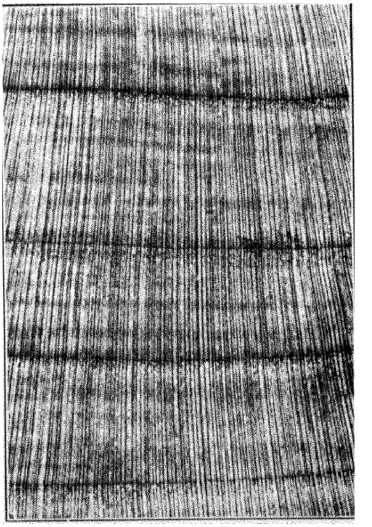


FIG. 58.—Transverse section of *Prunus* wood (magnified 2½ times). Very numerous narrow medullary rays.

[*To face p.* 114.

magnifying glass, as fine, light coloured lines, which sometimes extend fairly regularly parallel to the ring boundaries (*Ulmus effusa*), sometimes run in an undulating fashion (*Ulmus montana* and *campestris*), are often frequently interrupted, change their thickness during their course and often enclose the vessels. In the horse chestnut each individual ring finishes off with a layer of wood parenchyma (terminal parenchyma). The pines possess wood parenchyma only as a sheath for the resin ducts, whilst, in conifers in which there are no resin ducts, it forms single, longitudinally running rows of cells scattered between the other elements. In the larches it occurs on the outside of the summer wood, in the spruces very irregularly in the late wood of the margin of the ring.[1] The silver fir, whose wood is almost without resin ducts, has little or no wood parenchyma in the inner annual rings, but more in the outer rings; though there are great variations from specimen to specimen.

However complicated the distribution of the wood parenchyma in individual cases, the living elements of the wood are always connected with each other and they may anywhere adjoin water-conducting elements of the wood. In such places, on their otherwise thick walls, there are roundish thin areas (pits) which, especially on the boundaries between medullary ray cells and tracheids in the pine, occupy almost the whole of the wall in question (Fig. 54). This points to an exchange of materials between the dead and living constituents of the wood. The latter, in fact, draw water and nutrient salts from the former and, on the other hand, they give up to the vessels their own stored up materials, which are carried in the water stream to other places in the body of the plant.

It is practically impossible to determine the proportion of wood parenchyma to the rest of the wood, but where broad medullary rays occur or wood parenchyma is almost absent, it is possible, by measuring and counting the rays, to get an approximate idea of the quantity of living tissue present. Thus in conifers the medullary rays are calculated to occupy about 3.5 per cent. of the transverse section and about $\frac{1}{18}$th of the area of the tracheids.[2] Essner[3] found the following numbers of medullary rays on 1 square millimetre of the tangential section of an old pine stem:

In annual ring.	Medullary rays.
1	76
5	54
10	46
20	36
40—90	ca. 30
125	34
150	37

Other measurements were carried out by Robert Hartig[4] in the oak, and gave the important result that the proportion of broad medul-

[1] Bailey, Structure of the wood in *Pineae*. Bot. Gaz., Vol. XLVIII, Chicago, 1909.
[2] Dixon and Marshall, Sc. Proc. Roy. Soc., Dublin, XIV, N.S. No. 29, 1915.
[3] Quoted by Kny, Wandtafeln, etc.
[4] Untersuchungen über Entstehung und Eigenschaften des Eichenholzes. Forstl. naturwiss Zeitschr., III, 1894.

lary rays in the wood is the greater the more extensive the feeding activity of the leaves and consequently, presumably, the amount of the reserve materials to be stored up in the tree. The proportion of large medullary rays to the mass of the xylem is at a minimum in youth. It then increases and remains the same from a certain age onwards. Hartig found in a 400-year-old oak 4.1 per cent. of medullary ray tissue in the 40th year of life. From then onwards the medullary rays increased in number and breadth so that they finally formed 8 per cent. of the wood. In its 140th year the oak was isolated and grew as a standard in the young beech crop. The crown was fully lighted, the soil sheltered, and under these favorable conditions of nutrition the medullary rays thenceforward formed 10-12 per cent. of the wood. The proportion of medullary rays in the American red oak (*Quercus rubra*, L.[1]) was found by Eichhorn to be 18.5–20.9 per cent. in the broad annual rings of the first forty years. It remained almost the same at different ages in dominant stems. The formation of the individual medullary rays is, according to Hartig, also guided according to the activity of the crown. Trees which are favored in growth by the free development and illumination of the crown also tend markedly to produce broad medullary rays. It may at once be stated here that this has no influence on the quality of the timber. Hartig also investigated the variations in the proportion of medullary rays according to the portion of the stem and found a conspicuous diminution in the proportion of medullary rays from below upwards in the stem ; which he traced to a diminution in the number of the broad medullary rays. In 400 year old oaks, in the growth period from 360 to 400 years, there occurred four rays to 2 centimetres of the stem's circumference below and only 1.7 above. Bertog [2] has made similar investigations on very narrow medullary rays in the silver fir. Here the proportion of medullary rays was shown to be smaller than in the oak and smallest in the branch-free bole from a height of about 4 metres upwards. In a stem of the first class, for example, it amounted to 8 per cent. in the roots, to 6.1 per cent. in the 115th annual ring at 1.3 metres, to 4.0 per cent. at 10.9 metres and to 6.1 per cent. at 26.9 metres. The roots, the lowest part of the stem and the crown were thus richest in storage tissue. According to Mayr [3] these parts are also specially rich in resin. For the spruce Bertog calculated the proportion of medullary rays as 3–4 per cent. of the xylem. It is to be assumed, as Bertog declares, that the conifers require reserve materials and reserve storage tissue less, as they do not, like the broad-leaved trees, lose the whole of their leaves in the autumn, but retain needles over the winter, which are already producing new building materials when the young shoots are developing in the spring and are utilised during the winter as storage organs. This idea is supported by the fact [4] that the larch has a medullary ray percentage of 6.5 to 9.50, while the evergreen spruce has one of only 4 to 7.25, that it is greater in the deciduous bilberry (*Vac-*

[1] Unters. über das Holz der Roteiche. Forstl.-naturwiss. Zeitschrift., IV, 1895.

[2] Untersuchungen über Wuchs und Holz der Weisstanne und Fichte. Forstl.-naturwiss. Zeitschr., 1895, 177 ; also Jaccard, Ber. Dtsch. Bot. Ges., XXIII, 1915.

[3] Harz der Nadelhölzer, etc., 1894, p. 66.

[4] Simon, Ber. Dtsch. Bot. Ges., Bd. XX.

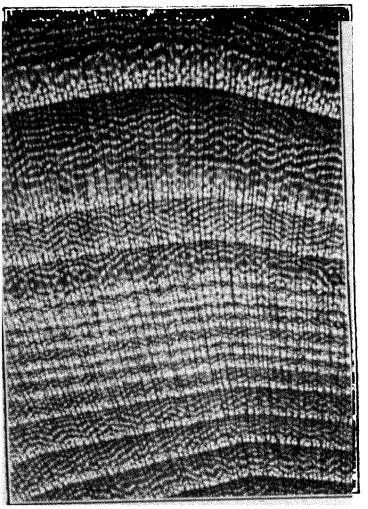


FIG. 59.—Transverse section of the wood of the English Elm (magnified 2½ times), with wavy lines of wood parenchyma. H.W.

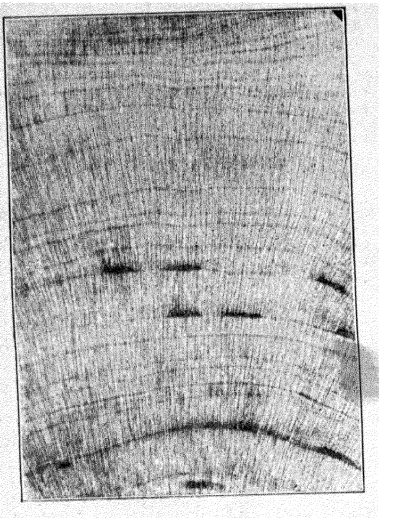


FIG. 60.—Transverse section of the wood of *Crataegus oxyacantha* with pith flecks (magnified 2½ times).

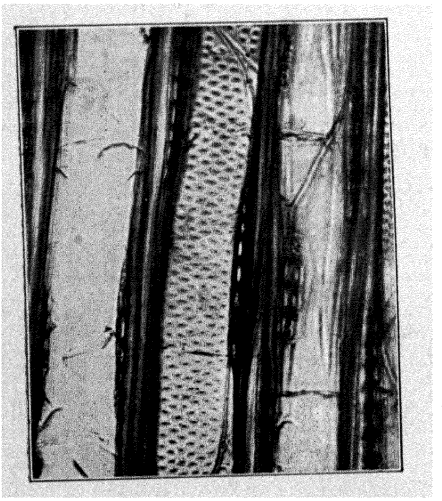


FIG. 64.—Part of longitudinal section of wood of a broad-leaved tree (Aspen). In the middle, wall of a vessel with bordered pits. (X 150.)



FIG. 65.—Longitudinal section of wood of a Conifer (Pine), showing the large bordered pits of the tracheids. (X 75.) From a photograph by Wigand, Zeitz., as also are 55–60, and 64.

[*To face p.* 117.

cinium myrtillus) than in the evergreen cowberry (*Vaccinium vitis idaea*), smaller in the evergreen mahonia (18 per cent.) than in the barberry (20 per cent.) and smaller in the evergreen oak than in deciduous species, with the exception of the cork oak (*Q. suber*), in which, perhaps, the great expenditure of material in the formation of cork makes more storage tissue necessary.

In connection with the normal living elements of the xylem the so-called "**Pith Flecks**" may be mentioned. They are longish flecks, generally on the outer side, though also not infrequently in the inside of an annual ring, their longest measurement following the periphery of the ring and often representing large segments of a circle, even 90 degrees or more [1] (Fig. 60). In the vertical direction they extend like paths in stretches several feet long, some ending blindly and some branched here and there in irregular directions and not infrequently crossing each other. In the alder, birch and species of *Sorbus* the pith flecks are characterised by a brown colour, in poplars and other trees they are colourless. They consist of parenchyma cells and are proliferations caused by the gnawing of the larvæ of gnats (*Agromyza carbonaria* Zett) in the cambium.[2]

3. The Dead Constituents of the Xylem.—Up to now, when we have been speaking of cells, the protoplast has always appeared to be the most important constituent. In the xylem of trees, however, we find only comparatively few protoplasts. The greater part of it consists of cell walls which fill their place in the life of the tree through the properties of their no longer living masses. These cell walls appear in three forms: as **Tracheae** or **Vessels**, as **Tracheids** or **Vessel-like Constituents** and as **Wood Fibres** (Figs. 61 to 63). The term tracheae is also used for both vessels and tracheids.[3] The vessels are the widest elements in the wood. They appear in transverse section as holes or pores, in longitudinal sections as grooves, in so far as they are recognisable by the naked eye at all, and arise from cells situated in a row one above another uniting to form tubes by the complete or partial (ladderlike) dissolution of their dividing walls, after their side walls have undergone very characteristic thickenings. With the dissolution of the dividing walls the protoplasmic bodies of the constituents of the tube fuse together,[4] later to contract to a thin film, the nucleus first swelling and then shrinking and becoming invisible. The vessels of the hazel and the tracheids of the larch still contain protoplasm for a long time after their formation—the larch for 2–3 years and in older rings remains of it are still found in the bordered pits. In ash wood, protoplasm has been found in the vessels of the last annual ring in winter. The tracheids (Fig. 61, *a–d*, 62, *B*) are narrower than the vessels and are fundamentally differentiated from them by each arising from a single cell and thus possessing a completely closed cell wall. Narrow vessels

[1] De Bary. Anatomie der Vegetationsorgane, etc., p. 507, Leipzie, 1877.

[2] Kienitz, Bot. Zentralbl., XIV, 1883; Nielsen, Zool. Jahrb. f. System, 23, 1906, p. 725; v. Tubeuf, Nat. Zeitschr. f. Forst.-u. Landw., 6, 1908.

[3] Meyer, J., Beih, z. Bot. Zentralbl., 33, I, 1917.

[4] Lange, Flora, hrsg. von Goebel. Marburg, 1891, Elwert; Lakon, Ber. Dtsch. Bot. Ges., 1911.

and wide tracheids are, however, not always easily distinguishable from one another. The tracheids in the first ring of the conifers were long taken for vessels. It is now known that vessels, often together with tracheids, occur only in the broad-leaved trees, but that our conifers contain tracheids only. Whatever the thickness of their walls, both elements have still comparatively wide internal cavities which, so long as they are capable of functioning, contain water in which many kinds of substances are dissolved, and in places, gas bubbles. Later, especially on the formation of heartwood, they are usually stopped up by tenacious, brownish substances. In the wood fibres (Figs. 61 *g*, 62 *A*), in contrast to the tracheids, the cell cavity almost entirely disappears in consequence of greater thickening of the walls. Elongated, narrow and pointed at both ends, they form solidly compacted, dense, wood masses, on the percentage proportion of which in the structure of the xylem the hardness and specific gravity of the wood for the most part depend.

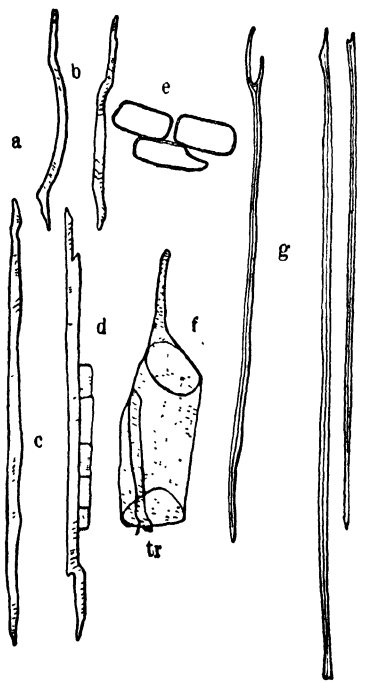


FIG. 61.—Constituents of the wood of broad-leaved trees. (*a*), (*b*), (*c*), tracheids; (*d*) tracheid with adherent wood parenchyma cells (magnified 60 times); (*e*) wood parenchyma cells (magnified 260 times); (*f*) part of a vessel with a tracheid attached (*tr*); (*g*) wood fibres (magnified 60 times). The bordered pits of the tracheids and the vessel have been rendered indistinct by the preparation (treatment with potassium chlorate and nitric acid). H.W.

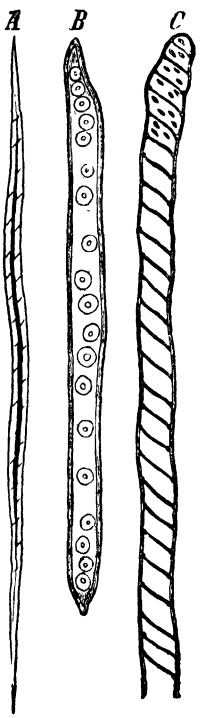


FIG. 62. — (*A*) Wood fibre; (*B*) tracheid; (*C*) upper part of a vessel-like tracheid with spiral thickening and pits. Magnified about 100 times.

The wall thickenings characteristic of vessels and tracheids (Fig. 63) appear in the first formed vessels of the shoot in the form of rings or spiral bands.

The spiral bands are connected to the cell wall by a narrow ridge which is the first to appear during their formation and is easily torn so that rupturing of the vessel by cutting it up often leads to the unrolling of the spiral bands.[1] Annular and spiral vessels also take part in the longitudinal growth of the shoot so that the windings of the spiral bands, which are lignified before the rest of the membrane, or the rings

[1] Körnicke, Sitzungsber. d. Niederrhein. Gesellsch. f. Natur- und Heilkunde, Bonn, 1899, p. 1.

are drawn apart.[1] In other cases of wall-thickening, oval or slitlike places in the vessels remain thin, producing the effect of a network of ridges deposited upon the wall (reticulated or scalariform vessels). All these strengthenings of the membrane place the vessels in a position to sustain the pressure of their surroundings without reducing too much the intercourse between their contents and those of neighbouring elements, as this finds its way through the gaps in the thickening material. The most remarkable of such gaps are the "**Bordered Pits**": often circular unthickened areas of the membrane over which, from the periphery of the circle, the thickening masses arch in a domelike manner, leaving only, over their centre, a round or slitlike opening (Fig. 64). As the bordered pits of two neighbouring elements usually coincide exactly with each other, the vaultings of the thickening on both sides enclose a lens-shaped cavity which is divided into two parts by the unthickened portion of the membrane and possesses on each side a narrow entrance, the opening on the summit of the dome.

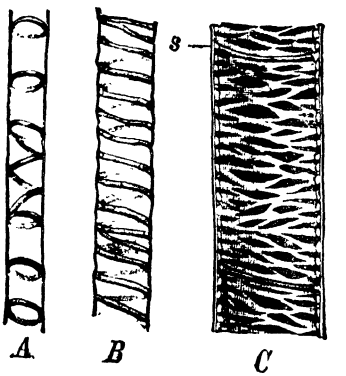


FIG. 63.—Portions of vessels. (*A*) annular vessel; (*B*) spiral vessel; (*C*) reticulate vessel cut longitudinally; (*s*) dividing wall broken through. 240 times magnified. B.L.

The bordered pits are especially conspicuous in coniferous wood (Fig. 65). They[2] are situated on the tracheid walls running in the direction of the radius of the stem and are particularly numerous towards the narrowing ends of the tracheids. They occur more sparsely in the narrow tracheids formed in the height of summer than in the wider ones of the spring wood. In the narrow tracheids they move round also on to the tangential walls which follow the direction of the circumference of the stem. In the main, however, it is only the last tangential tracheid walls, forming the boundary of the annual ring, that bear bordered pits which then facilitate water movement between the rings. In fresh sapwood the thin wall in the middle of the cavity of the pit, the **Closing Membrane** appears freely extended or only lightly stuck to the wall of the pit, in air-dry sapwood and in heartwood, however, it is so firmly pressed towards it that the "**Torus,**" a somewhat thicker and chemically somewhat differently constituted part in the middle of the closing membrane, firmly closes up the entrance to the pit. The border of the closing membrane has very fine perforations and radial ridges of thickening reticulately united.[3] Pits bordered on one side only are without the torus, the placing of which against the opening prevents the rupturing of the closing membrane even under high pressure. In the late wood tracheids of the heartwood, the medullary ray tracheids (*Pinus*) and in the pits on the tangential walls, the closing membranes are stretched

[1] Schellenberg, Jahrb. f. wiss. Bot., 29, 1896; Nathansohn, the same, 32, 1898 (sliding growth); Koernicke, M., Über d. Ausziehbarkeit d., spiraligen Verdickungsleisten d. Wasserleitungsbahnen. Ber. Dtsch. Bot. Ges., XLIII, p. 34, 1925.

[2] Strasburger, Leitungsbahnen, p. 31.

[3] Bailey, Forestry Quart., Ithaca, N.Y., 1913, Vol. XI (Pitmembrane and its permeability).

tightly in the middle of the pit cavity. These conditions are important in the theory of the impregnation of timber.[1]

The thickening of the membrane of the wood fibres is also not unbroken; though the unthickened areas are mostly confined to narrow slits running obliquely upwards. It is worthy of note that in the cork elm, hazel, sweet chestnut, birch, alder and others, an unlignified layer, apparently as soft as jelly, occurs in the walls of the wood fibres. These wood layers give the cellulose reaction and contain quantities of hemicelluloses; carbohydrates which differ from cellulose by being easily hydrolysed and may serve as reserve materials. In willows a re-dissolving, and in *Vitis* and *Robinia*, at least a corrosion of such layers was observed in winter, naturally only in fibres with still living protoplasm.[2] If the fibres have already lost their protoplasm any possible hemicellulose layer is no longer dissolved.

In order to convey an idea of the manifold transitions which occur between the kinds of living and dead wood elements already described, the following table, compiled on Haberlandt's [3] model, is given, which at the same time states the functions of the different organs in the life of the tree:

Description of forms.	*Main function.*	*Secondary function.*
1. Dead wood fibres with slit-like pits.	Strengthening.	—
2. Dead wood fibres with small bordered pits.	Strengthening.	Water conducting.
3. Thick-walled prosenchyma fibres with large bordered pits, without spiral wall-thickenings.	No distinction between main and secondary functions; the elements are employed equally in strengthening and the conducting of water.	
4. Fibre-shaped tracheids with spiral wall-thickenings.		
5. Thick-walled tracheids and vessels.	Water conduction.	Strengthening
6. Thin-walled tracheids and vessels.	Water conduction.	—
7. Wood fibres with living protoplasts.	Strengthening.	Storage and transfer of reserve substances.
8. Thick-walled wood parenchyma cells.	Storage, transfer of reserve substances.	Strengthening.
9. Thin-walled wood parenchyma cells and thin-walled living fibres (substitute fibres).	Storage and transfer of reserve substances.	—

The dimension of the elements of the xylem vary with age and the different levels in the individual tree, but not so greatly that particular widths for the vessels are not characteristic of individual trees (Figs. 66 and 67).

In figures,[4] the width of the large vessels in the oak reach 2–3/10 millimetres, while those of the elm and ash do not reach 0.2 millimetre (elm 0.158 millimetre, ash 0.140 millimetre) and those of the birch, alder and lime are less than 1/10 millimetre (birch 0.085 millimetre, alder 0.075 millimetre, lime 0.060 millimetre).[5] A few examples of

[1] Troschel, E., Handbuch der Holzkonservierung. Berlin, 1916, Springer.

[2] Schellenberg, Ber. Dtsch. Bot. Ges., XXIII, 1905, p. 36. Further literature: Czapek, Biochemie der Pflanzen, 2 Aufl., 1913, p. 685.

[3] Haberlandt, Physiol. Pflanzenanatomie, 2 Aufl., 1895, pp. 504 and 505.

[4] Strasburger, Leitungsbahnen, 1891, and Adler, Untersuchungen über die Längenausdehnung der Gefässräume, etc. Inaug- Diss., Jena, 1892.

[5] Haberlandt, Physiologische Pflanzenanatomie, 2 Aufl., 1896, 281.

the length of vessels [1] are: pedunculate oak: vessels 2 metres long numerous, many 3.6 metres long; birthwort (*Aristolochia clematis*): numerous vessels 3 metres long, a few over 5 metres; *Robinia pseudacacia*: 0.69 to 1 metre long. On the average, however, the length of the vessels is less than the dimensions given and does not exceed 10 centimetres. The length of the tracheids and wood fibres is considerably less. The highest values observed are: 4.91 millimetres in conifers and only 1.51 in broad-leaved trees.[2] Still longer tracheids occur in the roots (*q.v.*). Their dimensions generally remain however considerably below these figures. A compilation of the lengths of vessels in many woods is given in a treatise by Czapek,[3] from which it also appears that the length of vessels increases with the age of the branch and is different in the stems and branches.

In the majority of broad-leaved trees[4] (*e.g.* willows, poplars, alders, walnut, lime, robina), vessels, tracheids, wood fibres and wood parenchyma, as well as living fibre cells are present, but the last are absent in the oak, sweet chestnut and hornbeam. Our three species of maple, as well as the black and red-berried elders (*Sambucus nigra* and *racemosa*) are without wood fibres but possess vessels, tracheids, wood parenchyma and living fibre cells. Ash and plane have vessels, wood fibres and the living cells mentioned but have no tracheids.

FIG. 66.

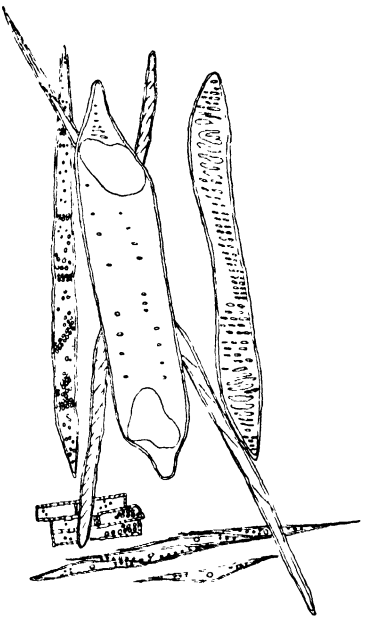


FIG. 67.



FIG. 66. Constituents of the wood (vessel components, tracheids, wood fibres, wood parenchyma) prepared from the wood of a 140 year-old beech. After R. Hartig.

FIG. 67.—Vessel components, tracheids and fibres from the wood of a 5–6 year-old Beech, under the same magnification as Fig. 66. After R. HARTIG.

The nature and arrangement of the wood elements in cross section provide, besides the medullary rays, a good additional guide for the identification of timbers (*see* Table, page 130).

4. Change from Sapwood to Heartwood.—In many stems and branches the outer portions of the wood differ conspicuously from the inner parts. Frequently the woody sheath formed by the younger annual rings only appears moister than the older wood; in other cases,

[1] See note 4, p. 120.

[2] Schulze, Grössenverhältnisse der Holzzellen bei Laub- und Nadelhölzern. Inaug.-Diss., Halle, 1882; Stone, Bot. Zentralbl., 99, 1905, p. 325.

[3] Czapek, Progr. rei botanicae, I, 2, p. 445, 1907.

[4] De Bary, Vergleichende Anatomie, 1877, p. 510

however, the latter has quite a different colour and a different specific gravity from the former and the colour often directly invests it with a special technical value. Thus the valuable dye stuffs of the dye woods are found only in the inner wood, where they permeate the cell walls and cell contents or sometimes only the latter.[1] A differently coloured central part of the wood is called "**Heartwood**" or "**Duramen,**" whilst internal groups of annual rings which are only dryer but are not markedly altered are called "**Ripewood.**" The colorations of the heartwood sometimes appear only after felling and under the influence of air and light, which also produce the dark browning of wooden houses in the Alps,[2] in so far as it is not artificially assisted, and, in conjunction with the iron-containing ash, the greying of spruce timber, *e.g.* in fences. Atmospheric oxygen also produces, without light, the marked orange coloration of the cut surfaces in felled alders.[3] The blue colour of stored pine timber is evoked by fungi of the genus *Ceratostomella*, and verdigris-like coloration of decaying wood by the fungus *Peziza aeroginosa*. The green of stored lime timber is a stain which originates from the tannin and iron contents of the wood in the presence of atmospheric oxygen (Schramm). Sapwood, ripewood and heartwood may occur side by side in the same stem. In the oak and the apple only sapwood and heartwood may be detected, in the beech and hawthorn only sapwood and ripewood. In the Norway maple and bladdernut no real distinction between heartwood and sapwood is perceptible to the naked eye. Trees of this sort are called **Sapwood trees.** In the following table from Nördlinger's treatise some trees are compared with respect to the characteristics mentioned.[1]

Sapwood trees.	**Heartwood trees.**	**Ripewood trees.**
Acer negundo.	*Acer tataricum.*	*Acer campestre.*
Acer platanoides.	*Acer dasycarpum.*	*Tilia parvifolia.*
Acer pseudoplatanus.	*Quercus sp.*	*Fagus silvatica* (in old stems "False Heartwood").
Aesculus hippocastanum	*Berberis vulgaris.*	
Aesulus rubicunda.	*Castanea vesca.*	
Alnus glutinosa.	*Cornus mas.*	*Sorbus torminalis.*
Alnus incana.	*Cornus sanguinea.*	*Crataegus oxyacantha.*
Betula alba.	*Juglans regia.*	*Picea excelsa.*
Carpinus betulus.	*Juniperus communis.*	*Abies pectinata.*
Corylus Avellana.	*Larix decidua.*	
Populus tremula.	*Pinus Austriaca.*	**Heartwood-Ripewood trees.**
Sambucus nigra.	*Pinus montana.*	*Rhamnus frangula.*
Sambucus racemosa.	*Pinus strobus.*	*Ulmus campestris.*
	Populus sp. except *tremula.*	*Evonymus europaeus.*
	Prunus sp.	*Fraxinus excelsior.*
	Robinia pseudacacia.	*Salix caprea.*
	Taxus baccata.	

[1] Will, A., Inaug.- Diss. Bern, 1899.
[2] Schramm, Jahresber. d. Vereinigung, f. angewandte Botanik, 1906.
[3] Neger, Naturw. Zeitschr. f. Forst.- u. Landwirtsch., IX, 1911, p. 96, Alder coloration. The same, 1910, p. 305, Greening of Lime wood.

The breadth of the different zones varies between wide limits in the trees mentioned. For example the sapwood of the pine may include 25 to as much as 80 annual rings, while in the silver poplar it only extends over about seven rings.

Generally, the boundary between sapwood and heartwood [1] does not follow a particular annual ring either at different heights in the tree or in the same cross section. Even in the same cross section it can vary by many years. The breadth of the sapwood does not always run parallel with the number of annual rings of which it consists. In the spruce and silver fir the cross sectional area of the sapwood falls off from below upwards, at first rapidly, then more slowly up the region of the crown, inside which it again diminishes very rapidly. The breadth of the sapwood diminishes from below up to about the middle of the clear bole. From there onwards it increases again in spite of the diminution of the number of rings included in the sapwood. It is noteworthy that the formation of sapwood conforms to the quantity of foliage. Strasburger [2] had already asserted this and Bertog [3] and Pilz [4] have obtained more exact data. Bertog determined the dimensions of spruce and silver fir crowns by weighing the green twigs. The following were thus obtained for spruce stems of three classes:

	Sapwood per cent. of stem volume. %	Green twigs per 1 cu. m. stem. kg.
I	52.3	74.0
II	52.0	57.9
III	46.8	48.6
IV	46.5	41.4

It is thus seen that the larger crowns of stems I and II correspond with a greater proportion of sapwood in the timber. In the sessile oaks of the Spessart, Robert Hartig [5] also found the absolute breadth of the sapwood was the greater, the larger the stem and consequently the crown of the tree, and that it markedly increased with age in the dominant stems. Especially in oak is the breadth of the sapwood of the greatest importance because it is quite worthless as timber. It readily decays and is destroyed by "wood worms" (*Anobium*). In silver firs, according to Bertog, the above relationship between the size of the crown and the breadth of the sapwood does not exist.

According to Kienitz the formation of heartwood is greatly accelerated by the admission of air to the interior of the stem, *e.g.* through large, dry stumps of branches which are often present near the upper end of the stem; hence the more rapid formation of heartwood in this region. The favorable effect of the admission of air was also observed by Coster in the teak tree, in which all injuries accelerated the formation of heartwood in the neighbourhood of the wound.

[1] Bibliography in: Bertog, Forstl.-naturwiss. Zeitschr., 1895, 108, and Münch, Naturwiss Zeitschr. f. Forst- u. Landw., VIII, 1910; Gurnik, Beitrag zur Kenntnis der Kernholzbildung. Bern, 1915.

[2] Leitungsbahnen, etc., 1891.

[3] Wuchs und Holz der Weisstanne und Fichte. Forst-Naturwi Zeitschr., 1895.

[4] Pilz, Allg. Forst- u. Jagdzeitg., 1907, p. 265.

[5] Untersuchungen über Wachstumsgang und Ertrag der Eichenbestände des Spessarts. Forstl-Naturw. Zeitschr., 1893, 249.

According to Harsch heartwood formation in the pine generally begins with the 30th to the 35th year and proceeds from above downwards in the stem. At any rate it does not begin at the bottom of the stem, but is on the average in the upper end of the stem (not of the tree), 29–33 years ahead as compared with the lower (butt) end. Differences of 0–60 years were observed. In 5 per cent. of the 151 stems examined the sapwood at the upper end was wider than at the butt, in 2 per cent. both rings of sapwood were of the same width, whilst in 93 per cent. of the stems the sapwood in the upper end was narrower than at the butt, and in fact the width of the sapwood at the upper end amounted to 0.4 to 0.6 of that at the butt end. The extent of heartwood formation increases with the quality of the locality and is thus a function of age and locality. The appearance of the heartwood at the butt end does not afford a correct representation of the heartwood formation of the stem generally. The upper parts of the stem contain fewer rings of heartwood than the lower. According to Pilz, in another locality the heartwood showed a smaller diameter and a conspicuously light colour, with high rates of growth. For this locality Pilz gives :

	Heartwood years.	Sapwood years.	Heartwood diameter.	Width of sapwood zone.
I Class	50	60	220	115
II Class	50	60	120	93
III Class	53	52	110	80

Strasburger has given an explanation of these concepts founded on the physiological condition of the sapwood and heartwood rather than on external appearances. He understands by heartwood the part of the xylem which no longer contains living elements, quite apart from its condition in other respects. As it is of importance, apart from the question of heartwood formation, how deep into the interior of tree stems life and respiration extend, I will quote a few of Strasburger's observations on these points. He was able to trace living medullary ray cells in a 60 year old spruce, from the outside inwards through 24 years, though in diminishing numbers from the twelfth annual ring. The breadth of this living zone amounted to 5.5–3.6 centimetres, whilst the remaining dead part of the wood had a radius of 12.5–6.3 centimetres. In a pine stem grown on very wet soil isolated living elements were found even into the 36th annual ring from the outside. In accordance with this, Märker states (Forstliche Blätter, 1885) that externally recognisable heartwood formation begins on the average about the 39th year. In extreme cases, however, he was able to count as many as 70 rings of sapwood. In an osier stem (*Salix viminalis*), 30 centimetres in diameter, according to Strasburger, starch and with it life, extended as far as the seventh annual ring from the outside ; in a 124 years old beech, in quantity as far as the 30th, in diminishing amounts, even to the 80th annual ring. The first to die are the parenchyma and fibre cells, and the last, the medullary ray cells. Wood fibres live as a rule eight weeks.[1]

[1] Fritzsche, Unters. über die Lebensdauer und das Absterben der Elemente des Holzkörpers. Inaug.-Diss., Leipzig, 1910.

In general, according to Strasburger, the sapwood, both as regards its thickness and the number of its annual rings, extends most deeply into the xylem in the roots. It is thicker in the stem than in the branches, though it often includes more annual rings in the latter. Finally, according to many observations, some of them cited by Strasburger, the percentage of heartwood in the pine is greatest in the crown section.

In the heartwood all the living cells have died. Instead of their content of plasma and reserve materials there are found drops or formless masses, generally of a brown colour, which are called "**Heart Substance.**" These substances also occur as pluglike stoppers in the vessels and also saturate the cell walls. Further, considerable quantities of calcium carbonate [1] are deposited, which in many broad-leaved trees (elm, wild service tree) occasionally completely fill the vessels. In the heartwood of extra-European trees silica and also calcium phosphate (teak wood) have been found. Under the term " heart substance " a variety of substances are included, among which tannins play a part. For example, the brown coloration of oak heartwood depends on the oxidation of the wood tannin whereby an insoluble brown substance finally arises. Besides this, dyes as well as gum-, bassorin- and resinlike substances are mentioned as constituents of heart substance. Assertions of the gummy nature of the heart substance are, according to Münch, very doubtful, and for false heartwood certainly erroneous. The rich tannin content of oak heartwood may be readily demonstrated in sections by means of iron solution, which colours the heartwood much more deeply than the sapwood. The heartwood of oak and also of sweet chestnut is, on this account, utilised technically for the extraction of tannin.

In the heartwood of most hardwoods there takes place in addition, the peculiar formation of new special cell elements, the **Complementary Cells** or **Tyloses.** These are sacklike outgrowths which grow into the vessels from the neighbouring wood parenchyma cells through the bordered pits or the thin places of annular or spiral vessels and finally completely stop them up. The sacks may be shut off by a dividing wall from the parenchyma cells to which they owe their origin, and may undergo thickening of their membranes and form connections with each other by pits. The complementary cells have mostly only a short period of life, after their formation is completed they soon die and then turn brown. Tyloses still arise in the living inner sapwood just before heartwood formation ends with brown coloration ; in the pumpkin the large vessels are stopped up within a few months of their formation. Many species,[2] like the cherries, birches and maples, never have tyloses, and conifers [3] only possess them as normal structures

[1] Molisch, Sitzber. d. Wiener Akad. Bd. LXXXIV, 1881.

[2] V. Alten, Beitr. z. vergl. Anatomie d. Wurzeln. Inaug.-Diss. Göttingen, 1908 ; the same : Kritische Bemerkungen und neue Ansichten über die Thyllen. Bot. Ztg., I, 1, Jahrg. LXVII, 1909. Gerry, Tyloses. Their occurence and pract. signif. in some American woods. Journ. of Agric. Research, I, p. 445, Dep. of Agric., Washington, 1914 ; Stauffer, Forstl.-Naturw. Zeitschr., 1892, I, p. 163.

[3] Über Thyllenbildung in den Tracheiden der Koniferenhölzer. Ber. Dtsch. Bot. Ges., X, 1892, p. 188.

in ageing resin ducts in the heartwood and, in certain circumstances, in the resin ducts of the needles.

An alteration of the wood exactly similar to this normal heartwood formation also occurs as a pathological phenomenon in the vicinity of wounds. In all species of plants where tylose formation is at all possible, if branches are cut off or other transverse wounds made and the wound is not immediately hermetically reclosed, tyloses appear which stop up the vessels. Fungi also regularly make their appearance in exposed wounds, and penetrate more or less deeply, often only quite superficially, according to the susceptibility of the plant and the kind of fungus that happens to be present. In so far as the wood dies in consequence of this or through other causes, brown colorations make their appearance,[1] either in tyloses or independent of them, which in every way correspond to the normal formation of heartwood. To such cases one applies the term **Wound Heartwood, Pathological Heartwood** or **False Heartwood,** and, as such heartwood affords a certain amount of protection against further injury, also **Protective Heartwood.** False heartwood is formed extensively also in ripewood species which normally form no heartwood, especially in the beech, but also in the birch and certain poplars. The false heartwood of the beech has been more thoroughly investigated.[2] From large branch wounds, which lay bare the inner, well aerated ripewood, the mycelia of certain wood fungi penetrate and spread into large tracts of the ripewood, at first killing and browning only the living cells. They soon come to a standstill, owing, according to Münch,[3] to the failure of oxygen after they have used up the air enclosed in the stem. In proportion as the oxygen is renewed and the stem grows in thickness, they advance by pushing their way outwards from time to time. As far as the fungoid infection extends, the cell contents are browned and the vessels filled with tyloses. These structures are found most plentifully between dead wood unattacked by the fungus and living wood, in a marginal zone a few millimetres wide,[4] which in cross sections looks like a dark brown border to the heartwood, and when the fungus has spread outwards repeatedly, forms almost concentric, or sometimes irregular, cloudlike figures (Fig. 68). If there are radial cracks in the wood, the formation of false heartwood follows these so that star-shaped figures may be produced.[5] In certain circumstances the false heartwood may become decayed by reason of the fungal hyphae also attacking the woody substance.

Dark heartwood, normal and pathological, has, as a rule, a higher specific gravity than the sapwood of the same tree, apart from the fact

[1] v. Tubeuf, Über normale und pathogene Kernbildung der Holzpflanzen. Zeitschr. f. Forst.- u. Jagdwesen, 1889, p. 385; Gaunersdorfer, Beitr. zur Kenntnis der Eigensch. d. Kernholzes, Wiener Sitzber. d. Ak. d. Wiss., 85, Bd., 1882, 1. Abt., p. 9, 41; Praël, Vergl. Unters. v. Schutz- u. Kernholz d. Laubbäume. Diss. Berlin, 1888.

[2] Hartig-Weber, Das Holz der Rotbuche, Berlin, 1888, p. 31 ff. Herrmann, Kernbildung der Buche. Zeitschr. f. Forst.-u. Jagdwesen, 1902, p. 596. Tuzson, Anatom u. mykol. Unters. u. Zersetzung u. Konserv. Rotbuchenholzes. Berlin, 1905.

[3] Münch, E., Über krankh. Kernbildung, Naturw. Zeitschr. f. Forst.- u. Landwirtsch., Bd. 8, 1910, p. 533.

[4] Lindroth, Beitr. z. Kenntn. d. Zersetzungsersch. d. Birkenholzes. Naturw. Zeitschr., Forst.- u. Landwirtsch., 1904, p. 393.

[5] Havelik, K., Warum ist der falsche Kern der Buche nicht von Jahrringen begrenzt . . . ? Ber. d. D. Bot. Ges., Bd. 43, 1925, p. 128.

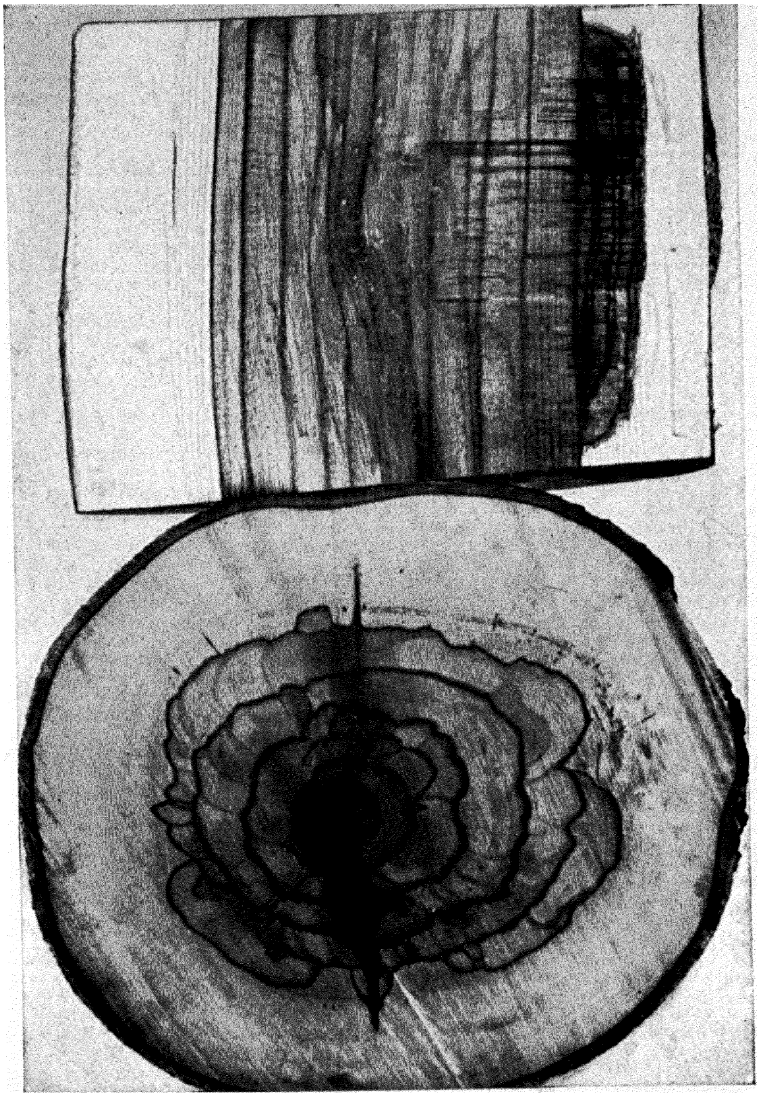


FIG. 68.—False heartwood of the Beech, longitudinal (medullary rays much browned) and transverse. Cloudlike appearance of the margins of the periodically advancing heartwood. Note also the favoring influence of the heart crack below. (Mch.)

[*To face p.* 126.

that the interior of the stem, even without the formation of heartwood, contains heavier wood. Coster [1] found, however, no such difference in weight in teak. The increase in weight cannot be ascribed to the addition of oxygen in the oxidation of the tannin alone; it must be assumed that substances flow to the wood which is in process of transformation into heartwood while it is still in a living condition and that oxidised substances, especially tannins, are also deposited even in the dead heartwood. This, according to Wislicenus, is brought about by adsorption, which is increased by progressive oxidation and condensation, because by this means colloid-soluble substances of high molecular weight, *e.g.* phlobaphene, are produced and coagulation and gel-membrane formation may take part. Wislicenus pointed out in 1909 the increase of the adsorption of wood-forming substances after their oxidation [2] and with Baerthel and Kräss [3] followed out thoroughly the process of heartwood formation. The results confirm the adsorption theory, also for the colloid chemical processes in wood formation which we mentioned in Chap. IV, 1. The dark boundary zone between the false heartwood and the living wood is particularly hard. Coloured heartwood, including also the pathological, is less prone to shrinkage and cracking and, above all, more durable than the sapwood because it is more resistant to decay-producing fungi, and wood destroying insects, furniture beetles, etc. Heartwood is, therefore, much more valuable than sapwood, which, in oak for example, is worthless as timber. If beeches with false heartwood are less highly valued than white hearted ones, it is only because such stems not infrequently contain decayed heartwood. Schwappach states that in the pine the specific gravity rises 6-8 per cent. as a result of heartwood formation. In this case the specific gravity of the wood membrane itself sinks in consequence of the access of resin, from 1.56–1.52. The wood membrane in the heartwood of the oak, however, becomes heavier by the deposit of heartwood substance; according to Hartig, up to a specific gravity of 1.625.

The brown heartwood substance in false heartwood arises, according to Münch (confirmed by Rudau,[4] Neger [5] and others) not, as was formerly thought, as a secretion of the living cells as a protection against fungi, but only after the death of the cells as an oxidation product of the cell contents, when these are no longer protected from access of oxygen by the living plasma membrane. In this process, according to Coster, enzymes participate, which can be rendered inactive by boiling but will withstand heating to 50–60 degrees. According to Coster, heartwood formation is possible without the access of oxygen, but his proof is inadequate. Münch observed also in fungal hyphae which produce false heartwood, exudations of heartwood substance which may play a part in the formation of false heartwood.

The causes of the formation of tyloses, in spite of many attempts,

[1] Coster, Ann. d. jardin botan. de Buitenzorg, Vol. XXXIV, 1, P. A.
[2] Wislicenus, H., Tharandter Forstl. Jahrbuch, Bd. 60, 1909.
[3] Unpublished Diploma works from the Tharandt Forest High School.
[4] Rudau, B., Beitr. z. Biologie d. Pfl., 13 Bd., 1917.
[5] Neger, F., Die Rötung des frischen Erlenholzes. Naturwiss. Zeitschr. f. Forst.- u. Landwirtsch, 1911, p. 96.

have not yet been fully explained for all cases. In false heartwood, according to Münch, they arise before the death and browning of the wood, in consequence of the access of air and also, without this, as the result of the stimulus of dilute fungal excretions or decomposition products which are carried in the sap stream and act as stimuli. They are structures quite comparable with wound-cork and other parenchymatous outgrowths which follow injuries, as is also remarked by Brieger.[1] That decomposition products of injured cells do operate as causes of such new formations is shown, especially by Haberlandt [2] who calls such bodies "**Wound Hormones.**" That access of air by itself sets up tylose formation, as Klein,[3] in ignorance of the pathological literature, declares, is contradicted by the fact that tylose formation in beech heartwood occurs only in the sphere of fungal infection and the products arising therefrom, but is absent in the uninfected but equally well aerated ripewood. The view of Lohse [4] and Schilling [5] that it is not wound hormones and external factors that set up tylose and similar new formations but "correlative tension differences," "balance disturbances," "cells becoming more independent," deserves to be further followed up.

It is less easy to see what causes bring about the appearance of heart substances and tyloses in normal heartwood. The ageing cells of the oldest sapwood layers which are ceasing to function, die off after having formed tyloses a short time beforehand. Their contents undergo changes, just as in false heartwood, in consequence of oxidation in the presence of sufficient moisture, into heartwood substance whose colour and composition depends also on outer circumstances. For example, *Cryptomeria japonica* contains in the heartwood a substance which turns dark with alkalis. The alkaline reaction and so also the dark colour of the heartwood depends on the locality and may proceed from wounds in which ammonia is produced by decomposition from organic substances.[6]

It is important from the point of view of impregnation practice that Gerry found tyloses plentifully developed in the white oaks (to which, in addition to American species, our two chief species, the pedunculate and sessile oaks belong) not, however, in the red oaks (*Quercus rubra*), though not without exception (*Quercus marylandica*). In this lies the reason that *Quercus rubra*, which is also cultivated in Germany, is rejected by coopers. The absence of tyloses makes the wood permeable. In *Robinia pseudacacia* the pitted vessels begin to fill themselves with tyloses even in the autumn of the year of their

[1] Brieger, F., Unters. ü. d. Wundreiz II, Die Ätiologie der Thyllen. Ber. d. Dtsch. Bot. Ges., Bd. 43, p. 343, 1925.

[2] Haberlandt, Wundhormone als Erreger von Zellteilungen. Beitr. z. Allgem. Bot., Bd. 2, p. 46, Berlin, 1923. Reiche, H., Über Auslösung von Zellteilungen durch Injektion von Gewebesäften. Zeitschr. f. Bot., Bd. 16, 1924.

[3] Klein, G., Zur Ätiologie der Thyllen. Zeitschr. f. Botanik, Bd. 15, p. 417, 1923.

[4] Lohse, Entwurf. einer Kritik d. Thyllenfrage . . . Bot. Archiv., Bd. V, p. 345. (With bibliography.)

[5] Schilling, E., Beiträge z. Physiol d. Verholzung u. d. Wundreizes. Jahrb. f. wiss. Bot., Bd. 62, 1923.

[6] Mitsunaga Fujioka and Kenzo Takahashi, The cause of the darkening of the heartwood of *Cryptomeria japonica*, Don., Journal of Forestry, Vol. XIX, No. 8, 1921.

formation and such were also found by Raatz in the oak even in the youngest vessels.

The part played by tyloses in the life of the tree is a many sided one. As protrusions of the living cells into the vessels from which they take nutrient substances and water they may serve as extracting organs [1] (hausteria), which increase the osmotically active surface of contact between the absorbing cell and the contents of the vessel, though the necessity of this is not apparent; secondly, considerable quantities of starch may be stored in the tyloses; thirdly, in the neighbourhood of wounds they take part in the closing up of the wound surface and this may be their most essential function in the heartwood. With this we come to the question of the place occupied by the formation of heartwood in the life of the tree in general.

The tree no longer utilises the inner parts of its wood for the transport and storage of materials. No further current outlay is made on their behalf, and in consequence death overtakes them. The dead wood remains of permanent value to the tree by reason of its mechanical function of supporting the crown, and is, therefore, so to speak, antiseptically impregnated once for all by the formation of heartwood substance from the contents of the dying cells. By this means and by the stoppage of the vessels, the further decomposition of the dead xylem itself is slowed down in an extraordinary degree, and the living outer parts of the wood are also protected from loss of water towards the interior of the tree and against the attacks of decay-producing organisms from thence. Obviously the protection given to the wood by the formation of heartwood cannot be absolute or permanent. Unlimited durability is given to no organic structure. Against the trivial rot fungi the heartwood is excellently protected—the tannin-rich heartwood of the oak and sweet chestnut resists even the dry rot fungus—not, however, against certain specially adapted heartwood parasites among the fungi; thus *Polyporus igniarius, sulphureus, dryophilus, Stereum rugosum*, etc., live by the preference in the heartwood of the oak, and *Trametes pini*, the dreaded Pine-stem rot fungus, attacks the pine exclusively in the heartwood. The sapwood of the living tree is protected against fungi by its high water and low air content [2] and is often spared when the heartwood is completely hollowed out by fungi. But when, after felling, the physiological difference between heartwood and sapwood disappears, sapwood decays much more rapidly than heartwood. Branches of conifers are very resistant to decay on account of their great density, richness in resin and brown masses (horny knots *q.v.*). Such properties may, to a large extent, form a substitute for heartwood formation in conifers. Spruce poles are the more durable the more slow grown and narrow ringed they are. Thus, in a fence erected in the Tharandt Forest Nursery in 1835, many of the very dense narrow-ringed poles are still utilisable to-day (1926).

5. The Pith.—The pith does not possess the importance in the life of the tree which is popularly ascribed to it. Rather does it become

[1] Haberlandt, Physiol. Pflanzenanatomie, 3 Aufl., p. 292. Leipzig, Engelmann.
[2] Münch, E., Naturwiss. Zeitschr. f. Forst.- u. Landwirtsch, 1909, 1910.

quite unimportant soon after the formation of the conducting tissues. It serves only temporarily for the storage of starch and also of tannin and crystals. In *Alnus*, *Betula*, *Carpinus*, *Quercus*, *Fagus*, *Castanea*, the pith is homogeneous, in *Fraxinus* and *Corylus*, heterogeneous, in that active and empty cells are intermingled.[1] The duration of life of the pith is one year in *Sambucus*, 42 years in the beech.[2] In *Juglans* the pith is torn apart even in the elongation of the shoot so that it appears chambered. Since the pith, as has been stated, is absent in the roots of most tres, the point at which it appears at the bottom forms a welcome basis for determining the boundary between the stem and root in estimating the age of old trees. The transformation of the radial vascular bundle of the root into the tubular bundle of the stem is carried out in the hypocotyl section by means of certain complicated windings of the bast and wood constituents.[3]

As characteristic of the alder may be mentioned the medullary cords of roundish section which consist of a group of unlignified elements, in part sieve tubelike, which is enclosed in a sheath of lignified constituents, partly prosenchymatous and partly resembling medullary ray cells.[4]

[1] Solereder, Systematische Anatomie der Dicotyledonen. Stuttgart, Enke.

[2] Massopüst, Über die Lebensdauer des Markes im Stamme, etc. Lotos, 1906. Ref. Bot. Zentralbl., CV, p. 535, 1907.

[3] Schoute, Die Stelärtheorie. Gröningen, 1902. Meyer, F. J., Beih. z. Bot. Zentralbl., XXIII, 1916, Abt. I.

[4] Künkele, Bot. Zentralbl., LXXII, 1897.

6. Summary of the Characteristics of Important Timbers.

I. Without vessels, ring-boundaries very sharp, medullary rays only recognisable by the naked eye on radial section: Conifers.

1. Without resin-ducts:
   (*a*) White, without heartwood. Rind grey, remaining smooth for a long time: *Abies pectinata.*
   (*b*) Reddish heartwood, fragrant. Rind dark reddish, fibrous: *Juniperus communis.*
2. With resin-ducts:
   A. Without heartwood:
      (*a*) Resin-ducts sparse, best recognised as "needle scratches" on radial sections. Rind reddish-brown with thin scales: *Picea excelsa.*
   B. With heartwood:
      (*a*) Heartwood red-brown, resin-ducts numerous. Late wood sharply bounded on both sides. Thick, longitudinally fissured bark with light brown cork (periderm) layers: *Pinus sylvestris.*
      (*b*) Heartwood redder. Resin-ducts sparse. Cork (periderm) layers carmine red: *Larix europaea.*
      (*c*) Whitish. Resin-ducts numerous. Very light. Rind thin and for a long time smooth: *Pinus strobus.*
      (*d*) Heartwood reddish, darkening, soft. Knots red to red-brown, very conspicuous: *Pinus cembra.*

II. With vessels, sometimes visible to the naked eye and sometimes only with the help of a lens, as pores on the transverse section and as scratches on longitudinal sections: Broad-leaved trees.

1. Ring-pored:
   A. Medullary rays unrecognisable:
      (*a*) Outside the zone of large pores, small pores and wood parenchyma are arranged in light-coloured branching strips in the direction of the stem radius: *Castanea vesca.*
      (*b*) Brown. With light brown lines running parallel to the ring boundary or deviating little from that direction, between the zones of large pores: *Ulmus.*
      (*c*) Light yellow. Between the zones of large pores, fine light dots which, in the late wood, often form tangential lines: *Fraxinus excelsior.*
      (*d*) Sapwood very narrow, light yellow; heartwood dark yellow-brown. Vessels plugged with shining tyloses. Rind thick-barked, longitudinally fissured, dark brown: *Robinia pseudacacia.*
   B. Some medullary rays very broad. Otherwise resembling *Castanea*: *Quercus.*

2. Pores scattered:

A. Vessels wide. Grey: *Juglans regia.*

B. Vessels small, mostly only visible with a lens:

(i) Some at least of the medullary rays broader than the width of the vessels.

(*a*) Medullary rays thick, conspicuous on all sections. Sapwood broad, light-coloured, heartwood grey-brown, rind grey-green, loosening itself in smooth scales: *Platanus.*

(*a*) Medullary rays fine but very distinct. Early wood zone particularly rich in pores and therefore spongy. Heartwood brownish: *Prunus.*

(*c*) Many medullary rays broad, very distinct, reddish in tangential section and often forming obliquely running groups: *Fagus.*

(*d*) Light-coloured; medullary rays sharp but very fine, lustrous in radial section: *Acer.*

(*e*) Broad medullary rays not sharply bounded.

(*aa*) White, hard, rings wavy: *Carpinus betulus.*

(*bb*) Reddish, soft, rind dark brown. Pith flecks present: *Alnus glutinosa.*

(*cc*) Ring-boundaries with small undulations. Rind thin, smooth. Wood white: *Corylus avellana.*

(ii) Medullary rays not broader than the diameter of the vessels, mostly invisible:

(*a*) Hard to medium hard:

(*aa*) Reddish tinted. Pith flecks not uncommon. Rind fairly hard, dark brown with white zones (hard bast): *Pyrus communis.*

(*bb*) Reddish. Transverse section as if dusted with flour: *Betula.*

(*b*) Soft:

(*aa*) Reddish, medullary rays occasionally distinct, 2 millimetres high (tangential section, lens). Rind watered: *Tilia.*

(*bb*) White to light brown (heartwood of *P. nigra*), needle scratched. Rhombic lenticels, rind two-layered: *Populus.*

(*cc*) Very light-coloured sapwood, pale reddish heart. Rind thick, longitudinally fissured, fibrous; *Salix alba.*

CHAPTER V

THE TREE RIND

In the summary on page 96 we applied the term "**Rind**" to all the tissues of the tree lying outside the cambium sheath and distinguished in it the parenchymatous, green "**Outer rind**" derived from the ground tissue, and for the most part prosenchymatous "**Inner rind,**" the "**Bast,**" produced by the cambium. To these is added in the course of further development the "**Cork,**" which either forms an outer covering or appears later also in the interior of the rind, when it converts the outer portion of the rind tissue into "**Bark.**"

1. The Bast.—In all trees the bast (inner bark, phloem) consists of **Sieve Tubes**—which in broad-leaved trees always appear in company with **Companion Cells**—**Bast** Parenchyma and **Cambiform Cells.** These elements together form the "soft bast." To the "hard bast" belong the **Bast Fibres** and other **Sclerenchymatous Cells.** The medullary rays also, in so far as they extend into the bast, are, in trees, to be assigned to the bast and not to the ground tissue, as they are formed only from cambium cells (*see* Chap. III, 4).

Like the tracheae or tracheids in the wood, so the **Sieve Tubes** are never absent from the bast of any plant. They form elongated tubes, mostly four-angled in cross section, which are made up of sieve tube components of the length of cambium cells, like the vessel components and tracheids of the wood. Like the components of the wood vessels, those of the sieve tubes are connected together openly in a longitudinal direction, though less completely so. While the transverse walls of the vessels are generally completely absorbed or very much broken through, the connection between the components of the sieve tubes is confined to the sieve pits in the transverse walls (sieve plates) and longitudinal walls (sieve fields). The analogy of structure of the sieve tubes in the bast and the tracheids in the wood is especially evident in coniferous wood (Fig. 73) where the sieve fields arise from similar rudiments in the cambium cells and in the same places in the radial walls, especially their pointed ends, as the bordered pits of the tracheids, and moreover, the shape, length and approximately also the width of sieve tubes and tracheids is the same. In the conifers, just as in the case of the tracheids, they do not form tubes but are connected together through sieve plates with unbroken walls as the

tracheids are by bordered pits. The width of the sieve tubes generally amounts to about 0.02–0.03 millimetre, rarely up to 0.08 millimetre in some twining plants. The most important physiological difference between sieve tubes and the corresponding conducting elements in the wood lies in the fact that the sieve tubes when they are transformed from the cambium cells retain their plasma lining and, for some time, their nucleus, whilst on the conversion of cambium cells into tracheae and tracheids the plasma disappears when they are completely formed. The impermeability of the plasma membrane to dissolved substances adapts the sieve tubes for osmotic forces and differences of pressure and for the transport of highly concentrated saps, without the dissolved contents being able to pass out in all directions If the plasma membrane were absent the contents would diffuse into the surroundings and miss their object. The plasma membrane clothes the sieve tube walls and also the pores of the membrane of the sieve plates and sieve fields on the inside, so that a cell cavity arises which, without being interrupted by plasma, extends from one component cell of the sieve tube to another. In tall trees gigantic cell cavities up to 100 metres long are created, reaching from the tips of the roots to the ends of the veins of the leaves, continuous and enclosed in a common plasma membrane, in which solutions and suspensions can move throughout the whole length without having to pass through a plasma wall. These long tubes thus act as a single cell. It is important to emphasise this anatomical condition as it solves in the simplest way the puzzle of the transportation of large quantities of organic, difficultly diffusable and non-diosmotic substances in the rind. The open connection is to be seen under the microscope in large-pored sieve tubes, especially in twining plants. In conifers, in which according to Strasburger, the sieve plates are closed by swollen parts of the primary cell wall, the solutions must pass through these walls, which, however, like all cellulose walls, are easily permeable for solutions and likewise form no obstacle to the movement of materials.

If the sieve tubes are opened by a cut across the stem reaching to the cambium, part of the sieve tube sap is squeezed out by turgor and flows out for a few seconds as a watery or cloudy fluid. (Fig. 71.) In microscopic preparations, therefore, the plasma membrane is generally found empty and the plasma separated from the wall in the form of a loose membrane.[1] By the exudation of the sap the turgor pressure is reduced and this diminution of pressure is transmitted, according to Münch,[2] often at a rate of 10–30 centimetres per second, to a distance of a metre downwards in certain trees, and after some time to as much as 5 metres—less far in an upward direction. A second cut then made within the distance results in no further outflow of sap. The open connection of the sieve tubes through the sieve plates is thus clearly proved. The outflow of sap from the wounds stops after a few seconds, as the sieve tubes immediately close up. Within a day they fill up again. The conifers and many broad-leaved trees, however, especially the pomaceae, *Cytisus* and others, allow no perceptible amount of sap to escape and

[1] Fischer, Ber. d. Dtsch. Bot. Ges., 18.

[2] According to a still unpublished work from which the other observations in this section, in so far as they differ from the previous editions, are taken.

poorly foliaged or overshaded trees also of other species, only a little, as the movement of sap in them is small.

The content of the cell cavity of the sieve tubes of the tree consists, according to Münch,[1] of a solution of sugar, especially cane sugar, with which are mixed small quantities of other substances of whose composition in trees little is known. At any rate protein substances or their dissociation products also occur. The plasma of the sieve tubes also contains leucoplasts with starch grains. In the air, colloids, mostly of a red-brown colour, are precipitated from the previously almost water-clear, colourless sap as the result of oxidation. These, however, only account for a small fraction of the total solid substance.

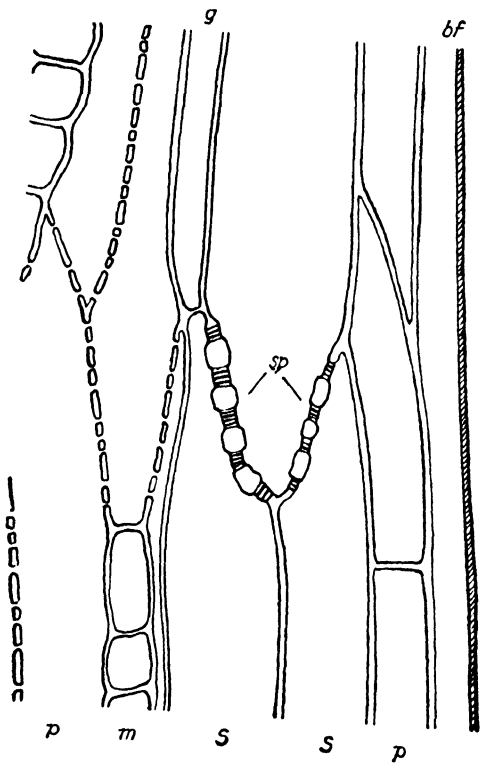


FIG. 69.—Bast tissue of *Tilia parvifolia*, tangential. (*p*) parenchyma; (*m*) medullary ray; (*SS*) sieve-tubes with sieve-plates (*sp*); (*g*) companion cells; (*bf*) bast fibre. Drawing by Beyreuther.

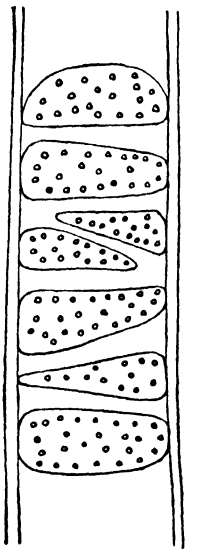


FIG. 70.—Sieve-plate from the radial section of the bast of *Tilia parvifolia*. Beyreuther (M.).

In microscopic preparations also, the remnants of the cell sap remaining in the sieve tubes are mostly found to be coagulated, so that the error arose that the sap consisted mainly of protein and that the sieve tubes served only for the transport of protein. According to Münch,[1] the following parts by weight of solid, dissolved or suspended substance to 100 parts of water are found in exuded sieve tube sap: *Quercus rubra*, 14.0–22.8 (average 18.4), *Acer pseudoplatanus*, 22.4, *Acer platanoides*, 27.8, *Carpinus betulus*, 16.8, *Castanea vesca*, 17.4, *Tilia* sp., 20.0, *Robinia pseudacacia*, 16.2–31.2 (average 25.0). In herbaceous plants the concentration is much smaller, being, according to Münch, in the hop, 7.1, in the

[1] See Note, 2, p. 134.

pumpkin, 8.2, according to Kraus,[1] in the sieve tubes of the pumpkin fruit on the average, 8.8. The osmotic value of the exuded sieve tube sap of the red oak corresponded with that of a sugar solution of a concentration somewhat higher than that found in the sieve tube sap for total dissolved substances.

The moving forward of the sap in the sieve tubes from the leaves to the places of consumption results from the wall pressure of the sieve tube walls, which, for its part, is produced by the osmotic pressure of the cell sap. The pressure already appears in the leaf parenchyma which forms sugar from the carbon dioxide of the air and draws to itself water from the tracheids in the leaf veins. By means of the bundle sheaths and other transition cells the sugar solution is then forced by turgor pressure into the sieve tubes in the way described on page 85. When sugar in the sieve tube sap is used up at the place of consumption, *i.e.* is converted into wood or starch, etc., the sap loses osmotic power in this region and water is forced out by the counter pressure of the sieve tubes and passes into the wood. In this way room for the inflow of sieve-tube sap and the necessary pressure gradient to overcome frictional resistance is provided. (*Compare* also Chap. XII, 2.) The movement of sap in the sieve tubes is thus a simple pressure filtration, the driving force being provided by the osmotic energy of the newly formed assimilates in the leaves and the fall in pressure by the destruction of osmotic force at the place of consumption.

The sieve-tubes only retain their activity for a short time. After one or a few years they lose their plasma, become filled with air and collapse. It is therefore only the youngest and innermost layer of the bast, generally only 0.1–0.2 millimetre thick and in living trees somewhat watery looking, which possesses active sieve tubes and is employed in the transmission of sap. Before they are cast off the sieve pores are stopped up by masses of a peculiar substance called " callus " which accumulates on the sieve plates and whose nature is still little understood. Plugs of callus also appear at the beginning of the winter to be again dissolved in the spring.

From the structure of the sieve tubes and other cells of the rind, their arrangement in the plant and other anatomical considerations, the nature of their contents and the results of ringing experiments (*see* Chap. XII, 2) as well as the whole behaviour of the outflow of sap from openings, it is established beyond doubt that the sieve tubes alone are engaged in the rapid transmission to a distance of the assimilates from the leaves, and that the other living cells conduct sap over only short distances, such as from the nearest sieve tubes to the place of consumption. The direction and arrangement of the pits and plasmodesms through which the transmission of sap goes on, indicate the great probability of the medullary rays being the paths from the bast to the cambium and through this to the storage parenchyma cells of the wood and the rind.

In accordance with their elongated form, the distribution of the sieve pores and the greater width of the latter in the transverse walls,

[1] Kraus, Über die Wasserverteilung in d. Pflanze. Sonderabdr. aus Abh. d. Natur-forsch. Ges. Halle, XVI, 1885.

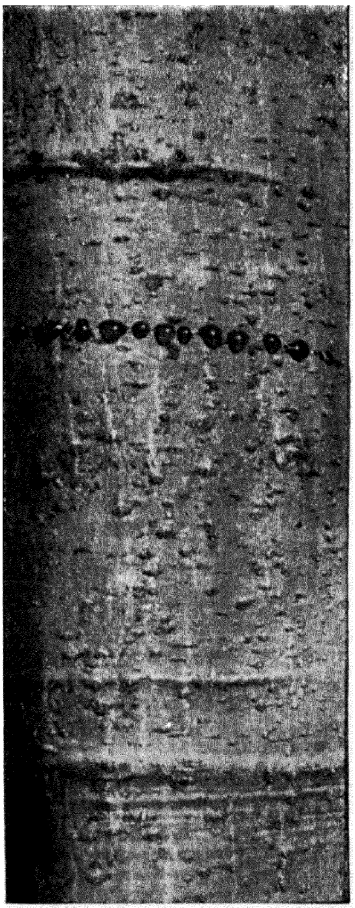


FIG. 71.—Drops of sieve-tube sap issuing from the rind of the Red Oak from an incision made between the two crosses. The drops have not yet reached their full size. After Münch.

the transport of materials in the sieve tubes proceeds mainly in the direction of the fibre and only slowly and slightly in the direction of the circumference of the stem. This is demonstrated with special clearness in experiments in which the rind is interrupted by horizontal cuts. In an experiment of this kind in which the severing of the rind was done in the way shown in Fig. 72, new, transverse sieve tubes were formed in the healing tissues which conducted the sap round the corners. This is the explanation of the uninterrupted transmission of sap round branch wounds and snags or along the spirally running constrictions made by twining plants which threaten to strangle the tree. (Fig. 137.)

The **Companion Cells,** as sister cells of the sieve tubes, run along near them. They are thin walled cells, rich in protoplasm, elongated and often transversely chambered, which may be arranged together in short chains of cells. Every companion cell is in contact with a sieve tube on one side and a medullary ray parenchyma cell on the other and is freely connected with both by pits and plasmodesms. The companion cells are absent in the gymnosperms. They are replaced there by border cells of the medullary rays, rich in protoplasm and proteins, which we will call "**Strasburger Cells,**" after their discoverer. They are connected, in the same way as companion cells, with sieve tubes and medullary ray parenchyma cells. The want of a continuity of great longitudinal extent excludes the companion cells and the Strasburger cells from the transport of substances over a distance; on the contrary it is concluded from their arrangement that they take in the contents of the sieve tubes, apparently also bringing them into a suitable form for consumption and give them up to the medullary ray parenchyma cells to forward to the place of consumption.

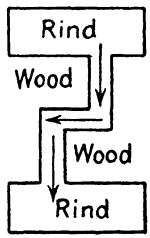


FIG. 72.—Rind-bridge after Teodoresco and Popesco.

The other parenchyma of the bast serves for the storage of organic reserve materials, and the accumulation of tannin, crystals and other substances still to be referred to in detail. The parenchyma cells arise by transverse division of cambium cells. If this division does not occur cambiform cells arise, which outwardly resemble cambium cells. They play a part especially in the finer leaf-veins.

All these living cells of the soft bast possess cellulose membranes. On the other hand the bast fibres (also called "**Libriform Fibres,**" on account of their resemblance to the sclerenchyma fibres of the wood) have thickened walls, generally also lignified, which often reduce the lumen to vanishing point, but frequently also leave room for living contents. In the larch they are much branched and penetrate between the cells of the adjacent tissue with their irregularly running ends. They are completely absent in many species of trees, such as the pine. Some also of the parenchyma cells of the bast convert themselves into hard bast. They lignify and thicken their walls and then no longer participate in the life processes of the tree.

These elements, best called hard cells or "**Stone Cells,**" may, by themselves or together with the bast fibres, form real woody walls in the young rind which, assisting the protecting cork, surround the

tender sieve tube-containing parts of the tissue with a second rampart. In transverse sections of the shoot such walls appear as rings which, as they are composed of bast fibres and stone cells, are termed mixed sclerenchyma rings. They are found for example in the young rind of birches, hazels, beeches and their varieties and in the horse chestnut. They sometimes persist for years, but they may be interrupted by rind parenchyma. The rings then present only isolated groups of stone cells and bundles of fibres which, however, may still be arranged in a circle in transverse section. Irregularly distributed groups of stone cells are found, for example, in the primary rind of the abietineae

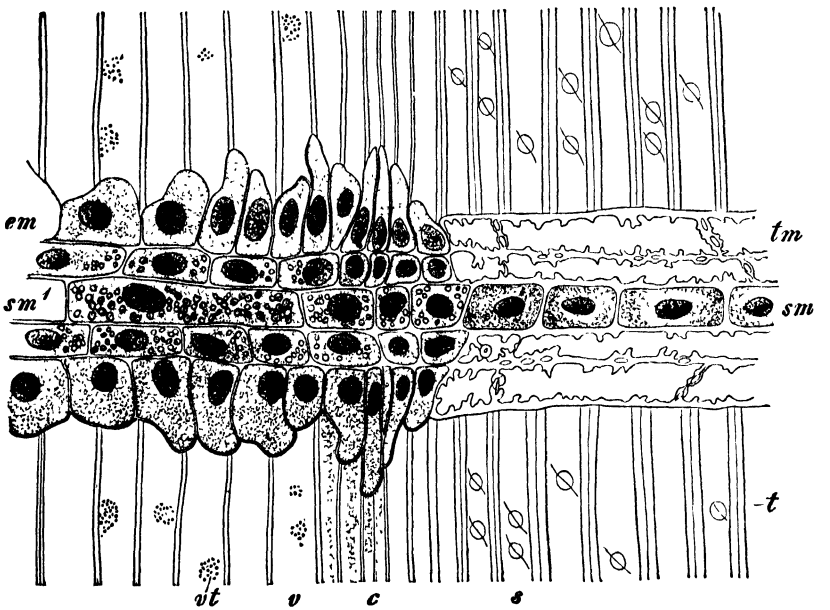


FIG. 73.—Radial longitudinal section of a Pine stem at the boundary between wood and rind (*s*) late wood; (*c*) cambium; (*v*) sieve-tubes; (*vt*) sieve-plates on the radial walls of the sieve-tubes; (*sm*) living medullary ray cells; (*tm*) tracheid border on the upper and lower margins of the medullary ray; (*em*) protein-containing medullary ray cells (Strasburger cells) in contact with sieve-tubes. Magnified 240 times. BL.

(except the pine, which, however, contains stone cells in the bark), the ash, lilac (*Syringa*) and the privet. Where, as in the juniper, elms and lime, stone cells are not present in the primary rind, they are replaced by bast fibres or a strong hypoderm. All these hard structures are generally regarded as "strengthening contrivances," or "stiffening contrivances," and the bast fibres and the closed walls of hard cells will, in fact, be useful in this direction in quite young and otherwise soft shoots. Scattered groups of hard cells cannot, however, serve as such; rather, in fact, are they somewhat injurious as regards the effects of pressure connected with growth in thickness as they must favour the crushing of the living cells.

In the silver fir, larch, birch, plane, etc., bast fibres are found in the secondary rind instead of the stone cells, whilst the juniper, *Taxus*, elm, elder, lime have bast fibres only there but no stone cells; in the

hazel, oaks, willows and species of maple, etc., however, both are present. The bast fibres of the lime are of practical interest. They have a length of from 0.875–1.255 millimetres with a maximum diameter of 0.031–0.25 millimetre and, according to measurements, carried out, it is true, on bast fibres of other plants, are equal in tensile strength to metals such as wrought iron and steel which they exceed in extensibility.

The behaviour of the medullary rays in the rind requires a few words. Among other changes, they undergo a considerable widening through the enlargement of their cells, in connection with the stretching of the rind caused by growth in diameter, as for example the medullary rays of the lime (*see* Fig. 75) and the hazel. Moreover it is worthy of note that the medullary ray mother cells in the cambium may also give rise to hard cells when the medullary rays pass between groups of hard cells. The best known examples of this are the hard ridges in beech rind projecting towards the wood, which consist of medullary ray constituents whose elements have become stone cells. Examples of trees whose medullary rays always remain thin-walled are the conifers, elms, willows and the spindle tree.

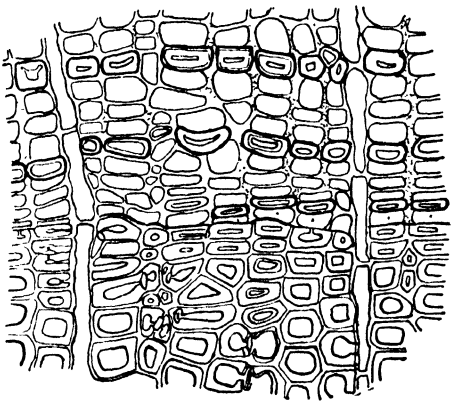


Fig. 74.—Part of the cross section of a Juniper shoot. Through the middle of the figure from right to left runs the boundary between the wood and the bast (cambium cells). At right angles to it, up and down in the figure, run two medullary rays. The black-bordered elements in the bast are the cross sections of the bast fibres which are arranged in tangential rows. After De Bary.

Hard bast and soft bast and also the separate elements of the soft bast, generally occur in concentric peripheral layers. The cambium of conifers, for example, generally forms alternate layers of sieve tubes and parenchyma cells.

Two layers of fibres are formed annually by the lime, more only in the first two years, 2–3 annually by the robinia; pines, larches, spruces and silver firs produce each year one row of parenchyma, two only in case of great increment. In the juniper (Fig. 74), there appear between each pair of layers of fibres, a layer of sieve tubes, a single layer of parenchyma and again a layer of sieve tubes, and this series is generally repeated twice a year. On the other hand it is said that, in the sycamore, only 20–25 layers of fibres appear in a hundred years. The fibres of the rind are generally united into bundles which form the valuable raw material known as "bast" for the manufacture of textiles and for binding. From them the term bast has been transferred to the whole portion of the rind which contains not them only but also the sieve tubes.

2. The Outer Rind and Epidermis.—The primary rind, originating in the ground tissue, at first consists of roundish parenchyma

cells. It is rich in chlorophyll, especially in the outer layers, giving the young twig a green appearance, but also still remains so after the formation of an external cork covering and has earned for the outer rind

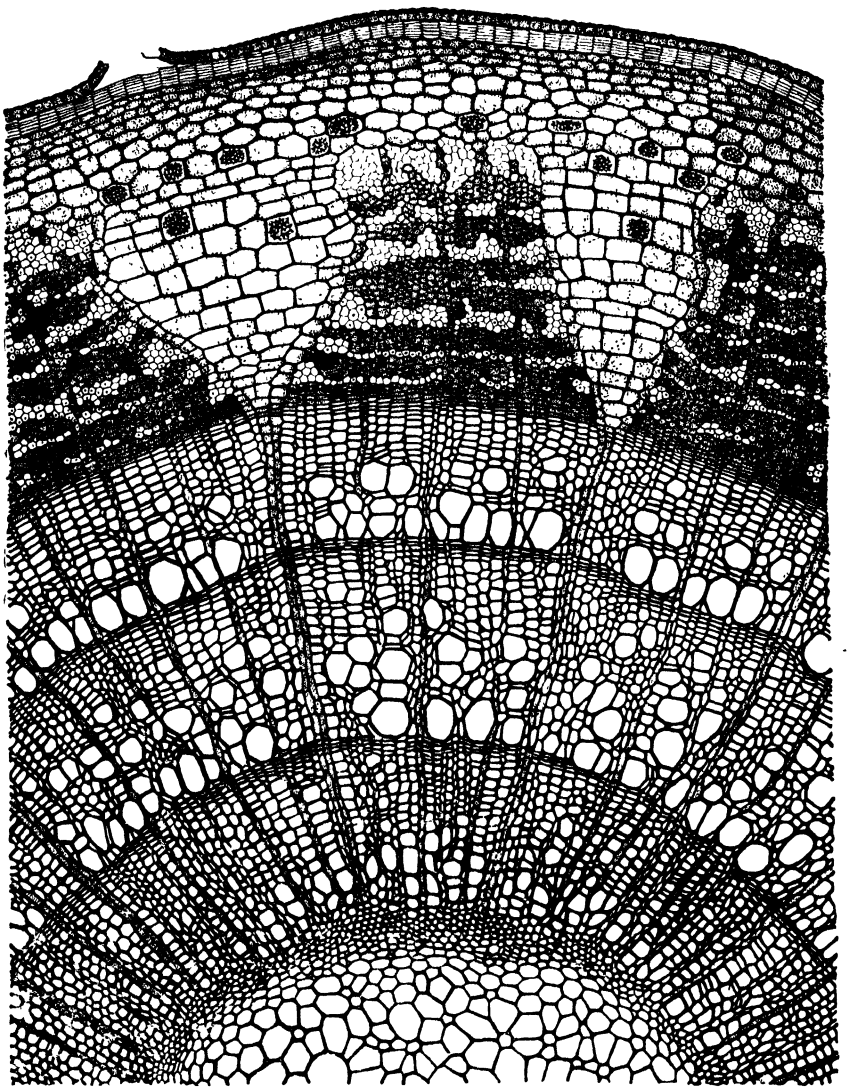


FIG. 75.—Traverse section of a three-year-old Lime twig. Under the ruptured epidermis are cork cells. Between the parts of the medullary rays in the rind, which are much broadened by the stretching resulting from growth in thickness—alternate layers of hard and soft bast. In the parenchyma of the primary rind and the broadened parts of the rays—druses of calcium oxalate. After Kny, Wandtafeln.

the name "**green rind.**" The green rind, especially when the shoot is young and so long as light is not excluded by cork, participates in the assimilation of carbon dioxide, which penetrates through the stomata and later through the lenticels of the epidermis. It may be assumed that with suitable access of light, it also assimilates the carbon dioxide

produced by the respiration of the wood and bast, which is passing to the outside through the lenticels, and so enables the plant to make use of it a second time. In plants with vestigial leaves, like the broom (*Sarothamnus scoparius*) and also the heather, assimilation by the rind of the shoots must contribute a very substantial amount to the total production of material; some species which broaden their shoots into leaf-like phylloclades and restrict the actual leaves to inconspicuous scales, like the Mediterranean Butcher's Broom (*Ruscus aculeatus*), hand over assimilation entirely to the rind of the shoots. In the roots the rind parenchyma is very fleshy and thin-walled and often filled with starch; chlorophyll, on the other hand, only appears in it if the root is laid bare and exposed to the light.

In many cases the outer layers of the rind, under the epidermis, are developed as **collenchyma** by the walls of the elongated cells being strongly thickened, especially at the angles of contact, by parts of the membrane which are highly refractive and swellable. The collenchyma, as the **Hypoderm,** supports the epidermis and gives the still young shoot a certain amount of rigidity. The thickenings on the walls appear to be dissolved again in spring.[1]

In proportion as the circumference of the shoot increases by secondary thickening the rind grows by cell division in the direction of the circumference. The cells thus newly formed may assume various forms and functions. Some of the new cells also contain chlorophyll, others become stone cells or contain tannin, crystals or secretions of various kinds. Mucilage cavities occur between the rind cells of the lime. The outer rind of conifers also regularly contains resin ducts (*q.v.*).

3. Cork and Bark.—The fresh green colour of the young twig is wont to give place to a brown one towards the end of the summer. This change is due to the replacement of the epidermis of the shoot by a **Periderm** which possesses, in an enhanced degree, the protective properties of the epidermis. The periderm arises through the cells of the green rind-parenchyma immediately adjacent to the epidermis, beginning to divide parallel to the surface of the twig (Fig. 76). The daughter cells cut off towards the outside become cork cells, those towards the inside of the twig (phelloderm) becoming cells of the green rind-parenchyma and between these two kinds of products, there remains a sheath of cells capable of division after the manner of the cambium. It is called the "**Cork Cambium**" (**Phellogen**).

Cork cells are above all conspicuous by having no living contents, but containing air, whose property of being a bad conductor of heat is here, as will be seen later, of importance for the tree. They have the form of flat, tabular, or also ordinary, parenchyma cells, and their walls for the most part remain without considerable thickenings. The physical properties of these walls are those of the cuticle, that fine skin, so impervious to water and water vapour, which covers the outer walls of the epidermal cells. Chemically they differ somewhat from the cuticle. According to Kügler, fatty acids (40 per cent.) and cellulose

[1] Schellenberg, Ber. d. Dtsch. Bot. Ges., 1905, XXIII, p. 36.

(22 per cent.), besides other substances take part in their composition.[1] The middle lamellae turn red with phloroglucin and hydrochloric acid like lignified cell walls, and their ash content is strikingly small (½ per cent.).

The cork cambium appears in the manner described, immediately under the epidermis in most woody plants (*Abies*, Betulaceae, Corylaceae, Cupiliferae, Ulmaceae, *Platanus*, *Populus*, *Sambucus*, *Viburnum opulus*, *Cornus mas*, *Aesculus*, etc.). In the pomaceae, Rosaceae, our *Viburnum* species and the willows, the epidermis itself becomes the cork cambium. It is formed further inside in *Pinus*, *Larix*, *Ribes*, *Robinia*, *Taxus*, *Lonicera*, *Philadelphus*, *Spiraea*, amongst others. Cork formation may begin very early. Thus in the beech even in the older parts of the current season's twigs a cork sheath is developed, under the epidermis which is dying as a result. Early formation of cork generally takes place completely round the young twig at about the same time, which is not the case when the epidermis lasts through several growing seasons, as in *Taxus*, the spindle tree, birthwort, ash-leaved maple (*Acer negundo*), etc. Cork formation begins in such cases in limited areas from which it spreads out in different directions, only after some years to completely cover the twig, as may be clearly seen especially in the spindle tree. In the beech, hornbeam, hazel and barberry the cork cambium, formed immediately under the epidermis, remains active for many years, as it keeps pace with the progressive increase of surface of the growing branches, by itself extending by growth and cell division. The epidermis, and afterwards ever the outermost cork cells, imperceptibly crumble off and are lost, whilst the cork cambium provides suitable substitutes. In this way arise the smooth, unfissured, comparatively thin, rinds of the trees mentioned. In the birch the cork attains a thickness of 3–4 millimetres and breaks up into 20–30 thin sheets easily separated from one another, each of which consists on the inside of a few layers of thick-walled, flat, cork cells, empty or filled with the brown remnants of their contents and, on the outside, of thin walled, less flattened, cork cells. The easily torn walls of the latter account for the rind of the birch splitting readily into sheets. The cells contain betulin or birch camphor, a combustible white substance without odour or taste which sweats out of birch rind on heating and can be extracted from it by boiling alcohol. It melts at 258 degrees, consists of carbon, hydrogen and oxygen, and is responsible for the white colour of birch rind. It is not unlikely that the comparative cleanness of birch rind as regards algae and lichens is also connected with its content of betulin ; but perhaps more effective is the fact that its outer layers are being constantly shed and that consequently many organisms that have settled on it are removed before they have become really properly established. Tannin (up to 3 per cent.) together with the betulin and the toughness of the rind account for the birch being less damaged by animals than other broad-leaved trees. The dark coloured, barky, transverse lines in the rind of the birch have to do with the lenticels, to be described below. In one of the German and British species of birch, generally characterised

[1] See Czapek, Biochemie, 2 Aufl., Bd. I, p. 695.

by pendant twigs, the formation of a stone-hard, almost black bark takes place at the bottom up to a height of a few metres, whilst in the other, the downy-barked birch (*B. pubescens*), the less pure-white, smooth, superficial cork is retained and continues to be slowly renewed from the inside. Cork layers have been counted [1] in the beech: in the first year 8, later 10–11; in the birch: in the first year 11, in the 10th year 20, in the 20th 88, in the 40th 150.

If the cork cambium is formed deeper in the rind its activity generally ceases early—sometimes even in the year of its appearance. It is then continually replaced by new secondary cork cambiums still further from the surface of the tree, which may extend into the bast and by means of the cork layers they produce, cut off the connection of the green rind tissue, resin galls, crystal cells, resin ducts and bast elements with the living portions of the rind. Such masses of material inevitably die and then, together with the cork layers which cut them off, form the "**Bark.**" If the inner cork cambiums encircle the shoot like a sheath, there results "**Ring Bark,**" such as is found in the vine, fly honeysuckle (*Lonicera xylosteum*) and the syringa (*Philadelphus coronarius* L.). The forms in which bark is produced in other cases are extremely manifold, among which longitudinally fissured barks as in the ash and Norway maple, sheet barks as in *Taxus* and the plane, and finally all sorts of different "**Scale Barks**" (field maple, sycamore, horse chestnut, spruce) may be distinguished. Long known, but always being reinvestigated as a striking phenomenon, is the bark [2] which many beech stems produce. It appears to characterise a variety whose timber is declared by woodcutters to be specially hard. For the rest, there exist all intermediate stages between the ordinary smooth-rinded form and the true hard "**Stone Beeches.**"

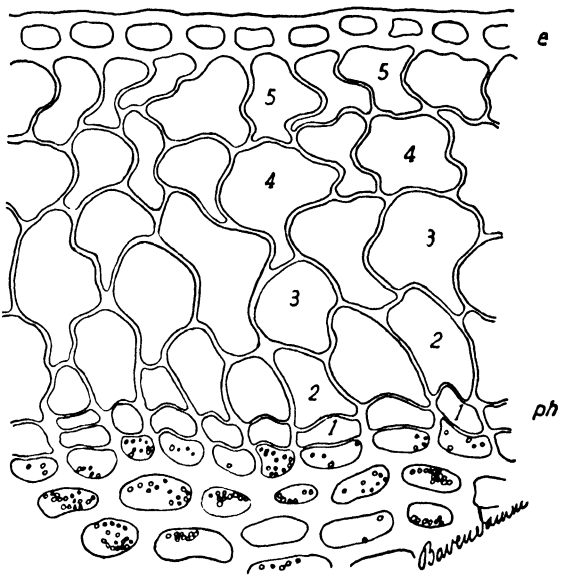


FIG. 76.—Cork formation in a young Ash twig. (*ph*) phellogen; (*e*) epidermis. The phellogen cell 1 has cut off in succession the cells 5–2. Drawn by Dr. Bavendamm (M.).

The hardness of a bark or a cork depends upon the form of the cell walls of its elements. If the latter are thin-walled and with large lumina, sponge cork is formed such as is met with in the English elm,

[1] Gerber, Inaug.-Diss. Halle a. S., 1883.

[2] Areolate-rinded Beech: Thomas, Die Verbreitung der gefeldertrindigen Buche, *Fagus silvatia* var. *quercoides Persoon*. Naturw. Zeitszch. f. Forst- u. Landwirtsch, VIII, 1910, 16; IX, 1911 (Feucht); IX, 1911 (Lorge); XII, 1914, p. 216 (Münch).

robinia and spindle tree. The cell walls of such sponge corks sometimes consist in part of cellulose (V. Höhnel's Phelloid [1]). The cork of *Quercus suber*, L. (the cork oak) and *Quercus occidentalis*, to which we owe sheet cork, belongs to this class. The normal cork rind, the "**Male Cork**" of these trees, which are found in Spain, southern France and Algeria, is too fissured and therefore worthless. If, however, it is pared off superficially—which is done from the 10–15th year onwards—a new cork cambium is formed in the rind parenchyma which produces the useful, light, "**Female Cork.**" This is removed after 8–12 years, during which time it reaches a thickness of several centimetres, whereupon formation begins afresh. In a similar fashion the birch is used for its white cork covering in northern Russia.[2] A suggestion that a similar advantage might be taken of our field maple and English elm [3]—*Ulmus suberosa*, Ehrh., the cork elm, is no longer regarded as a separate species—appears to have had no result. The name "**Stone Bark**" is given to bark formations which are very hard in consequence of the great thickness of the walls of their elements.

The raggedness of the surface of bark is caused by the stretching of the rind associated with the growth in thickness of the stem of the tree. The cork cambium and the other living constituents of the rind follow it by cell multiplication, cell growth and the formation of larger intercellular spaces,[4] so that these parts of the rind behave like a coat which enlarges of its own accord with the growth of the wearer. The dead bark cannot do this and therefore acquires fissures whose direction generally follows the length of the stem and depends in individual cases on the constitution of the bark. The more the cork separates into scales the more is the direction of the fissures obliterated. The separation of the scales occurs, *e.g.* in the larch, at the boundary between the, in this case red coloured, cork sheets of the secondary cork and the dead rind tissues lying between them. In the pine the shedding of the scales in the upper part of the stem occurs early and in thin layers, while further down the scales remain on for a long time. Above, therefore, there are always present new, brightly coloured scales, whilst below every scale has time to change colour under the influence of the weather and the impurities that settle upon it. The cork layers between the bark scales of the pine consist of alternate layers of thick-walled stone-cork and thin-walled cork cells. The form and arrangement of the bark scales is characteristic for species of trees and forms an important means of distinction.

The significance of the cork and bark structures described above, in the economy of the tree has already been suggested. They come into consideration as a protection against loss of water, temperature influences and against damage by animals. The regulation of the temperature of the interior of the tree is partly done by the water current which flows from the roots to the leaves, there to provide for the replace-

[1] Sitzunbsber. d. Wiener Akad. d. Wissensch., LXXVI, 1877; quoted from Haberlandt, Physiol. Pflanzenanatomie, 3 Aufl., 1904.

[2] v. Merklin, quoted in De Bary, Vgl. Anatomie, 1877, p. 573.

[3] Wessely, in Wiesner, Rohstoffe des Pflanzenreichs, p. 475. Leipzig, 1873.

[4] Devaux, Accroissement tangential des tissus situées à l'extérieur de cambium. Mém. de la soc. phys. et nat., Bordeaux, 1899, T.V., p. 47. Ref. Bot. Zentralbl., 1900, Bd. 83, p. 352.

ment of the loss due to evaporation. If the crown is deprived of its leaves or needles, that current is checked and the temperature of the interior of the tree begins to rise.[1] The measurable deviations of the internal temperature from that of the outside are brought about exclusively by the physical conditions [2] and have no relation to the life processes. Production of heat in the living tissues, which undoubtedly exists, is so small that, having regard to the sources of error, it cannot be proved with certainty. On long exposure to the sun a stem may warm up to 40 degrees C. in spite of the bark covering. Temperature excesses of 8–10 degrees above air temperature are not infrequent on the sunny side. At 30 degrees C. in the shade at 3 p.m., Vonhausen found in the rind and the outermost layer of wood in the beech, temperatures of 45 degrees on the sunny S.S.W. side, 35 degrees on the south side and 31 degrees on the north side. Too high temperatures give rise to **Bark Scorching,** which is a dreaded phenomenon, especially on thin-rinded trees without bark (beech and hornbeam) and, in youth, so long as the bark is not fully formed, also in spruce, maple, lime and fruit trees. It consists in the death and drying up or even the loosening and scaling off, of the rind on the sunny side and appears especially on trees which, grown up in close order, are suddenly isolated. In such " coddled " specimens the rind is more weakly developed than in those which have grown in full light from their youth up. When isolation is gradual, an adaptation of the rind to the altered exposure to the sun takes place. If damaged trees in a rashly opened up wood margin are removed, bark scorching spreads to the stems now exposed to the sun and may thus penetrate deep into the crop. The rind of felled beech stems also soon dies as the result of overheating on the side on which the rays of the sun fall, whilst it generally remains green throughout the summer on the shaded side. In any case bark scorching is hindered by anything that slows down the penetration of the heat of the sun into the interior of the stem. There is a certain connection between the character of the surface of the tree and its requirements as regards habitat, which is worth noting. Species which like an open stand, like oak, robinia, pine and larch, are protected against rapid heating of the cambium by particularly thick bark. In the equally open-stand loving birch the same protection is provided by the white colour which reflects the sun's rays as well as by the betulin and air content of the cork layers. Stems exposed to the tropical sun are often characterised by a light-coloured rind (*Eucalyptus*, leguminosae [3]). It is true that the light colour is not infrequently provided by a covering of lichens. The pine is practically fully protected, below by a coarse scaley bark, above by smooth, thin bark which reflects the sun's rays. The bark scales of the spruce shrivel and bend when exposed to solar radiation in such a manner that protective air-spaces are formed between

[1] Hartig, R., 1892.

[2] Leick, Temperaturzustand verholzter Achsenorgane. Greifswald, 1913, Hartmann; Vonhausen, Rindenbrand: Allgem. Forst- u. Jagdzeitung, 1873. Böhm und Breitenlohner, Temperatur im Bauminnern. Biblioth. Bot. VI, 336, Sitzber. d. Kgl. Akad. d. Wiss. Bd. 75, Mai, 1877.

[3] Further examples of protection from the sun by light-coloured bark, *see* v. Tubeuf. Naturwiss. Zeitschr. f. Forst- und Landw. 12, 1914, p. 36.

them and the stem. Beeches and spruces like to stand so close that their stems are shaded by the crowns and when they grow up isolated, the branches drooping far down and, in the beech also the shoots springing from dormant buds, take over the protection of the stem. In normal circumstances, therefore, they do not require the protection of a particularly thick bark against heat. The aforementioned rule is not contradicted by the usually dark colour and freedom from bark of the younger twigs, including those of the birch, because for such twigs, in part shaded by the leaves, any protection against heat other than their great surface in proportion to the heat storing mass is unnecessary because it cools itself to air temperature by radiation and by conduction through its contact with the air, and the air temperature in our latitudes never reaches the fatal height of 50–54 degrees.[1] Only direct solar radiation can become injurious. Protection by the bark against heat also plays an important part in forest fires, which, especially in the primeval forests as the result of lightning, etc., are of great importance for tree life.[2] A ground fire generally kills only the smooth-rinded trees and spares the tough barked species. The latter are therefore favoured as against the former and may attain dominance even when, without this help in the struggle for existence, they would not have achieved it. Without forest fires, the oak could not have maintained itself to the extent it has against the beech, which surpasses it in growth. The famous oak woods of the Spessart owe their establishment and preservation only to the protection afforded by their thick bark against fire and the many-thousand year-old giant trees of California (*Sequoia gigantea*) owe their great age to the unique character of their massive bark in being practically incombustible, and as surely effective as a fire-proof safe. Examples of the efficiency of the bark as regards late frosts are mentioned by Robert Hartig.[3] In the younger parts of the pine he found late frost rings which were absent in parts of the stem six years old and upwards as their thick bark prevented the penetration to the cambium of low temperatures of brief duration. Larches behaved similarly. In them in fact the frost rings did not extend beyond the fourth year. In the thin-rinded spruce, on the other hand, the formation of frost rings extended down to the 10–12 year-old parts of the stem and Hartig counted no less than ten frost rings in a specimen about fifteen years old.

Finally, on the character of the rind depends, in a great measure, the behaviour of the tree towards lightning.[4] The oaks, with the poplar, pear tree, elm, willow, acacia and ash, are among the broad-leaved trees which are often and seriously damaged by lightning. Deeply penetrating root systems, easily split wood (poplar), but especially the great slowness with which the stem is wetted in thunder showers are, as Stahl convincingly demonstrated, the reasons for this. The crooked branches of the oak, often carried horizontally, conduct the water badly to the stem; the fissured, thick, scales absorb it and

[1] Münch, E., Hitzeschäden an Waldpflanzen. Naturwiss. Zeitschr f. Forst- u. Landw. 11, 1913. The same, 12, 1914; 13, 1915.

[2] Schenck, Der Waldbau des Urwaldes. Allg. Forst- u. Jagdztg., 1924.

[3] Doppelringe als Folge von Spätfrost. Forstl. Naturw. Zeitschr., 1895, I.

[4] Stahl, E., Die Blitzgefährdung der verschiedenen Baumarten, 1912.

the cork layers, reaching the surface at their base hinder its spreading. Thus the electricity does not find good surface conduction from the wet crown to the earth and destruction is wrought by its passage into the stem like that found elsewhere in its passing from a good conductor to a bad one.

A complete protection, and one of importance for tree life, is provided by the bark against the browsing of animals. When there is an excessive stock of game and a monotonous diet for them, most trees are peeled in their youth by red deer, so long as the rind is smooth, but as soon as they form a thick bark they are entirely left alone. The dry dead bark, which because of its poverty in nutriment and production of cork is never attacked by decay-inducing fungi, is inedible by animals and so protects the living bast, rich in nourishment, which they do not understand how to free from the bark and devour separately. There is in addition the great toughness of many barks, the effect of the bast fibres and stone cells. The mechanical resistance which the rind presents to the attack of the larger animals has been measured by Räuber.[1] He found a considerable increase to result from the formation of bark.

In conclusion it remains to be said that cork and bark also provide protection against disease-producing fungi. It is true that cork is not poisonous, but it cannot be utilised by fungi. Fungi germinating on the surface can therefore penetrate it at the most by the lenticels. As a rule they require a wound as an opening for ingress, in so far as they do not, like the rust fungi, make their way through the stomata or the still tender epidermis of young leaves or twigs.

4. Substances contained in the Cells of the Rind.—The value of most useful tree-rinds depends on their containing substances with valuable chemical properties. Such substances are not wanting in the rinds of our trees also, though they are inferior in variety and abundance to the products of more favorable climates. These substances are partly dissolved in the sap of the living cells of the rind, partly accumulated in storage organs which no longer possess protoplasm. The first to be mentioned are the tannins which are indeed absent from few rinds, though they occur in useful quantities only in a few of our trees.[2]

In the oak the barky rind of old trees is poorer in tannin; the smooth rind of young wood, free from bark, of 14–20 years old stems forms the most valuable material, because the tannin content of the bark is about half as great as that of the "flesh," *i.e.* the living portions of the rind. The best smooth rinds, *i.e.* bark-free rinds with glossy cork covering, of poles under 10 inches diameter, in a dry condition, contain 16–20 per cent. of tannin. Warm situations favour the formation of tannin, which, for the rest, is found in practically the same quantity at all seasons in oak and spruce rinds.[3] Perhaps, in the latter,

[1] Der natürlichen Schutzmittel der Rinden, etc. Jenaische Zeitschrift f. Naturwissenschaften, 1910, Bd. 46, p. 1–76; Heikertinger, Gibt es natürliche Schutzmittel der Rinden, etc.? Zeitschr. f. Forst- u. Landwirtsch., XII, 1914, p. 97.

[2] Schwackhöfer, Forstlich-chem. Technologie in the Handbuch der Forstwissenschaft, begr. von Lorey, hrsg. von Chr. Wagner, 1912, 3 Aufl. Bd. II, p. 562. Tübingen, Laupp; Fischer, Handbuch d. chem. Technologie. Leipzig, 1893; V. Höhnel, Die Gerbrinden. Berlin, 1880.

[3] Paessler, Mitteilungen der Deutschen Versuchsanstalt für Lederindustrie in Freiberg i. S., 1915 and 1916. Berlin S.W. 11, Günther & Sohn, Schöneberger Str. 9–10.

it increases somewhat towards the winter. The tannin content of oak rind falls off from the root to the top by 3–5 per cent. (earth, middle and top quality). Spruce rind contains 7–13 per cent., the quantities being equal throughout the different heights in the stem, larch rind 10 per. cent., silver fir rind 5 per cent., birch rind 3 per cent., alder rind 16–20 per cent., willow rind 8 to over 13 per cent. of tannin. In elm rind 3–4 per cent. of tannin is found, in young horse chestnut rind about 2 per cent., in beech rind 2 per cent. The wood with rind of young coppice shoots of sweet chestnut contains, according to Paessler, 6.6 per cent. of tannin, young chestnut growth from seed, 5.2 per cent. In Germany oak and spruce rinds especially are employed. The function performed by the tannins in the economy of the tree is, in accordance with the many sided nature of these bodies, not a simple one.[1] Some of them keep off slugs, which may also appear as pests of trees, from parts of the plant. To this extent they may be described as protective substances. The rind tannins form no protection against the attacks of animals. Indeed oaks and spruces are particularly resorted to by roe deer. To the rabbit, tannin seems to be agreeable, as, at least in captivity, it gnaws oak twigs with remarkable avidity. At any rate, many of the rind substances which are characterised by special physiological effects are of service as protectives, like the poisonous oils of the juniper and the savin tree (*Juniperus sabina*). The fluorescent glucosides of horse chestnut (aesculin with the enzyme aesculase) and ash rind (fraxin), the salicin of the willows and poplars, the secretion which exudes as a milky juice on cutting the young shoots of the Norway maple and many other rind substances might also give a positive result if tested from the above point of view. The maple secretion is found in vacuoles about 1 millimetre long arranged in vertical rows between the sieve tubes and the bast bundles laid down before them. They are largest and most numerous in the Norway maple and remain filled with sap for about ten years. The view here presented, worked out and established by Stahl, which has not remained unopposed,[1] finds substantial support by experiment and by the fact that the substances named and other protective means against animal attack, in a manner replace each other. Thus the lime rind contains no poisons but contains, like the elm, slime cells whose contents form a good protective means against slugs, for example, as Stahl has proved. A similar role to that of the stone cells is played by a solid substance very widely distributed in rinds—**calcium oxalate**—which in no way precludes this compound from performing other functions in the life of the plant. It appears in the form of single crystals (*Pinus, Acer*), masses of crystals (*Lonicera, Viburnum, Tiliaceae*), single crystals and masses (*Betulaceae, Corylaceae, Ulmaceae, Platanus, Salicaceae*), as crystal sand (*Cupressineae, Sambucus*), or crystal needles (*Fraxinus, Tulip tree*), as single crystals, especially in the vicinity of the resin cells, and, to every animal attacking the rind, is at least a disagreeable addition. For oxalate needles, especially

[1] Stahl, Pflanzen und Schnecken. Jena; Räuber, Schutzmittel der Rinden, etc. Jenaische Zeitsehr. f. Natürw., Bd. 46, 1910. Opposing Stahl: Heikertinger, Über die beschränkte Wirksamkeit der natürlichen Schutzmittel der Pflanzen gegen Tierfrass. Biol. Zentralbl. XXXIV' Nr. 2, 1914. Leipzig, Thieme.

the so-called raphides, a powerful protective action against slugs has been proved with certainty, again by Stahl. If the needles are associated with poisonous substances their protective effect is increased; but the action of the needles alone is not unimportant in this direction.[1] The alkaloid of *Taxus*, taxin, is fatal to cats and dogs even in small quantities. Our wild animals [2] and domestic ruminants, however, are not harmed by not over-large quantities of yew needles. Horses are more susceptible but have a strong antipathy to the taste of the yew.

5. Resin.—Not indeed confined to the rind, but allied in their functions to the substances treated of here, are the resins [3] of the conifers. They consist of a mixture of non-nitrogenous bodies composed of carbon, hydrogen and oxygen, dissolved in oil of turpentine to form a fluid mass which solidifies in the air with the absorption of oxygen and the loss of the fluid turpentine oil. The original clear yellowish liquid is called **Balsam** or **Turpentine**—the **Raw Resin** of industry—the solid product which is obtained from it by distillation is called **Colophonium** or **Resin** in the narrower sense. Besides this the liquid oil of turpentine is obtained in the distillation. The resin of the silver fir is the most fluid; then follows that of the pine, then that of the larch, which is the least fluid. The masses of resin which appear on wounding and are utilised technically, are present in special canals, the **Resin Ducts.** These are passages running between the cells, produced by the drawing apart of neighbouring cells which have previously multiplied by division [4] (Intercellular spaces). In the resin ducts in pine wood these cells swell up and so, to some extent, crush the surrounding parenchyma cells, which then die and become lignified, thus forming a sheath of dead, crumpled, cells, mostly filled with air, round the resin duct [5] (Fig. 77, *s.*). The resin originates in the interior [6] of the cells bounding the resin canal (Epithelial Cells) and is excreted through the wall into the inter-cellular passage, and indeed, according to Münch, under a high "secretion pressure" which pushes apart the epithelial cells and finally compresses them into thin bands which line the walls of the resin duct. In the case of the resin ducts of the wood the ducts are already laid down in the cambium. With the complete lignification of the tissues surrounding it, the resin duct has reached its mature form—that of a cylindrical tube filled with balsam. It is still doubtful in what way the balsam passes out of the interior of the epithelial cells through the water-impregnated membrane into the lumen of the resin canal; probably some kind of emulsifying process is involved.[7] Accord-

[1] Lewin, Ber. d. Dtsch. Bot. Ges., 1900, Bd. 18, p. 53.

[2] Ehrenberg und v. Romberg, Giftigkeit der Eibe. Landwirtsch. Versuchstationen, 1913.

[3] Chief work: Tschirch, Die Harze und Harzbehälter, 2 Aufl. Berlin, 1906. Several of the anatomical and physiological data in this work are now superseded.

[4] Sanio, Jahrb. f. wiss. Bot., IX, 1893, p. 99.

[5] Münch, E., Naturw. Grundlagen der Kiefernharznutzung. Arb. a. d. Biolog. Reichsanst. f. Land- u. Forstw., Bd. X, H, 1, 1919. There further literature. The same, Zur Anatomie de Harzgänge v. *Pin. silv.*, Bot. Archiv., 9. Bd., 1924, p. 195.

[6] Mayr, H., Das Harz der Nadelhölzer. Berlin, 1894. Bailey, Bot. Gaz., 1909, XLVIII, p. 47; Tschirch, Ber. d. Dtsch. Bot. Ges., XIX, 1901; Haberlandt, Physiologische Pflanzenanatomie, 3 Aufl., 1904; Schwabach, Ber. d. Dtsch. Bot. Ges., XVII, 1899; Höhlke, Beihefte z. bot. Zentralbl., XI, 1901; Nottberg, Zeitschr. f. Pflanzenkrankheiten, VII, 1897.

[7] Pfeffer, Pflanzenphysiologie, 1897, p. 85-87. *Comp.* Heller, Flora, 1904.

ing to Hannig [1] the resin appears in the form of droplets in a secretion field on the surface of the protoplast from small, rupturing, vacuoles, only then passing out through the cell wall into the resin canal. The mode of passing through the wall is not thereby explained; the droplet must again dissolve or emulsify in order to be able to pass through the water-saturated membrane. Tschirch's statement that the resin

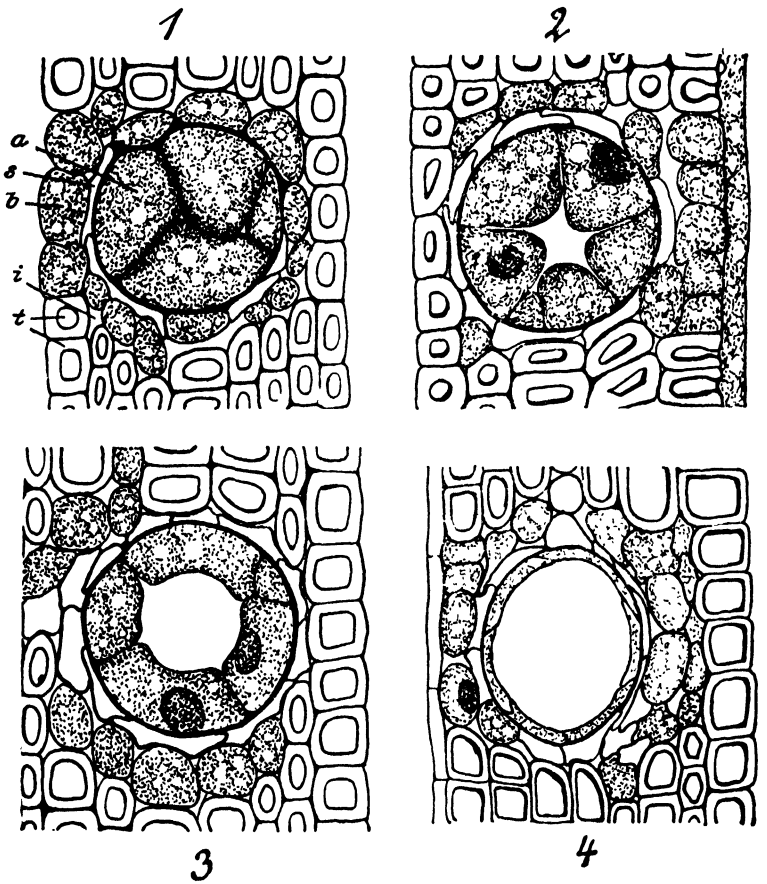


FIG. 77.—Resin ducts in pine wood filled to different extents. 1. Completely emptied; the secreting cells fill up the lumen. 4. Full; the secreting cells compressed into thin plates on the wall. 2 and 3. Intermediate conditions. (*a*) Epithelial or secreting cells, (*b*) parenchyma, (*s*) cells of the air sheath, (*i*) intercellular spaces, (*t*) tracheids. After Münch.

is first formed outside the secreting cells in a " resinogenous membrane " which lines the resin canal, could not be confirmed by recent investigations and is refuted by Hannig (*loc. cit.*).

In spruce and larch some of the epithelial cells become thick-walled and no longer capable of multiplication. In the conifers, resin ducts appear only in the parenchyma, and longitudinal parenchyma bands always contain at least one resin duct. In the spruce, resin is also formed in glandular hairs on young shoots. At the boundary between

[1] Hannig, E., Unters. über d. Harzbildung der Konifernnadeln, Zeitschr. f. Botanik, 14, p. 385, 1920. Franck, A., Bot. Archiv. III, 1923, p. 173.

heartwood and sapwood the resin canals close up by the growing out of the epithelial cells into the resin canal (tyloses *see* Heartwood formation) and die off. This is of practical importance, because the resin in the heartwood, in any case less fluid, further loses in mobility. Heartwood therefore does not suffer any loss of resin or of value in the process of tapping for resin. In winter the horizontal resin canals are stopped up by the cambium. If they are cut through by the cork cambium in the process of formation of bark, closing up by the formation of tyloses takes place in the same way. In the wood, longitudinal ducts run in the direction of the fibre and narrow transverse ducts along the medullary rays (Fig. 79). Longitudinal and transverse ducts communicate at all crossing-points, which, indeed, according to Münch, are often formed by the longitudinal ducts bending out of the direction of the fibres peripherally so as to join on to transverse ducts. Many millions of such open connections may be counted in a cubic metre of pine wood. The transverse ducts always originate from longitudinal

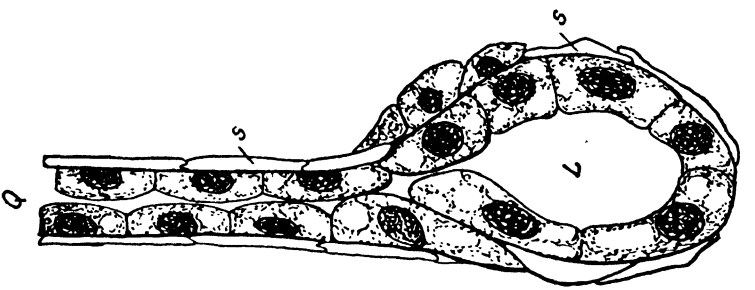


FIG. 78.—A medullary ray resin duct (*Q*) arises from a longitudinal duct (*L*). Transverse section of pine wood. (*s*) sheath cells. After Münch.

ones (Fig. 78). In the pine, the bast contains no resin ducts of any kind. The length of the vertical resin canals in the spruce amounts, in the lower half of the stem to 70 centimetres, in the upper half to 40 centimetres, in the larch to 15–30 centimetres. In pine wood the length of the resin ducts is from 0.10 up to over 1 metre—on the average about 0.5 metre. The ducts end blindly or connect with other ducts.[1] Their course is curved, with the convexity towards the centre of the tree at about the middle of their length. Besides this, their course is somewhat winding, so that they occasionally encounter each other laterally (tangentially) and may run united for a space.

Mayr distinguishes an outer and an inner canal system in the arrangement of the resin canals. The first runs in the original rind of the young shoot, where, *e.g.* in the spruce, over 100 resin ducts could be counted in the cross section of a stout annual shoot. All these canals are lost on the formation of bark. Thus, for example, in isolated spruces in which bark-formation was rapid, none of these outer resin ducts was any longer active in the cross section of the three-year-old stem. In suppressed stems with very small cross sections, they survived on the north side up to the sixtieth year of life. In the silver

[1] On the arrangement of the resin ducts *see* Mayr (*loc. cit.*) and Strasburger, Bau und Verrichtung der Leitungsbahnen. Jena, 1891, p. 1, ff.

fir they are cut off by the formation of bark, only from the eightieth year onwards. The outer canal system of the larch consists only of short ducts which, in the long shoots are involved in the formation of bark a few weeks after their appearance, but in the dwarf shoots are preserved for several years. The resin blisters of the balsam fir, Douglas fir and others, arise from the massing of resin producing cells and their segregation in isolated places in the resin canals. During diameter growth they may lose connection with the canals and continue to grow on their own account. The rind canals are always much larger than the resin ducts of the wood.

The inner resin canal system runs between the products of the cambium. Mayr reports, for example, 804 longitudinal resin ducts in the transverse section of a ten-year-old spruce and 44,000 in the middle of the bole of a mature one. In spruce, larch and pine over 60 transverse resin ducts emerge, on the average, on 1 square centimetre of the outer surface of the external annual ring.

In the pine, Münch found that the number of the longitudinal resin ducts regularly depended on the breadth of the annual ring. The side of the stem, the height in the stem, age, vigour of growth, etc., have an influence on the number of resin ducts only in so far as they influence the breadth of the annual ring. The cross section of an annual ring has, on the average, $3 + 4b$ resin ducts to 1 centimetre of the circumference, where b is the breadth of the ring in millimetres. The number of resin ducts in 1 square centimetre of the cross section of the wood was as $(40b + 30) \div b$ — the resin ducts thus stand the more closely the narrower ringed the wood. They therefore become generally closer in old trees from within outwards and are closer in slow grown trees than in fast grown ones. The volume content of the resin ducts increases correspondingly; it amounts, *e.g.* in 1 millimetre wide annual rings, inclusive of the transverse ducts in the medullary rays, to about 4 litres per cubic metre. When the cambium is injured, pine wood immediately forms two or three times the normal number of pathological resin ducts, which may be traced for several metres from the wound, —in young plants, up to the tips of the twigs.

In the silver fir, normal vertical resin ducts are almost completely absent in the wood and its timber can in this way be distinguished from that of the spruces, pines, larches and Douglas firs. Resin canals are absent also in the wood of the common and Virginian junipers, the common arbor vitae, and Lawson's cypress (*Chamaecyparis Lawsoniana*). The last named, however, exudes resin from the occluding tissues at wounds. Occluding wood in the silver fir is also rich in resin ducts.

Of a more abnormal nature are "**Resin Galls**" and "**Resin Cracks.**" The former arise when resin from the horizontal canals, through high pressure, ruptures the cambium at the time of its activity and lifts up the rind in blisters. Assertions to the contrary by Tschirch (wounding of the cambium with dissolution of tissues) cannot be confirmed, at least for the pine. They remain in the timber and may cause a depreciation in its value. The resin cracks are fine fissures in the heartwood at the base of the stem of the larch and Douglas fir, proceeding from the pith and filled with resin, which become visible on felling, but,

however, apparently originate in the earlier years of the tree's life.

In the pine, to a much less extent in the spruce, balsam flows out when the resin ducts are opened by wounding. As the resin ducts of the stem are to a great extent, perhaps entirely, in open communication with each other by means of the transverse ducts, balsam can flow to the wound from extensive regions, apparently from the whole tree, also, according to Schierlinger[1] in considerable quantities in the direction of the circumference. The driving force overcoming the great frictional resistance of the viscous balsam in the narrow canals, is the osmotic pressure of the epithelial cells which has been investigated in the pine by Münch (1919). When the resin duct is opened the compressed epithelial cells suck in water from the surrounding wood and swell until they to a great extent fill up the lumen of the resin duct and squeeze out the balsam from it (Figs. 77 and 79). They develop thereby an extraordinarily high osmotic pressure, which, according to Münch, may exceed 100 atmospheres. On reaching the air the balsam stiffens into solid colophonium through the loss of the turpentine oil and stops up the resin duct, whereupon the latter again fills up through the formation of new balsam by the epithelial cells which again resume their original flattened form. The refilling is complete after about two weeks. It proceeds rapidly at first, then, in accordance with the growing counter pressure of the accumulating balsam, at a continuously diminishing rate, according to an exponential function determined by Münch. On this repeated emptying and filling depends the possibility of the continuous extraction of resin from pines. The pine timber does not become poorer in resin by the extraction; rather is the resin which flows out completely replaced. In the spruce the resin ducts of the wood give only a little outflow of balsam, but on the other hand, the occlusion cushions on the margin of wounds afford considerable quantities of resin, which was also formerly technically extracted from

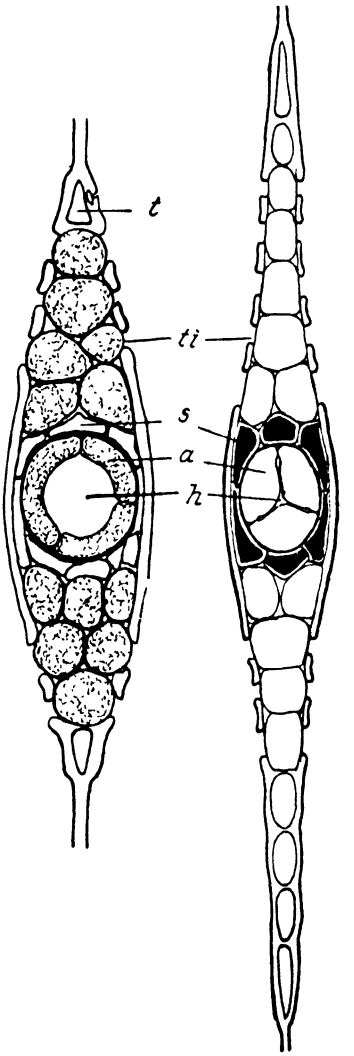


FIG. 79.—Medullary rays in pine-wood with resin ducts; left, filled with resin; right, emptied and filled up with the secreting cells. (*t*) tracheids, (*ti*) pits, (*s*) air sheath, left, shown white, right, black. (*a*) epithelial cells, (*h*) lumen of resin duct. After Münch.

[1] Schierlinger, Naturw. Zeitschr. f. Forst- u. Landwirtsch., 1919.

specially made, longitudinal wounds, the so-called resin grooves or resin streaks. Resin is only obtained from the larch by boring into the stem so as to reach internal wood cracks filled with resin (Venetian turpentine). From the silver fir " Strasburg turpentine " was formerly obtained in small quantities by puncturing the resin blisters of the rind. The resin cracks of the larch provide for as many as thirty years, yields of 120–500 grams of resin per stem per annum. The following figures give an illustration of the quantity of resin contained in a tree. Mayr, by boiling shavings in alcohol and calculating, found in 1 cubic metre of sapwood: in the pine 22.21 (22.1 kilogrammes) of resin, in the larch 18.11 (18.3 kilogrammes), in the spruce 9.31 (9.4 kilogrammes) and in the silver fir 3.31 (3.2 kilogrammes).

Ramann obtained the following figures for a 165-year-old pine by extraction with chloroform:

At	1.00m.	stem ht.	7.99% resin.
,,	4.30m.	,,	5.04% ,,
,,	8.45m.	,,	5.56% ,,
,,	12.60m.	,,	3.66% ,,
,,	16.75m.	,,	3.93% ,,
,,	20.90m.	,,	3.17% ,,
,,	24.05m.	,,	5.05% ,,

Mayr gives the average resin-content of the whole stem in percentages of the dry wood as follows:

Silver fir . . .	1.003
Spruce . . .	1.68
Larch	4.19
Pine	4.81

Finally, determinations by the Eberswalde Forestry Research Station[1] (boiling with soda at 170–180 degrees under a pressure of 8–10 atmospheres) gave for the pine 3–4 per cent. of raw resin of which almost a half was fat, for the spruce 1 per cent. of raw resin of which half was fat. The lowest part of the stem always showed itself richest in resin, the clean part of the stem above it was poorest and the crown section again somewhat richer than the latter. In branch and root wood the upper side is always richer in resin than the lower. The annual production of resin increases with the age of the tree in accordance with the increasing frequency of resin ducts in the stem, so that the inner heartwood is poorer in resin than the outer. The heartwood is always richer in solid resin than the sapwood. The formation of new resin is indeed at an end when the formation of heartwood begins. According to Münch's calculations, these quantities of resin are only to a small extent contained in the resin ducts as fluid balsam, because the ducts have a much smaller volume than the space occupied by the amount of resin obtained by boiling and washing out. The resin thus obtained will come, for the greater part, from the wood walls which are richly impregnated with it especially in the heartwood. Besides the resin, the extracts always contain much fat, which cannot be separated from the resin.

Sub-tropical pines, *Pinus palustris* (longleaf) and *Pinus caribaea* (slash) especially, are utilised for resin extraction in the United States of North America. Of the European pines the most productive are the Maritime pine, *Pinus maritima*, on the west coast of France (the Landes) and the Black pine, *Pinus Austriaca*, in Lower Austria, which,

[1] Tetzner, Zeitschr. f. Forst- u. Jagdwesen. Berlin, 1915, J. Springer; Schwalbe, *ibid.*, 1915.

on the average, produces 3–4 kilogrammes of resin per stem. Two to three kilogrammes per stem a year and, under favorable circumstances, up to 1,000 kilogrammes per hectare and year may be obtained from our native *Pinus sylvestris*, though with a considerable expenditure of labour, because the balsam solidifies more quickly and the resin wounds must be renewed more frequently than with other species of pines. In actual production of resin our pine is not inferior to other species. The spruce furnishes only little resin and that of small value and suffers very much from stem rot when worked for resin production. Spruce, larch and silver fir can no longer be regarded for practical purposes as resin trees. The technique of resin production for our native pine was first worked out during the world war. The rind is cut through down to the wood by means of a timber scribe in oblique grooves, on certain areas which should not exceed two-thirds of the circumference of the stem. The resin flows down the grooves and is collected in a suitable manner. The cuts are renewed along their lower margins at intervals of several days, the proper duration of which was accurately determined by Münch. The cut furnishes on the average about 1 gramme of resin per centimetre of the cut circumference of the tree, the amount increasing with the length of the pauses in utilisation and especially with the size of the crown and roots and consequently with the growing space. The weather, though not simply the temperature, also has an influence, as also various other conditions which are set forth in the individual works.[1]

The significance of resin in the life of the tree is that of a protective substance. The protective action of solid resin especially affects fungi and bacteria, against which it appears to be an excellent means of protection. Wounds in the sapwood of the resinous pine almost never result in decay of the wood even after many decades, as the exposed wood becomes permeated with resin, while the spruce, poor in resin, is on the other hand regularly infected with rot fungi through wounds in the wood. Fluid resin effectively wards off insects as it flows out under pressure when a resin duct is accidentally injured, overwhelms the attacker and kills it. On the other hand, it is true, the flow of resin is of use to the larva of one of the twister moths (*Tortrix resinella*) as it constructs its protective dwelling out of resin.[2] If, in spite of resin protection, the resin-rich pine suffers more from insects than any other species of tree, it does not mean that this protection is useless, but at the most, that without it the tree would be exposed to many more enemies, and perhaps, indeed, would be quite incapable of surviving in the face of our animal world.

6. The Lenticels.—It is a pertinent question, how, when the epidermis with its stomata has been replaced by cork and bark, the

[1] Petraschek, Naturw. Ztschr. f. Forst- u. Landwirtsch., 1916; and Wiener Allgem. Forst- u. Jagdzeitung, 38, 1920, Nos. 45, 46 and 47. (Complete collection of the whole of the war literature.) Kienitz, M., Zeitschr. f. Forst- u. Jagdwesen, 1919, and 1924. Cieslar, A., Zentralb. f. d. Ges. Forstwesen, 1918, p. 65. Roth u. Austerweil, Gewinnung und Verwertung von Harz und Harzprodukten, München u. Berlin, 1917. Wislicenus, H., Nat. Ztschr. f. Forst, u. Landwirtsch., 16, 1918; v. Tubeuf, *ibid.*, Schierlinger, *ibid.*, 1919, and other works mentioned in Münch (*loc. cit.*) and Petraschek (1920).

[2] Büsgen, Entwicklung von *Tortrix resinella*. Allgem. Forst- u. Jagdztg., 1898, p. 380.

aeration of the interior of the tree is effected. That such aeration must take place is undoubted, because in the higher plants there is no living cell which can do without respiration. Communication with the outer air of the air passages which accompany the living elements of the tree takes place through the **Lenticels.** These are the, mostly light-coloured, points or short horizontal stripes on the rind, which often afford good distinctive marks for the identification of the species, especially on young twigs. They consist of masses of roundish cells, sometimes closely, sometimes loosely united together which, as it were, burst out above the rind and are permeated by numerous air passages. In many cases (*Ulmus, Robinia, Alnus, Betula, Sorbus, Prunus, Aesculus, Conifers*, etc.) the masses of loose cells are interrupted by solid intermediate strips of sclerophelloid [1] which are ruptured from time to time during growth and replaced by new ones. These layers of solid impermeable cells are, according to Neger,[2] so arranged that on the drying up of the rind, when the loose, permeable cells contract, they often form a complete stoppage of the lenticels. In this way a substitute is provided for the regulation of transpiration by moving stomata. The formation of the lenticels proceeds from portions of the cork cambium, generally beginning under a stoma. Where they are absent, as in the honeysuckle (*Lonicera periclymenum*), the Traveller's Joy (*Clematis vitalba*), *Philladelphus coronarius* and *Vitis*, the ventilation of the stem is effected by means of the medullary rays which penetrate the rind to the outer surface and so maintain communication between the atmosphere and the interior by means of their intercellular spaces.[3] The formation of bark-fissures usually commences from the lenticels, as is easily recognised in the Poplar, whose rhombic lenticels amalgamate later to form the longitudinal fissures of the bark.

The perviousness of the lenticels for gases has been proved by Weber by means of ammonia vapour, which penetrates the pervious lenticels and kills and browns the tissues in their neighbourhood. Winter lenticels exhibit great differences in perviousness. In *Sambucus nigra* for example, the vapour did not penetrate by any means easily, whilst, on the other hand, the lenticels of *Fraxinus excelsior* were shown to be permeable. Klebahn has already shown earlier that the winter closing layer is pervious to CO_2. Stahl was able to squeeze air through the lenticels of twigs immersed in water, by pressure of mercury.

[1] Neger und Kupka, Beitr. z. Kenntn. d. Baues u. d. Wirk. d. Lent. I, Ber. d. Dtsch. Bot. Ges., 38, p. 141, 1920.

[2] Neger, *Ibid.* II. The same 40, p. 306, 1922.

[3] Klebahn. The same, I, 1883; Weber, the same, 34, 1916.

CHAPTER VI

THE ANNUAL RING

1. Survey.—Everyone is familiar with the ring shaped markings on the surface of the cross section of felled tree stems but only a few are aware of the amount of scientific work which has been expended on the interpretation of this phenomenon, without, indeed, up to the present having led to a result satisfactory on all points.[1]

These marks are the expression of seasonal variations in the mode of formation of the wood of the tree, which correspond in most cases to the change from one vegetation period to another. The elements of the wood formed at the beginning of a period of growth activity are of a different character from those which are formed later, and the differences which are present between the last wood of a period and the first of the following one are, in most species, so great that they are evident to the naked eye.

The annual rings are the transverse sections of the layers of growth formed in the various years, which are in the form of conical sheaths piled up one over another, the younger of which always overtops the older by the length of an annual shoot. Strasburger [2] has made the condition clear in a diagram (Fig. 80). It shows how the individual sheaths, which are represented in longitudinal section, become thinner towards the upper end and the shading in these regions indicates that an alternation in the structure of the wood occurs. In conifers the tracheids become narrower there and, instead of pitting of their walls, scalariform thickening occurs which passes over into the spiral thickening of the first elements of the new annual shoot. In broad-leaved trees all the wood elements disappear except the vessels which diminish in width and pass over, through forms with transversely elongated pits, into spirally thickened, vessel-like tracheids which are again continuous with the first vessels of the new shoot. The cambium of the new shoot joins on completely to the old and afterwards works in conjunction with it. The transition in the rind proceeds in the same way.

Applying the term " annual rings " to the ring-shaped markings requires some limitation. In actual fact, so generally does a ring include

[1] Antevs, E., Die Jahresringe der Holzgewächse u. d. Bedeutung ders. als klimatischer Indikator, eine Literaturzusammenstellung. Progr. rei botanicae, 5, 1917. Gives about 300 references.

[2] Bau und Verrichtungen der Leitungsbahnen in den Pflanzen. Jena, 1891. G. Fischer.

the wood production of one year, that the age of a tree may be determined by counting the annual rings. Cases in which several rings appear during one year are, however, not altogether rare and, on the other hand, there are cases, *e.g.* in the lower and middle parts of the stem, as well as in the lower branches of trees growing under unfavorable conditions, where no ring is formed for years. Thus, according to Nördlinger, the sparingly produced wood of clipped hedges or garden shrubs not infrequently extends scarcely or not at all to the bottom of the plant and long, twigless branches of " snake spruces " exhibited only eight annual rings at the base of a structure consisting of thirteen annual long-shoots. The production of two rings in one year is generally associated with the production of two sets of foliage.[1] It was observed, for example, in limes and horse chestnuts which, having shed their leaves in August, had developed fresh green leaves and a few flowers in September. In the mountain ash, pedunculate oak and the small leaved lime, Kny found a second annual ring formed after complete defoliation by insects in June followed by a fresh production of leaves, whilst, the birch, in similar circumstances, produced no double annual ring. In conifers, according to Nördlinger, " false rings " are not infrequent and Strasburger also found in a larch about twenty years old, the second, third, fourth and sixth rings doubled ; though the autumn wood boundary was more strongly marked than that formed in the middle of the season. Lammas shoots do not appear to be associated as a rule with a doubling of the annual ring ; though Jost saw this occurring in *Forsythia*, especially when the formation of the second shoot was late and proceeded from an already closed bud. Finally, the frost rings described in detail by Robert Hartig should be remembered. Kühn, by artificial defoliation of the horse chestnut, hazel and mountain ash, brought about a doubling of the ring in which the boundary between the two false annual rings was formed by abnormally thin-walled cells.[2] Experiments by Wilhelm on oaks had little result.

Counting of the rings can only be done without difficulty when they are sufficiently sharply defined and their breadth is not too small. Distinctness and breadth, however, vary between wide limits. In the wood of the plum (*Prunus domestica*) mistakes may be caused by the zonelike variations in colour. To avoid them the wood must be discoloured by bleaching water. The examination of thin shavings between two plates of glass by transmitted light may also be of good service. The conifers especially, possess clearly defined annual rings, then the oaks, robinia, ashes, alders and birches, whilst those of the hornbeam and lime are less conspicuous. The boundaries of the annual rings of the gorse (*Ulex Europaeus*) and the olive (*Olea Europaea*) are sometimes difficult or almost impossible to detect even under magnification, though they are not entirely absent from any European woody plant. De Bary, in his Anatomy (page 19), cites, as plants in which he was unable to find any annual rings, only the woody Piperaceae, Cacti and the

[1] On double annual rings *comp.* : Jost, Bot. Ztg., 1891, 608 ; Kny, Verh. d. bot. Vereins. d. Provinz Brandenburg, 1879 ; De Bary, Vergleichend. Anatomie, 1877, 529 ; Strasburger, Leitungsbahnen, 1891 ; Wilhelm, Ber. d. Dtsch. Bot. Ges., I, 1883 ; R. Hartig, Forstl.-Naturw. Zeitschr., IV, 1895.

[2] Bibliotheca botanica, LXX, 1910.

climber *Cobaea scandans*. Sanio[1] mentions as the only plant without annual rings, *Muhlenbeckia complena*, one of the Polygonaceae. Ring formation also occurs in tropical trees but it is not always annual-ring formation.

In markedly pendant branches of the spruce annual rings are, as a rule, not present in their full numbers.[2] Growth becomes very small, especially at the point of attachment and then ceases entirely so that the branch can soon no longer sustain its own weight and consequently hangs down. In the dwarf shoots of the beech, spring-wood and late-wood can no longer be distinguished after the eighth year.[3]

(On the anatomy of dwarf shoots *see* above, page 23.)

Irregularities in ring breadth often occur which lead to irregular longitudinal ridges and furrows, as in yews, hornbeams[4] and elms. Such trees are termed "fluted." The

[1] Quoted after Jost, Bot. Ztg., 1891.

[2] Rubner, Mitteil, d. Bayr. Bot. Ges., II, 1911, p. 307. The same, Das Hungern des Kambiums und das Aussetzen der Jahresringe. Naturw. Zeitschr. f. Forst- u. Landwirtschaft, VIII, 1910, p. 212.

[3] Daniel, Compt. rendu. Paris, CL, 1910, p. 1611.

[4] Well-grown hornbeams in eastern Germany (Rev. Gertlauken) are less fluted than the hornbeams of western Germany. Büsgen Cupuliferen, p. 182, in Lebensgeschichte der mitteleuropäischen Blütenpflanzen, Bd. II, 1913.

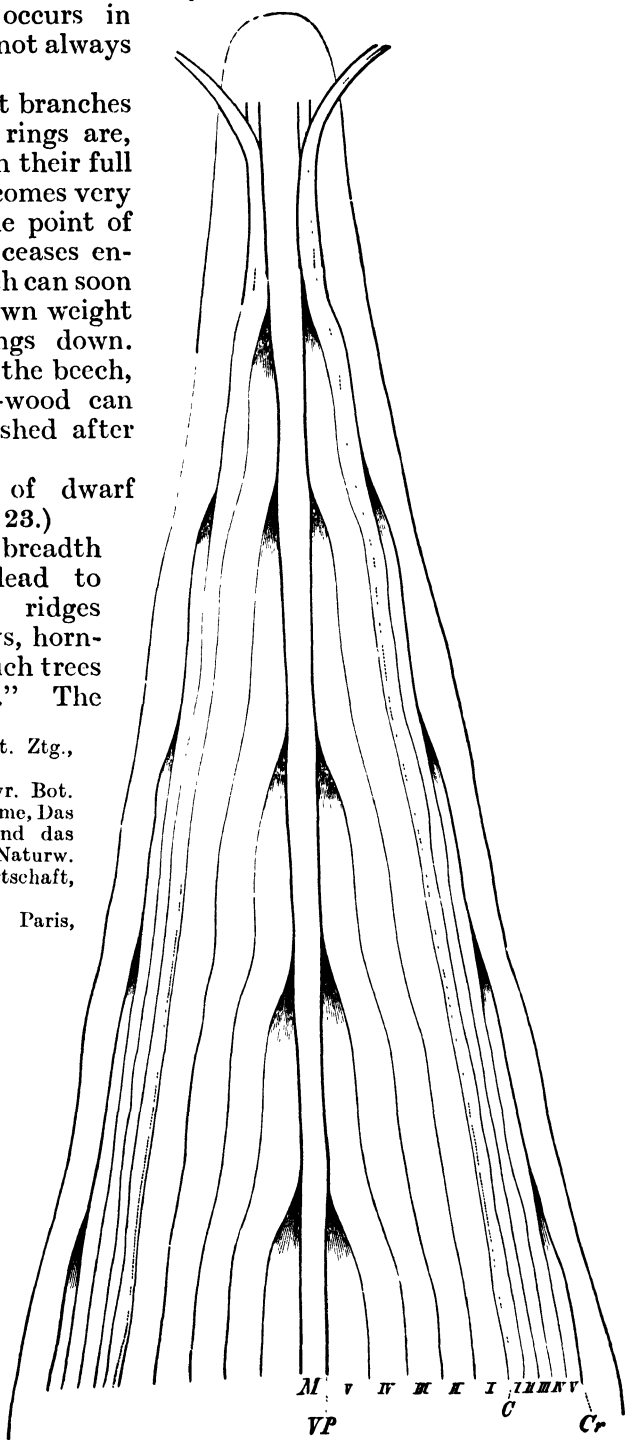


FIG. 80. — Longitudinal section through the middle of a tree showing the sheaths of growth. Much shortened. (*M*) pith, (*VP*) primary wood, (*C*) cambium (dotted line), (*Cr*) cork cambium. Below the tip, two leaf traces. (From Strasburger, Leitungsbahnen, etc.)

fluting of the hornbeam is associated with the occurrence of false medullary rays. These woody bands without vessels, which look like medullary rays to the naked eye, remain in growth behind the neighbouring tissue which is rich in vessels, because of the absence in them, not only of the vessels, but also of the wide elements which make up more than half of the vessel-containing parts of the wood.

If the annual increase in the cross sectional area of a stem is the same everywhere throughout its length, the linear breadth of the annual rings must increase from below upwards, because the circumference of of the stem, which together with the breadth of the ring determines the sectional area of the annual increment, diminishes in an upward direction. Consequently the annual rings are as a rule widest immediately below the living crown. Inside the crown they fall off in breadth with each branching.

In conformity with the slowness of development in youth, the breadth of the annual rings increases in an outward direction from the pith for a number of years and then slowly diminishes towards the outside. The falling off of linear width with age does not, however, imply a diminution in the area of the annual rings because the circumference increases from year to year. Rather, according to the investigations of R. Weber,[1] does the sectional area of the annual rings tend to remain the same up to an advanced age, where growth is unchecked. This is to be taken into consideration in determining the age of old trees when only borings which do not reach the centre of the tree are available. If the average area of the rings in the last decade has been determined from borings, the approximate age is found by division into the total stem area of the tree ; an allowance being made for the slower period of youth. At any rate the right age is more nearly obtained in this way than from the breadth of the annual rings in the outer layers of wood, although serious errors are unavoidable because of the never absent irregularities in the course of growth.

The annual rings of the roots [2] differ from those of the stem by their irregular form and also by their smaller average breadth. They are much more difficult to count as a rule, even in species whose stem rings are easily recognised. " Dozens of annual rings may unite together there to form one or a few in the interior or on the circumference or along one narrow side. Countable rings alternate with indefinite ones, simple ones appear, by reason of deceptive rings of wide-meshed tissue, to be double, and only rarely (Hickory) is the absence of a good mark of distinction such as the pore zone in the stem, replaced to some extent by unusually dark boundaries to the rings." Thus does Nördlinger describe the characteristics of the cross section of the root.

After this survey we turn to the individual problems of annual ring formation which have perpetually occupied both Phsyiology and Forestry. Of particular importance to Physiology is the question as to what causes ring formation to take place at all, to what internal and ex-

[1] Weber, R., Lehrb. d. Forsteinrichtung m. bes. Berücks. d. Zuwachsgesetze der Waldbäume. Berlin, 1891. Further mathematical expressions of the law of increment, *see* Tischendorff, Wuchsges. von *Pinus silvestris*, Forstwis. Zentralbl., 1926, p. 578, etc.

[2] Mohl, Bot. Ztg., 1862.

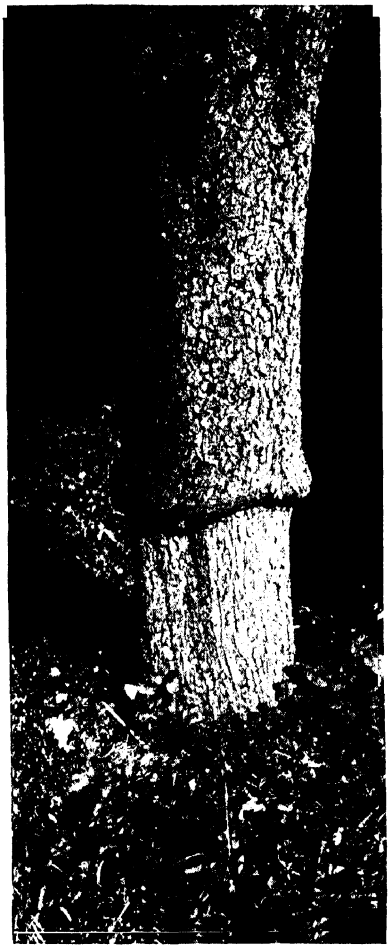


FIG. 81.—Grafted Apple tree. The scion has grown in diameter more rapidly than the stock. (Mch.)

ternal factors is to be attributed the rhythmical alternation in the nature, size and shape of the wood organs with the changes of the seasons. For Forestry the question of the breadth of the annual rings is of the greatest importance because, more even than the magnitude of the height-growth, it determines the yield by volume and value. To both sciences, the distribution of annual increment at different heights in the tree and at different ages, are of equal importance. It touches the most important questions of the physiology of nutrition and the knowledge of its laws is of importance to Forestry, especially as the basis of yield and volume determinations.

The breadth of the annual rings varies with the species of tree; under similar conditions the spruce forms broader annual rings than the yew, common pine broader ones than the cembran and mountain pines, the Canadian poplar broader than the aspen, the Norway maple broader than the field maple, the lowland races of the pine and spruce broader than the mountain and northern races. If a vigorous species or variety is grafted on a slow growing one or vice versa, the difference in their specific ring breadth becomes especially conspicuous. A very marked change in the thickness of the stem often appears at the place of grafting (Fig. 81). The vigorous variety retains its inborn tendency to form broader rings even under these otherwise exactly similar conditions of nutrition. But even more than these specific dispositions does nutrition, expressed as the quality of the locality, determine the breadth of the annual rings, and we shall learn to recognise as causes of the distribution of the increment in various parts of the tree, phenomena which we are compelled it assign to the sphere, still fundamentally little understood, of stimulus effects.

2. Breadth of the Annual Rings and Nutrition.—Obviously the breadth of the annual ring depends above all on the amount of organic building material which can be produced by the leaves and supplied to the growing cambium. The better the soil, the more favorable the climate and weather in warmth, length of growing season and moisture, the larger the growing space and so the mass of leaves and roots, the less the competition of neighbouring trees and ground vegetation, the smaller the damage by frost, insects, leaf- and root-fungi, etc., so much the more abundant is the assimilation and the wider the annual ring. All that follows in later sections about the conditions of nutrition and assimilation applies here. In this place only a few details especially affecting the breadth of the annual rings will be explained.

The dependence of ring breadth on climate is shown by G. Kraus's [1] observations on Greenland trees. It is less a question here of the immediate influence than of the development of narrow-ringed races and species. A billet of *Salix antarctica* 3 decimetres long was found to be 100 years old with a stem radius of 16 millimetres and an annual ring breadth of 0.16 millimetre. A 40-year old specimen of *Betula nana* of the thickness of a quill grown in 73½ degrees north latitude had ring breadths of 0.1 millimetre, whilst a small stem in the Würzburg Botanical Garden showed one of 1.6 millimetres. In Jämtland in Sweden,

[1] Bot. Ztg., 1873, p. 513.

between 600 and 680 metres elevation, the height of the birch is 4–13 decimetres, the diameter increment measures 1.45–3.05 millimetres annually. Fuel wood of 15–20 centimetres in diameter is produced in 50–140 years, according to the elevation and soil conditions.[1]

Other examples from Sweden [2] are :

Betula pubescens	80	years,	diameter	128	mm.,	height	12	m.
	50	,,	,,	60	,,	,,	8	,,
	60	,,	,,	75	,,	,,	8	,,
	100	,,	,,	102	,,	,,	14	,,
Pinus sylvestris	40	,,	,,	47	,,	,,	6	,,
	80	,,	,,	127.5	,,	,,	9	,,
	50	,,	,,	120	,,	,,	6	,,
Pinus abies	80	,,	,,	83	,,	,,	5	,,
(Spruce)	125	,,	,,	70	,,	,,	6	,,
	70	,,	,,	70	,,	,,	7	,,
	45	,,	,,	59	,,	,,	6	,,
	45	,,	,,	38	,,	,,	4	,,

Within its natural region of distribution, the timber increment of the spruce rises with the earlier awakening of the vegetation and the longer growing season, for, in general, the length of the growing season is more important for the rate of growth than summer warmth or total heat. Danckelmann [3] finds no considerable variations in the beech in the interior of Germany, where the length of the growing seasons is approximately the same, whilst Wimmenauer [4] proves, that its timber increment shows a falling off from the south-west to north-east, with the exception of Schleswig Holstein, similar to that of the length of the growing season. At the tree limit [5] in the Alps the breadth of the annual rings in all woody plants is much smaller than in lowland specimens of the same species. Partial suspension and irregularity of ring formation is there very widespread, because, where tree life is only just possible, every unfavorable alteration of the external conditions makes itself strongly evident. At the tree limit in Siberia the small increment makes the forest look young, whereas it consists of old, dwarfed specimens (Middendorf). A great diminution of the thick-walled late wood portion was noticed in conifers at high elevations.

How greatly dependent on climatic influences the breadth of the annual rings is, may be seen on any stem section (Fig. 82). A marked alteration of the prevailing weather expresses itself in irregularities in the breadth of the ring just as definitely as in the length of the leading shoot (*see* Chap. I, 5).

Hesselmann [6] gives some examples of this. The diameter increment

[1] Andersson, G., in den Mitteilungen der schwedischen Forstversuchsanstalt, Stockholm 906.

[2] Sterner, Botaniska Notiser, for 1911, Häftet 1, Lund, 1911.

[3] Phänologie der Holzarten. Zeitschr. f. Forst. u. Jagdwesen, 1898, p. 288.

[4] Hauptergebnisse 10 jähriger forstlich-phänologischer Beobachtungen in Deutschland, 1885-1894. Berlin, 1897.

[5] Rosenthal, Über die Ausbildung der Jahresringe an der Grenze des Baumwuchses in den Alpen. Inaug.-Diss., Berlin, 1904.

[6] Hesselmann. Mitteil. d. forstl. Versuchsanstalt Schwedens, 1904, Heft. 1. Ref. Bot. Zentralbl., Bd. 99, 1905, p. 55.



FIG. 82.—Stem-section of a Spruce. The area increment was reduced to less than a third of its previous value after the drought year 1904 and has not recovered since. (Mch.)

[*To face p.* 162.

of Swedish pines was greater in 1901 than in 1902; on the other hand the annual shoot of 1902 was longer than that of 1901. 1901 was very warm and dry, 1902 cold and wet. The favorable summer of 1901 influenced the annual shoot of the, in itself, unfavorable year 1902, but did not counteract the working of the unfavorable weather on diameter increment. The latter depends especially on the weather of the current year. Nördlinger[1] had already pointed out that diameter increment occurs, for the most part, in the spring and early summer and that on the one hand the wetness or dryness of the preceding winter, on which the store of water present in the soil depends, may have an effect; whilst on the other hand a dry heat in the latter half of July and in August can no longer seriously prejudice the increment of the current year. Still, however, the notorious summer drought of 1911, which first set in in July, may be clearly recognised in many stem cross sections, in the diminished breadth of the annual ring, especially the ring of late wood. Thus, for example, the narrow wood ring of 1858 is explained, not only by the great summer drought of 1858, but also by the unusual dryness of the winter of 1857–58. The greater abundance of light[2] and higher average temperature of a cloudless summer do not appear to exert any substantial influence in good situations, shortage of moisture may, however, come into consideration. Thus Henry[3] quotes a lowering of the increment in oaks, beeches and hornbeams to 70–30 per cent. of the normal production in consequence of drought, the size of the loss being more dependent on the shallowness or depth of the root system than on the condition of the soil. Not only shallow-rooted spruces but also deep-rooted pines may be much checked in growth by drought. The diameter growth of silver firs was reduced by up to one-third or a quarter in the very dry year 1893[4] and this at the middle and base of the stem, and Oelkers[5] found the ring of 1911 narrowed at breast height in dominant spruces. Schwarz[6] found the temperature of early spring to affect the ring breadth of the pine. Schwappach[7] pointed out that the drought years 1892–1894 reduced the increment for the quinquennium 1891–1895 by as much as 50 per cent of the normal rate. Wiedemann's[8] detailed investigations showed enormous damage by drought to the increment of spruces and pines in the middle and lower elevations in Saxony. The diameter growth of middle-aged spruces sank, in consequence of repeated summer droughts from 1911 for over ten years, to a half, the volume increment to a quarter, of its previous value. (Fig. 82.)

During the last century, the summer droughts of 1858–59, 1865, 1874–76, 1887, 1892–93, 1903–04, 1911, 1915, 1917, 1921, showed them-

[1] Forsthotanik, I, 1874.

[2] Jaccard, Accroissement en épaisseur de quelques Conifères en 1911 et 1912. Journ. forestier suisse, 1913.

[3] Compt. rend. Paris, 1894, II, p. 1025. Ref. Bot. Ztg., 1895, p. 303.

[4] Influence de l'état climatérique sur la croissance des arbres. Compt. rend. Paris CXX, 1895, p. 275.

[5] Oelkers, Zeitschr. f. Forst- u. Jagdwesen, 1914.

[6] Schwarz, F., Physiol. Unters. ü. Dickenwachstum u. Holzqualität von *Pinus silvestris*, Berlin, 1899.

[7] Schwappach, Laufender jährl. Zuwachs in Buchenbeständen. Ztschr. f. Forst- u. Jagdwesen, 1904. Die Kiefer, 1908.

[8] Wiedemann, E., Zuwachsrückgang u. Wuchsstockungen der Fichte. 2 Aufl. Tharandt, 1925.

selves particularly harmful. (*Compare* also the remarks on the dependence of height-growth on the weather, Chap. I, 5). Cold wet years also seriously depress the increment.[1]

The strongest influence in changing the breadth of the annual rings is exerted by those factors of climate which, in a given locality, differ most widely from the optimum—in the north the temperature, in our and more southerly lowlands, the moisture.

Defoliation of the crown by insect attack, frost and the like, immediately diminishes the increment. Nördlinger was able to trace the cockchafer years back into the eighteenth century by the aid of the narrow wood ring appearing in each case in the oak. It is interesting that the ring following the cockchafer year has already the normal breadth. It appears from this that the breadth of the ring depends much more on the materials newly formed by the leaves of the current year than on reserves stored up in the wood and rind. The same effect of defoliation was found by Schwarz (*loc. cit.*) in the pine and R. Hartig in spruces stripped bare by nun moth caterpillars. If less than one-sixth of the needles remain old spruces invariably die; when damage is less extensive they suffer a consequent loss of increment for many years, in which the scanty assimilated materials are extracted from the descending sap-stream by the starving cambium in the upper part of the stem and growth in the lower part of the stem may be at a standstill. The whole annual ring then often consists of only two rows of cells, an early wood and a late wood tracheid row, which remain very thin-walled but are distinguished by different widths.

In years of plentiful seed production, the fruit requires so much assimilated and reserve material that diameter growth is diminished, especially in the beech in full mast years.

An extensive literature has been called forth by the broadening of the annual rings which sets in when trees are given a more isolated position.[2] In already well developed crowns and in crops in a youthful condition, it appears in the first year. As a rule, however, the rising of the increment sets in first in the 2nd to the 4th year after isolation. Its amount depends less on the grade of thinning than on the species of tree, age, condition of the crop, and the quality of the locality. It may last until the crop is again closed above and below the soil by the spreading of the crowns and root systems, but its duration seems also to be not unlimited even in completely isolated trees. True "**Light Increment**" in a practical sense begins when more than 0.2 of the volume of the normal full crop is removed.[3] There then occurs not only a raising of the increment but also an alteration of the form of the stem (*see* Chap. VI, 3). The causes of light increment are sought in the stronger development of the crown and root system made possible by the increase in the space available. The improved lighting, together with the simultaneous increase in supplies from the soil, may be assumed to lead to increased

[1] Hartig, R., Lehrb. d. Anatomie u. Physiol. d. Pflanzen. Berlin, 1891, p. 264. Christison, D., Transact. Proc. Bot. Soc. of Edinburgh, Vol. 19, p. 101, 1891.

[2] The statements made here are based on the presentation of the subject by R. Weber in his Lehrbuch der Forsteinrichtung. Berlin, 1891.

[3] Handbuch der Forstwissenschaft. Hrsg. v. Chr. Wagner, 3 Aufl., Bd. II, p. 186. Tübingen. Laupp.

production of building materials which must be to the benefit of diameter growth. Moreover an increase, temporary it is true, in the transformation of the nutrient capital of the soil, in consequence of the more rapid decomposition of the humus constituents and nitrification (Hesselman, 1926) as a result of the open stand, is also brought into the explanation. A rise of increment on one side, right at the bottom of the stem, is, as is shown below, to be traced to a stimulus action of the wind, which operates more strongly in open stands.

The influence of the weather day by day on diameter increment and its course from spring to autumn was investigated by Friedrich [1] with the aid of a sensitive self-registering increment measurer, by which besides the daily variations of the diameter of the stem, the actual daily growth of the wood was measured and compared with the meteorological data. According to this, diameter growth proceeds especially well when the giving off of water is diminished and the water saturation of the cambium increased and thus particularly at night, by day only when atmospheric humidity is high.

Under certain conditions, which, however, must be regarded as pathological, the distribution of the increment over the different parts of the tree may depend on whether the part in question can be more or less abundantly fed by a supply of building materials. If the stem is girdled so that the descending stream of assimilates is interrupted, the increment below the level of the girdling does not take place ; above it, where the building materials accumulate, it is increased. If a branch is shaded so that it nevertheless remains alive but cannot send down any building materials to the main stem, the increment ceases in a long groove reaching from the branch to the ground, until the branch dies. Then new, transversely running, transmission channels [2] are formed in the healing tissues round the dead snag, which make the nourishment and diameter growth of the previously non-growing strip possible. The phenomenon is especially noticeable in mixed woods of beech with pines, larches and other light-demanding trees. In pure woods of beech, the shaded branches die off too rapidly by reason of the heavy shade for the formation of grooves to be clearly apparent.

3. Annual Ring Breadth and Growth Stimulus, Stem Form, Eccentricity, Pressure Wood.—Even on superficial observation of tree stems it is recognised that the breadth of the annual rings may not be equally great in all parts of the stem and may not be distributed in every stem in the same way at different levels and on different sides. In every wood, besides slender, almost cylindrical, regular, " full timbered " stems, there are also found " tapering " stems, diminishing rapidly in size from below upwards, and it will soon be noticed that the latter are always bigger crowned and freer grown, whilst the full timbered specimens are to be sought among the small-crowned members of the crop, restricted and hemmed in by their neighbours. Similar differences

[1] Friedrich, Über d. Einfl. d. Witterung auf den Baumzuwachs. Mitt. a. d. forstl. Versuchsw. Österreichs, 22 Wien, 1897.

[2] Mäule, Faserverlauf im Wundholz. Bibl. botanica, 33, 1895 ; De. Vries. Flora 59, 1876 ; Küster, Pathologische Pflanzenanatomie, 2 Aufl. Jena, 1916.

are presented by a comparison of crops in various localities. In narrow, windless valleys and ravines the stems are more slender and more cylindrical than on open slopes. The increment may also be unequally distributed on the sides of the stem. Many stems, especially of the pine, are found by measurement and often even by mere inspection, to be elliptical in cross section and show considerable differences in the breadth of annual rings on different sides of the stem, whilst the pith in elliptical stems is always eccentric and lies somewhere about one of the two foci of the ellipse. Generally even more uneven is the cross section of the branches and roots. Most conifer branches show furtherance of growth on the lower side, hardwood branches on the upper side, lateral roots always on the upper side (Fig. 87) often in such a manner that actual " board roots " (buttress roots) arise which always stand on their edges. On mountain slopes, the upper side of the stem is often favoured in growth, on the margins of woods, sometimes the strongly branched outer side, but not infrequently also the opposite side, is more strongly developed.

It was for a long time sought to trace these and other inequalities in the distribution of growth to differences in the nutrition of the cambium. The great importance mentioned above, of the total amount of nourishment for the amount of growth as a whole, lent support to this idea. Reasons were sought for the better supplying of food materials sometimes to the upper, sometimes to the lower parts of the stem or sides of the branches, sometimes to the branched side, sometimes to the unbranched side of the stem and thus leading to stronger growth of the cambium. All these researches directed to explaining the distribution of growth in individual regions of the cambium by local differences in nutrition, must now be regarded as having miscarried. The nutrition theory—apart from the pathological processes as described above—has missed fire all along the line. All observations on trees as on all other organisms agree that, in cases of undisturbed development, growth does not take place where the materials flow in, but the materials flow in to the place where growth is going on. Heinrich Cotta [1] as early as 1806 set up the position, which to-day may be almost regarded as prophetic, that " All saps are contained in their vessels under perpetual pressure and go by preference to where the greatest need for their utilisation is felt." Growth draws building materials to itself, it is not itself set in motion by building materials previously streaming in but by causes which, so long as nothing further is known of their nature, we call for the time being **Stimuli**, it being understood that this is only a very indefinite, provisional conception set up in default of more accurate knowledge, which is to disappear again as soon as their chemical or physical nature is better cleared up.

Clearness and order first came into the confusion of phenomena when Metzger,[2] in continuation of the classical work of Schwendener [3]

[1] Cotta, H., Naturbeobachtungen über die Bewegung und Funktion des Saftes. . . . Weimar, 1806, p. 47.

[2] Der Wind als massgebende Faktor für das Wachstum der Bäume. Mündener forstliche Hefte, III, 1893, and Studien über den Aufbau der Bäume nach statischen Gesetzen ; the same, V, VI, both 1894, VII, 1895 ; Konstruktionsprinzip des sekundären Holzkörpers. Naturwissensch. Zeitschr. f. Forst- u. Landwirtschaft, VI, 1908. E. Ulmer, Stuttgart.

[3] Schwendener, Das mechanische Prinzip im Bau der Monokotylen. Leipzig, 1874.

on the mechanical principle of plant structure, investigated stem-form from the point of view of the requirements of the tree as to mechanical strength.

Metzger's theory, confirmed by Schwarz [1] and supported by many works by physiologists on other plants, proceeds on the assumption that the principle of wood formation in the stem is governed by the requirement of the tree for mechanical strength.

The straining of the stem by the wind, whose pressure on the crown is conveyed to the lower part of the stem and increased by leverage the higher the tree and consequently the longer the arm of the lever, requires a reinforcement of the stem increasing downwards, and of the roots which anchor the tree in the soil, in proportion as the tree becomes higher and as it is more exposed to the wind. Crowded, small-crowned trees are less exposed to the pressure of the wind; they can, therefore, be more weakly constructed in the lower part of the stem and so more slender than isolated, full-crowned trees. The weight of the crown necessitates resistance in the stem to breakage which threatens whenever it is bent out of the position of equilibrium, especially when accumulations of ice and snow multiply the weight of the crown. The forest tree requires, moreover, a certain stiffness and immobility, because violent shaking and bending of shoots is shown by pathological investigations to be highly prejudicial to growth. The fulfilling of all these demands is opposed, however, to the tree's endeavour to expand its crown and root system as much as possible and to produce seed, because strengthening of the stem requires building materials which must be taken from the crown, roots and fruits. If both requirements are to be satisfied the stem must be so formed that it may possess the highest possible bending-strength in all parts, with the smallest possible expenditure of material. In fact, the stem, especially in conifers, less accurately in broad-leaved trees, nearly always satisfies the requirements of a **Beam of Uniform Resistance.**

If a beam is fastened at one end and bent by a force applied at the other, it breaks most readily at the fixed end. All the remaining portions of the beam are less exposed to danger. When, therefore, material has to be economised, the beam will not be made of the same thickness all along but may be allowed to decrease in thickness from the fixed end towards the other. Near the point of application of the force much thinner parts of the beam will sustain it than towards the fixed end where it works with greater leverage. A beam whose taper is so adjusted that it presents the same resistance throughout its entire length to a bending force applied to the end, or which, in other words, is equally likely to break in every cross section is called a "**beam of uniform resistance** (*see* Fig. 83). According to Metzger, the shafts of spruces are such beams and the changes which their form undergoes during life in consequence of altered requirements are also the same as those which must be carried out in such a beam according to mathematical laws. The greater the demands made on a beam of uniform resistance by a bending force applied to one end, the more

[1] Schwarz, F., Physiolog. Unters. ü. Dickenwachstum u. Holzqualit. von *Pin. silv.* Berlin, 1899.

rapidly must its strength increase from the free end towards the fixed one; the more does it resemble a tapering tree. And, in fact, trees are the more tapering, the stronger the hold the wind is able to get of them. The tapering form of trees grown in complete isolation, the specially great increment in the lower parts of the stem when trees previously crowded are opened up, the increased deviation from the cylindrical form of trees with increased elevation [1]—in all these phenomena Metzger sees a consequence of the mechanical action of the wind. When the mechanical requirements are very small, as in the suppressed trees of the dominated crop, the strengthening of the base of the stem is checked even to the temporary cessation of the formation of annual rings.[2] If the action of the wind in a wood is diminished by the growing up of the underwood, by the crowns of neighbouring trees entering the canopy or finally by the crowns being greatly reduced by the removal of the lower branches, the reason for strengthening the lower part of the stem disappears. The increase in diameter growth towards the base—always excepting the root swelling—becomes less and the stem more cylindrical. The relations which Metzger finds between the above mentioned behaviour of the stem and the height-growth of the tree are of special interest. The short-stemmed character of isolated trees in contradistinction to the long-stemmed character of those in close woods, the sudden falling off in height-growth after (selection) thinnings, the relatively greater height-growth of crowded stems, finds its explanation for him in the competition for building materials between the crown and stem. In all the cases mentioned, diminished height-growth goes hand in hand with increased demands due to the wind. Diminished height-growth, however, means nothing more nor less than feebler development of the leading shoot, and indeed also of other new annual shoots. The greater requirement for rigidity of the stem, brought into being by the action of the wind, has withdrawn building materials from the crown.

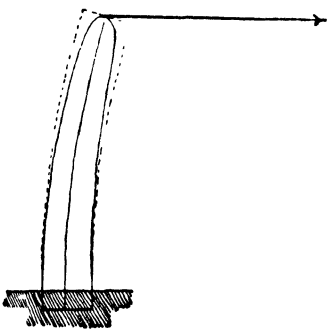


FIG. 83.—Beam of uniform resistance.

The mode of action of the wind in the diversion of food materials in one direction or another is called by Metzger an " impulse " (Anreiz). This may be understood as a true stimulus action like that of gravity on the direction of shoots and roots. The wind pressure bends the stem and places the cambium cells on one side under pressure and those on the other side under tension. These forces of pressure and tension act as a growth stimulus which is greatest and most frequent where the bending is greatest, and so where the stem is proportionally weakest. The form of the beam of uniform resistance of the dimensions required by the locally prevailing strength of the wind results automatically.

[1] Seiroku Honda, Einfluss der Höhenlage der Gebirge auf die Veränderung des Zuwachses der Waldbäume. Allgem. Forst.- u. Jagdzeitung, 1892, 361.

[2] Flury, Über gewisse Störungen in der Jahresringbildung. Schweiz. Ztschr. f. Forstwesen., 1926, p. 141.

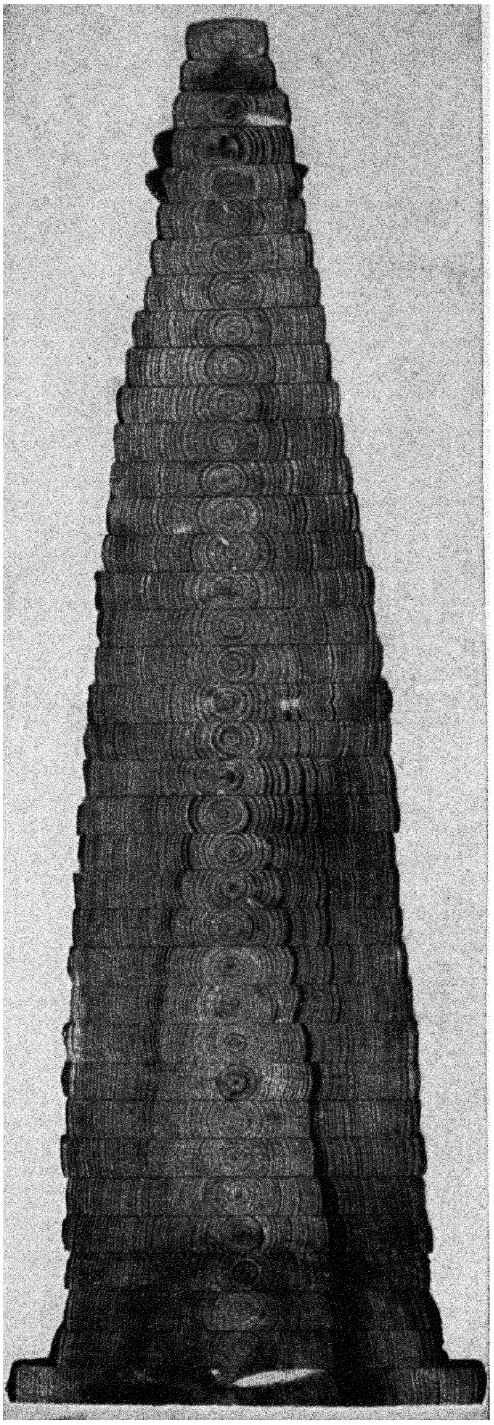


FIG. 84.—Stem pyramid of a 76-year-old Spruce formed of cross sections taken from the stem at intervals of 50 cm.; *see* also Fig. 85. Scale 1 : 3.6.

[*To face p.* 169.

The pressure and tension stimulus on the cambium occurs most frequently and strongly in the direction of the prevailing wind—in Germany south-west and west winds predominate—because the stem is more frequently bent in this direction. This results in the cross section of the stem taking the form of an ellipse whose long axis lies in the direction of the wind, or in sloping stems, in the direction of the

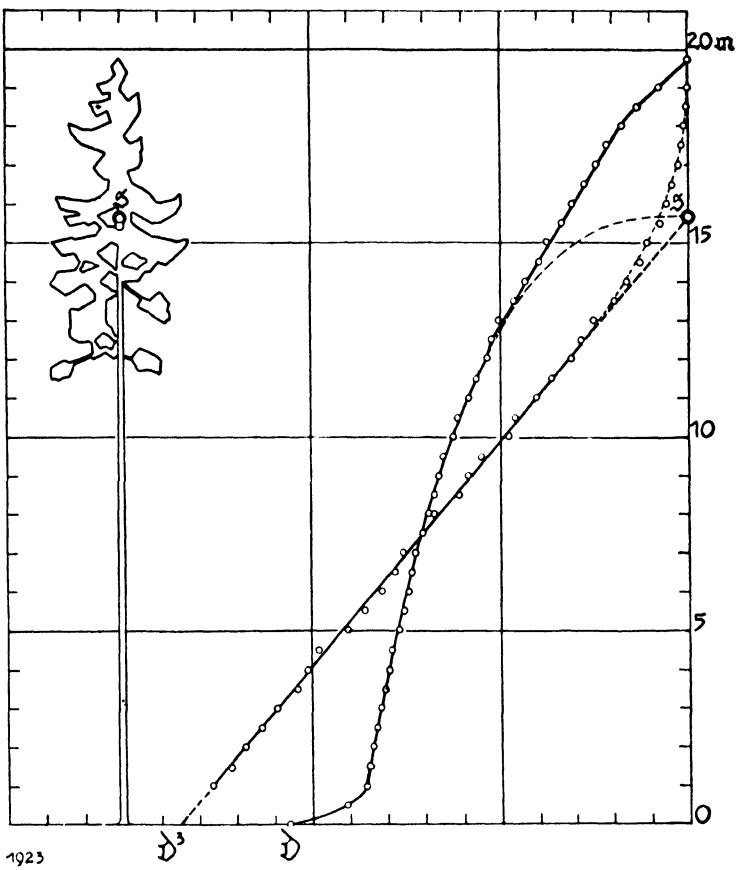


FIG. 85.—Stem analysis of the 76 year old Spruce (Fig. 84) from the Tharandt Forest Garden. The branch-free part of the stem, from a height of 1 m. to the beginning of the crown, forms a cubical paraboloid d (the cubes of the diameter, d^3, lie in a straight line through the centre of gravity s of the crown). Inside the crown, except for a short piece at the top, the stem forms a cone. The stem thus has the form of a beam of uniform resistance. Scale for the height 1 : 200, for the diameters 1 : 4. (Mch.).

slope. In conifers the side of the stem turned away from the winds always shows the greatest growth.[1] The advantage of this form for strengthening is obvious. A horizontal beam loaded on one side would not be made with a square but with a rectangular section placed on edge. The circular section of the beam is the best for strength only when forces act upon it from all sides. Exceptionally, in trees exposed to the wind on one side, thickenings of the rings occur at right angles to direction of the pressure. We shall come to this phenomenon again.

[1] Nördlinger, Forstbotanik, 1874. Hartig, R., Forstl-Naturwiss. Ztschr., 1896, p. 212

According to the laws of statics, a beam of uniform resistance is a cubical paraboloid, in which the third power of the diameter D_x in every position, is proportional to the distance x between the place of measurement and the point of application of the bending force. For every point in the beam, therefore, the equation $D_x^3 \div x = C$ holds; in which C is a constant, increasing with the bending force. The stronger the prevailing wind and the larger the crown on which the wind impinges, so much the stronger is the wind pressure and so much the greater the proportion between the diameter and the height of the tree, measured to the centre of gravity of the crown, which may be regarded as the point of application of the wind (Figs. 84 and 85).

This relation is thus the measure of taper. Inside the crown the area of attack of the wind falls off with the diminution of the crown.

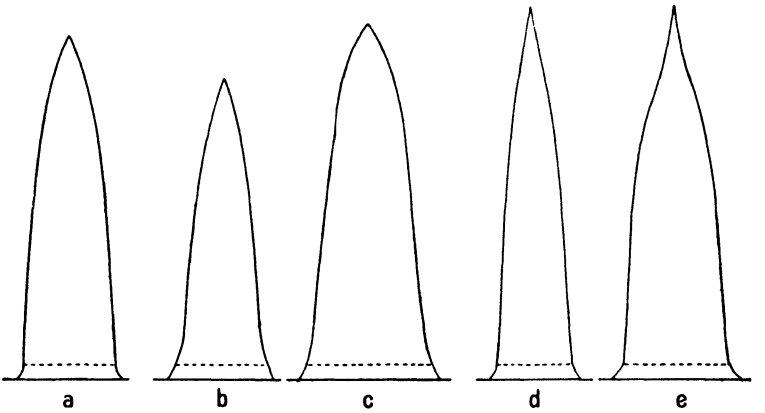


FIG. 86.—Stem-forms of the Silver Fir, Pine and Beech in longitudinal section. After Guthenberg in: Handbuch der Forstwissenschaft, hrsg. v. Chr. Wagner, 3 Aufl. Bd. III, p. 162. Tübingen, 1912, Laupp. The heights reduced compared with the diameters in the proportion 20 : 1. (*a*) 180 year Silver Fir; (*b*) 110 year and (*c*) 200 year Pine; (*d*) 120 year Beech grown in close stand; 160 year Beech grown, heavily branched in opener stand.

The part of the stem inside a regularly diminishing crown is therefore a cone. Extensive forestry experience shows that regularly grown stems do, in fact, form in the branch-free portions, a cubical paraboloid.[1] The cubic content if the stem is most exactly measured by the area of the middle section of the stem and its length, which, only in a paraboloid gives the correct volume.[2] Schwarz found the form of the cubical paraboloid very accurately realised. Numerous, as yet unpublished, measurements of spruces, pines and larches, on sites with the most varied wind-strengths, carried out at the institute of the editor of this edition gave the same result. The stem pyramid in Fig. 84 and the analysis of this stem in Fig. 85 may serve as an example from which it is to be seen that the whole stem, with the exception of a short root-swelling and a short piece at the top, damaged by the droughts of the last decade, corresponds in form with a beam of uniform resistance. Complications which may produce many deviations from the regular

[1] Maass, A., Die Ausbauchung in den untersten Teilen des Stammes bei Kiefer und Fichte. Mitt. d. forstl. Versuchsanst. Schwedens, 1913, H. 10.

[2] Kunze, M., Unters. über d. Genauigkeit der Inhaltsberechnung d. Stämme aus Mittenstärke und Länge. Mitteil. Sächs. forstl. Versuchsanstalt. zu Tharandt, Bd. I, H. 1. Berlin, 1912.

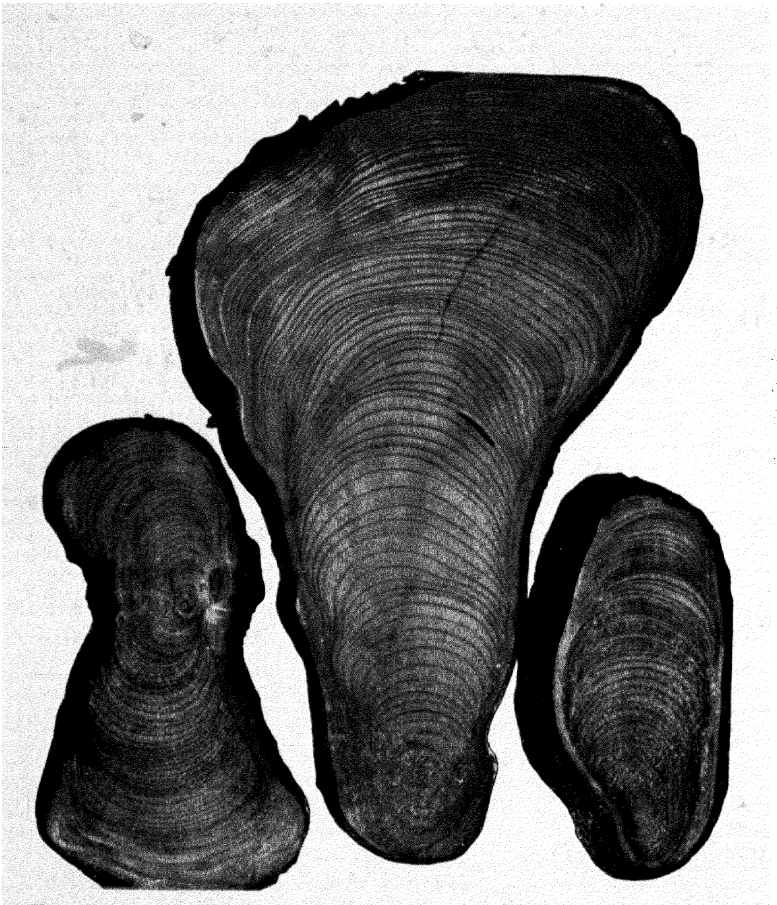


FIG. 87.—Eccentric diameter-growth of Spruce roots. Left: tendency to the T-girder form. (Mch.)

[*To face p.* 171.

form are produced by the strength of the stem timber not being the same in all parts. Especially is the strength determined by the ingrown branches which seriously weaken the wood. The values for the strength of timber found in branch-free pieces of wood cannot consequently be used for static calculations and since strength determinations in branchy wood do not exist in sufficient quantity, the question whether the stem is a beam of uniform resistance not only in form but also in strength, is not yet clearly answered. Below, in the region of the root-swelling, the stem is overthickened in form, also for mechanical reasons, not however comprehensible mathematically, which are connected with the transmission of the stresses from the stem to the horiontal lateral roots.[1] The deviation of the root-swelling from the form of a cubical paraboloid may extend upwards for several metres, especially in tapering isolated trees. When the root-swelling extends high up, the "neiloid" expresses the extreme form of tapering. The amount of tapering varies also with the species on account of the different shape and size of the crown resulting in unequal wind pressures. Pines, especially lowland pines are, as a rule, less slender and cylindrical than the highland pines, spruces and silver firs [2] (Fig. 8). The greatest irregularities in stem-form are often present in the stems of broad-leaved trees, which are partly the result of ingrown branches and are partly not explainable by any theory.

The oval- and board-form of lateral roots (Fig. 87) is most strongly developed in the angle where strong, surface-running, lateral roots branch from the stem at right angles and where, in consequence of the shallowness of the soil, tap-roots are absent—most finely in spruce stands in peaty soil. Often, also, the upper lateral roots have the form of railway metals. The strengthening recalls the struts with which the carpenter support vertical pillars and their usefulness for strengthening the stem against windfall is obvious. Fundamentally, the same pressure stimulus as in the one-sided thickening of the stem is doubtless operative here. The swaying stem produces by leverage a longitudinal pressure on the upper side of the lateral roots, and this pressure is the greater the less these lateral roots are relieved by deeply penetrating tap or sinker roots.

The increased formation of strengthening tissues, and one-sided eccentric growth by the one-sided movement of the stem, were produced artificially, among others, by R. Hartig [3] in spruce and Rasdorsky [4] in sun-flowers. Rasdorsky moved the stem of the experimental plant continuously to and fro by means of a mechanical device. The stem then developed an oval transverse section by the promotion of secondary wood formation, in which the greatest diameter was in the plane of bending. Only when damage was done by excessive movement did variations occur. If potted sun-flowers were supported with the tip of the stem free so that all pressure stimuli were absent, strengthening tissue was developed so feebly that the stem, left to itself, could not

[1] Leon, Technik und Naturwissenschaft. Zentralbl. f. d. ges. Forstwesen, 1915, p. 254.
[2] Münch, E., Beitr. z. Kenntn. d. Kiefernrassen Deutschlands. Allgem. Forst.- u. Jagdzeitung, 1925, p. 99 ff.
[3] Hartig, R., Holzuntersuchungen, Berlin, 1901.
[4] Rasdorsky, Ber. Dtsch. Bot. Ges. 43, p. 332, 1925.

sustain its own weight and bent over. Hofmeister had already proved the influence of wind experimentally by a comparison of free and tightly tied up stems. On the other hand oft-repeated experiments in which tension and pressure were applied in the direction of the longitudinal axis of plant members had generally no anatomical result.[1] The conclusion therefore is, that it is differences in tension on different sides of the shoot which bring about increased diameter growth. The negative results are, however, apparently explainable on the assumption that it is not static pressure or tension, but the frequent dynamic stretching and compression which acts as the growth stimulus.

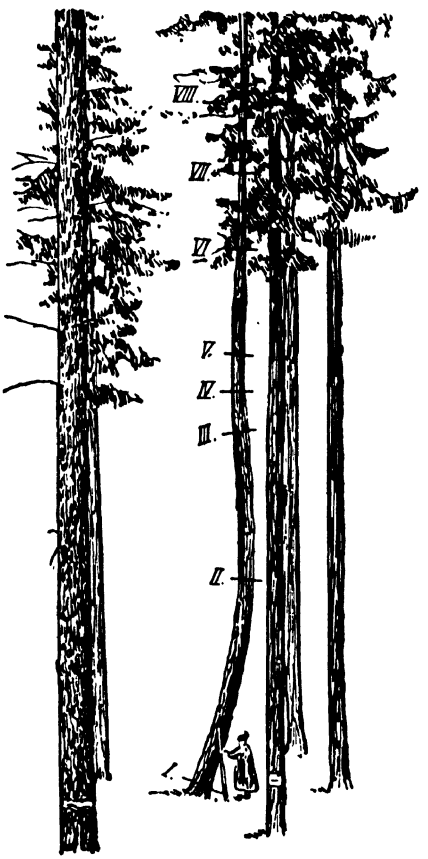


FIG. 88.—Spruce 30 m. high, set aslant by the wind, which has subsequently curved upwards. Note the over bending between II and IV. The stem sections in Fig. 89 were taken at the places marked. (Mch.)

The dissimilarity in structure of the upper and lower sides of horizontal branches [2] and sloping stems may indeed be explained by mechanical stimulation. According, however, to R. Hartig's [3] account, a similar result also occurs in fallen spruces when the stem is in contact with the ground in several places in such a way that it is never under tension. Here the force of gravity, whose strong formative action we have already recognised in geotropism, is alone able to act. In this case occurs one of those instances not rare in biology, where the form of an organ is influenced by causes which have nothing to do with the functions of that organ.

It must be assumed that a stimulus action of gravity, to which in this case conifer twigs react in an opposite sense to the broad-leaved trees, also plays the most important part in the eccentricity of branches (Epi- and Hypotrophy, Wiesner, 1868; also Epi- and Hyponasty). This stimulus effect is, however, altered by the mechanical stimuli and perhaps also by still other influences acting in the plant, so that it occasionally comes to light differently even in one and the same branch. It is

[1] Urspring, Beih. z. Bot. Zentralbl. XXIX, Abt. 1, 1913. Ball, Jahrb. f. wiss. Bot., 1903, p. 305. Tension does not increase the tensile strength of the tissues. The variations which occur are at present not fully explainable. Pennington, Bot. Gaz. L, 1910, p. 257 (Poplar, Robinia). Literature; Wiedersheim, Jahrb. f. wiss. Bot., XXXVIII. Bordner, Bot. Gaz., XLVIII, 1909, p. 251. Bücher, Jahrb. f. wiss. Bot., XLVIII, 1906, p. 271.

[2] The total increment appears to be the same in eccentric as in regular growth (Jaccard, Mem. Soc. Vaud, Sc. nat., 1925, 2, p. 141. Quoted from Bot. Zentralb).

[3] *Loc. cit*

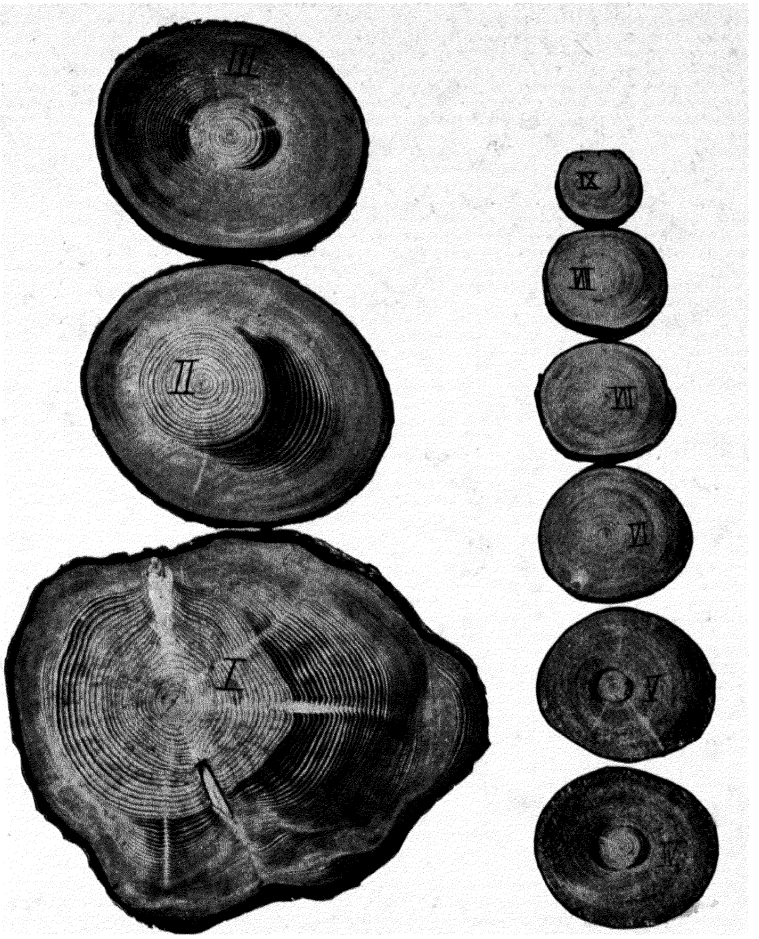


FIG. 89.—Cross sections of the stem of the Spruce represented in Fig. 88. The stem, now 30 m. high and 45 cm. thick at the base, was tilted to the right by the wind 80 years ago. The stem, at that time 25 cm. thick and 14 m. high, bent itself upwards and then with the leader over to the opposite side. The bending was completed in Section II in 15, in Section III in 4, in Section V in 3 years. Every deviation of the stem from the vertical led to eccentric growth and the formation of red wood on the side underneath at the time. In consequence of the bending going too far the formation of red wood in II and III passed from the right to the left hand side of the stem. As a result of repeated displacement of the direction of the stem, the red wood periodically takes up a different position. In the basal section this gives rise to a wavy course of the red wood and of the circumference of the stem. Not retouched. Scale: left, 1 : 8, right, 1 : 12. (Mch.)

[*To face p.* 172.

striking that it spreads from the horizontal or sloping shoots into the upright axis. Thus it is noticed that in vertically growing daughter twigs of mother branches which are thickened on the lower side, the pith is displaced towards the inside of the crown, *i.e.* towards the side near the main axis; and where the mother branch is thickened on the upper side, the opposite condition obtains.[1] In horizontal branch systems the influence of the position of the mother branch may make itself felt in a tilting of the plane of symmetry of the daughter twigs, as is to be observed in Fig. 90. It can also be seen here that, with thickening on the lower side (*Taxus*) the pith of the secondary shoot is directed towards the mother axis, with thickening on the upper side (Lime), away from it. In the lime the eccentricity has also extended to the rind.

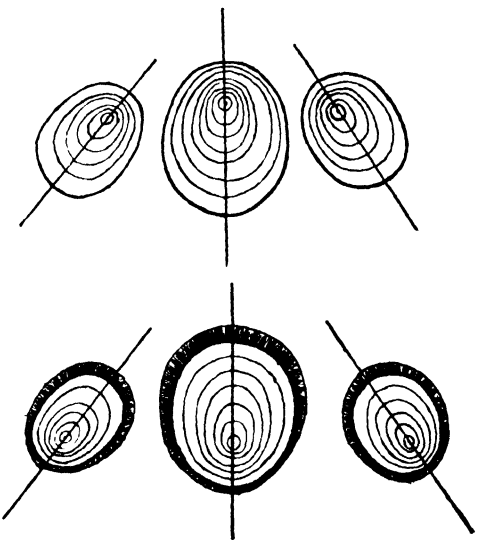


FIG. 90.—Above: Section of a horizontal branch of *Taxus* and a pair of its lateral twigs (Hypotrophy). Below: The same of a Lime (Epitrophy). After Wiesner.

The eccentric growth of the Vosges silver firs, whose annual rings become wider on the under side of the stem than on the upper side, for several years after tilting over, Mer[2] ascribes to the action of gravity, which in this way may contribute to the setting of the tree upright again.

Cieslar,[3] at the request of Wiesner, made experiments on the spruce which prove that here eccentricity with a thicker wood mass on the under side may be produced by altering the position of a shoot. The leading shoots of four eight-year old spruces were brought into a horizontal position in May by a gradual curve. After the lapse of two growing seasons, both the bent main stem and also the side shoots developed in the compulsory horizontal position, irrespective of their position on the main shoot, showed the promotion of xylem formation on the lower side. Thus the influence of position here outweighed that of their attitude towards the mother twig. Experiments by R. Hartig (*loc. cit.*) on spruces and Karzel[4] on broad-leaved trees had similar results.

In bendings by mechanical forces, only the sides of the stem lying in the plane of the direction of the force are stretched and compressed; on the two flanks of the stem at right angles to the direction of the force

[1] Wiesner, Untersuchungen über den Einfluss der Lage auf die Gestalt der Pflanzenorgane. I. Sitzber. d. Wiener Akad. d. Wiss., Bd. CI, 1892, and Ber. Dtsch. Bot. Ges., Bd. X, 1892.

[2] Recherches sur les causes d'excentricité de la moelle des sapins. Paris, 1889. Extr. de la Revue des Eaux et Forêts.

[3] Zentralbl. f. d. ges. Forstwesen, Wien, 1896. Also under Wiesner, Ber. Dtsch. Bot. Ges., 1896.

[4] Karzel. Stzgsber. Akad. d. Wiss., math.-natur. Kl. CXV, Wien, 1906.

there is a neutral fibre which is neither elongated nor shortened longitudinally by bending but is only curved. As these neutral fibres, apart from exceptions to be mentioned later, do not apparently alter their growth, it is to be concluded that only forces acting in the direction of the fibres act as growth stimuli. In conifers growth is promoted on the side made concave by bending and thus shortened, but is checked on the convex, elongated side as compared with the neutral flanks. In broad-leaved trees this is reversed.[1] The same thing holds good if the mechanical stimulus is replaced by the gravity stimulus. In extreme cases the check on the narrower side is so great that thickening stops for years, so that the number of annual rings on each side becomes different.[2]

Arnold Engler [3] has cleared up these questions to a large extent by thorough investigations, especially on broad-leaved trees. In broad-leaved trees diameter growth is promoted by the gravity stimulus on the upper side, by pressure stimulus on the lower side. As a rule the gravity stimulus preponderates in broad-leaved trees. If both stimuli act equally the strengthening occurs in the direction of the resultant of the two forces, *i.e.* in horizontal branches to right and left. The branches by this means acquire the mechanical advantage of greater flexibility and elasticity. The thickening on bent stems is often displaced laterally from the plane of bending, a phenomenon which, like other occasional variations, is not yet fully explained. They may be connected partly with resultant action and partly with the bending being accompanied by torsion.

Hand in hand with eccentric diameter growth go peculiarities in the structure of the wood. In eccentric roots and shoots in dicotyledons there occurs a multiplication and a widening of the vessels, a greater breadth of the pore ring and relatively more late wood. Multiplication of the parenchyma cells, medullary rays [4] and mechanical elements and the dissimilar development of the bark on opposite sides are also observed.[5] In *Pinus strobus* [6] the tracheids of the upper side of the branches are longer than those of the more strongly developed lower side. The difference falls off gradually from the base of the branch towards the tip ; from which it may be conjectured that in this instance loading conditions are not without influence on the length of the tracheids.

In spruces, silver firs, pines and many other plants the formation of **Red-Wood (Pressure Wood)** occurs in eccentric stems and branches.[7] This term is applied to the dark- or brownish-red portions of wood

[1] Konstruktionsprinzip des sekundären Holzkörpers. Naturw.-Zeitschr. f. Land- u. Forst.-wirtsch, 1908.

[2] Mer, Causes des variations de la densité des bois, etc. Bull. de la soc. bot. de France, T. XXIX, 1892.

[3] Engler, A., Tropismen und excentrisches Wachstum der Bäume. Zurich, 1918.

[4] Jaccard, Verteilung der Markstrahlen bei den Coniferen. Ber. Dtsch. Bot. Ges., XXIII, 1915.

[5] Lämmermayr, Sitzber. d. K. Akad. d. Wiss., math. nat. Kl., Wien, 1901.

[6] Baranetzki, Flora, 1901.

[7] Cieslar, Rotholz der Fichte. Österr. Zentralbl. f. d. ges. Forstwesen, April, 1896 ; Hartig, R., Rotholz der Fichte. Forstlich. naturw. Zeitschr. V, 1896 ; the same, Holzuntersuchungen, 1901 ; Schwarz, Frank, Dickenwachstum und Holzqualität von *Pinus silvestris*. Berlin, 1899, Parey. Ursprung, *see* below p. 175 ; Petersen, Bot. Tidsskr., XXXIII, Kjöbenhavn, 1914.

which appear in the under sides of conifer branches, on the leeward side of conifer stems exposed to the wind, sloping and prostrate stems, in natural curves as in the erection of lateral shoots and on the concave side of forcibly bent shoots and crooked roots—in short in all cases where gravity acts across the stem axis or bending produces a one-sided pressure (Fig. 89).

In such places the tracheids are shorter than in other parts of the wood, very thick-walled and of round section. Spiral markings are found on their walls and the unlignified inner layer, which is so strongly defined in white-wood, is absent. Red-wood is poor in water and has a high specific dry weight. The causes of red-wood formation [1] are allied to those of eccentric growth. Where red-wood and eccentricity are artificially produced by the bending of branches or stems, the concave side of the bend is compressed, the convex side is under a tensile strain and the pressure acts as a stimulus as the result of which red-wood formation occurs. The same stimulus is the cause of red-wood formation on the compression side of trees exposed to the wind. It is consistent with this that red-wood is more resistant to pressure,[1] and richer in lignin than white-wood, which, on the other hand, possesses twice as great a tensile strength. The meaning of red-wood formation in these cases lies in its acting against the bending. It is also asserted,[2] however, that the pressure resistance of red-wood is not higher, and in fact is lower than that of white or normal wood. This is still to be further cleared up. It is certain that red-wood possesses an extraordinary hardness, so that it is scarcely possible to drive a nail into it. Wood-cutters speak of a red, hard side of the spruce, handicraftsmen of a hard, nailfast and a soft side of the pine, meaning thereby red and white-wood. That the combined action of pressure and tension cannot be always the sole cause of the formation of red-wood, is apparent from experiments [3] in which twigs of pine and cypress were bent into circles and ellipses. Red-wood appeared here on the sides directed towards the earth, irrespective of whether this was the concave or the convex side of the curve. The red-wood forming cambium thus found itself now under tension and now under pressure. Here the most important role in the formation of red-wood is to be ascribed to the stimulus action of gravity and this is also to be assumed for the normal formation of red-wood on the under side of spruce branches and slanting or prostrate stems.[4]

Böning [5] examined a large number of woody and herbaceous plants and found it in the main confirmed, that it is pressure and tension conditions which produce hypotrophy in conifers and epitrophy in broad-leaved trees, as well as red and white-wood (Pressure and Tension

[1] Sonntag, Jahrb. f. wiss. Bot. XXXIX, 1903.

[2] Schwappach, Unters. über Raumgewicht und Druckfestigkeit, etc. I, Die Kiefer. Berlin, 1897.

[3] Ewart and Mason-Jones, Ann. of Botany, XX, 1906.

[4] Further observations and experiments *see* Jaccard, Abnorme Rotholzbildung. Ber. Dtsch. Bot. Ges., XXX, 1912. Ursprung, Über das exzentrische Dickenwachstum bei Wurzelkrümmungen und die Erklärungsversuche des exzentrischen Dickenwachstums. Beihefte z. bot. Zentralbl., Bd. XXIX, Abt. 1, 1913. Ball, Jahrb. f. wiss. Botanik, 1903, p. 305.

[5] Böning, K., Über den inneren Bau horizontal geneigter Sprosse und seine Ursachen. Mitteil. der Deutschen Dendrologischen Ges., 1925, p. 86. Ber. Dtsch. Bot. Ges. 40, p. 279, 1922.

wood). In the ash the branches are eccentrically formed, and the upper and lower sides lignified to a different extent. Generally in broad-leaved and coniferous wood the secondary membrane is unlignified in tension wood and strongly lignified in pressure wood (red-wood). In the majority of species of plants examined, including bushes and herbaceous plants with a continuous ring of wood, dissimilarities in structure are found in the sides under tension and pressure in shoots exposed to the action of one-sided tension and pressure (branches and artificially bent shoots). In several species of trees and bushes, however, including *Pyrus* and *Crataegus* and in many herbaceous plants whose woody elements are arranged not in a continuous wood ring but in separate vascular bundles, the difference is absent.

The literature contains no account of the nature of the bending stimulus and the reasons why one-sided pressure and tension promotes or hinders growth in thickness. As for growth in general, it has been conjectured that it must be set in motion by particular stimulating bodies, called **Growth Enzymes** or **Growth Hormones.** It must consequently be assumed that cessation of growth is caused by the absence of growth enzymes or the presence of inhibiting substances. Moreover in our case, it appears, according to Münch,[1] that changes in the composition of the formative sap are involved. According to an old, apparently too little noticed work of Kraus,[2] mechanical movements of shoots have in a very short time an extraordinarily great influence on the composition of the sap. When shoots of various plants, including woody plants, were shaken so that they were bent into a bow-shape with the tip hanging over, the concentration of the cell sap on the convex side became immediately higher than on the concave side, actually in consequence of a higher content of sugar, which was freshly formed at the moment of shaking. The shaking did not need to be very violent; it might be kept within the limits found in nature in moderately moving air. Sugar was also produced by movement without the production of permanent bending. With the new formation of sugar the disappearance of free acids from the cell sap was observable. According to experiments by Münch,[1] a moderate bending of stems of various broad-leaved species, results instantaneously in a great alteration in the turgor pressure of the sieve tubes. If the rind of a standing tree at rest is cut through as far as the cambium, large drops of sieve tube sap exude, with especial abundance in the lime and red oak (Fig. 71). This exudation is, however, absent if the stem is somewhat bent beforehand. A moderate amount of bending, such as might occur in a thin stem in a strong wind, was sufficient to check the outflow of sap. The turgor pressure in the sieve tubes must have so diminished by some process or other, perhaps in the way established by Kraus, that it no longer suffices to squeeze out the sap. It is hardly conceivable that extensive changes in the composition and turgor pressure of the formative sap remain without influence on the nature and extent of

[1] In an, as yet unpublished, work.

[2] Kraus, Gregor. Abhandl. d. Naturforsch. Ges. zu Halle, Bd XV, II, 1880. *Comp.* also Gabnay, Ref. Bot. Zentralbl., 1892, III, 237. Schley, E., Bot. Gaz. 69, p. 480, 1920. Philipps, Bot. Gaz., 69, p. 168, 1920.

growth. It is easy to imagine a hypothetical cause for the alteration of the cell-sap by pressure and tension. It recalls the re-formation of sugar by frost which, it is supposed, comes about by the sugar-forming enzyme being brought into contact with the starch by the freezing, whether it be by a purely mechanical process or by the alteration of the permeability of the plasma in which the enzymes are enclosed. Mechanical pressure and tension may act in the same way. In Münch's experiments the full cell-pressure in the sieve tubes re-established itself in about fifteen minutes. The bending must therefore be oft repeated if it is to markedly influence growth, which agrees with the observations mentioned. The growth stimulus and so also ring-breadth and stem-form could thus be traced to quite simple, purely physical and chemical causes, if a fundamental connection could be proved between the alterations described in the sap and the alterations in growth after bending. Gravity also, when it acts across the direction of the shoot, according to a similar work by Kraus, results in a variation of the sugar content on the opposite sides of the shoot. If this phenomenon is not explainable on such an easily comprehensible hypothesis, it does appear to point to the gravity stimulus and its effect on the quality and breadth of the annual ring being a simple chemical process.

Other theories of annual ring breadth and stem form may be briefly discussed. Hohenadl [1] conceives the stem, not as a beam of uniform resistance to bending, but as a beam of uniform resistance to pressure. The increase of thickness of the stem from above downwards would be proportional to the increasing weight of the stem itself above the place of measurement. This theory is, however, not adequately proved. It is also hard to understand, because a minute part of the cross section of the stem possesses sufficient resistance to crushing to take up the whole of the vertically acting pressure of the shaft. With a resistance of only 150 kilogrammes per square centimetre a stem of 7 square centimetres would suffice to carry a tree with a wood volume of 1 cubic metre and 1,000 kilogrammes weight, whereas such a stem has a basal area of about 700 square centimetres, so that it is overstrengthened 100 times in its resistance to crushing.

Jaccard [2] has sought more thoroughly to establish the theory, already many times discussed before his time, that the breadth of the annual ring and the form of the stem are governed according to the water-transport requirement of the tree, so that the stem should be a body of uniform water-conducting capacity. In fact earlier researches by Jost on bean seedlings demonstrated a certain correlation between the formation of the conducting system and the mass of the leaves, and in the beech Hartig and Weber [3] found over the whole length of the branch-free stem a constant number of tracheae in each annual ring and so a constant conducting capacity of the annual ring (*compare* p. 189). As, however, the lumena of the conducting elements only form a part of the cross section of the wood, the breadth of the annual ring

[1] Hohenadl, W., D. Aufbau d. Baumschäfte. Forstw. Zentralbl. 46, 1924.

[2] Jaccard, Neue Unters. über die Ursachen des Dickenwachstums der Bäume. Naturw. Zeitschr. f. Forst- u. Landwirtsch., XIII, 1915. The same, 1913, p. 241.

[3] Hartig and Weber, Das Holz der Rotbuche. Berlin, 1888.

may follow quite other laws, even when the conducting capacity is uniform, as indeed follows from the Hartig-Weber measurements. Moreover it is not one single annual ring but a large number of annual rings, apparently varying according to requirements, which are employed for the conducting of sap, and since the breadth of the water-conducting sapwood and the rapidity of the transpiration stream in different annual rings and at different heights in the stem, are not yet sufficiently known, the water-conductivity theory of stem form is not capable of proof. As has been shown by ringing and sawing experiments,[1] a very small portion of the existing wood passages suffices to provide for the transpiration stream for years. Part of the material presented by Jaccard besides forms rather an argument for the mechanical resistance theory.

A small experiment of the editor's may serve to strengthen the idea that the importance of diameter growth lies more in the strengthening of the stem than in providing for sufficient water transport. A 3 centimetres thick goat willow was ringed in the spring. The stem and crown above the ringing place developed vigorously and showed no apparent shortage of water; but below the ring the stem, which remained thin, was unable to bear the meanwhile increased load of the crown and broke off at the ring after as little as two months.

4. Causes of Annual Ring Formation.[2]—In colloid substances such as gelatine, layering and zone formations may be brought about by the addition of suitable substances, which recall the marks on striped leaves, the fairy rings of fungi and also the annual rings and other zonal markings in timber. Such zones are formed also under absolutely uniform external conditions. They depend only on the properties of the mutually reacting substances in the gelatine. Küster [3] has pointed out that in such processes there is to be found a possible explanation of the above mentioned phenomena in plants. According to his deductions it might be conjectured that chemico-physical processes, themselves rhythmical, may be acting in the setting up of rhythmically recurring structures in cells, tissues and plant members. A serious application of this to annual ring formation is so far quite out of the question.

In order to acquire a full insight into the causes of the formation of annual rings it is first necessary to determine wherein this actually consists, *i.e.* it must be quite clear what properties of the xylem give rise to the ring-like markings on the cross section.

To superficial observation, the difference between early and late wood consists in the former appearing more porous and open than the latter and often differently coloured. For a full determination the help of a microscope is necessary. Then the commonest and often the only mark of the boundary of the annual ring, is the flattening of the last wood elements of the summer in the direction of the stem radius. It may go hand in hand with alterations in their mean length and

[1] Strasburger, Bau und Verrichtung der Leitungsbahnen. Jena, 1891.

[2] Küster, Rhythmus im Leben der Pflanze. Zeitschr. f. allgem. Physiologie, 1916. Kniep, Rhythmischer Verlauf pflanzlicher Lebensvorgänge. Die Naturwissenschaften, 1915.

[3] Über Zonenbildung in kolloidalen Medien. Jena, 1913, G. Fischer.

extends to the medullary rays in the same way as in the actual wood. The transition from the elements formed earlier in the year to these flattened elements may occur suddenly, but may also be quite gradual, whilst the unflattened first-formed wood of the following spring always joins on abruptly. In the broad-leaved trees, to the flattening of the late-wood elements is added a narrowing or a diminution of the vessels in favour of wood-fibres and tracheids. The meaning of this phenomenon is conceived by Haberlandt [1] and Hartig [2] to be as follows. The greater number of vessels and the greater width of the other water conducting organs in the spring wood, corresponds with the requirements of the tree for suitable water conductors which makes itself felt at the beginning of the growing season. Once these are formed the requirements of increased strength may be satisfied by the narrower elements of the late wood. In conformity with this idea, heartwood trees especially, exhibit a spring zone with numerous or large pores. The heartwood does not take part in the conducting of water. As, however, the formation of heartwood affects new annual rings each year, it is especially important, on account of the narrowness of the remaining zone of sapwood, to provide substitute channels for the conduction of water as early as possible. The willows present an exception, in which, in spite of the formation of a conspicuous heartwood, the vessels are regularly distributed in the ring. Hartig considers this to be associated with the fact that the annual shoots do not unfold suddenly and all at once, as in the oaks, but increase the number of their leaves by prolonged growth throughout the summer, thus making a regular progressive increase in the number of conducting channels in the annual ring necessary. To apply this explanation to the ash is difficult because it does not unfold its leaves with a rush (*see* Fig. 10) and yet forms a spring wood zone of large vessels. Perhaps its generally greater water requirement plays a part. It is not, however, in any way possible to conceive the formation of open wood in the spring as a consequence of an increased demand for water. The broad-leaved trees begin to form wood and, in fact, open wood in the spring, often before coming into leaf, and the spruce produces pronounced open wood before the breaking of the buds and thus when it is practically in the same condition as regards foliage as when it formed close wood in the previous summer. It is also very doubtful if more water is required in the spring than in the height of the summer when the formation of close wood has already begun.

A third, but less constant characteristic of the boundary of the annual ring, is the special thickness of the membranes of the late wood. In the pine the walls of the last tracheids of a ring may be almost twice as thick as those of the first, and in the hornbeam also they show a marked increase in thickness. In other cases, however, as in the vessel-like tracheids of the birch, alder, poplar, willows and elder, likewise also in the wood parenchyma, the wood fibres and fibre-like tracheids, the thickness of the walls remains about the same throughout the whole breadth of the annual ring and in many cases even diminishes towards the autumn boundary. In the conifers thick cell walls in the

[1] Physiologische Pflanzenanatomie. [2] Lehrbuch der Anatomie, etc., and *loc. cit.*

late wood are widely distributed but not constant. Indeed the various parts of one and the same branch, like the various parts of the same annual ring, behave differently. Thus, according to Kny,[1] in the common juniper and others, the late tracheids in side branches have thinner membranes than the tracheids formed before them in the same year and the early tracheids of the following year; albeit only in the more strongly developed wood of the underside of the branch. Repeated alternation of unusually thick-walled, late-wood-like tracheids with thin-walled elements in different regions of one and the same annual ring, are instanced for the pine (De Bary, Anatomie), *Thuya occidentalis* and *Tsuga canadensis* (Kny, *loc. cit.*).

The question of the reason for annual ring formation or the importance for the plant of the anatomical differences between early and late elements of the annual layer, is not the same as that of the cause of the formation of rings. It is necessary to distinguish here between the two; first the fact of growth in thickness by layers and secondly the occurrence of anatomical differences which give rise to the ringed appearance. The first does not necessarily include the second. Growth in layers may quite well take place without the layers being visibly differentiated from each other. For the explanation of growth in layers *per se*, everything which has been said above (p. 11, 61, etc.) on the periodic phenomena of plant life is applicable. The power of growing in thickness by layers is inherent in the organisation of woody plants, but conditions outside the inherited organisation determine when the formation of a layer shall begin or end.

Also in reference to the second question, that of the causes of the formation of early or late wood, a distinction must be made between the inherent capacity to produce this or that woody element and the conditions under which it actually happens. These conditions are discoverable by research. That capacity may continue to be termed the, for the time being inexplicable, inner cause of annual ring formation.

Older attempts by Sachs [2] and De Vries [3] to explain the increasing density of the annual ring by a rind pressure increasing in the course of the summer with the circumference of the stem, have been refuted by Krabbe.[4] He showed that the supposed increase of rind pressure in the summer did not, in general, occur. If a ring of rind on a branch or stem is loosened from the wood, it shrinks spontaneously in such a way that, if an attempt is made to replace it, its two ends will no longer meet. To bring the band of rind to its original length a certain force is necessary, which gives a measure of the condition of tension under which the rind is on the untouched tree. This tension—the tangential strain on the rind—when divided by the radius, gives the pressure exerted by the rind in the direction of the radius of the tree.

$$\text{Radial pressure} = \frac{\text{Tangential tension}}{\text{Radius}}$$

[1] Kny, Wandtafeln. VI, Berlin, 1884, Parey.
[2] Lehrbuch. 1. Aufl., 1874.
[3] De l'influence de la pression du liber sur la structure des couches ligneuses annuelles. Extr. d. Archives Néerlandaises, T. XI, 1876.
[4] Sitzber. d. Berliner Akad., LI, 1882, p. 1093.

Krabbe determined the tangential tension by stretching the loosened rind ring to its original length by weights over round wooden discs of the diameter of the stem in question. He found that, so long as the rind has not undergone any considerable alteration by bark-formation or other processes, it does indeed increase with the diameter increment of the wood but not so greatly that the radial pressure likewise increases with the increase of the stem radius. The pressure remained the same or showed rather a decrease, because the rind extended in area by growth on its own account and became wider.

The only exception was presented by an ash branch, and here the pressure of the rind, with an elongation of the radius from 18 to 25 millimetres, had only undergone an increase of 0.1 gramme. Moreover, sometimes, as in the lime and pine, the transition from the other wood elements to the flattened form is so abrupt that, as Krabbe says, it is quite impossible to understand whence the sudden pressure which would bring about such a flattening of the cells in a radial direction, could come. Krabbe [1] observes in a later work that growth in thickness, and in particular the radial diameter of the wood elements in conifers, may indeed be reduced by artificial pressure, but only by one of 3–5 atmospheres, which far exceeds the natural rind pressure. This latter Krabbe in the work of 1882 had determined in May, June and August as 1.11 (*Populus alba*); 1.7 (*Castenea vesca*); 0.5 (*Pinus strobus*); 0.32 (*Pinus sylvestris*), etc., atmospheres with a maximum of 1.7 and a minimum of 0.227. Krabbe had calculated the growing force of young cambium cells at 10 atmospheres in conifers and at least 15 atmospheres in broad-leaved trees. J. Friedrich [2] was able to confirm these results and gives 8–10 atmospheres as the pressure at which injury to growth begins. Through all these observations of Krabbe the experiments of De Vries lose their demonstrative power. De Vries's artificially produced "spring wood" and "autumn wood" are to be regarded as the pathological results of injury and must be sharply differentiated from natural products.

Krabbe did not link up a well-founded theory of annual ring formation to his statements. Moreover explanations attempted later have not fully attained their object. They are based on the mutability of the wood elements, especially the tracheids of conifers, under the influence of changing water supply. The observations of Lutz [3] have been particularly instructive in this regard. Lutz defoliated seven 6–10 year old beeches and five 5–7 year old pines at different times of the year and removed all newly formed buds each time. The pines stood defoliation badly; they died off, but produced woody growth beforehand when the defoliation took place after the breaking of the buds. In this case they formed wood until their reserve of starch was used up. The elements formed after the defoliation, strangely enough, exhibited the form of early tracheids, even when the operation was carried out at a time when otherwise autumn wood is

[1] Sitzber. d. Berliner Akad., 1884.
[2] Einfluss der Witternug auf den Baumzuwachs. Mitteil. a. d. forstl. Versuchswesen Österreichs, XXII, Wien, 1897, p. 146.
[3] Beitr. z. wissecschaftl. Botanik, hrsg. von Fünfstück I, 1. Stuttgart, 1895.

wont to be formed. He concluded from this, as well as from observations on the dependence of tracheid-width on the weather, that the width of the tracheids depends on the water content of the stem. His proofs are, however, insufficient and are in disagreement with other observations.

Thus Christison,[1] in Uruguay, in a climate with irregularly alternating, long, dry and rainy periods, nevertheless found clear annual rings in robinias corresponding in number to the age of the tree. In this connection may be considered the deductions of P. Groom,[2] who found the American species of pine with narrow tracheids (24–39 /1000 millimetres) generally xerophilous as regards distribution and locality and those with the widest tracheids (up to 50 /1000 millimetres) hygrophilous. The width of the wood elements in the pines, junipers and oaks is certainly a species and group characteristic; the species with wider elements are, however, at home in moister places. Exceptions are explained probably in part by the sources of error which are not small, since tracheid widths vary with the height in the stem, with the side of the tree even in the same annual ring and with the locality, and, on the other hand, the climatic and edaphic conditions are difficult to determine exactly.

Strasburger has suggested a hypothesis as to the way in which the water supply acts on the cambium which gives a physiological basis to the connection, supposed by Haberlandt and R. Hartig to exist, between the water supply and the change from porous early wood to solid late wood. Strasburger supposes the conditions prevalent in the water channels to exert a quite definite stimulus on the wood elements which are in process of development and to determine thereby the nature of their construction. As long as the water channels to the places of demand are not yet set up, such a stimulus may consist, *e.g.* in water being given up to the young wood cells; it may, however, also be given by any other consequence of the springtime superfluity of water. The stimulus leads to the formation of vessels or other wide-lumened elements. As soon as new water channels are provided in this way it ceases, and now the influences become effective which express themselves as the need for mechanical strengthening.

The first to undertake to explain, on experimental grounds, annual ring formation by the water supply to the cambium as apart from nutrition as a whole, was Wieler, after R. Hartig [3] had suggested such a connection. Hartig had brought into the explanation the worse or better nourishment of the cambium at different times of the year; though, by reason of the want of closer knowledge, quite opposite hypotheses may be constructed about this. Wieler [4] observed that in small robinias and sessile oaks which were raised in nutrient solutions,

[1] Transactions Proc. Bot. Soc. Edinburgh, 1891. Ref. Beih. z. Bot. Zentralbl., 1891, p. 533.

[2] Tracheid caliber in Coniferae. Bot. Gaz., Vol. LVII, 1914; East Indian Pines: Linn. journ. Bot., Vol. XLI, 1913.

[3] Holzuntersuchungen, 1901.

[4] Über Beziehungen zwischem dem sekundären Dickenwachstum und den Ernährungsverhältnissen der Bäume. Tharandter forstl. Jahrb. Bd. XLII, 1892. Über Anlage und Ausbildung von Libriformfasern in Abhängigkeit von äusseren Verhältnissen. Bot. Ztg., 1889, p. 517. Über die Beziehungen zwischen Wurzel und Stammholz. Tharandter forstl. Jahrb., Bd., XLI, 1891.

in those parts of the stem which had developed under water or in a very moist atmosphere, the new wood was poorer in wood fibres and that its elements were abnormally widened in the direction of the stem radius. Wiel r was also able to bring about anatomical changes by chemical action. In shoots of *Phaseolus multiflorus*, the common scarlet runner, and of *Vicia faba* (the broad bean), the vessels remained smaller when the plants were raised in phosphoric acid free or in mannite-, cane sugar-, gum-, potassium saltpeter- or potassium nitrate-containing solutions, without the reduction of the cross section of the vessels being in proportion to the osmotic power of the solution.

Dassonville [1] showed that in the lupin, under the influence of salts dissolved in the water, the number and diameter of the vessels increase and a closed ring appears in the stem, whilst on cultivation in distilled water, only isolated vascular bundles are formed. The composition of the nutrient solution also influences the lignification of the endodermis, the number and wall-thickness of the fibres and the size of the parenchyma cells. Kohl [2] found that the number and diameter of the vessels increase and diminish with changes in transpiration and that the strengthening tissue (collenchyma and sclerenchyma) develops more strongly in moist soil with dry air than in a moist atmosphere or with a general shortage of moisture. Lothelier [3] also observed a reduction of the bast- and wood-fibres in cultures in a moist chamber. Frank Schwarz [4] opposed Wieler and Lutz. According to his observations annual rings of specially dry years (*e.g.* 1893) are distinguished by the falling off of the percentage of late wood and also in other years with a dry August, little late wood was formed.

If the cause of late wood formation is to be found in shortage of moisture in the cambium, it is to be expected that conversely much late wood would be formed in dry periods. The large irregular variations in water-content of older trees, whereby maxima may occur in the height of summer, the incomplete formation of late wood in young plants which deprives the observations of Lutz of part of their validity, the increased activity of growth in places of compression, which at any rate does not point to a shortage of water there, though it may nevertheless be associated with the formation of cells of the late wood type, further the fact that cells flattened in the direction of the radius ought not to be summarily identified with true, late wood cells; these and other details of Schwarz's copious work, again show the mutability of the wood elements, the explanation of whose formation must however not be sought in a single cause alone. Schwarz is of opinion that the appearance of late wood may, in the first place, be the consequence of the pressure conditions prevailing in the cambium, whereby he must, it is true, assume that the pressure effect remains "latent" at the time of the formation of early wood.

[1] Compt. rend., T. CXXV, p. 794, 1897; Vöchting, Anatomie und Überernährung beim Wirsing. Nachr. d. K. Ges. d. Wiss., Göttingen, 1902, und Untersuchungen zur experimentellen Anatomie u. Pathologie d. Pflanzenkörpers. Tübingen, 1908, Laupp.

[2] Die Transpiration der Pflanzen und ihre Einwirkung auf die Ausbildung pflanzlicher Gewebe. Braunschweig, 1886. Experimental plants were *Tropaeolum*, *Hedera*, *Lamium album*, *Phragmites*.

[3] Rech. anat. s. l. épines et les aiguillons d. plantes. Mem. I. Ann. d. soc. nat., 1893.

[4] Physiologische Untersuchungen über Dickenwachstum und Holzqualität von *Pinus sylvestris*. Berlin, 1899. Parey.

Klebs [1] has very efficiently represented the standpoint that the essential inner conditions for the growth of the cambium as well as of the growing point are to be found in *chemical reactions*. The same conditions which are generally favorable to the activity of the growing point and to growth in general, also promote the activity of the cambium cells. Favorable conditions for growth are rapid supply of water and nutrients and active breaking down of reserve materials by ferments. They involve the diminution of the quotient C : N (carbon compounds : mineral substances) whose growth by the increase of carbonaceous reserve substances always denotes a decrease in the stimulation to vegetative growth and an increase in the tendency to flower production. These conditions for the decrease of the quotient C : N are present in spring. André [2] succeeded in inducing ring-formation in species of *Nicotiana* and *Lantana ramosa* (Verbenaceae) which under constant external conditions produce homogeneous wood, by altering the nutrient salts. Changing the supply of water alone had no such result. At the time of the breaking of the buds, the water- and ash-content of the cambium rises rapidly, apparently with increase of potash and decrease of calcium in the ash.[3] The awakening cambium forms early wood. Gradually, however, the leaves begin to supply carbohydrates to the cambium and while the carbon assimilation increases with the increasing amount of light in early summer, a great excess of carbohydrates is stored up in the rind and the wood. The water-content of the cambium still rises but the ash-content remains constant, whilst calcium is again brought in and potassium apparently passes out in consequence. Magnesium increases and decreases with the dry substance of the cambium. In proportion as the carbon assimilates predominate, the growth conditions of the cambium must alter; simultaneously with the increase of its calcium content, it forms wood elements which slowly take on the character of late wood. Finally, owing to excess of accumulation, wood forming activity is paralysed. Since in July and August, Klebs continues, the water-content of the soil is on the average very small and on the other hand the demands of transpiration are very high, relative shortage of water may contribute to promoting late wood formation, and this is supported by the researches of Wieler (1887) and Lutz (1895). One will readily agree with Klebs when he states his opinion that the question of the causes of annual ring formation is not finally solved. For much more distinct narrow and wide wood is formed, for example, by the evergreen spruce, which in the spring immediately assimilates carbohydrates with its old needles and transmits them to the cambium, than by many broad-leaved trees which do not possess such a supply of carbon in the spring. It is always a step in advance that this question is now placed in the realm of problems to-day ripe for treatment.

The terms " spring wood " and " autumn wood " have, in the light

[1] Über das Treiben der einheimische Bäume, speziell der Buche. Abhandl. d. Heidelberger Akad. d. Wiss., math.-nat. Kl. Abt. 3. Heidelberg, 1914, Carl Winter.

[2] André, H., Über die Ursachen des periodischen Dickenswachstums des Stammes, Zeitchr. f. Bot. 12, 1920.

[3] Sieber, Physiologische Rolle von Kalzium, Magnesium, Phosphorsäure im Kambium. Inaug.-Diss., Würzburg, 1912. (*Ulmus, Paulownia.*)

of better knowledge of cambium activity, had to give place to the words " early " and " late " wood. It appears to be more in accord with the present position to allow these expressions to drop and with Klebs, to replace them by " wide " and " narrow " wood. These terms allow research a free course and do not bind it to time relations, which in practice do indeed exist, but need not be marked out as the main factor among the causes of annual ring formation.

By way of supplement a few observations on the climatic influences on the structure of wood may be mentioned. Trees and bushes originating in Fontainbleau, propagated in Toulon, multiplied the fibres in the late wood formed in dry periods and enlarged the vessels in the early wood (Bonnier, Compt. Rend., 1902) and Zdarek found, at high elevations, three or four rows of pits in spruce tracheids, as in the larch, whilst at low elevations the pits in spruce wood are arranged in 1–2 rows.[1] Perhaps experiments made on ashes would be fruitful as they are represented as being especially sensitive to shortage of moisture during growth.[2]

Gaston Bonnier [3] described alterations in the anatomical structure of the leaves and shoots of pines, beeches, oaks and birches under the influence of electrical illumination applied day and night. They are of a pathological nature. It will therefore only be remarked here that feeble lignification played a part and that the plants which were only illuminated electrically for twelve hours daily, seemed to be less altered than those mentioned above.

[1] Österr. Forst- u. Jagdztg., 1903, Wien. No. 21, p. 185.

[2] Heck, Verhalten erwachsener Fichten gegen Dürre und Frost. Forstwirtsch. Zentralbl., XXXIV, 1912.

[3] Compt. rend. h. des séanc. de l'acad des sciences, T. CXV, 1892, p. 447 and 475. *Comp.* also Flammarion. Bot. Zentralbl., 1900, IX, p. 224.

CHAPTER VII

ANATOMICAL BASIS OF THE TECHNICAL PROPERTIES OF TIMBERS [1]

1. Relation between the Strength, Specific Gravity and Structure of Timber.—Among the important technical properties of timber, apart from the size and shape of the pieces available and its durability, are first the character of its external appearance—colour, lustre and marking (grain)—then strength, elasticity, toughness, fissibility and hardness, and finally specific gravity and constancy of form. According to the purpose which the timber has to serve, sometimes one and sometimes another of these properties is regarded as the measure of its quality. As a rule by quality is understood the strength of the timber and, so far as it goes hand in hand with this, its specific gravity—its density in an air-dry condition. By it, at the same time, is indicated also the hardness of the wood, which rises and falls approximately with the specific gravity. Janka [2] has proved in the case of spruce that, with the same moisture content, the strength properties of the timber rise with increasing specific gravity. For the spruce, therefore, the specific gravity is a fairly certain indicator of quality, at least in a certain experimental area, though the remarkable fact, proved by Bauschinger,[3] should be noted: that resistance to crushing is greatly increased by storage for a year without the specific gravity being altered. In comparative investigations of different kinds of timbers, resistance to crushing or bending must be determined, which then serves as a good measure of quality. The experiments carried out by Schwappach [4] at the Hauptstation des forstlichen Versuchswesen at Eberswalde and the Konigl. technischen Versuchsanstalt at Charlottenburg, showed that in the pine, spruce, silver fir, Weymouth pine and beech, resistance to crushing and specific gravity depended, apart from the species, on the part of the stem, age, region of growth and quality of the locality and on the proportion of summer wood in the annual ring, and this moreover in

[1] General: Exner-Janka, Dei technische Eigensch. d. Hölzer, in Handbuch d. Forstwiss., 3 Aufl., 2 Bd., p. 342, Tübingen, 1912; Gayer-Fabricius, Forstbenutzung, 11 Aufl. Berlin, 1919; Lang, G., Das Holz als Baustoff, Wiesbaden, 1915.

[2] Mitteilungen a. d. forstichen Versuchswesen Österreichs. K. k. Versuchsanstalt Mariabrunn, Heft, XXXV, 1900, u. XXXIX, 1915.

[3] According to Exner, *loc. cit.*

[4] Untersuchungen über Raumgewicht und Druckfestigkeit des Holzes wichtiger Waldbäume. I. Kiefer, 1897. II. Fichte, Weisstanne, Weymouthskiefer und Rotbuche. ,1898. Berlin, J. Springer.

such a way that not only does their size but also their relationship alter. In the spruce, to the low crushing strengths corresponds a relatively low, to the higher ones a proportionately high, volume weight. The relation between crushing strength and specific gravity is termed the "**quality coefficient.**" The relationships mentioned between volume weight and technical properties only obtain however when the water-content of the pieces compared is the same. The water-content is by far the most important factor in strength; for example:—the crushing strength of pine timber falls from 500–700 kilogrammes per square centimetre in the absolutely dry condition to 150–200 kilogrammes per square centimetre when fully saturated with water. It is mainly the water of imbibition of the cell walls that is concerned here, liquid water in the lumena of the wood organs has a smaller influence. As regards water-content, a distinction is made between **Green Weight, Air-dry Weight** and **Oven-dry Weight** (in an absolutely dry condition).

We owe the first information as to the connection between the technical properties,[1] particularly of coniferous timbers, and their anatomical structure, especially to R. Hartig[2] and his school, who, following the lead of Sanio, proved by thousands of measurements, that quite generally, in all spruce and silver fir stems examined and in all age classes of mature trees, the width of the tracheids in one and the same annual ring increases up to a certain height in the shaft and then falls off again so that it is about the same at the base of the crown as at breast height. From there on, within the crown, a rapid diminution of the width of the tracheids takes place up to the top of the tree. Bertog[3] showed that these regularities are most clearly apparent when only the first five rows of tracheids in each annual ring are considered.

The length of the tracheids alters in the same sense as their width so that the increase at first up to the base of the crown and the decrease within the crown, applies also to their total size. The thickness of the walls of the first five tracheids of each ring first diminished and then increased with the height in the tree. The width and the wall thickness of the tracheids of one annual ring at various heights in a silver fir stem are quoted from Bertog's work as an example:

Unit of measurement: 0.00001 square millimetre.		Unit: 1μ = 0.001 millimetres.	
			Wall thickness.
Tracheid width at	1.3m. = 95	at 1.3m.	6.4
,, ,,	4.5m. = 98	at 4.5m.	4.9
,, ,,	7.7m. = 100	at 7.7m.	4.8
,, ,,	10.9m. = 101	at 10.9m.	4.5
,, ,,	14.1m. = 109	at 14.1m.	4.5
,, ,,	17.3m. = 108	at 17.3m.	4.5
,, ,,	20.5m. = 99	at 20.5m.	4.2
,, ,,	23.7m. = 84	at 23.7m.	4.2
,, ,,	26.9m. = 48	at 26.9m.	4.6

[1] Hollendonner, Holzelemente der Nadelhölzer. Budapest, 1913. With 40 plates. Hungarian. Could not be utilised.

[2] Das Holz der deutschen Nadelwaldbäume. Berlin, 1885.

[3] Bertog, H., Untersuchungen über den Wuchs und das Holz der Weisstanne und Fichte. Forstl. naturw. Zeitschr., 1895.

The variations in specific gravity of conifer timbers are fully explained by the structure of the tracheids. Thus in the pine, Weymouth pine and silver fir, the wood of the lowest part of the stem, where the smallest tracheids are found, has also the highest specific gravity. The specific gravity falls off upwards at first rapidly and then slowly, again increasing immediately under the crown and taking quite an irregular course within the crown. In the spruce the heaviest wood is found at a height of 2 metres in the stem and a second, smaller maximum weight, in the middle of the stem. According to an analysis made by Münch,[1] in the pine, the quality falls off from below upwards in an "inter node" between the whorls of branches, more rapidly than in the stem as a whole.

The changes in the specific gravity of wood with the age of the tree may also be traced to the constitution of the wood elements (Omies [2]) Examples of such changes are given in Fig. 91. Regularities are only to be detected with difficulty in the experiments in question, as accidental differences in nutrition, crop density, red-wood formation, etc., often conceal the age function.

The percentage of narrow-lumened late wood, "summer wood," in the annual ring, which generally increases with age, has been shown to be specially important for the quality of the timber (Schwappach in Handb. d. Forstw., p. 409). As a practical rule for the determination of timber quality from outward appearance, it follows from this that it is not the annual ring breadth itself, but the proportion of late wood that is the determining factor. A small proportion of summer wood (30 per cent. or less) corresponds with a low volume weight and a low crushing strength, and both rise rapidly with an increase in this percentage. All circumstances and processes that raise the percentage of summer wood improve the quality of the timber. The structure of the wood is also of importance in impregnation. For example under the low pressure of the Boucherie process [3] the impregnating fluid does not penetrate well into the narrow annual rings on the windward side of the tree.

Our knowledge of the anatomical causes of the variations in quality of timbers of broad-leaved trees, is again based especially on the investigations of Sanio and R. Hartig and his school.[4] In the beech [5] the specific gravity falls irregularly from below upwards, so that the highest volume weight often lies at about 4 metres and a very distinct minimum at about two-thirds of the total height. Here, according to Hartig, as well as in the oak, it is the percentage of wide-meshed elements and narrow-lumened fibres in the wood which determines the alteration in quality of the timber from below upwards. In general the proportion of

[1] Münch, Blaufäule. Naturwiss. Zeitschr. f. Forst.-u. Landwirtschaft, 1908.

[2] Untersuchungen des Wachstumsganges und der Holzbeschaffenheit eines 110 jährigen Kiefernbestandes. Forstl.-naturwiss. Zeitschr IV, 1895.

[3] Handbuch der Holzkonservierung, hrsg. von Troschel, 1916.

[4] Sanio, Bot. Ztg., 1863; R. Hartig und Weber, Holz der Rotbuche; Treatises in the annual volumes 1892, 1893, 1894, 1895 of the Forstl.-naturwiss. Zeitschr. on the timber of the oaks, Canadian poplar and Robinia; Eichorn, Holz. der Rotbuche, *loc. cit.*, 1895; Stauffer, Holz der Birke, *loc. cit.*, 1892; Schneider, Zuwachsgang und anatom. Bau der Esche, *loc. cit.*, 1896; R. Hartig, Untersuchungen a. d. forstl.-bot. Institut in München, II, 60.

[5] Schwappach, *loc. cit.* II.

the latter falls off from below upwards. Within the crown of the tree, the wide elements decrease upwards more rapidly than the narrow ones, so that the timber becomes heavier there in an upward direction. R. Hartig counted 115 vessels in the square millimetre cross section in the beech at breast height; 175 at a height of 10.7 metres. Taking into account the circumference of the stem at the two places, he calculated the absolute number of vessels in the whole annual ring to be 200,100 and 197,750, *i.e.* it remains approximately the same. The difference is so small that it may be ascribed to errors in the method of enumeration

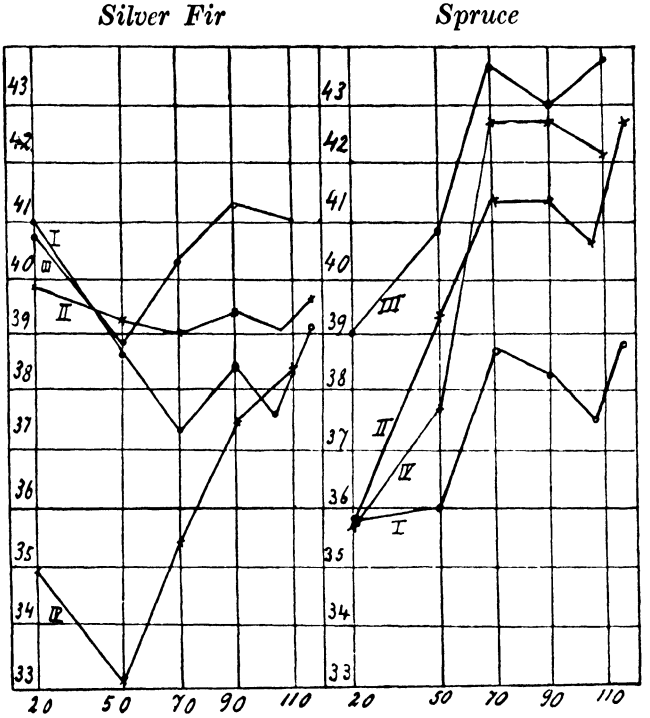


FIG. 91.—Relation between size of stem, age and timber weight in Silver Fir and spruce. After Bertog, Forstl.-naturw. Zeitschr., 1895, p. 677. *I–IV*, stem classes (*I* the largest). Ordinates: dry substance in the fresh volume, abscissae: ages.

The greater number of vessels to the square millimetre in an annual ring in the upper part of the stem, is explained by the fact that, owing to the falling off in the sectional area increment from below upwards, the same number of vessels must be crowded into a smaller space. Inside the crown the absolute number of vessels in the annual ring falls off rapidly. At a height of 21 metres only 57,500 were found. At the same time their size sank from 0.003 square millimetre in the stem, to 0.002 and even to 0.001 square millimetre. The birch behaves in many respects differently from the beech. In it, according to Stauffer, the weight of the wood increases with the age of the tree, and thus from within outwards in the stem, because the thickness of the walls of the wood fibres increases with each year, whereas the proportion of vessel lumena and parenchyma diminishes. The timber weight falls off in the stem from

below upwards for the same reasons as in beech, *i.e.* because, in spite of the absolute number of the vessels remaining constant in the whole ring, more vessels are crowded together per square millimetre of cross section in the upper part.

Distribution of vessels found in the birch:

Height in the stem.	No. of vessels in 1 sq. mm.	No. of vessels in whole ring.
1.3m.	55	46,050
3.5m.	72	45,590
5.7m.	80	46,576
7.9m.	82	48,937
10.1m.	124	43,970
12.1m.	221	27,249

In the crown of the tree the number of vessels sinks considerably. In spite of this the quality of the timber in the birch does not improve there because at the same time the proportion of parenchyma in the wood rises and the thickness of the walls of the wood fibres diminishes.

In the pedunculate oak, sessile oak, red oak and beech the wood elements in individual trees are smaller in youth than later on, so that Theod. Hartig already recognised that the wood of young beeches possesses "wood tubes" one-quarter to one-third narrower than the young wood of older parts of trees. R. Hartig found the wood elements in five-year old beeches only half as long as in 120-year old ones, the length increasing rapidly up to the 60th year and more slowly afterwards. From the 120th year onwards the length again diminished. The wood fibres were always the longest, the individual components lying above each other in the vessels, the shortest and the lengthening of both occurred in the same proportions. The width of the elements altered analogously with their lengths, and this is important for the quality of the timber. The vessels widened from a diameter of 0.05 millimetre in the 1–30th years to 0.064 in the 30–60th years, retaining this size up to the greatest age attained. In the pedunculate and sessile oaks—whose timbers, R. Hartig incidentally noted show no characteristic differences—this investigator found that the maximum size of the wood elements was reached in the 80th year and then remained the same, not again diminishing. The increase with age of the number of vessels in 1 square millimetre of surface is further worthy of note. R. Hartig quotes, for example, in a 120-year old beech stem at 1.3 metres height:

Age from	0–30 years	85	vessels on	1	sq. mm.	cross	section.
,, ,,	30–60 ,,	110	,,	1	,,	,,	,,
,, ,,	60–90 ,,	140	,,	1	,,	,,	,,
,, ,,	90–120 ,,	135	,,	1	,,	,,	,,

For the pedunculate and sessile oaks Hartig further states that the percentage of wood fibres in the annual accretion in young plants is higher than later on, and that the development of parenchyma wood elements, which increases up to between the 80th and the 100th year, is very small in youth. A similar condition is found in the beech, according to Eichorn.

In estimating the quality of oak timber by means of ring breadth, it must be taken into account that the early wood zone with its wide vessels remains the same under various conditions of growth. Broadening of the rings involves the increase of the summer wood portion which is rich in fibres. For this reason broad-ringed oak timber is heavier than narrow-ringed, in which the very large vessels are close together. Thus originates the "mild" timber of oaks from high elevations, *e.g.* the Spessart, which is very easily worked.

All the factors mentioned unite to reduce the specific dry weight of the wood formed in the later periods of the life of a tree, as against the production of its youth. The quality of the stem seems to be the better the younger it is. A hundred-year-old broad-ringed beech on very good soil, Hartig declares, has, under similar methods of cultivation, the same timber as a hundred-year-old beech which, on poorer soil, has formed only narrow rings. Owing, however, to the great difference in diameter of the two trees, the latter is perhaps only fit for felling at 200 years old, whilst the former has reached the necessary size in half this period. At the time of maturity, therefore, the narrow-ringed stem is much older than the broad-ringed one, and for this reason the quality of its timber is poorer than that of the latter; not, however, because any kind of connection exists between rate of increment and timber quality.

With regard to the influence of the region of growth and locality; in the case of the pine, timber from poorer localities is not so good as that from better ones, and in Germany the best quality of pine timber is raised between the middle and lower course of the Oder and Weichsel. Within the same region of growth and at the same age, the timber of stems grown in poor soil has always a lower specific gravity than timber from better localities. The silver fir of the Thüringian Forest has a lower specific gravity than the spruce of the same region, whilst within a region equally suited to both species the difference is only small. In the Bavarian Forest, approach to the vertical limit, in the Thüringian Forest, to the northern limit of distribution, appears to act unfavorably on the specific gravity. The spruce [1] mixed with it in such woods, which has a more extensive horizontal and vertical distribution, is less unfavorably affected, so that the difference between spruce and silver fir timber alters to the disadvantage of the latter with increasing altitude and progress towards the north. The specific gravity of the beech falls off within Germany from the south towards the north.

The influence exerted by summer- and winter-felling on the quality and durability of timber has often been discussed, but still requires further investigation. The method of drying and other conditions as to infection with wood fungi, are of greater importance than differences in the chemical composition of the contents of the wood elements in summer and winter. Winter-felled timber decays just as rapidly as summer-felled, if it remains lying in the summer, under conditions of moisture which are favorable to wood-destroying fungi.

[1] Schwappach, Einfluss der Herkunft und Erziehungsweise auf die Beschaffenheit des Fichtenholzes. Zeitschr. f. Forst- u. Jagdwesen, 1911.

2. Specific Gravity.—The above derivation of the quality of timbers from anatomical structure was based on the tacit assumption that the specific gravity depends only on the proportion between the share of actual wood substance and of air spaces in the timber, and not on changes in the weight of the substance forming the walls of the wood elements. It does in fact appear, that the specific gravity of the wall substance of tracheids, vessels, fibres, wood parenchyma and medullary rays, is everywhere the same, if there is no great impregnation with resin or especially high mineral content. This has been determined by placing very thin wood shavings, from which all air had been removed by boiling, into salt solutions of various specific gravities. The specific gravity of the liquid in which the shavings neither sank nor rose but just remained suspended, must be the same as that of the wood. From such experiments [1] a figure of about 1.56 (see also Heartwood formation) was obtained for quite different woods.

Since therefore all wood membranes have about the same specific gravity, the causes of the differences in weight of timbers must be sought in their structure. The more wood substance present in a given volume of timber the heavier will it be. In fact R. Hartig found the timbers of broad-leaved trees richer in substance than the specifically lighter conifers, so that, for example, the oak showed 37.6, the beech 36.6, the birch 32.6 volume per cent. of wood substance, the pine, on the other hand, only 27.3 per cent. and the spruce only 24.0 per cent. The greater porosity which characterises oak and other hardwood timbers as compared with the conifers, by reason of their possession of wide vessels, is compensated by the presence also of wood fibres, which, with almost vanishingly small internal cavities, possess thicker membranes than most of the tracheids of the conifers.

A few examples [2] of the specific gravity of timbers (I) in the air-dry and (II) in the absolutely dry condition are :

		I	II			I	II
Oak	Sap.	0.712	0.672	Spruce	Sap.	0.472	0.453
	Heart.	0.722	0.690		Pith & Heart.	0.441	0.424
Beech	Sap.	0.727	0.695	Pine	Sapwood	0.503	0.484
	Heart.	0.718	0.692		Pith & Heart.	0.487	0.464
Birch	Sap.	0.626	0.600	Larch	Sapwood	0.537	0.516
	Heart.	0.618	0.574		Pith & Heart.	0.522	0.503

Other estimates of the specific gravity of timbers in the air-dry condition are taken from Exner and others :

White beam (*Sorbus aria*, Grantz) . . .	0.88	(0.73–1.02)
Pedunculate oak (*Quercus pedunculata*, Erh.) .	0.86	(0.69–1.03)
Sessile oak (*Q. sessiliflora*, Lm.)	0.75	(0.53–0.96)

[1] Sachs, Abhandlung über die Porosität des Holzes. Arbeiten des bot. Instituts zu Würzburg, II, 1879 ; Hartig, R., Unvers. a. d. forstl-bot. Institut der Universität München, II, 1882 ; Omeis, Forstl.-naturwiss. Zeitschr., 1895, 150. He determined, by means of solutions of calcium nitrate, the specific gravity of pure wood-membranes to be 1.51-1.55 ; in a strongly resinous piece of the stump, 1.37. Eichorn, *ib.*, 1895, 292. Red oak, 1.545–1.565. Henze, A., 1883, gave the specific gravity of woody fibres as 1.60–1.62, that of pure cellulose as 1.63 (Göttingen, Inaug.-Diss).

[2] Hartig, R., Unters. a. d. forst.-bot. Inst. der Universität München, III, 5, 1883.

Plum (*Prunus domestica*, L.)	0.79	(0.68–0.90)
Ash (*Fraxinus excelsior*, L.)	0.76	(0.57–0.94)
Beech (*Fagus sylvatica*, L.)	0.75	(0.66–0.83)
Hornbeam (*Carpinus betulus*, L.)	0.72	(0.62–0.82)
Pear (*Pyrus communis*, L.)	0.72	(0.71–0.73)
Apple (*Pyrus malus*, L.)	0.75	(0.66–0.84)
Norway maple (*Acer platanoides*, L.)	0.69	(0.56–0.81)
Field maple (*Acer campestre*, L.)	0.68	(0.61–0.74)
Sycamore (*Acer pseudoplatanus*, L.)	0.66	(0.53–0.79)
Robinia (*Robinia pseudacacia*, L.)	0.72	(0.58–0.85)
English elm (*Ulmus campestris*, L.)	0.69	(0.56–0.82)
Walnut (*Juglans regia*, L.)	0.68	(0.65–0.71)
Plane (*Platanus occidentalis*, L.)	0.65	(0.61–0.68)
Horse chestnut (*Aesculus hippocastanum*, L.)	0.58	(0.52–0.63)
Goat willow (*Salix caprea*, L.)	0.53	(0.43–0.63)
Alder (*Alnus glutinosa*, Gärtn.)	0.53	(0.42–0.64)
Aspen (*Populus tremula*, L.)	0.50	(0.43–0.56)
Birch (*Betula alba*, L.)	0.64	(0.51–0.77)
Small-leaved lime (*Tilia parvifolia*, Ehrh.)	0.46	(0.32–0.59)
Yew (*Taxus baccata*, L.)	0.84	(0.74–0.94)
Pitch pine (*Pinus palustris*, Mill.)	0.70	(0.50–0.90)
Juniper (*Juniperus communis*, L.)	0.62	(0.53–0.70)
Larch (*Larix europaea*, DC.)	0.60	(0.44–0.80)
Austrian pine (*Pinus laricio* var. *Austriaca* Tratt)	0.57	(0.38–0.76)
Douglas fir (*Pseudotsuga Douglasii*, Carr.)	0.55	(0.49–0.61)
Scots pine (*Pinus sylvestris*, L.)	0.52	(0.31–0.74)
Silver fir (*Abies pectinata*, DC.)	0.49	(0.37–0.60)
Spruce (*Picea excelsa*, Lk.)	0.48	(0.35–0.60)

Among exotic timbers the ebony (*Diospyros ebenum*) may be mentioned, whose specific dry weight, like that of many other tropical woods, is greater than unity.

As is seen above, the dry weight varies between quite wide limits from species to species and from individual to individual within the species. These differences may be due in part to differences in the water-content of the sample pieces, for they were all examined in an air-dry condition and, by reason of the hygroscopicity of wood, vary in weight. Wet or even only moist wood is much heavier than dry wood because, on drying, air enters in place of the water contained in the wood and shrinkage does not correspondingly reduce the size of the samples.

Exact estimations of the total water-content of a piece of timber are not quite easy to carry out [1] because the last traces of water are difficult to remove, and even by drying at 100 degrees C. decomposition of the wood substance may set in, which is not taken into account in many determinations. Exner [1] states that timber which has been stored for a long time in dry, occasionally heated places has a moisture content of about 10–18 per cent. (room-dry), wood in closed sheds (air-dry) 13-17

[1] Schild, H., Mitteil. d. Königl. technischen Versuchsanstalten zu Berlin, 4 Jahrg., 1886; Exner, Die technischen Eigenschaften der Hölzer, in Handb. d. Forstwissenschaft. 3 Aufl. hrsg. v. Chr. Wagner, Bd. II, p. 372. Tübingen, 1912, Laupp.

per cent., stored in the open under a roof or in a cellar (cellar-moist) 17–22 per cent. R. Hartig[1] gives the water-content of air-dry oak, beech and birch as 8 per cent., pine and larch wood as 10 per cent.

It may be stated that H. Mayr [2] brings the relations between wood weight and the amount of increment into relationship with the climate, without, however, bringing forward adequate proofs.

3. Tensile Strength. Shrinkage. Fissibility.—The tensile strength [3] of spruce and pine timber depends essentially on the strength and proportional width of the late-wood zone. The early wood is also concerned but is of less importance for differences in tensile strength within one and the same species of timber, because its condition is very constant, as has already been noted. The breadth of the annual ring in itself, has no influence on tensile strength. " A high tensile strength is always accompanied by a fibrous, a low one by a short or jagged fracture and the great variations which the tensile strength shows in the same stem and even within the same cross section, may depend on the variability of the arrangement and joining of the fibres." Many timbers in the naturally moist, or especially in a steamed condition, possess great plasticity or pliability ; *i.e.* they stand considerable alterations in shape beyond the elastic limit without breaking down. This makes them suitable for the production of crooked sticks and for wicker work, and enabled Thonet to establish the manufacture of furniture made from bent, round staves of beech wood. By treatment with hot water and pressure the middle lamallae may apparently be altered so that a diminution of strength and even a break down of the timber is observed.[4]

Timber, being hygroscopic, alters its own degree of moisture with changes in the moisture content of its environment. This leads to changes of form. The timber is " living " or it " warps " and even cracks or splits in the process. It shrinks with diminished and swells with increased moisture. Not only the size but also the shape of the specimen alters in consequence, because these processes proceed unequally in different directions in the wood. Timber is anisotropic, like a crystal in which light travels at different speeds in different directions. This is due simply to its being composed of longitudinally arranged fibres, tracheids, and vessels and, directed across them, medullary rays, whose mass becomes especially clear to the observer in a tangential section with its numberless medullary ray cross sections.

Shrinkage amounts on the average to 0.1 per cent. in the direction of the grain, 10 per cent. in the tangential direction and 5 per cent. in the radial direction. Conifers generally shrink least. Among broad-leaved tree timbers, maple, oak, ash, elm, shrink little; aspen, birch, pear and poplar fairly strongly; beech, lime, walnut, hornbeam, very greatly. One measure against shrinkage is making wooden objects not out of one piece but out of smaller pieces stuck together with their grains crossing. Nördlinger [5] investigated shrinkage with special

[1] Untersuch, a.d. forstl.-bot. Institut der Universität München, III, 5, 1883.
[2] Das Harz der Nadelhölzer usw., 1894, 9. 66. Berlin, Springer.
[3] Bauschinger, quoted from Handbuch der Forstwissenschaft. Bd. II, p. 408 *et. seq.*
[4] Handbuch der Holzkonservierung, hrsg. von Troschel, Berlin, 1916, Springer.
[5] Technichen Eigenschaften der Hölzer, 1860.

thoroughness and stated that the medullary rays shrank more than other wood elements, both in length and cross section. Seasoning cracks nearly always run near the medullary rays and also often traverse them throughout, splitting them into two parts. The anisotropy of timber is most obvious in splitting. That the **fissibility** of timber is greatest in the direction of the radius depends on the fact that in this way the medullary rays do not have to be torn apart, as in splitting in the direction of the boundaries of the rings, but the split follows the medullary rays.

Nördlinger finds fissibility $\frac{1}{3}$–$\frac{1}{2}$ times as great radially as tangentially. Otherwise no simple connection exists between fissibility and the condition of the medullary rays. Timbers with high rays, *i.e.* those broad on the radial surface, do not always split more easily than those with low rays. Thickness of the medullary rays, *e.g.* in the elm, makes the split uneven. As splitting depends on the connection between fibre and medullary ray, their bounding layer is of the first importance. The poor fissibility of hornbeam timber is indeed bound up with the penetration of fibres into the medullary rays which takes place in that species.

Changes in fissibility from the pith towards the rind, Nördlinger ascribes to the smaller water-content and less regular ring formation of the inner portion of the wood, and also, on the other hand, to the smaller number of included branches in the outer wood of the stem. Green wood splits, as a rule, more easily than dry wood. For the most part the surface of the split follows the course of the fibres. The lignum vitae wood of skittle balls does not split and splinter because its fibres run wavily and also change their course according to the annual rings. Tangential seasoning cracks in oak timber go through the large vessels of the early wood zone and will occur the more easily, the more distinctly the timber is disposed in layers in the direction of the rings.

4. Hardness.—By the hardness of timber is understood the resistance which it offers to penetration by a solid body. Strictly speaking, owing to the varied nature of the attack of wood-working instruments, hardness towards the axe, saw, nails, etc., must be distinguished. In testing hardness,[1] iron hemispheres 5.642 millimetres in diameter, that is with a maximum section of 1 square centimetre, are employed, which are driven by continued pressure into the smoothed surface of the wood to be tested, until their maximum section lies in the plane of the surface of the wood. The resistance overcome is the measure of the hardness of the timber.

Hardness depends on the species of timber and, in samples of the same species, runs parallel with the specific dry weight. Resistance to crushing follows the same rule. The rule may be concealed by differences in the moistness of the samples, because, as Janka's investigations showed, hardness and resistance to pressure diminish with increasing

[1] Österr. Zentralbl. f. d. ges. Forstwesen, 1906 and 1908. Quoted from Exner, *loc. cit.* Mathematical treatment of hardness of wood, *see* Lorenz: Analytische Untersuchung des Begriffs der Holzhärte. Mitteil. a. d. forstl. Versuchsw. Österreichs, hrsg. v. d. k. k. Versuchsanstalt, Wien, 1909; Janka, Die Härte der Hölzer. The same, Heft 39, Wien, 1915.

moisture content. The quotient: Hardness ÷ Specific gravity, is smaller in conifers and larger in broad-leaved tree timbers than the quotient: Resistance to pressure ÷ Specific gravity. It therefore follows that coniferous timbers are more suitable for building purposes in which the greatest possible strength with the smallest possible specific gravity is important, whilst the hardwoods are more suitable for uses in which hardness and thus resistance to wear and tear are more important than lightness (furniture). Janka found the minimum hardness 200 kilogrammes per square centimetre (*Paulownia*), the greatest hardness 2000 kilogrammes per square centimetre (African Blackwood.) Büsgen [1] first determined numerically the hardness of 182 timbers by driving in a steel needle to a depth of 2 millimetres. The pressure in grammes necessary for this, divided by 100, gave him the respective figures. The hardest timbers (African Blackwood of the leguminous *Dalbergia melanoxylon*) showed more than 55 times the hardness of the softest (Ambatsch, *Aeschynomene elaphroxylon*, Leguminosae), and the following series could be set up: Hardness I, very soft 1–10: *Salix*, *Populus*; Hardness II, soft, 11–20: Pine, alder; Hardness III, somewhat hard, 21–30: Oak, cherry; Hardness IV, hard, 31–50: Mountain ash, *Taxus*, Hornbeam; Hardness V, very hard, 51–70: Dogwood, *Ilex*; Hardness VI, stone hard 71–140 and over: *Buxus*, *Casuarina*, *Quebracho*, African Blackwood. As the piercing method requires the careful choice of places for penetration and a large number of them, the following series by Janka is of more practical importance:

I. Very soft, 0.350 kilogrammes /square centimetres: Spruce, poplar, Weymouth pine, lime, Scots pine, willow, silver fir, horse chestnut, Austrian pine.

II. Soft, 351–500 kilogrammes /square centimetres: Larch, white alder, pubescent birch, mountain pine, goat willow, black alder, teak, juniper, bird cherry, common birch, guelder rose.

III. Medium hard, 501–650 kilogrammes /square centimetres: Sweet chestnut, grey willow, plane, wych elm, English elm, hazel.

IV. Hard, 651–1000 kilogrammes /square centimeters: Oak, mountain ash, walnut, sycamore, wild cherry, maple, apple, ash, yew, beech, pear, plum, robinia, hornbeam, wild service tree.

V. Very hard, 100–1500 kilogrammes /square centimetres: Dogwood, privet, pubescent oak, fly honeysuckle, box.

VI. Stone hard, over 1500 kilogrammes /square centimetres: Ceylon ebony, *Quebracho colorado*, lignum vitae, African blackwood.

Among 285 kinds of timber Janka found 97 hard, 40 medium hard, 40 soft, 62 very hard, 39 very soft and 9, all exotic, stone hard.

Anatomically the resistance of timber to penetration into its surface depends in the first place on its content of solid substance which the penetrating needle or hemisphere only displaces with difficulty. To this is due the general correspondence of hardness and specific gravity. Further the greater or lesser deposit of mineral matter, on which for instance the wearing out of tools depends, is also involved. The hardness of the actual cell membranes of wood when not excessively

[1] Zeitschr f. Forst- u. Jagdwesen, 1904 u., 1905.

charged with ash constituents, corresponds, like that of plant cell membranes in general, with that of gypsum ; one of the lowest members in the scale of hardness of mineralogists. The hardness of the longitudinal section appears to be greater than that of the cross or transverse section. The broad-ringed red-wood zone on the side of the wood turned away from the force of the wind in isolated coniferous trees, is harder than the narrow-ringed opposite side, but the former has a smaller compression resistance than the latter (Janka, *loc. cit.*). For the rest, hardness, like other mechanical properties, does not depend on the ring breadth as such, but on the actual proportions of late and early wood.

A comparison with metals shows that timber is characterised by greater lightness, less brittleness, fissibility, small heat conductivity, softness and pliability with often greater resistance to external influences. The elastic limit, *i.e.* the weight that produces a permanent elongation of 0.00005 of the length of the rod, lies lower in timber than in the most useful metals, apart from lead. Determined on wires of 1 square millimetre cross section it lies at 3–11 kilogrammes for silver, 3–12 kilogrammes for copper, 5–32 kilogrammes for iron and 15–43 kilogrammes for steel wire. The elastic limit of the wood of robinia lies at 3.2 kilogrammes, of the pine at 1.6 kilogrammes, of the silver fir at 2.2 kilogrammes, of the oak and beech at 2.3 kilogrammes, of the maple at 2.7 kilogrammes, of the poplar at 1.5 kilogrammes.[1]

[1] According to Müller-Pouillet, Lehrbuch der Physik und Meteorologie. Bd. I, p. 329, ff. Braunschweig, 1906.

CHAPTER VIII

THE LEAVES

1. General.—It is in the summer that the form of the leaf in our broad-leaved trees reaches its highest development. If the stipules or the leaf base, developed into the bud-scale, might be called the winter-leaf, it is the leaf-blade which becomes important to the tree [1] in summer. The characteristics of the leaf-blade are at once understood from its function of creating the carbon compounds required by the tree, for building up its rigid framework, multiplying its living substance and as fuel for the maintenance of respiration and its working activities. Further, it promotes the water current which, passing through the tree from the root to the crown, supplies it, not only with water itself, but also with mineral nutrients derived from the soil and moreover favorably influences the temperature of the interior of the tree.[2]

In addition to the above, there are still other special functions assigned to the leaves of forest trees as well as those of herbs and shrubs, namely that the leaves, which form the main bulk of what falls from the tree, must not injuriously affect the soil on which the trees have to maintain themselves for many decades. They are fixed in their growing site, whilst smaller plants strive to change theirs by spreading rhizomes or by the help of runners, as every gardener knows to his cost.

The fallen leaves of trees, together with the moss and other lowly ground vegetation is called by the forester, the **forest litter.**[3] It is indispensable for the maintenance of the forest, especially on the poorer soils, because on its decay, it gives back to the soil the greater part of the store of nutrients, especially the indispensable nitrogen, taken up by the roots, protects the soil from consolidation and drying out, nourishes the micro flora and fauna of the soil and enriches it with humus, which in its favorable forms, increases fertility. The action of the forest litter is the more favorable, the more rapidly and completely the leaves decay. The leaves of broad-leaved trees generally behave better than needles in this respect; the beech especially, acts under most conditions as a soil improver, as the " mother of the forest." Oak litter acts less favorably,[4] and pure needle litter of the spruce and also of other species,

[1] Berthold, II, p. 31. In *Robinia* often simple leaves at the base of the shoot. Very often the first leaf with terminal leaflet and two very deciduous stipules.

[2] Böhm u. Breitenlohner, Sitzungsber. d. K. Akad. d. Wiss., Abt. I. May, 1877; Bot Jahresber., 1877, 552; R. Hartig, Forstl.-naturw. Zeitschr. II, 1893, p. 345.

[3] Ebermayer, Die gesamte Lehre der Waldstreu. Berlin, 1876. Gayer-Fabricius, Die Forstbenutzung, 11. Aufl. Berlin, 1919. Ramann, Die Waldstreu und ihre Bedeutung f. Boden u. Wald., 1890.

[4] Büsgen, Kupuliferen in Lebensgeschichte der Blütenpflanzen.

may even become harmful when, as especially on soils which are poor in plant food or dry, it decays too slowly and forms unfavorable and sour kinds of humus. Its decay-resisting resin content makes difficult its breaking down by bacteria, fungi and worms; sour, raw humus or dry peat layers may arise which acidify, bleach out, and solidify the mineral soil.[1] Such ill effects occur especially in the dense, pure coniferous woods, which foresters have been establishing for more than a hundred years very extensively in the place of poorly growing hardwood forests, in order to obtain a yield also in poor localities by means of the less exacting and therefore more valuable conifers. In the primeval forest [2] the decay of the litter and the formation of humus are generally more favorable; dead remains of trees lying on the ground, extensive mixing of species, inequality of age and irregularity of canopy such as are present in many, though in by no means all, primeval forests are favorable to the breaking down of the litter; windfall catastrophes which heave up the soil and forest fires, destroy in the primeval forest conditions, the unfavorable accumulated humus coverings and lead to an advantageous alternation of tree species. Forest science and forest management have actively endeavoured to find means of bringing about a favorable decomposition of the litter and formation of humus also in the cultivated forest, and to retain for the soil the food capital which annually circulates in the leaves. Mixing of species, underplanting with beech, regulation of the density of the crop, suitable arrangement of the fellings, avoidance of large cleared areas, soil cultivation, sowing of lupins and gorse on areas to be artificially stocked, liming, etc., are measures by which it is hoped to achieve this aim, even in difficult localities.

Ebermayer, 1876, estimated the quantity of foliage by the dry weight of the leaves falling annually. Their dry substance amounted to 3331 kilogrammes per hectare for the beech, 3007 kilogrammes for the spruce and 3186 kilogrammes for the pine.

These figures are only rough approximations for, as Ney pointed out,[3] the method of obtaining them leaves much to be desired and very great variations occurred in individual cases.

Burger, 1925, gives as the dry weight of the foliage on a hectare: 2,400 kilogrammes for the beech and 12,600 kilogrammes for the spruce, which retains its needles for several years.

The quantity of leaves varies greatly in individual cases round the mean value, according to Ebermayer even on the same area from year to year, but especially according to the quality of the locality. Thus the following figures were obtained as the yield in air-dry leaf litter in kilogrammes: [4]

Quality class:	I	II	III	IV	V
	3047	2213	1462	1149	617

[1] Chief works: Müller, P. E., Studien über die natürl. Humusformen, 1887, Classic basic work. Ramann, Bodenkunde, 3. Aufl., 1911. Hesselman, Acta forestalia Fennica, 1926.

[2] Schenck, Der Waldbau des Urwaldes. Allgem. Forst.-u. Jagdztg. Rubner, Pflanzengeographische Grundlagen des Waldbaues, 2. Aufl., 1925.

[3] Ney, C. E., Der Wald und die Quellen, p. 23. Separate reprint from the Wochenblatt f. Forstw. "Aus dem Walde." Tübingen, 1894.

[4] Bühler, Der Waldbau, Bd. 1, p. 473. Stuttgart, 1918.

2. The Size and Form of the Leaves.—The extension of the leaf in one plane gives it the form in which as many of its green cells as possible make use of the light necessary for their chemical activity. In this form also the largest surface is offered to the atmosphere for the exchange of gases and water vapour. Where, as in our conifers, the leaves are shaped otherwise, the number of the needles is a substitute for the size of the broad leaves. The total surface of the covering of needles of a spruce or pine reaches quite considerable dimensions. V. Höhnel[1] states the total leaf surface of 5–6-year-old deciduous trees to be at the most 4–4½ square metres, whilst P. Groom[2] found the following leaf areas in conifers of the same age: *Picea excelsa* 14,250 square centimetres (1.4 square metres), *Abies pectinata* 12,400 square centimetres (1.2 square metres), *Pinus sylvestris* 5,300 square centimetres (0.5 sq. metres).

Büsgen found 6,577 needles and a needle surface (one-sided) of 0.066 square metre on a four-year-old spruce. The one-sided leaf surface of a lime with 46 leaves amounted to 0.26 square metre, or only four times as much. Some two-year-old broad-leaved trees gave the following figures:

	No. of leaves.	Surface area (one side).
Ash	10 leaves with 66 leaflets.	0.0188 sq. m.
Hornbeam	17 leaves.	0.0161 sq. m.
Beech	30 leaves.	0.0230 sq. m.

The measurements were carried out with a polar planimeter on the dried leaves. In the spruce the mean needle surface was determined on drawings made with the microscope.

Some more of V. Höhnel's figures for the total leaf surface of young plants are as follows:

Carpinus betulus	Shade	842–1829 sq. cm.
	Sun	1385–1624 ,,
Fagus sylvatica	Shade	365–1776 ,,
	Sun	798–1803 ,,
Betula alba	Shade	462–707 ,,
	Sun	987–1418 ,,
Fraxinus excelsior	Shade	1503–1940 ,,
	Sun	1385–3067 ,,
Acer pseudoplatanus	Sun	1085–2858 ,,
Acer platanoides	Shade	1466–2677 ,,
	Sun	3412–4435 ,,
Tilia grandifolia	Shade	1015 ,,
	Sun	1138 ,,

It is evident from V. Höhnel's figures that the total leaf surface of trees standing in sunny situations is, as a rule, greater than that of

[1] Mitteil. a. d. forstl. Versuchsw. Österreichs, Bd. II, Heft 1 u. 3, 1879 u. 1880.
[2] Remarks on the Ecology of Coniferae. Ann. of Bot. Vol. XXIV, 1910.

shaded ones. The same thing appears from Ramann's [1] measurements on the beech. In pole forest he found the total leaf surface of trees 13–14.5 metres high:

On a dominant tree = 24.45 sq. m.
On a dominated „ = 12.08 „
On a suppressed „ = 8.62 „

In a dense beech crop, 25 years old on the average, the differences were much greater.

According to Knuchel [2] the number of leaves on a beech 37 centimetres in diameter was 119,000, the surface, both sides (upper and lower) = 285 square metres. Spruces and silver firs of 40 centimetres diameter, grown in selection forest, may bear 10–20 million needles, those of 60–70 centimetres diameter, 30–40 million. Knuchel found the leaf surface area (two sides) in a spruce with about 20 million needles to amount to 702 square metres, one with 4 million needles to 147 square metres, in a silver fir with 20 million needles to 930 square metres, one with 39½ million, to 1,825 square metres. According to his measurements, silver firs have almost twice as large a total needle surface as spruces of the same size of stem and tree class; the total (two-sided) leaf surface of a beech lay between the total needle surface areas of two equally large spruces. The one-sided leaf surface of the beech is three times, the needle surface of small spruces three to five times, of large trees about ten times, as large as the growing space of the tree. One of Knuchel's beech experimental plots with 198 stems to the hectare, had 23.6 million leaves and a total leaf-surface (upper and lower sides) of 5.6 hectares. A 55-year-old spruce wood with 790 stems to the hectare had 4,128 million needles with a total surface area of 12.8 hectares; *i.e.* more than 10 times the area of the wood.

According to Stalfelt [3] the number of leaves, the leaf surface and the amount of chlorophyll, are much greater in conifers than in broad-leaved trees. Burger [4] found the weight of leaves in percentage of the total green weight of the parts of the plant above ground.

	Spruce.	Beech.
4 yrs. old	60%	30%
50 „	6%	2%
100 „	3.5%	1%

The total leaf surface depends upon the number and on the size of the individual leaves and both vary with the lighting conditions within wide limits. Thus Ramann's dominant pole-forest tree had 10,950, the dominated tree 6,710 and the suppressed tree 3,145 leaves. In the dense 28-year-old wood, the dominant tree had 22,740, the dominated 2,270 and the suppressed only 586 leaves. Fifty to sixty-year-old beeches (V. Höhnel) had 35,000 leaves with an air-dry weight

[1] Blättergewicht und Blattflächen einiger Buchen. Zeitschrift fur Forst-und Jagdwesen, 43, 1911.

[2] Spektrophotometrische Untersuchungen im Walde. Mitteil d. Schweiz. Zentralanstalt f. d. forstl. Versuchswesen, hrsg. von A. Engler, XI, 1, p. 87. Zürich, 1914.

[3] Stalfelt, Mitteil, d. forstl. Versuchsanstalt Schwedens, 1924.

[4] Burger, Die Transpiration d. Waldbäume, Zeitschr. f. Forst- u. Jagdwesen, 1925.

of 4,482 kilogrammes, an isolated birch 200,000 leaves in the total weight of 214,000 grammes (197.8 grammes fresh birch leaves weighed 100 grammes air-dry).

The size of the individual leaves generally increases with the illumination. In close beech and spruce crops however, Stahl [1] saw that, on passing from places fully exposed to the sun to shaded ones, the stout, proportionally smaller leaves in the former increased gradually in size until they reached a maximum from which they again fell off with further diminution of the illumination. The surface of a beech leaf grown in the sun measured 33.2 square centimetres, that of one grown in the shade 54.6 square centimetres; direct action of the sun may thus be detrimental to the size of the leaf. This was also observed by Ramann, who found the surface area of a leaf grown in the sun on a dominant beech to be 19.78 square centimetres, that of a shade leaf 21.27 square centimetres. The total surface of the 5,590 light leaves amounted to 11.06 square metres and was therefore smaller than that of the shade leaves which amounted to 11.39 square metres, although the number of shade leaves was only 5,360 and thus much less than that of the sun leaves. The leaves of the suppressed tree reached 27.4 square centimetres and were thus considerably larger than the shade leaves of the dominant tree. On the 25-year-old over-dominant tree of the dense wood, light leaves were measured up to 25.45 square centimetres, shade leaves to 19.36 square centimetres. Larger than both, 30.9 square centimetres were the leaves of the sub-dominant tree, which were certainly grown under less exposure to direct sunlight than the above mentioned light leaves. In the deep shade of the dominated tree the leaves only attained 13.93 square centimetres. That the leaves in full light remain smaller, is in accordance with the general phenomenon that light checks growth, or rather opposes an over elongation which, in the complete absence of light, leads to etiolation.

After transplanting, young conifers produce conspicuously short needles.[2] If the transplanting takes place between late autumn and May, the whole shoot of the next year appears shortened and thickly set with abnormally short needles (*see* also Brush shoots). The number of needles remains the same, as they were already laid down at the time of transplanting. If the damage is done during May and June, the rudiments of the needles intended to develop in the following year are injured. The shoot in question remains small but its few needles stand at normal intervals and reach normal size. Pine needles formed in the dry year 1911 were found by Hergt [3] to be half as long as needles of 1912.[4] The extraordinarily large leaves found on stool shoots owe their size to the greater power of growth of these shoots, which have at their disposal the whole root system of the tree. The persistent needles of the pine and spruce go on growing in later years and, accord ing to Stalfelt (*loc. cit.*), gain in weight from year to year.

The average size of simple leaves of the tree species is connected

[1] Über den Pflanzenschlaf usw. Bot. Ztg., 1897.
[2] Thomas, Notjahr einer jungen Fichte. Bot. Zentralbl., Bd. 105, 1907, p. 325.
[3] Bot. Zentralbl., Bd. 123, 1913, p. 220.
[4] *Comp.* also Chap. II, 3.

with climate and locality. Evergreen simple leaves of considerable size are found especially on trees of the wet tropical region, whilst evergreen simple leaves in regions with long dry periods are usually small. Short-lived, simple, seasonal leaves also reach their largest dimensions (teak, Umbrella tree) in the tropics. They are less dependent on constant moisture as they fall during dry periods. Large pinnate leaves occur in the moist warm forest as well as in the tropical steppes (Acacias). The size of their pinnae is larger in many, but not in all, leguminosae of the moist, hot, tropical forest than in leguminosae of the steppes.

The size of the individual leaves of one and the same tree depends on the reciprocal relation (correlation) of the leaves with each other.

Fig. 92.

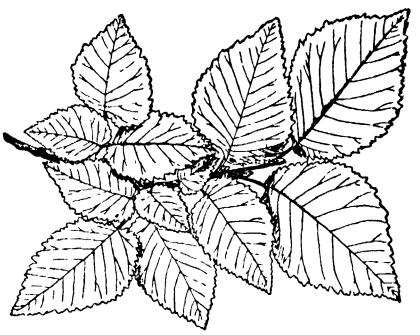


Fig. 93.



Fig. 92.—Leaf mosaic of the Elm. After Kerner v. Marilaun.

Fig. 93.—Part of a twig of Norway Maple with three decussate pairs of leaves. In the top and bottom pairs the leaves which spring from the upper side of the twig are smaller and shorter-stalked than those on the under side.

If we examine closely the dwarf shoot of an oak or beech, we note that the uppermost leaves are very much larger, often twice as large, as those formed further down the shoot. Under the influence of light the different leaves place themselves so that the smaller ones fill the gaps between the large ones and in this way all the light which falls is, as far as possible, intercepted (Fig. 15, p. 24 and Figs. 92 and 93).

Specially striking is the unequal size of the leaves in maples and other plants with decussate leaves (ash, horse chestnut). If we hold a maple twig, which has grown in a horizontal position, horizontally before us, we find the leaves of one pair on the right and left flanks, those of the previous and following pairs springing from the upper and lower sides of the twig. By means of twistings and bendings, carried out especially by the base of the leaf stalk, all the leaf-blades are spread out nearly horizontally on the upper side. It is at once noticed that the two leaves of the pair arranged above and below (the top and bottom pair of leaves in Fig. 93) are quite different in length of leafstalk and size of blade. All the leaves springing from the under side of the shoot are longer stalked and much larger than those of the upper side of the

twig, while the leaves on the flanks do not show similar differences.[1] There is no doubt of the ecological meaning of the phenomenon. A glance at the illustration above shows that the elongation of the stalk of the leaf in the under side brings the latter out of the shade of the others, and it is at once seen that the reduction in the size of the upper leaves must act favorably on the lighting of those below. The physiological explanation presents difficulties,[2] because the inequality of the leaves is already introduced in the bud. The under leaves of the pairs are better lighted than the upper ones because their longer stalks push them further out of the shade of the neighbouring leaves. They therefore form starch earlier and also produce more starch in a given time.[3] With the stronger growth thus made possible there is connected a greater transpiration of water. The better lighted and consequently more actively working leaf, draws away water from the opposite leaf and so also prejudices its growth.[4] Gravity may also co-operate as a stimulus since it influences the disposition of the whole shoot. That exchange relationships of leaves and twigs between themselves co-operate is shown by the fact that on lateral shoots of higher order, the leaves directed towards the mother shoot are larger. The regular increase in size of the conifer needles of one year as well as their subsequent decrease which Copeland[5] determined (in the spruce an increase in the size of the needles from 18.8 millimetres to 20.1 millimetres, then a decrease to 10.6 millimetres) belongs, like the multiplication of dwarf shoots, to the phenomena correlated with the increase in size of the tree. In an especially flourishing 14–16-year-old wood of Austrian pine (*Pinus laricio*) whose trees bore green needles up to four years old and, in addition, dried up needles up to eleven years old, Meissner[6] found that their lengths increased for some time from annual shoot to annual shoot, then steadily diminished for a time, only again to increase and so forth. The length of the needles of different years in conifers depends on the wetness of the year and the amount of reserve materials accumulated (*compare* Chap. II, 3). The length of the internodes has no influence on the length of the needles. Long shoots often produce quite sort needles and short shoots long needles. Among needles of the same age, those of the main shoot are longer than those of the lateral branches of the first order and the latter again larger than those of the lateral branches of the second order, and when the needles on the main shoot become larger or smaller the same thing occurs on the side branches. Finally when a lateral branch erects itself in the place of a destroyed leader and becomes itself the leader, it also acquires longer needles from then onwards. Meissner was not able to detect growth in length of pine needles over a period of several years. They grew, however, in thickness in the course of time, by the multiplication of the

[1] On anisophylly of silver fir needles *comp.* Chap. VIII, 6.
[2] Weisse, Ber. d. D. bot. Ges., XIII, 1895, 376, and the other works mentioned below.
[3] Schiller, Öster. bot. Zeitschr., LIII, 1903. Quoted from Bot. Zentralbl. 95, 1904, 121.
[4] Wiesner, Sitzungsber, d. Wiener Akad. d. Wiss., Math.-nat. Kl. CXIV, 1, 1905; Figdor, Ber. d. D. bot. Ges., XXII, 1904, 286.
[5] Bot. Gaz., XXV, 1898, 427; Heyer, Ber. Schweiz. bot. Ges., XX, 1911.
[6] Studien über das mehrjährige Wachsen der Kiefernnadeln. Bot. Ztg., 1894.

elements of their bast [1] and, to some extent also of their xylem. Exhaustive researches into the variations of needle size and allied phenomena were carried out by Renvall.[2] The largest simple leaves in our flora are produced on the large-leaved lime.

The leaves of most of our native trees are stalked. By this means their mobility is increased and the tree crown saved from a stiffness which would be a mechanical and physiological disadvantage. Stalked leaves oscillate round a point at the base of the blade, or they turn about the stalk and midrib. Thus stalked leaves give before the blast of rain and wind and so break their force. Every leaf movement promotes also the penetration of light into the crown and thereby the activity of the leaves and Jungner [3] has developed the theory that the inflow of nutrients to the leaves and consequently their growth is influenced by movements. Stahl [4] was able, by holding the leaves of the aspen still, to cut down the water evaporation of the twig by more than 50 per cent. Promotion of transpiration involves, however, an increased supply of mineral matters from the soil. The aspen has thus in its trembling leaves somewhat of an advantage over the elms, ashes and willows which share its habitat, whose leaves are much less mobile. The same service is rendered to these by the so-called water-pores through which they are able to allow water to pass out when transpiration is insufficient. The same organs, which are absent from the trembling leaves, are present in the pubescent leaves, entirely lacking in the trembling movement, produced by seedlings as well as by coppice shoots and root suckers of the aspen.

Habenicht [5] has attempted to explain the form of leaves mathematically.

The margins of our leaves vary according to their average size. The smaller leaves, like those of the beech, hornbeam, alder, lime, poplar and birch, do not generally possess deep incisions or divisions, whilst such are the rule in the large leaves of the ash, robinia and horse chestnut. Undivided they would present a larger surface of attack to the wind than would be consistent with their actual strength and the carrying capacity of their stalks and twigs. The main point however of the division of the leaf-blade into smaller leaflets and also of the lobing and everything which increases the circumference whilst the area remains the same, appears to lie in the fact that every surface evaporates the more, the greater its margin in proportion to its area. A dome of water vapour is formed over the surface of the leaf which flows off at the margins, so that the giving off of water increases with the relative increase in the margins. This influence of the leaf margins is especially important in the wind, as Walter proved by experiment. The supply of carbon dioxide to the leaf surface should also be favorably influenced in the same way by increased margin action.

[1] Accounts of the occurrence of anomalous numbers of needles *see* Schneider, Vergleichende morphologische Untersuchungen über die Kurztriebe einiger Arten von *Pinus*. Flora, Bd. 105, 1913.

[2] Renvall, A., Acta forest. Fennica 3, 1914, Helsingfors.

[3] Jungner. Phyllobiologiska studier. Bot. Zentralbl. Bd. 119, 1912; Hertel, *ib.* Bd. 132.

[4] Über den Pflanzenschlaf und verwandte Erscheinungen. Bot. Ztg., 1897, p. 71.

[5] Beiträge zur mathemat. Begründung der Morphologie der Blätter. Berlin W., 30, 1905, O. Salle.

Broad leaves form on upright shoots a smaller number of longitudinal rows than narrow ones, because only thus do the members of neighbouring rows not overshade each other. The vertical interval between the leaves is so regulated that the rays of light penetrate into the space between each two leaves of the same longitudinal row and shine through the interior of the shoot system.

A very widespread phenomenon is the larger size of one half of a leaf as compared with the other.[1] In the elm (Fig. 94) this is easily seen at the base of the blade, of which one half is not infrequently greatly shrunken whilst the other extends further down the leaf-stalk and sometimes provides a protective cover for the young axillary bud against the rays of the sun. In other cases the unequal size of the halves of the leaf has only been determined by weighing. The inequality is usually greatest in the lower leaves of sloping twigs. Generally the rear half of the leaf, which is turned towards the base of the twig and the earth, is furthered in growth but in the elm it is actually the front half. The proportions of the two halves in the sun-leaves of the elm was found to be 1.88 : 1, in shade leaves 1.3 : 1. The inequality is not quite independent of outer influences; for the rest, however, it is an expression of the condition of the whole shoot, as it is perfected in the growing point [2] under the influence of its position (*see* pages 6 and 7). Baumert [3] considers that the unsymmetrical form of the leaf may have the advantage that such leaves, when heavily wetted, tilt sideways more readily and allow the rain water to flow off better than symmetrical ones.

The **teeth** found on so many leaf margins not infrequently fulfill their functions for the plant at the time when the leaves begin to unfold and even in the bud. In the case of the wild cherry and others, if a bud is taken to pieces and the small leaves are closely examined, the strong development of the leaf-teeth is at once apparent. They—and sometimes in the earliest youth also the whole leaf surface—excrete resinous (*Pinus, Alnus, Salix, Carpinus*) or mucilagenous (*Acer, Fraxinus, Ulmus, Viburnum*) substances [4] which provide protection against the attacks of many pests of the animal world. Even in the later stages of life, secreting glands are often found seated in the teeth of mature leaves, as, for instance, in the crack willow.

In mature leaves the teeth are often important as emergency exits of the water conducting system which runs through the whole leaf in the form of veins. They bear the water pores which always lie above the ends of veins and, when there is a superfluity of water, as is the case on every cool summer morning, serve to allow water to pass out in drops, whether, when this happens, it actually flows out directly from the vessels or, what is much more common, is secreted into the pores through a special living tissue (Epithem).[5] More or less copious water shedding

[1] Nordhausen, Untersuchungen über Asymmetrie von Laubblättern usw. Jahrb. f. wiss. Bot. XXXVII, 1901; Ber. d. D. bot. Ges., XXX, 1912, p. 493; Figdor, *ib.* p. 134; Boshart, Flora, Bd. 103, 1911, p. 91

[2] Goebel, Organographie der Pflanzen, 2 Aufl. I, p. 263, Jena, 1913.

[3] Baumert, P., Mitt. d. D. dendrol. Ges., 1925, p. 132.

[4] Reinke, Jahrb. f. wiss. Bot., hrsg. v. Pringsheim, X, 1875.

[5] Burck, Versl. kon. Akad. Wetensch. In *Corylus* and elms at first resin or mucilage, later only water is excreted. Amsterdam, 1909 (Bot. Zentralbl., 1910, 572).

was found by Stahl [1] on the leaves of willows, wych elm, ashes, black and red berried elders (*Sambucus nigra* and *racemosa*), not always in the hazel. In hornbeam and elms, only some of the teeth emitted water and Stahl found no emission in sweet chestnut, lime (*T. ulmifolia*), sycamore, mountain ash, black and aspen poplars.

The small ears at the leaf base of *Quercus pedunculata* are inhabited by mites, like the tufts of hairs which occur widely in the angles of the veins on the underside of leaves.[2]

The further end of the leaf-blade is often drawn out into a point which is specially conspicuous in red oaks, limes, birches (*Betula verrucosa*) and poplars, but also occurs in a less marked form elsewhere. Such points promote the running off of rain water from the leaf, especially when, as in the lime, and oftener in trees in rainy tropical regions, they are somewhat sharply bent. They have been called "**drip points.**" [3] It is important that the leaf should be soon freed again from rain water because the covering of water on the blade checks transpiration, favours the establishment of parasites and even occasionally, by acting as a lens, gives rise to sun scorching. In trees and shrubs of drier localities where the drying of the leaf-blade proceeds more rapidly by simple evaporation or where hairs effect rapid distribution of the water over the whole leaf-blade and consequently accelerated evaporation, as in the wayfaring tree, the leaves are often without points. Considering the vegetation of the earth as a whole, it undoubtedly appears that drip points are chiefly associated with climates with high rainfall. Leaves which in such climates take up an upright position, like the leaves of *Lophira alata*, which is a common forest tree in the Cameroons, may be without points, because water flows off from them towards the stalk. The trembling leaves of the aspen crown [4] are without drip points because their continuous movement provide adequately for getting rid of the water which wets them. The leaves of aspen seedlings or root suckers which are nearer the ground and surrounded by humid or stagnant air and also the first leaves of the Lammas shoots are, on the other hand, so formed that water lodging on them flows off rapidly sometimes over the base, sometimes over the tip or by reason of the hairy covering of these leaves (which at the same time may protect them from many animals) by distribution over the whole surface of the leaf. Water collects in large drops on the edges of aspen leaves. The draining off of water from the whole

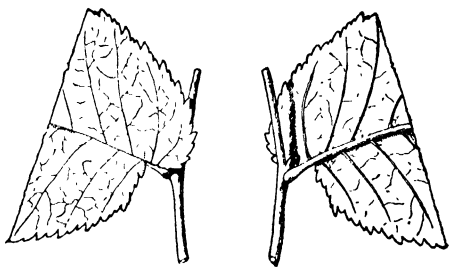


FIG. 94.—Parts of the leaf of the Wych Elm; left: seen from above; right: from below. They show the covering of the axillary bud by the unsymmetrical base of the leaf.

[1] Der Sinn der Mykorrhizabildung. Jahrb. f. wiss. Bot., Bd. 34, 1900.

[2] Lundström, Pflanzenbiol. Studien, II. Nova acta reg. soc. Upsaliensis., Ser. 3, Vol. XIII. Upsala, 1887.

[3] Stahl, Regenfall und Blattgestalt. Ann. d. jardin botan. de Buitenzorg, Vol. XI, 98. Leiden, 1893.

[4] Stahl, *loc. cit.*

crown of the tree proceeds as a rule centrifugally.[1] In the lime the water trickles from the upper leaves over their tips on to those next below, which pass it on downwards and outwards until, having reached the lower margin of the crown, it falls to the ground. A partially centripetal system of conducting away water is possessed, for example, by the beech, with its upright branches which conduct the rain water to the stem down the outside of which it trickles. Evergreen leaves with drip points, and also always of some size, may be designated hygrophilous leaves, because, according to experience, they appear in regions with high rainfall. Small evergreen leaves of plants in dry regions have been called xerophilous (*q.v.*).

The form of the leaf margin is not independent of external influences. Brenner [2] found pedunculate oak leaves grown in a damp place, dark green and tough, feebly incised, with only slightly marked nervature, blunt leaf tips and shortly wedge-shaped leaf base. Leaves reared in dry air exhibited lighter colour, stronger nervature, deep marginal incisions with sharper lobes and a generally heart shaped base. In nature also, according to Brenner, the lobes of pedunculate oak leaves in dry localities are more pointed and the incisions deeper, than in wetter regions. Oak leaves of warmer and drier localities have a closer network of the finest nerve ramifications.

3. The Anatomical Structure of the Leaves.—Three kinds of tissue are found in the leaf: the green cells which are concerned with the provision of carbon for the plant; the network of leaf veins, an extremely many branched irrigation system for supplying those cells with water and mineral substances and for the removal of the substances formed in the leaf; and the epidermis which shuts off all the rest from the outer world. We will consider first the leaf veins, the course of which is recognisable even by the naked eye and stands in close relation to the shape of the leaf. It is explained by the form of the outline of the leaf and the necessity of providing transport to and fro in as direct a line as possible. Every leaf outline leaves different possibilities open, among which that which conforms to the whole organisation of the plant comes into being (Habenicht). In parallel veined leaves the strengthening elements follow the straight main conducting veins, in reticulately veined leaves the latter have amalgamated with the former.[3] In the case of the smaller veins, regard for the watering of every possible cell and as direct a contact as possible between each and the outflow elements the veins, are natural considerations.

In beeches, oaks, hornbeams, willows etc., a main cord runs from the leaf-stalk through the middle of the leaf up to near its tip, and from this midrib lateral veins branch off and very often terminate in one of the leaf-teeth. Their course often affords good marks for distinguishing the different species of trees. In our sessile oak, the lateral veins of the first order almost all terminate in the lobes, in the pedunculate oak, to a great

[1] Kerner v. Marilaun, Pflanzenleben; Wiesner's works on ombrophile and ombrophobe plant organs. Sitzungsber. d. Wiener Akad., Bd. CII, 1894, and Anzeiger d. Wiener Akad., Bd. V, 1894.

[2] Klima und Blatt bei der Gattung *Quercus*. Flora, Bd. 90, 1902, p. 122.

[3] Habenicht, *loc. cit.*

extent also in the incisions. Glatfelder [1] has utilised the venation of willow leaves for determining the species. He groups the species according to the course of the secondary lateral veins, as those of the first order almost always run parallel with each other. As characteristic for *Salix amygdaloides* Anders., for example, star shaped points in the meshes between the finest ramifications of the veins are put forward. The above described arrangement of the veins in oaks and willows is called **pinnate**; a second arrangement has received the name **palmate** venation. In this, several nerves of approximately equal importance extend from the point of attachment of the leaf-stalk out to the leaf margin. Both systems may occur in the same genus. Thus the leaves of the black poplar are pinnately veined, while those of the aspen have palmate venation. Between the stronger veins in both cases is built up a veritable labyrinth of finer veins which are thousands of times interconnected and break up the whole leaf into innumerable small units, measurable only in fractions of a millimetre, in which their ultimate ends, no longer to be discerned without a microscope, reach almost every individual cell.

As regards anatomical structure, the conducting system of the leaves consists of the same elements as the conducting xylem of the tree stem; in particular, tracheids or vessels with lignified walls are never absent from the half of the vein directed towards the upper side of the leaf and the accompanying groups of sieve tubes on the under side. Even the finest bundle terminations always contain two kinds of elements, namely, beside the tracheids, also long thin, tube-like cells, which stand in direct connection with the bast of the ends of the thicker veins.[2] There are present, in addition, parenchymatous and also thick-walled, mechanically acting elements, and every bundle so formed is surrounded by a parenchyma sheath [3] whose constituents resemble in size the green assimilating cells but betray a different function by poverty in chlorophyll and elongation in the direction of the veins. In them are collected temporarily, the carbohydrates and protein substances which make their way in the bast of the veins to the leaf stalk, from there to be forwarded further into the twigs.

The starch content of the cells of the sheath has given it the name starch sheath (endodermis). The cells of the endodermis have a greater power of making starch out of sugar than other leaf cells. By the solidification of the sugar flowing into them from the palisade cells, in the form of starch, a fall of concentration towards them is set up. This fall sets going and maintains the transport of the assimilated sugar from the palisade cells to the vascular bundle. When the leaves are being emptied starch disappears first from the palisades, because there must be a higher concentration of sugar there if that substance is to pass out to the neighbouring cells. The summit of the concentration gradient must therefore lie in the palisade cells furthest from the leaf veins, the bottom of the gradient in the endodermis.[4] Corresponding to these

[1] 5th Annual Report of the Missouri Bot. Garden, 1893. Ref. Bot. Zentralbl., 1894, I, 56.
[2] Kruticky, Beihefte z. bot. Zentralbl., 1891, p. 417.
[3] Czapek, Ber. d. D. bot. Ges. XV, 1897, p. 124.
[4] Rywosch, Zur Stoffwanderung in Chlorphyllgeweben, Bot. Ztg., 1908, 66, I, p. 121.

differences in concentration, there must also exist similar differences in turgor, which, however, must be modified by differences in the amount of loss of water in cells which lie at different distances from the stomata. Ursprung and his collaborators found the absorptive power of cells to increase with the distance of the palisade cells from the leaf veins. He found this difference enormous; it amounted sometimes to a whole atmosphere from one cell to another. Such concentration- and pressure-differences must bring about in the leaf parenchyma, diffusions and sap currents in the direction of the leaf veins, which are to some extent opposed to the transpiration current. That the nearest way to the vascular bundle is not struck, but that several palisade cells always unite together in a bundle to form a common transport channel, follows from the arrangement of the cells (Fig. 100).

The protoplasm in the cells of the endodermis is often so fluid that the starch grains sink downwards whatever the position of the organ containing the sheath. Haberlandt based on this phenomenon, the theory that movable starch grains in the protoplasm give effect in this way to the directing action of gravity, like the statoliths in the balancing organs of animals.[1] The mobility of the starch grains has been recognised in geotropically sensitive stalks and roots and, in many cases, the cessation of geotropic sensibility when starch grains are removed from the organs in question, has also been observed.[2]

Each of the vascular bundles entering a pinnate leaf through the leaf-stalk [3] supplies with its lateral branches a definite region of the leaf-blade. Water conducting connections between these regions only become active when some of the supplying channels are interrupted, as for example when a leaf is broken. In such cases the whole leaf can be supplied by the undamaged veins if only the necessary connecting veins are present. A part of the leaf which is for any reason transpiring with special vigour can withdraw water from the other parts. The vein bundles running together from the blade into the leaf-stalk, separate from each other again in the broadened leaf-base and unite with the organs of the twig in such a way that the conducting tissues of their phloem and xylem are continuous with the corresponding parts in the soft bast and the wood. The formation of starch takes place only in those places in the leaf which are bathed in the carbon-dioxide-containing air. The movement of carbon dioxide is restricted, in reticulately veined leaves, by the veins, which are without intercellular spaces, whilst roomier intercellular spaces permit of a transport of several centimetres.[4]

In addition to the conducting of water, the veins have also a mechanical function to perform, as in the larger leaves, it is they which provide support for the membranous, spreading, blade. It is true that in the first place the tension of the leaf is the result of the tightness

[1] Physiol. Pflanzenanatomie. 3 Aufl., p. 523, Leipzig, 1904, Engelmann.

[2] Zollykofer, Ber. d. D. bot. Ges. 36, 1918.

[3] Gerresheim, Über den anatomischen Bau und die damit zusammenhängende Wirkungsweise der Wasserbahnen in Fiederblättern der Dicotyledonen. Ber. d. D. bot. Ges. XXX, 1912, p. 553; Rippel, Anatom. u. Physiol. Untersuchungen über die Wasserbahnen der dikotylen Laubblätter mit besonderer Berücksichtigung der handnervigen Blätter. Inaug.-Diss., Marburg, 1913.

[4] Zeijlstra, Acad. proefschrift, Groningen, 1909.

(turgescence) of its individual cells. If this is decreased by loss of water the veins are not able to prevent the whole leaf from becoming limp. Nevertheless they are important as supporters of the rest of the leaf. The branchings of the nerves in the neighbourhood of the leaf margin often help to prevent it from being torn ; curved vein connections with their convexity towards the leaf margin are especially effective in this direction.

The outer covering of every leaf is formed by a single layer of cells with very little or no chlorophyll, such as we have already become acquainted with under the name epidermis as the universal integument of the younger parts of plants (Chap. III, 3). In the shoot the epidermis generally soon becomes replaced by cork ; it is retained by the leaves throughout their lives. In them a peculiar double role is assigned to it. On the one hand it must protect the interior of the leaf from loss of water, but on the other hand it must present no obstacle to the exchange of gases between it and the outer air. The former task is undertaken by a very thin skin, impermeable to water, the cuticle, which, forming the external layer of the outer walls of the epidermis, also extends over the younger parts of the stem. The cuticle may be covered on the outside with wax, which forms a lustrous, smooth layer in the sessile oak, a granular, almost lustreless covering in the pedunculate oak, and a bluish bloom in various conifers : the *glauca* varieties of *Abies concolor*, *nobilis*, *Picea pungens*, *Pseudotsuga Douglasii*, etc., and the races of pine from high elevations in the south. Woolly hairs, which are found especially on the undersides of leaves (grey alder, white poplar), act as a protection against evaporation, in calm air only in thick layers, but in moving air even as a thin covering, whose efficiency rises in sunshine more than that of a wax coating. Hairs are therefore brought in as a protection against occasional intense evaporation, whilst wax acts as a check on evaporation at all times.[1] The hairs are already formed in the bud, where they are often strongly developed. In many cases they disappear later (beech, plane) or are retained only in the angles of the leaf veins, where they often provide, as " domatia," places of shelter for leaf mites. Equally repressive of evaporation, is the effect of the thickening of the walls of the cells of the epidermis which proceeds so far, *e.g.* in our pines, that all that remains of the cell lumen in our Scots pine is a point and in the mountain pine a thin line. Such epidermal layers are stiff and solid and these qualities are often increased by similar thick-walled hypoderm cells which adjoin them towards the interior of the leaf. They may also assist in protecting the interior of the leaf from loss of water by the mere fact that they increase the distance of the succulent green cells from the evaporating surface of the needle. This would explain the variability of their occurrence according to the locality, of which Stahl [2] made mention. In the needles of many species of silver firs, these hard cells form an almost continuous layer under the epidermis on the upper side in sunny situations, whilst in the shade they are only sparsely

[1] Wiegand, Bot. Gaz. IL, 1910, p. 430.

[2] Über den Einfluss des schattigen und sonnigen Staudorts auf die Ausbildung der Laubblätter. Jena. 1883.

developed. In accordance with this, species of southern regions, like *Abies Cephalonica*,[1] exhibit a stronger development of the hard cells than others, and the leaves of silver fir seedlings, adapted for living in the shade and thus exposed to no extreme loss of water, are almost without hard cells situated under the epidermis. Where large secretions of wax form the protection against transpiration, as in *Abies concolor*, the hypoderm disappears. Besides this, the hard cells are certainly not without value as a means of defence against gnawing tree pests whose injurious activities must be facilitated by their absence. Even the thickened outer wall of the epidermis itself is avoided, for example, by leaf mining insects. Stalfelt (*loc. cit.*) prefers to regard the whole xero-morphic structure of needlelike leaves as a method of providing strength. Cuticular transpiration is, it is true, reduced by the tough epidermis, but the total transpiration of conifers is equal to that of broad-leaved trees.

In the sphere of protection against small pests of the animal world, apparently also lies the significance of the mucilage which is contained in the walls of epidermal cells, *e.g.* in the birches, willows, *Prunus* species and oaks (*Q. pedunculata*) and in a layer of cells below the epidermis in the alder. It is accumulated in a thick layer on the otherwise generally very thin, inner wall of the epidermal cells, which swells up strongly when the cells are cut under water and also when they are bitten. The membrane mucilage has been regarded as a water reservoir from which the neighbouring cells can draw. It is, however, not easy to see how it can act in this way, as the mucilage rather absorbs water from its surroundings and retains it. For the rest the epidermis does actually act as a water storer. When shortage of water sets in in the leaf, its cells sink together because the green tissue draws water from them. According to the calculations of Haberlandt, the quantity of water which is liberated by the collapse of these cells to one half of their volume, can supply the loss of water which a leaf suffers by evaporation, in the horse chestnut for over two hours, in the pear for 39 minutes and in the hazel for 43 minutes. Epidermal cell walls curved outwards, lens-shaped thickenings of the same, and finally specially smooth-walled groups of cells between the ordinary epidermal cells (*Acer*), which like the cornea and lens of the eye, refract the rays of light which strike the leaf and direct them to particular points in the protoplasm, have been termed **Light Sense-organs** by Haberlandt.[2] Such contrivances cause great differences in the lighting of neighbouring parts of the living substance, and every alteration in the direction of the incidence of the light, leads to strong illumination of other places in the body of the cell. The protoplasm then works towards the re-establishment of the normal lighting conditions. This leads to bendings and twistings of the leaf-stalk by means of which the leaf-blade is brought into the proper position. Haberlandt's ideas have not remained uncontradicted. They can, indeed, hardly be strictly proved, because in

[1] Köhne in his "Dendrologie" has drawn upon the occurrence of hard cells as a characteristic for the identification of the species of *Abies*.

[2] Haberlandt, Physiol. Pflanzenanatomie, Leipzig, 1904, Engelmann; Sitzungsber. d. Wiener Akad., CXVII, 1908; Albrecht, Inaug.-Diss., Berlin, 1908; the same, Vorlaufig. Mitt. Ber. d. D. bot. Ges. XXVIa, 1908, p. 182; the same, Nordhausen u. Kniep, XXV, 1907.

judging plant sense-organs, it is not permissible to compare them with the human senses as in the case of animals. Haberlandt's conception has nevertheless the advantage over other possibilities, of dealing with visible things and not referring to plasma structures which are, so far, unrecognisable.

Finally, on the constitution of its epidermis depends the behaviour of the leaf towards rain. The slight bulging out of the areas enclosed by the veins has been looked upon as a measure of protection against the beating of rain and hail. Such a protection is hardly required, however, as the weight of a drop falling from a height of more than 5 metres, according to Wiesner's measurements,[1] does not exceed 0.2 grammes and the heaviest drops (0.16 gramme) observed by him reach the earth with a kinetic energy of about 0.0004 metre-kilogramme. Their rate of fall reaches at the most 7 metres per second. Hailstorms, however, are only exceptional. More important is Wiesner's[2] distinction between ombrophylous and ombrophobous foliage. Ombrophobous leaves, exposed to continuous rain-dropping, quickly perish, and protect themselves against the injurious action of the water by wax coverings which permit the raindrops to run off quickly (honeysuckle, conifer needles, oak leaves, tropical xerophytes). Ombrophylous foliage stands the action of rain even for weeks and without means of protection (our broad-leaved trees except the oak, and many leaves of the tropical xerophytes).



FIG. 95.—Leaf epidermis with sinuous cell walls and stomata. Magnified 160 times After Strasburger.

The connection of the ordinary epidermal cells with one another is firm and without gaps and is made even closer by sinuous interpenetration, as for instance in the shade-leaves, not however the sun-leaves, of the beech (Fig. 95). For the exchange of gases between the interior of the leaf and its surroundings special openings exist. The evaporation of water through the cuticle is to the total evaporation of a leaf, for example,[3] in the horse chestnut as 1 : 7.6, in the hazel as 1 : 8.1, in the birch leaf as 1 : 10.6. The openings in the epidermis in question are extremely small slits, each between two cells which differ widely in form from the other epidermal cells and are termed the "**guard cells,**" and with the cleft that separates them are called "**stomata.**" The small width of the slits, which are of the order of 0.01 millimetres in size, is made up for by their great number, which in most foliage leaves amounts to between 40 and 800 to the square millimetre. On green shoots of woody plants, they are often separated to a distance of a millimetre,

[1] Ann. du Jardin bot. de Buitenzorg, XIV, 1897.

[2] Über ombrophile und ombrophobe Pflanzenorgane. Sitzungsber. d. k. Akad. d. Wiss. in Wien, Bd. 102; the same, Biologie der Pflanzen, Wien, 1902, Hölder; Haböck, Österr. Bot. Zeitchr., LX, 1910.

[3] Haberlandt, Physiol. Pflanzenanatomie, 3 Aufl., p. 137, Anm. 17. Leipzig, 1904, Engelmann.

and their number is to a certain extent dependent on external circumstances. According to Dufour [1] more stomata are formed in sunlight than in shade (*compare* also Section VII, 6).

According to Yapp,[2] leaves of *Filipendula ulmaria* situated high on the shoot, have considerably more stomata than those lower down. Flat, herbaceous, leaves generally bear stomata on both sides; more, however, on the under side than on the upper, whilst leathery, glossy leaves such as those of the holly, indiarubber tree and oleander bear them almost exclusively on the under side. To them are added the hornbeam, birch (about 237 per square millimetre),[3] beech, pear and other tough leaves. Some of the maple species have stomata only on the underside, a smaller number have them also on the upper side.[4] In *Tilia grandifolia*, *Fraxinus excelsior* and *Acer platanus* they are most plentiful in the middle of the under side of the leaf and diminish towards the leaf-margin.[5] They are also completely absent from the upper side in these trees. In the horse chestnut, most of the stomata lie at the margin of the broadest parts of the leaves. In the conifers the stomata are recognisable even with a lens as white points which are arranged in longitudinal rows on the needles, sometimes only on the under side (silver fir), sometimes on the upper side (cotyledons of the silver fir) and sometimes on all sides.

The white colour is produced by accumulations of wax in the neighbourhood of each individual stoma, which in dew or rain, hinder the settling of water there and the closing up of the opening. Our pine has the stomata mainly, the Weymouth pine exclusively, on the upper side of the needles.[6] The latter is also the case in species of *Thuya* and the juniper, which betrays the position of the stomata, as in the silver fir, by wax stripes, which in it consequently occupy the upper side of the leaf.[7] In other cases protection against wetting is afforded to the stomata by hairs which are often found in special abundance on the lower side of the leaf. The arrangement of the stomata on the under side may enable the leaves of low plants near the ground to utilise more fully the carbon dioxide rising from the soil (*see* Chap. VIII, 10).

Leaves of similar form have generally, though not always, a similar distribution of the stomata, and leaves of dissimilar form may have the same distribution, family relationships expressing themselves in this. In many cases (horse chestnut) particular places in the leaf are specially rich in stomata. Bud scales and transition leaves have fewer stomata than ordinary foliage leaves (ash, horse chestnut). Out of 1,359 species of broad-leaved trees, Köhne [8] found the upper sides of the leaves in 222 provided with stomata. Espe found the following numbers of stomata

[1] Influence de la lumière sur la structure des feuilles. Bull. de la soc. bot. de France, T. XXXIII, 1886.

[2] Yapp, Annals of Botany, 26, p. 815, 1920.

[3] Weiss, Jahrb. f. wiss. Botanik, Bd. X, 1876, p. 119; Büsgen, Kupuliferen in Lebensgesch. der mitteleurop. Blütenpflanzen, hrsg. von Kirchner, Loew u. Schroeter, Bd. II, 1.

[4] Warsow, Beibl. z. Bot. Zentralbl., XV, 1903, p. 493.

[5] Espe, Beiträge zur Kenntnis der Verteilung der Spaltöffnungen über die Blattspreite. Inaug.-Diss, Göttingen, 1911, Dietrichsche Universitätsdruckerei.

[6] De Bary, Vergleichende Anatomie, etc., p. 52.

[7] Kerner v. Marilaun, Pflanzenleben.

[8] Mitteil. d. D. Dendrolog. Ges., 1899, p. 47.

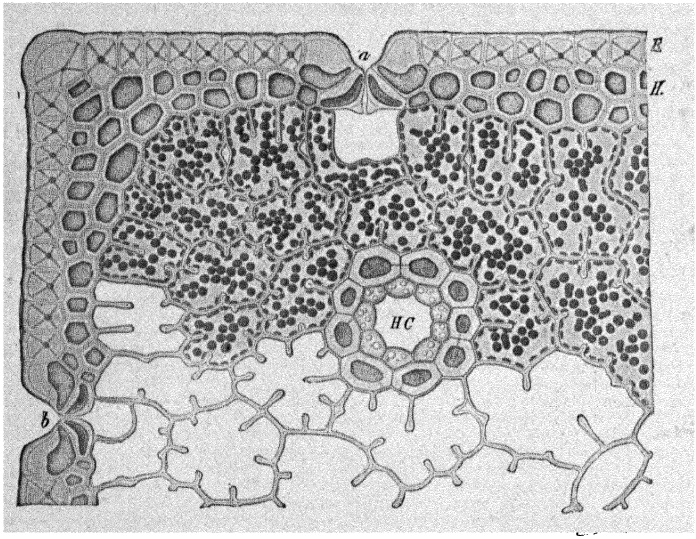


FIG. 96.—Corner of cross section of a Pine needle (*P. laricio*). (*a*) (*b*) Stomata, (*HC*) resin canals, (*E*) epidermis, (*H*) thick-walled hypoderm cells. Magnified 230 times. After Kny.

[*To face p.* 215.

per square millimetre of leaf surface on ordinary foliage leaves (under side):

Ash	321–667
Horse chestnut	186–451
Tilia grandifolia	173–272
Prunus avium	180–256
Juglans regia	150–240
Prunus avium	150–225
Acer pseudoplatanus	90–160
,, ,,	75–120
Pyrus malus	93–119
Prunus laurocerasus	74–85
,, ,,	68–85

Stomata on the under side may be differently shaped from those on the upper side, and stomata on rhizomes, stems and leaf sheaths differently from those on the leaves.[1]

4. Operation of the Stomata.—The giving up of water through the stomata to the surrounding air follows the laws of the diffusion of gases. The water comes from the moist cell walls of the interior of the leaf, which for their part draw it from the living cell contents and allow it to evaporate into the numerous intercellular spaces of the leaf, which communicate with the exterior through the slits. Immediately under the stoma lies, as a rule, a large intercellular space—the **Respiratory Cavity.** The slit has towards the respiratory cavity on the one side and towards the outer air on the other side, a widening, the inner and outer cavities, of which the latter is again somewhat narrowed towards the very outside by the projecting form of the cuticle. In the spruce, silver fir and pine (Fig. 96*a*, *b*), the actual opening is a canal about the same width throughout, without an inner and outer cavity. The opening is, however, deeply sunk between the neighbouring epidermal cells, so that it lies at the bottom of a funnel-shaped depression. This cavity, as an extension of the canal through which the water vapour must pass to come into contact with the outer air, acts as a check on evaporation, especially when it is partially stopped up with wax, or resin, as in the conifers.

A mere checking of the exchange of gases with the outer air could however be attained in a much simpler and more efficient way, namely by reducing the number and width of the stomata. The chief function of the outer cavity is protection against wind. According to Gradmann,[2] who studied the action of sunken stomata of various forms in models, evaporation is increased by strong winds to a much greater extent than the absorption of carbon dioxide. Calm air is favorable to the relation between carbon dioxide assimilation and water emission and the value of the sinking of the stomatal apparatus lies in the breaking of the wind by the outer cavity, so as to bring about a smaller loss of water with the same amount of carbon dioxide assimilation.

[1] Warnke, Jahrb. f. wiss. Botanik, Bd. L.

[2] Gradmann, Windschutzeinrichtungen der Spaltöffnungen. Jahrb. wiss. Bot. 62, H. 4, 1923.

On account of their small size, the total area of all the slits is only a small fraction of the leaf surface that bears them. The epidermis nevertheless permits of a really great evaporation of water because, as physics teaches,[1] even quite small openings allow comparatively enormous amounts of vapour to pass out. The size and distribution of the stomata on the epidermis is so favorable that, given calm air, evaporation from the interior of the leaf can go on almost as if the epidermis were not there at all. The effect of the epidermis as a protection against drying out, apart from its properties as a storer of water, is that of keeping the dry air at some distance from the moist cell walls of the interior of the leaf and by this means retarding loss of water. Movements of the air increase water evaporation by constantly removing from the leaf the air that has become moist and supplying new dry air and so maintaining at a high value that difference in vapour content between the interior of the leaf and the outer air on which the rate of evaporation depends.

The half-moon shaped guard cells have the power of reducing or increasing the evaporation by altering their curvature and thus allowing the slit to gape open to a smaller or greater extent. The movements are often facilitated by the accessory cells [2]; neighbouring cells of the epidermis of special structure and arrangement.

Whether the stomata of a plant are open or shut can be readily determined at any time by a simple experiment.[3] It is only necessary to place a little alcohol or ether on the stomatiferous side of the leaf to be tested. Alcohol penetrates only into fairly wide open slits, whilst ether passes even through narrow ones. The penetration of either liquid into the interior of the leaf is immediately recognised by the dark coloration which appears when they fill the intercellular spaces. If the slits are completely closed this coloration of the leaf does not take place. A special procedure was necessary to recognise the behaviour of evergreen conifer needles, in which the experiment with alcohol and ether does not work. The stomata of these plants [4] develop on the young needles still enclosed in the bud, later than the rudiments of the veins and resin canals, but soon reach the form which they retain throughout life. In the needles still enclosed in the bud scales the funnel over the stomatal opening is already filled by a spongy or granular mass permeable to air, which appears to be formed less out of wax than out of resin or is a mixture of bodies of a new group,[5] and is soluble in cold alcohol and ether. Neger succeeded in getting water to penetrate through the open stomatal slits in the needles of the yew, silver fir and hemlock spruce (*Tsuga*) after pumping out part of the air present in the interior of the needle. He determined in this way that the stomata of young needles were open for water, those of 1–2-year-old needles closed, though not fully so for air. Stålfelt (1924) dips pine and spruce

[1] Renner, Wasserversorgung der Pflanze in Handwörterbuch der Naturwissenschaften, Bd. X, p. 538. Jena, 1915, G. Fischer. Gives literature.

[2] Bennecke, Bot. Ztg., 1892.

[3] Molisch, Zeitschr, f. Bot., Bd. IV, 1912; Stein, E., Ber. d. D. bot. Ges., XXX, 1912; Neger, the same, Bd. XXX, 1912, p. 179; Dengler, the same, XXX, 1912, p. 452. In the last two works, accounts of the stomata of conifers.

[4] Schwabach, Ber. d. D. bot. Ges., XX, 1902.

[5] Bougault et Boudier, Compt. rend. Acad. sc. Paris, CXLVII, p. 1311, 1908.

needles into a narrow glass tube filled with ether so slowly that the intercellular air can be displaced by the entering ether. The infiltrated places are then distinguishable from those containing air. Another method [1] is based on the permeability of the slits to gases. The needles are placed in the vapour of ammonia or sulphurous acid. If the stomata are closed the needles remain unchanged; if they are open the cells die and blacken. Dengler inferred the degree of perviousness of conifer stomata from the way in which they allowed air bubbles to emerge under water when water was squeezed up the needle from the base. He was also able to prove the variability of the width of the slits under the influence of changing light and warmth.

The stomata only become fully movable in the mature leaf. In youth they are closed or only open under especially favorable conditions. The leaves situated lowest on the growing shoot are the first to have adjustable stomata.[2] But their mobility also decreases in age, especially in several-year-old needles, even if it does not completely cease. Incipient wilting leads, in many plants, to the closing of the stomata. Further wilting is thereby immediately very much retarded, whilst plants which are not able to close their stomata rapidly wilt completely, for example in the dry air of a room, even when they are placed in water.[3] If a transpiring twig is cut from the tree and the transpiration measured at short intervals, the hourly delivery of water is found to fall off rapidly to a small fraction of its original amount. This is only to a small extent due to physical depression of evaporation as the result of incipient drying up, much more to the closing of the stomata which sets in about half an hour after cutting.[4] The stomata are closed in winter. Not always completely so, however, for Huber found, also in winter, the above mentioned falling off of transpiration in cut twigs of *Sequoia*, which indicated that the slits were previously open.

The stomata are not equally adjustable in all plants. The aspen, which generally occurs on wet soil and there attains its finest development, is able to live in comparatively dry soil because it is able, when water shortage occurs, to close its stomata completely. On the other hand, many species of willow [5] are confined to moist localities because they are without the power of rapidly closing the stomata. The drying up of such plants may be hindered, as Stahl also states, by closing the stomata artificially, *e.g.* by smearing the under side of the leaf with vaseline. *Betula alba* and *Alnus glutinosa* also cannot regulate their transpiration to any great extent by closing the stomata. The poorly illuminated leaves in the interior of a tree crown do not open their stomata so wide as leaves in the sun. As they possess thinner epidermis outer walls than do leaves developed in the sunlight, evaporation of water through the cuticle plays a greater part in their water economy than elsewhere. The activity of the guard cells differs according to age, position in the leaf, and especially structure.[5] The nocturnal closing of the slits gives the tree an opportunity of again making up the loss of

[1] Weber, F., Ber. d. D. bot. Ges., 1916, Bd. 34.
[2] Linsbauer, K., Beitr. z. K. d. Spaltöffnungsbewegungen. Flora 109, 1917, p. 100.
[3] Stahl, Einige Versuche über Transpiration und Assimilation. Bot. Zeitg, 1894.
[4] Huber, B., Transpiration in verschiedener Baumhöhe. Zeitschr. f. Bot. 15, 465, 1923.
[5] Linsbauer, Spaltöffnungsbewegungen. Flora, IX, 1916.

water resulting from evaporation during the day. In shrubs the stomata are more often open also at night.[1]

The regulation of the width of the stomata has to serve two quite different requirements of the plant. On the one hand the slit should only be opened so wide that the giving off of water by the leaves shall not be excessive, but on the other hand they must admit as much carbon dioxide as possible in order not to hinder assimilation. These two requirements are very often in opposition and in many cases a compromise has to be effected which is fair on the one hand to the regulation of transpiration and on the other to the carbon dioxide requirement. The supply of carbon dioxide is only of use to the plant when the leaf is in the light. In conformity with this, the width of the stomata is dependent in the first place on illumination. Bright light causes the opening, darkness the closing of the slits. The greatest opening of the slits usually occurs about noon, from about 11 to 3 o'clock. The stomata may remain completely closed on dull windy days. At night or in artificial darkness the slits close rapidly. If darkness is prolonged a re-opening may take place. The withholding of carbon dioxide leads, in light as in darkness, to opening, and thus acts like access of light.

In most plants an efficient, self-acting, regulation of evaporation takes place through the automatic closing of the stomata when excessive loss of water occurs.[2]

The closing for the whole winter of the stomata of our evergreen shrubs and trees early in the autumn, is explained by the necessity of being sparing with water during the time when there is little or no root activity. If cut twigs of *Ilex* or *Taxus* are placed in water in a warm room in winter, re-opening of the stomata occurs, given sufficient atmospheric moisture, in *Ilex* even in a few hours, in *Taxus* only in a week, whilst *Hedera* and *Buxus* even then still keep them closed.

An important life phenomenon which is explained by the above behaviour of the guard cells of the stomata, is the reduction or cessation of the feeding activity of the leaves during shortage of water. The general standstill of vegetation during dry weather is well known and Kreussler has shown that very much less is assimilated in dry air than in moist. If the water shortage is so great as to cause wilting, the leaf forms no more starch whatever, as Stahl proved in limes, fly honeysuckles, lilacs and black elders. This failure to assimilate has been traced by Stahl to the closing of the stomata in consequence of shortage of water. Assimilation ceases if the passages are closed to the exchange of gases bound up with it. In plants which are unable to close their stomata, assimilation still continues during wilting. When, indeed, the assimilating cells themselves become limp, it is interrupted in these cases also. Respiration is less reduced than assimilation by the closing of the stomata with vaseline, which may be partly due to the passage through the cuticle being more open to the gas interchange connected with the former, partly however to the so-called internal or intramolecular respiration which becomes recognisable with insufficient

[1] Livingston & Estabrook, Bull. Torrey bot. Club, 39, 1912.

[2] Iljin, Flora N. F., Bd. 16, 1923, p. 360 ; the same, Jahrb. wiss. Bot. 61, 1922 ; Linsbauer, *loc. cit.* ; Stalfelt, *loc. cit.*, and others.

supply of oxygen.[1] The wave length of the light also influences the condition of the stomata and transpiration.[2]

Leaves that are not yet half grown and in which the final formation of the various tissues is beginning, transpire the most freely. The smaller transpiration of leaves that are more advanced, is explained by the completion of the cuticle whilst the intercellular spaces are not yet fully formed. Mature leaves transpire more weakly than leaves in the first stage but more strongly than those in the second, so that when only leaves in the second stage are present at the tip of the shoot, water is sucked away from the latter by the older leaves and a reversal of the sap stream may thereby occur.[3]

The alterations in shape of the **guard cells,** which effect the alternate opening and closing of the stomatal slits, are stimulus movements. The external influences in whose train they appear, such as alterations in the water content or in illumination, set free processes in the protoplasm which lead to changes in the osmotic pressure and so of the turgidity of the guard cells. Increase of their turgidity results in the widening of the opening and vice versa. They contain a supply of carbohydrates which at need takes the form of osmotically inactive starch or appears as soluble sugar which can set up osmotic pressure in the interior of the guard cells, independent of the pressure prevailing in the other cells of the epidermis. As the guard cells contain chlorophyll, being thereby distinguished from all other epidermal cells, they can supply themselves with carbohydrates, though they are not entirely dependent on their own chlorophyll, because the (exceptionally) chlorophylless guard cells of variegated leaves contain carbohydrates and are adjustable.[4]

Iljin [5] asserts he has observed in the guard cells with open slits very high pressures, which according to Ursprung and Blum were still to be proved. If the slits are to close, the sugar changes into starch and the pressure sinks to a half or less. The accessory cells also take an active part in this. When starch is built up in the guard cells it is decomposed in the accessory cells, so that a higher pressure arises in them which presses the guard cells together.[6] The conversion of starch into sugar and vice versa and the changes in turgidity consequent thereon may be completed in 1–2 hours. In stomata, closed in winter, of winter hardy leaves, the guard cells do not contain starch, but oil, sugar or tannin instead.[7]

The guard cells carry on a domestic economy of their own independent of their neighbours. They are, it is true, connected with the neighbouring cells by prolongations of the protoplasm,[8] but these

[1] Nicolas, Ann. d. sc. nat. Bot., 1909, p. 1. (Ref. Bot. Zentralbl, 117, 1911, p. 131.)

[2] Iwanoff u. Thielmann, Flora, 116, 1923, p. 296.

[3] Seliger, Inaug.-Diss., Göttingen, 1911; Schechner, Zur Kenntnis des absteigenden Saftstromes. Anz. d. Akad. d. Wiss. Wien, XLVI, 1909, p. 272; Löwi, Verhl. zool.-bot. Ges. Wien, LIX, 1909, p. 397; Wiesner, Biologie der Pflanzen, 2. Aufl., p. 67. Wien, 1902, Hölder.

[4] Kümmler, A., Jahrb. wiss. Bot. 61, 1922.

[5] Regulierung der Spaltöffnungen im Zusammenhang mit der Veränderung des osmotischen Druckes. Beih. z. bot. Zentralbl., XXXIII, 1, 1915.

[6] Strugger u. Weber, Ber. d. D. Bot. Ges. 44, p. 272, 1926.

[7] Hagen, Zur Physiologie des Spaltöffnungsapparates. Beiträge z. allgem. Bot., Berlin u. Leipzig. Borntraeger.

[8] Kienitz-Gerloff, Bot. Ztg., 1891; Kohl, Bot. Zentralbl., Bd. 72, 1897, p. 257.

connections are, as Hill [1] found, only very rare and difficult to detect. Thus starch remains in them when it has disappeared from all the other cells of the leaf. Recent researches show that the contents of the guard cells and so also their osmotic value and the condition of their openings, can be altered by influences of many kinds. The water content of the leaf, salt solutions,[2] wounds, may be effective besides the external factors already mentioned, in that they influence the starch forming and decomposing enzymes or the permeability of the protoplasm. The researches into these questions are still in progress and show that the problem is more complicated than it previously appeared. Further, the guard cells permit substances which are not recognisable in other places on the leaf surface, to pass out into dew drops, by diffusion through their cuticle, and this is apparently one of the reasons why the germs of leaf-inhabitating fungi make their way to the stomata, thence to penetrate into the host plant.[3]

5. The Leaf Parenchyma.—Let us now consider the green cells in the interior of the leaf. Generally they contain a large vacuole surrounded by protoplasm lining the wall, in which, besides the nucleus, as specially characteristic constituents, are deposited the **Chlorophyll Granules,** the bearers of the green colouring matter with whose presence is bound up the power of decomposing carbon dioxide or assimilation. So close is the connection between this function and the chlorophyll that green leaves usually soon die off if they are given no opportunity of carrying out assimilation.[4] Leaves which have been raised in the dark and have therefore not become green, are longer lived. Chlorophyll originates as a rule only in the light ; even if the granules in which it is formed are present in the cells. Plastids also, which are usually colourless (*see* p. 86), may often become green in the light and so become chlorophyll granules. Only in a few cases, as for example, in the embryo of the silver fir when still enclosed in the seed, does the formation of chlorophyll occur in the dark. In white spotted, variegated leaves, closely investigated by Küster and Lakon,[5] chlorophyll formation, for various reasons does not take place in isolated patches and strips.

Under the epidermis of the upper side of the leaf, which is exposed to the greatest intensity of light, are found one or more layers of cylindrical or prism-shaped cells, which are arranged at right angles to the leaf surface and are accompanied by narrow intercellular spaces. These are called **Palisade Cells.** The space between them and the lower epidermis is filled with loosely aggregated or **Spongy Parenchyma**—

[1] Hill, A. W., Phil. Trans. of the Royal Soc. of London, Ser. B. Vol. 194, 1901, p. 83.

[2] Iljin, Stad. plant. physiol. Labor. Prague 2, 1925 ; Jahrb. wiss. Bot. 61, 1922 ; Biochem. Z. 132, 1922 ; Schmetz, L., Bot. Archiv. 10 ; Arends, J., Planta, Archiv f. wiss. Bot. 1, 1925, etc. ; Kirschew, N., Veränderung der Durchlässigkeit des Protoplasmas der Schliesszellen. Beih. Bot. Zentralbl. 41, I, Abt., 1925 ; Nicolic, M., *ibid.* Further literature *see* Ber. Bot. Ges. 43, 1925, p. 437.

[3] Büsgen, Bot. Ztg., 1893.

[4] Jost, Über die Abhängigkeit des Blattes von seiner Assimilationstätigkeit. Pringsheims Jahrbuch f. wiss. Bot., Bd. 27, 1895 ; Vöchting, Über die Abhängigkeit des Laubblattes von seiner Assimilationstätigkeit. Bot. Ztg., 1891, 113.

[5] Küster, Mitt. der D. Dendrologische Ges. Nr. 28, 31, 32, 33, 34, 1919-1925 ; Lakon, G., Weissrandpanaschierung von *Acer negundo* L., Zeitschr. f. indukt. Abstammungs- und Vererbungslehre XXVI, 1921.

somewhat thick-walled cells, less rich in chlorophyll, which owing to their irregular shape leave large air spaces between them, either all in communication with each other, or *e.g.* in beeches, hornbeams, oaks and maples, uniting into several spaces separated from each other by the veins which form an almost air-tight boundary.[1] All the intercellular spaces of the leaf debouch to the outside in the stomata.

The leaves of the hop hornbeam (*Ostrya carpinifolia*) and many species of maple are centrically constructed, *i.e.* their spongy tissue resembles the palisade tissue.[2] Centric construction is however specially exhibited by the needles of our conifers. They are traversed by a single middle vein, whose vascular bundle, in many species, splits early into two bundles [3] in the young leaf. By employing this peculiarity it has been possible to divide the coniferous species into two groups: the one- and two-bundled (haploxylon and diploxylon) (Fig. 97). In the neighbourhood of the vascular bundle, besides parenchyma cells and transition cells from the bast to the assimilation tissue, are found short tracheids with bordered pits (Fig. 97 *g*, *b*), which serve as water storers and enlarge the conducting surface of contact between the bundles of the vein and the green tissue. Their number is small in the spruce and silver fir which are adapted to situations with ample water supply, great in the pines which prefer sunny localities.[4] In the abietineae, and especially in the pine, this tissue is surrounded by a thick-walled parenchyma sheath whose cells are suberised on the transverse walls, in part also on the tangential walls, like the cells of the endodermis,[5] whilst in other cases it is immediately in contact with the green leaf parenchyma. In these cases its cell walls are stiffened by spiral or reticulate thickenings. The tissue bears the name of **Transfusion Tissue.**[6]

The green leaf-tissue, which in the pine needle surrounds the leaf vein with its water storer in a fairly uniform circular manner, is here disposed in layers (Fig. 98). Generally, stratified layers of green cells alternate with air spaces along the length of the needle. In the needles of the silver fir, palisade and spongy parenchyma are distinguishable, in the spruce, as in the pine, the green tissue forms transverse plates (Fig. 99). This arrangement permits of a perfect gas exchange with the outer air, although the stomata are not so regularly distributed over the surface of the leaf as in the broad-leaved trees, but are grouped in a few narrow strips (Rywosch). The green cells of the pine needles have characteristic folds and ridges on their walls which project to a varying extent into the interior of the cells and, forming recesses, increase the area of the cell walls (Fig. 96). By this means room is provided for

[1] Neger, Spaltöffnungsschluss und künstliche Turgorsteigerung. Ber. d. D. bot. Ges., XXX, 1912, p. 189. Wegsamkeit der Laubblätter für Gase, Flora 111, 1918; Rywosch, S., Ber. d. D. Bot. Ges., 43, p. 67, 1925.

[2] Warsow, Beih. z. bot. Zentralbl., XV, 1903, p. 493.

[3] Chauveaud, Ann. sc. nat. Bot. 8me. sér. XIX, 1904, p. 336.

[4] Scheit, quoted from Haberlandt, Physiol. Pflanzenanatom. 3, Aufl., 1904, p. 324.

[5] Soar, J., The structure and function of the Endodermis in the leaves of the Abietineae. New Phytologist, 1922, 21, p. 269.

[6] For more on this *see* Strasburger, Leitungsbahnen, Jena, 1891, G. Fischer. Anatomical-theoretical on the transfusion tissue; Carter, Ann. Botan. XXV, 1911, p. 975; Bernard, Bois centripète dans les feuilles de Conifères. Beih. z. bot. Zentralbl. XVII, 1904, p. 241, and XXII, 1, 1907, p. 211.

more chlorophyll granules, which are wont to distribute themselves in a single layer under the outermost stratum of the protoplasmic body. The ridges [1] originate in the interior of plasma plates as deposits on the cell walls which project to a varying extent into the cell cavity from the beginning, grow at the same time as the rest of the cell wall and do not penetrate into the interior of the cell merely by way of an addition. The ridges may divide into two leaves and have an ear-like widening at the end. Thus apparent folds are formed from the ridges. The only actual folds which occur are those which enclose the respiratory chambers under the stomata.

Long lived conifer needles grow in thickness. In this process the elements in the vascular bundle, especially those of the phloem, multiply, and the outer layers of the cells of the green leaf-tissue elongate, after

FIG. 97.

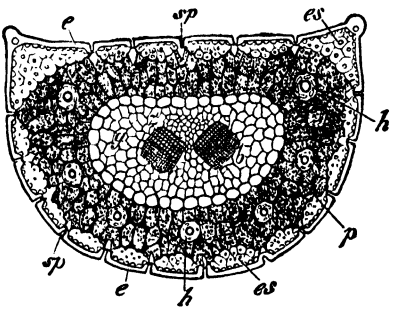


FIG. 98.

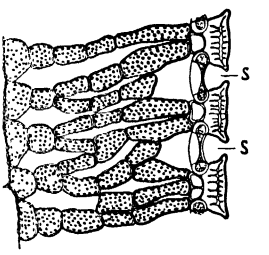


FIG. 97.—Cross section of a Pine needle (*Pinus pinaster*) magnified about 30 times. (*e*) epidermis, (*es*) thick walled cells under the epidermis (hypoderm), (*sp*) stomata, (*p*) green parenchyma, (*h*) resin ducts with sheaths, (*g*) (*b*) tissue without chlorophyll, containing two vascular bundles. After Sachs.

FIG. 98.—Longitudinal section of Pine needle from the outside to the transfusion tissue. (*s*) stomata. After Lebensgesch. d. mitteleurop. Blütenpflanzen.

the fashion of palisade cells, at right angles to the surface of the needle.[2] The remaining green cells extend themselves more in the direction of the latter.

The longitudinal development of the needles proceeds in such a way that they grow rapidly in their first youth but soon form a tip which puts an end to their growth. The further elongation then proceeds from a zone of growth lying at the base of the needle. The prolonged increase in length of several-year-old pine and spruce needles takes place by the enlargement of the cells, especially at the base of the needle, without however a continually active, dividing tissue [3] being present there. Meissner was not able to detect an actual growth in length of several years' duration in pines, silver firs, *Tsuga* and *Pseudotsuga*. The one-year-old needles are sometimes larger, sometimes smaller than those which have been on the tree for two years. On the other hand,

[1] Reinhardt, Die Membranfalten der *Pinus*-nadeln. Bot. Ztg. 1905, LXIII.

[2] Pergola, Ann. d. Bot., Vol. VI, 1907; Strasburger, Leitungsbahnen. Jena, 1891; *comp.* also Reinhardt, *loc. cit.*

[3] Strasburger, Leitungsbahnen; Meissner, Studein über das mehrjähriger Wachstum der Kiefernnadeln. Bot. Ztg. 1894 u. 1897.

Krauss [1] found that the needles of various species of pine are still able to grow in the second and even in the third year of their lives, and this at the base, enclosed in the sheath of the dwarf shoot, which contains fairly thick walled cells—not so those of other conifers. In the second year, in the most favorable cases, the length may increase in the proportion 46 : 62 or even 57 : 95.

The pulvini, *i.e.* the cushions which in the spruce run some distance down the shoot from the point of insertion of the needles, originate as regards their lower part from the shoot, as regards their upper part from the base of the needle.[2]

In pine needles just under the epidermis, there are two principal resin ducts, placed laterally, which extend down to within ½ millimetre of the leaf-base. In addition there are 2–20 accessory resin ducts which, likewise placed just under the epidermis, are distributed over the upper and under sides of the needle. These resin ducts end 5–7 millimetres above the leaf-base by the disappearance first of the resin-containing intercellular space and then of the resin-forming cells.[3] As a rule the ducts are surrounded by a sheath of very thick walled cells which protect them from the pressure of the living, green leaf-tissue (Fig. 96). The spruce needle [4] has, as a rule, two resin ducts near the under side. In young needles the two resin ducts extend into the rind of the shoot that bears them. The connection is interrupted, however, by the middle of June, by the formation of cork, whereupon the resin duct becomes filled with tyloses in the base of the needle. The ducts are often interrupted in their course, which makes their enumeration by cross sections uncertain.

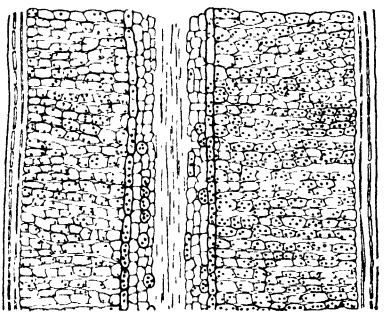


FIG. 99.—Sun-needle of the Spruce. Longitudinal section. Shows epidermis, hypoderm and stratified green parenchyma and its transition into the water storing tissue. Highly magnified.

In *Abies* the position of the resin canals may be used as a means of identification, according as to whether they adjoin the hypoderm or are embedded in the parenchymn. If a needle is cut across and slightly squeezed, small droplets of resin may be seen even by the naked eye, to exude at the places in question. It is to be noted in making comparisons that *e.g.* in *Abies pectinata*, the resin ducts in shade leaves are marginal, but those in light needles and on the main shoot internal. Only those needles are comparable which have all grown on main shoots or all on side shoots under similar lighting conditions.

The palisade cells contain the major portion of the chlorophyll

[1] Krauss, G., Mehrjähriges Dickenwachstum der Kiefernnadeln. Abhandl. der naturforschenden Gesellschaft zu Halle, XVI, p. 1–12.

[2] Celakovsky, Flora, XC, 1902, 433.

[3] Haberlandt, Physiol. Pflanzenanatomie, 3. Aufl., p. 460. Leipzig, 1904.

[4] Rywosch, Bot. Jahrbücher f. Systematik, XLI, 1908, and Strasburger, Leitungsbahnen, Jena, 1891; Rywosch, Beiträge zur Anatomie des Chlorophyllgewebes. Zeitschr. f. Bot., IV, 1912, p. 257. Jena, G. Fischer.

granules of the leaf which is, even to the naked eye, of a darker green colour on the upper side, and they are the best lighted. It is, therefore, in them in the first place, that the formation of carbohydrates, which depends on light and cholorophyll, is carried out. Under the same intensity of illumination more carbon dioxide is actually decomposed by the part of the leaf on the upper side than by the under one.[1] By this function, and by the necessity of conveying the newly formed substances to the veins by the shortest way and without unnecessary obstacles, for transport out of the leaf, the characteristics of the palisades are explained. Their elongation at right angles to the leaf surface reduces the number of cell walls to be passed through to reach the conducting tissue. Their convergence towards funnel shaped cells, which usually join on to the ends of several palisade cells and bring about the transition to the well aerated spongy parenchyma (Fig. 100),

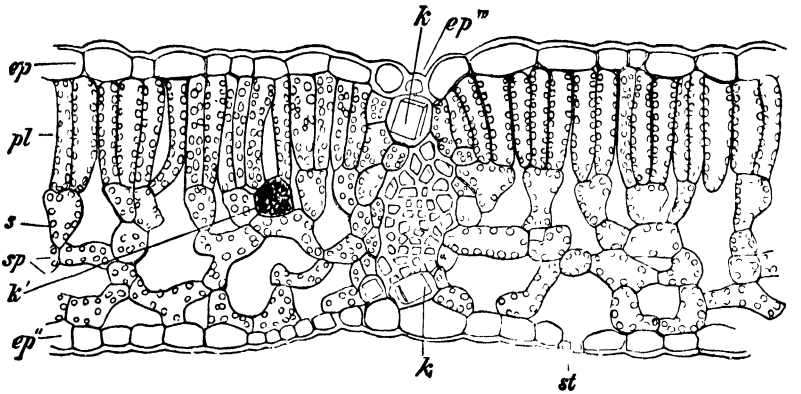


FIG. 100.—Cross section of a Beech leaf with palisades (*pl*), spongy parenchyma (*sp*), and funnel cells (*s*) ; (*ep*) epidermis, (*k*) crystals, (*st*) stoma. Magnified 360 times. B.L.

acts in the same way. These funnel shaped cells are equally well adapted for the distribution of the water coming in from the veins among the palisades and for the removal of the substances coming from the latter.[2]

In many trees, the sap of the leaf-cells contains anthocyanin which completely conceals the chlorophyll by its vivid red colour and gives the whole crown a dark red appearance. Such red-leaved sub-varieties are especially well known in the beech (copper beech), hazel, sycamore and many other plants.[3] Stahl[4] conjectures that to the red colouring matters falls the task of making serviceable for the plant, light-rays which are ineffective in the colouring matter of the chlorophyll.

6. Shade-leaves and Sun-leaves.—In many trees there is a difference in structure between the leaves which develop more in the interior of the crown and those which have unfolded on the outside of it. The former have been termed **Shade-leaves,** the latter, **Sun-leaves.**

[1] Griffon, Compt. rend., Paris, 1902.
[2] Rywosch, Ber. d. D. bot. Ges. XXV, 1907, p. 196.
[3] v. Schwerin, Über rotblättrige Pflanzen. Mitt. d. D. Dendrol. Ges., 1925, p. 156.
[4] Stahl, Über bunte Laubblätter. Annales du Jardin de Buitenzorg, XIII, 1896, p. 141.

The difference between them is very marked, especially in beeches, oaks and hazels. Shade-leaves (Fig. 104) have fewer stomata, they are thinner and more delicate than sun-leaves, because the latter possess thick walled, epidermal cells and a massive, many layered palisade parenchyma, whilst in the former the epidermal cells have delicate walls and the palisade tissue is developed as a single layer of cells, full of gaps and differing very little from the spongy parenchyma. Measurements [1] have shown that the air spaces in shade-leaves of *Sambucus nigra* and the beech have 10 per cent. more volume than those in the sun-leaves. The mean proportion of air spaces in the leaves of the former plant amounted to 24½ per cent. (extremes 16 and 26 per cent.), of the latter, 23 per cent. (extremes 19 and 29 per cent.). Sun-leaves of the sycamore (*Acer pseudoplatanus*) have palisades double as long as those of the shade-leaves, the collecting cells (funnel cells) being also absent from the latter. The stronger structure of the palisades and the strengthening organs involves a smaller proportion of surface to volume in light-leaves than in shade-leaves. Huber calls this proportion of surface to volume the "surface development." He found it to be as follows:

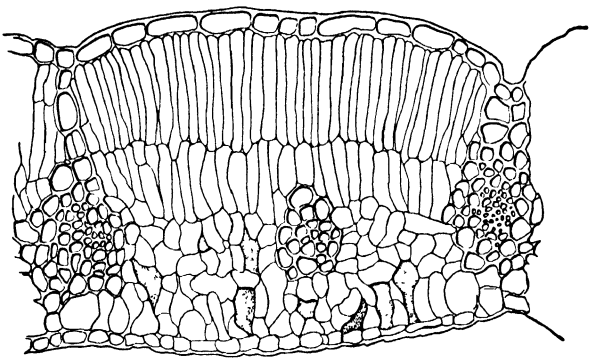


FIG. 101.—Sun-leaf of Beech. Highly magnified. Transverse section. After Stahl.

	Sun-leaf.	Shade-leaf.
Beech	123	153
Pedunculate oak	84	109
Silver fir	39	70
Spruce	30	40

The epidermal cells of the sun-leaf of the beech abut on each other with even walls, whilst in the shade-leaves the walls run in a wavy fashion.

Even more striking are the differences between the light- and shade-leaves of the spruce and silver fir species (Fig. 102, 103, 105–107) whose leaves, by reason of their power of bearing much shade, occur in very varied strengths of illumination. The shade-leaves of the silver firs [2] are pectinate and directed horizontally (euphotometric arrangement),

[1] Stahl, Über den Einfluss der Lichtintensität auf Struktur und Anordnung des Assimilationsparenchyms. Bot. Ztg., 1880; the same, Einfluss der sonnigen und schattigen Standortes auf die Ausbildung der Laubblätter. Jenaische Zeitschr. f. Naturwissensch., Bd. XVI, 1883. Reprint by G. Fischer, Jena.

[2] Taubert, Beitr. z. äusseren und inneren Morphologie der Nadeln bei der Gattung *Abies*. Diss. Tharandt- Leipzig, 1926, and Mitt. d. D. Denrol. Ges., 1926; Kirchner, Loew, Schröter, Lebensgeschichte d. Blütenpfl-Mitteleutopas.

the needles on the upper side of the twig are considerably shorter than those on the underside, so that they shade each other as little as possible (anisophylly). The structure of the needles is dorsiventral, stomata occur mostly on the under side, and in smaller numbers than in light-leaves. Palisade parenchyma is formed only as a single layer of cells on the upper side; the point of the needle is, in most species, notched. The thickening of the epidermal walls, the wax secretions on the needle surface, and the hypoderm are weaker than in light-needles. The light-needles, which are only fully perfected in older trees, and especially in the apical region, are thicker, sabre shaped, have their tips directed vertically upwards (panphotometric arrangement) and stand closer on the twig than shade-needles; the notching at the tip is absent. Stomata are formed in larger numbers and also on the upper side. The palisade parenchyma consists of several layers and also appears on the under side.



FIG. 102.—*Abies Nordmanniana*, shade-twig of an old tree. Needles pectinate. Reduced 1 : 2. After Taubert.

The structure and arrangement of the shade-needles allows of the fullest possible utilisation of the small amount of light falling on them, and the arrangement of the light-needles ensures that the excessive zenith light, rich in ultra-violet rays, only grazes their surface. The wax secretions which are found, especially on the leaves of coniferous species and varieties from dry high altitudes on continental mountains, such as the Rockies in North America, as well as the thick cuticle, epidermis and hypoderm layer of sun-leaves, act both as a protection against excessive light of short wave-length which they absorb and keep back from the chlorophyll tissue, and, in addition, especially as a protection against cuticular evaporation. If the stomata are closed, this protection becomes a very real one; on the other hand, when the slits are open, transpiration proceeds for the most part through the stomata and the reduction of cuticular water emission plays no part. It is then also unnecessary, for the stomata are only opened when there is a plentiful supply of water. In this condition light-leaves evaporate more than shade-leaves, in consequence of their greater number of stomata, since stomatal transpiration is many times greater than cuticular. Shade-leaves, because of their sheltered, shady position, have less need for cuticular protection against evaporation; being constructed to favour evaporation they are able to keep the vital water circulation going at the necessary rate even in the moist calm atmosphere of the interior of the crown.[1]

[1] On the transpiration of shade- and sun-leaves *see* Dietrich, Jahrb. f. wiss. Bot., 1925, p. 98.

In broad-leaved plants also, light-leaves have far more stomata than shade-leaves. Thus, according to enumerations by Schramm [1] the number of stomata per square millimetre of leaf surface was :

	In the sun.	In the shade.
Acer pseudoplatanus .	860	215
Carpinus betulus . .	365	170
Quercus sessiliflora . .	810	468
Tilia grandifolia . .	759	450



FIG. 103.—*Abies Nordmanniana*, light-twig from the top of an old tree. Needles directed upwards in a brushlike manner. (*a*) seen from above (0.6 : 1), (*b*) from the side (0.4 : 1). After Taubert.

Hesselman [2] found more stomata on sun-leaves than on shade-leaves, also in herbaceous plants. Dufour [3] found the same. For

[1] Schramm, Flora 104, 1912.

[2] Hesselman, H., Beih. z. Bot. Zentralbl., 17, 1904.

[3] Dufour, Influence de la lumière sur la structure des feuilles. Bull. soc. bot. de France, T. XXXIII, 1886. *Comp.* also Yapp, Ann. of. Bot. 26, p. 815, 1920.

accounts of the number of rows of stomata on light- and shade-leaves of various species of silver fir *see* Taubert.

Measurements of the water vapour given off by shade- and sun-leaves give different results according to as whether the loss of water vapour is related to leaf dry weight or to leaf area. If a beech grown in the shade seems to evaporate more per 100 grammes leaf dry weight than one grown in the sun, this may be due to the much greater lightness of the delicate shade leaves of the former, with their plentiful intercellular spaces, as compared with the tough leaves of the latter. Indeed the actual amount of water evaporated by the sun-beech may consequently have been greater. Hesselman [1] has proved that in the sun, in the same locality, plants with palisade cells actually gave up much more water in proportion to the leaf surface than those whose leaves possessed the shade-leaf structure. In the olive, Berger [2] found sun-leaves in nature evaporated 8–10 times as much as shade-leaves, and under similar though not quite natural conditions, still 1½ times as much.

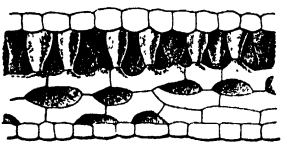


FIG. 104.—Shade-leaf of a Beech. Highly magnified. Cross section. After Stahl.

The form of the light-leaves, especially their thick palisade parenchyma, enables them to utilise the favorable illumination in proportion to their high chlorophyll content. Génau de Lamarlière [3] has also proved that, under similar external conditions, sun-leaves actually develop a greater assimilative activity than shade-leaves, which they also excel in rapidity of respiration. Whilst, for example, sun-leaves of the beech decomposed 0.038; 0.081; 0.023 cubic centimetres of CO_2, shade-leaves decomposed 0.024; 0.068; 0.017 cubic centimetres.

For the oak the following were given:

Sun-leaves . .	0.064	0.050	cubic centimetres carbon
Shade-leaves . .	0.037	0.037	dioxide decomposed.

The difference would be still greater if the activity of the small quantity of chlorophyll in the cells of the shade-leaves were not aided by the large intercellular spaces which facilitate the supply of carbon dioxide.[4]

The compensation point at which the assimilates formed are just again consumed by respiration lies, according to Harder,[5] higher in light-leaves than in shade-leaves of the same species, in the ivy for instance by 100 per cent. Light-leaves thus require more light than shade-leaves to keep them alive. Stalfelt [6] found the same thing.

[1] Zur Kenntnis des Pflanzenlebens nordischer Laubwiesen. Eine physiolog.-biolog. u. pflanzengeographische Studie. Jena, 1904, G. Fischer; *comp.* also Areschoug, Flora, XCVI, 2, 1906, p. 319.

[2] Bot. Gaz. XXXVIII, 1904, 285.

[3] Compt. rend. d. Pariser Acad., T. CXV, Nr. 9 and 12. Ref. Bot. Zentralbl., 1892, IV, 331, 1893, I, 148; Jensen, P. B., Studies on the production of matter in light- and shadow-plants. Botanisk Tidskrift, Kopenhagen, 1919, Bd. 36, p. 219. With extensive literature.

[4] Montemartini, Intorno alla anatomia e fisiologia del tissuto assimilatore delle piante. Atti d. Ist. bot a. R. Univ. Pavia, Ser. II, Vol. IV. Ref. Bot. Zentralbl., 1895, III, 74.

[5] Harder, Ber. Dtsch. Bot. Ges. 41, 1923, p. 194.

[6] Stalfelt, Mitt. forstlich. Versuchsanstalt Schwedens, 1922, H. 5.

According to his investigations the light value of the compensation point at 20 degrees C. for light-needles of the spruce lies at 7.5 per cent., for shade-needles at 3 per cent., of the full sunlight at the beginning of July. The power of the shade-needles to utilise poor light better is due in part to their relatively larger chlorophyll content.

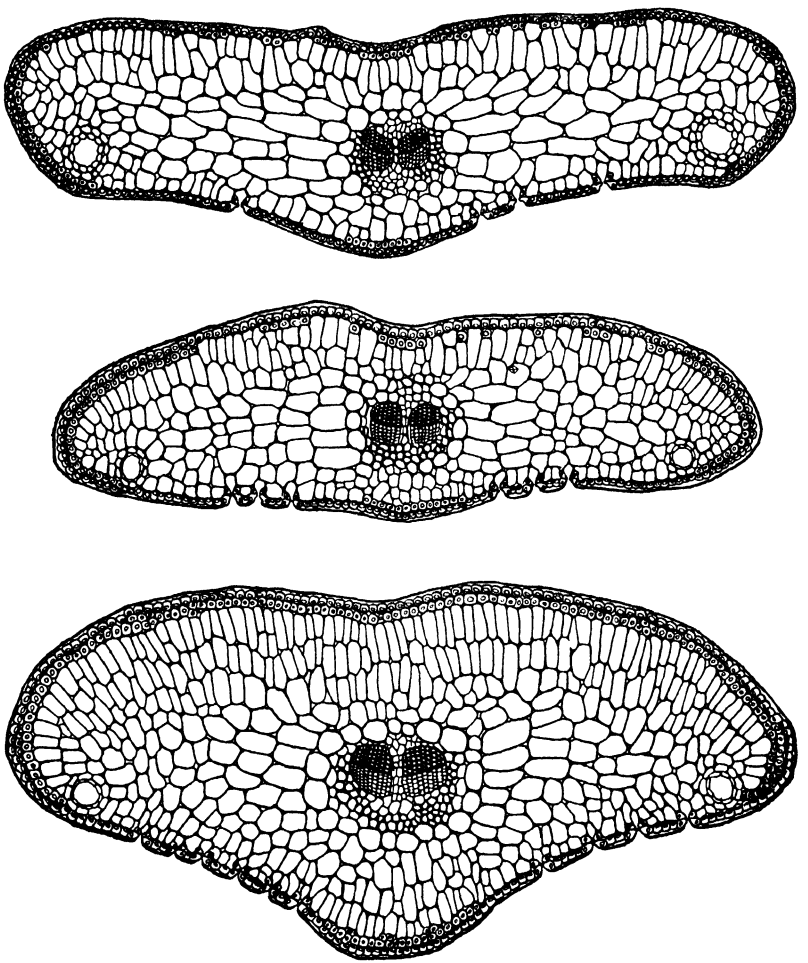


FIG. 105.—Transverse sections of needles of *Abies Nordmanniana* 1 : 56. Top: light-needle of a young plant. Middle: shade-needle from an older tree; both with weak hypoderm and single-layered plaisade parenchyma. Bottom: light-needle from the top of an old tree, with 2–3 fold hypoderm and 2–3 fold palisade parenchyma. After Taubert.

It is in agreement with this that, according to Engler,[1] beech plants raised in full light throve much worse after transplanting into the shade than did plants accustomed to the shade.

On a comparative examination of the structure of the leaves formed in the different life stages of the plant or the individual twigs, it is evident that in our broad-leaved trees, the juvenile leaves of the whole plant, like those of the individual twigs, possess the structure of shade-

[1] Engler, A., Mitt. der Schweiz. Zentralanstalt f. d. forstl. Versuchswesen, X, 2, 1911.

leaves. Thus the appearance of shade-structure in the older tree and in the later stages of growth of the individual twig, does not indicate the development of a new anatomical characteristic, but the retention of the juvenile form.[1] Taubert found the like for almost all species of silver fir. The faculty of reacting to strong light by the formation of highly differentiated light-leaves first appears with the increasing age of the plant. Epicormic branches (preventitious shoots) of the silver fir also, even when they appear in well lighted positions on old trees, begin with the juvenile form of leaf and are able to form light-leaves only after several years. Vischer [2] has demonstrated on xerophyllous plants and from the literature, that throw-backs to the juvenile form may be induced by the most varied conditions. The juvenile forms (shade-leaves), just like the throw-backs, are distinguished by a proportionally higher ash content,[3] the later forms (sun-leaves) by a higher content of assimilates, and everything which interferes to displace the proportions of these two groups of substances in one direction or the other, favours the appearance of the anatomical peculiarities in question. Thus severe cutting back, good rooting, cutting off of leaves, moist air, removal of reserve materials, manuring and cultivation in nutrient solutions, just like poor illumination lead to an increase in the ash content as compared with the assimilates, and thereby to the appearance of the atavistic form. Poor rooting, cutting of the roots, cultivation in sand or pure water, also the application of common salt which renders difficult the taking up of water, just like good illumination, upset the proportion in favour of the assimilates and lead to the appearance of the mature form. Klebs [4] found a higher concentration of carbonaceous assimilates as compared with nutrient salts, determinative for the formation of sun-leaves in the beech.

The external influences by which sun- and shade-leaf structure can be produced experimentally are, in nature, in hardly separable association with the arrangement (organisation) of the whole plant. Thus, in the spruce, sun-needles are found on strong upright-growing shoots, shade-needles on the horizontally extending, drooping side twigs. In broad-leaved trees (beech, etc.) sun- and shade-leaves may be distinguished in the buds even before sprouting [5] and, under the same illumination, the one or the other leaf-form appears on twigs according as to whether the twig itself has developed in the sun or in the shade the previous year. It should be noted, in experiments, that leaves which in the fully foliaged tree may lie in the shade, may have been exposed to the sun during their development. The formation of red colouring matter in beech leaves and, to a certain extent also, leaf thickness and the length of the palisades, are directly favoured by light. Tobacco leaves, when illuminated from all sides, form palisades also on

[1] Schramm, Über die anatomischen Jugendformen der Blätter einheimischer Holzpflanzen. Flora, hrsg. v. Goebel, IV, 1912, p. 225. Jena G. Fischer; Nordhausen, Über Sonnen- und Schattenblätter. Ber. d. D. bot. Ges., XXX, 1912, p. 61.

[2] Vischer, W., Experimentelle Beiträge zur Kenntniss der Jugend- u. Folgeformen xerophiler pflanzen. Flora, hrsg. v. Goebel, VIII, 1915, p. 1. Jena, G. Fischer.

[3] Leiningen, Nat. Zeitschr. f. Forst- u. Landwirtsch, III, 1905.

[4] Über das Treiben der einheimischen Bäume, speziell der Buche. Abhandl. d. Heidelberger Akad. d. Wiss., math.-nat. Kl., Abt. 3 Heidelberg, 1914.

[5] Nordhausen, Ber. d. D. bot. Ges., XXI, 1903, p. 30.

the under side where otherwise they are absent.[1] Sun-buds of the beech, *i.e.* those developed on twigs in the sun, differ from shade-buds in the number, size and inner structure of the scales. In consequence of the stronger development of all their tissues sun-twigs are thicker and longer than shade-twigs.[2] Their epidermal cells are smaller and thicker walled, their cork periderm appears earlier and more abundantly and has thicker tangential walls, and there are more stone cells embedded in their rind parenchyma. In the xylem wider vessels and more wood-fibres are present.

Shade-buds of the beech and some other broad-leaved trees expand in spring earlier than light-buds. This is perhaps associated with the shade-buds being less tightly enclosed in their thinner scaly covering. Thus, when a beech wood becomes green, it is the adventitious shoots and the buds of the inner and lower parts of the crown that unfold

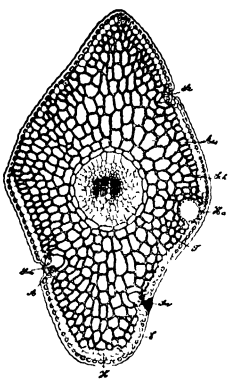


FIG. 106.—Shade-needle of the Spruce. Transverse section. Same magnification as Fig. 107.

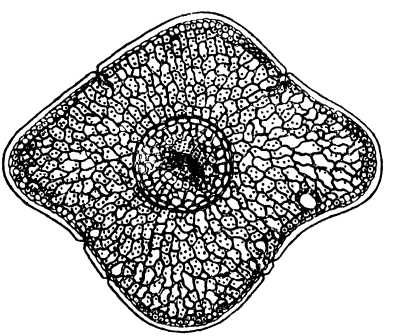


FIG. 107.—Sun-needle of the Spruce. Transverse section. Same magnification as Fig. 106.

first.[3] Moreover on northern slopes, the trees become green up to as much as a week earlier than on southern slopes, because the buds formed in the diffused light have fewer and thinner scales than the "sun-buds" of the southern slope; the latter are also larger and heavier than the former.

7. The Chlorophyll Granules.—An alteration which the leaves undergo immediately under the influence of light is the rearrangement of the chlorophyll granules. In the palisade cells the chlorophyll granules are generally distributed on the cell walls that are at right angles to the leaf-surface; they avoid those walls of the cells which are parallel to the surface of the leaf, at least when they border on other cells.[4] In this position they receive the slightly oblique rays of the diffused light from the clear sky. Rays which penetrate the leaf quite vertically "shine past the chloroplasts thus arranged." They

[1] Groslick, Bot. Zentralbl., XX, 1884.

[2] Fahrenholz, Einfluss von Licht und Schatten auf Sprosse von Holzpflanzen. Kieler Inaug.-Diss. Dresden, 1913. Also on the anatomical differences between dwarf and long shoots

[3] Engler, A. Mitteil. d. schweizer. Zentralanstalt f. d. forstliche Versuchswesen. X, 2, 1911.

[4] Stahl, *loc. cit.*, Rywosch, Zeitschr. f. Bot., IV, p. 257. Jena, 1912.

fall, almost undiminished, to the benefit of the spongy parenchyma. Here, in diffused light, the chloroplasts distribute themselves especially on the cell-walls parallel to the leaf-surface (**epistrophe** or surface arrangement). In bright sunlight they withdraw to the more shaded walls at right angles to the leaf-surface (**apostrophe** or profile arrangement); they flee from the sun's rays. Shade-leaves, especially, with poorly marked palisades therefore appear paler than usual in sunlight. If the leaf is illuminated with moderately strong rays made artificially parallel, some of the chloroplasts in the palisades also move to the small cell-walls which lie parallel with the leaf-surface.[1] The zoospores of the green algae of our waters seek certain light intensities and flee from others. The individual chloroplasts of a leaf behave in just the same way. They are "**phototactic.**" Stahl describes an experiment by which the position of the chloroplasts can be judged by the naked eye. If a shade-leaf of the elder is struck by sunlight falling vertically on its surface, it soon becomes paler owing to the migration of the chlorophyll granules. The leaf appears almost bleached if it is looked at in the same direction as that in which it is struck by the sun's rays. If the leaf is tilted the granules are seen partly in surface arrangement and partly in profile. The contrast between the sunned and unsunned parts decreases until in a certain position almost all the granules turn an equally large surface to the observer and the contrast entirely disappears.[2] In the palisades the chlorophyll granules adjust themselves to various light intensities by altering their shape. In strong illumination they are spread out flat against the longitudinal cell walls, in weaker light they project more into the cell cavity and so intercept more light. The palisades are the cell form adapted for strong light, the spongy cells, that for weaker intensities of illumination.

If leaves are placed in the dark, the chloroplasts in the spongy parenchyma distribute themselves on all the walls which abut on other assimilating parenchyma cells, leaving vacant the walls which are in contact with air-spaces, epidermal cells, raphide cells, and other chlorophyll-free elements.[3] If one of the factors concerned (light, heat, etc.) acts too excessively the chloroplasts draw together in clumps.

The chloroplasts are not only sensitive to light but also **thermotactic.** If hoar frost forms on the leaves they draw away from the cold outer walls of the palisades. Moreover they are **chemotactically** attracted by carbon dioxide, salts and organic substances. In such cases even small differences in concentration are effective so that such stimuli may be concerned when they are placed in the dark.

As far as their physical properties are concerned the chlorophyll granules [4] are tender structures, in many cases more like drops of liquid

[1] Senn, Gestalts-und Lageveränderung der Pflanzenchromatophoren. Leipzig, 1908. Gives further literature.

[2] Stahl, Einfluss sonnigen und schattigen Standorts auf die Ausbildung der Laubblätter, p. 5, Note. Jena, 1883, G. Fischer. The same, Bot. Ztg., 1880.

[3] Senn, Weitere Unters. ü. Gestalts- u. Lageänderungen d. Chromatophoren, IV u. V. Zeitschr. f. Bot. II, 1919.

[4] For everything about the chemical side of plant life the well-known chief sources are: Czapek, Biochemie der Pflanzen, 2, Aufl., Bd. I. Jena, 1905, G. Fischer; Wehmer, Pflanzenstoffe. The same, 1911. *See* also the relevant articles in the Handwörterbuch d. Naturwissenschaften. Jena, G. Fischer; Willstätter u. Stoll, Untersuchungen über Chlorophyll. Berlin, 1913, Springer. The same, Unters. ü. d. Assimilation der CO_2. Berlin, 1918.

than solid bodies. The colouring matter is distributed in colloid solution in a colourless matrix consisting of proteid-like hydro-colloids, out of which it separates very easily in droplets. The whole uninjured chloroplast only contains droplets or granules, however, when small starch grains or drops of oil appear. The colouring matter is easily extracted from the leaves by alcohol, though it does not remain unaltered by the process. The solution soon decomposes and changes colour, especially in the light.

The chloroplasts contain a considerable amount of lipoid substances which stand in close relation to the chlorophyll colouring matter.[1] From comparisons of more than 200 very varied kinds of plants, it appears that chlorophyll is everywhere chemically identical. It consists of the blue-green chlorophyll a and the yellow-green chlorophyll b. Both are complex Mg. compounds of similar constitution.

$$\text{Chlorophyll a} = (MgN_4C_{32}H_{30}O)\ CO_2CH_3.\ CO_2C_{20}H_{39}.$$
$$\text{Chlorophyll b} = (MgN_4C_{32}H_{28}O_2)\ CO_2CH_3.\ CO_2C_{20}H_{39}.$$

In the chloroplast the chlorophyll colouring matters are always accompanied by two yellow pigments: carotin $C_{40}H_{56}$ and the xanthophyll $C_{40}H_{56}O_2$. The chlorophyll content of normal green leaves amounts generally to about 0.8 per cent. of the dry weight and varies between rather narrow limits, 0.15–0.35 grammes per 100 grammes green weight, 0.6–1.2 grammes per 100 grammes dry weight of the leaves, 0.3–0.7 grammes per 1 square millimetre of leaf surface. Substances may be obtained from chlorophyll by decomposition which are chemically closely allied to bodies which may be obtained from the colouring matter of the blood. Iron is indispensable for the formation of chlorophyll in the leaf but is not a constituent of the chlorophyll molecule. Pure chlorophyll together with the yellow pigments and other accompanying substances, in colloidal distribution, is unable to decompose any CO_2 outside the chloroplast.

8. Assimilation and Respiration.—The importance of chlorophyll for the plant lies in the fact that it is only in green cells that the decomposition of carbon dioxide, the process which supplies our trees with carbon, is carried on. The dry matter of wood contains 49.5–51.5 per cent. of carbon, of which, for example by the technical processes of carbonisation, 24–25 per cent. of wood charcoal is obtained from barked beechwood. Not a single one of the innumerable plant substances is free from carbon. All the substances formed in animal and plant bodies, the so-called " organic substances " are carbon compounds, and the whole of the carbon contained in the animal and plant world—with the exception of certain bacteria—is extracted from the atmospheric carbon dioxide in the green cells.

The particular activity of the green cells under consideration is called **Carbon Assimilation** or, briefly, **Assimilation.** The word means " making similar " and rightly describes the process which makes the dead carbon of the carbonic acid into a constituent of the living plant body. The carbonic acid gets into the plant almost entirely in gaseous

[1] Biedermann, Flora, 1918, Stahl-Festband, p. 591.

form as carbon dioxide (CO_2) by means of the gas-exchange between the interior of the plant and the outer air through the stomata. Although the latter only occupy 1–3 per cent. of the leaf surface on which they occur, they are, under ordinary circumstances, the only means of ingress for the carbonic acid. If they are closed by smearing with a mixture of wax and cocoa butter assimilation ceases. The cuticle only allows appreciable quantities of carbonic acid through when the content of the surrounding air amounts to 30 per cent. or more, a figure which can only occur in nature in the neighbourhood of carbonic acid springs. The small quantities of carbonic acid which reach the leaves with the soil water from the roots and the carbonic acid formed by respiration hardly come into account for assimilation.

High concentrations act as a certain poison. A replacement of carbonic acid by other carbon-containing gases such as hydrocarbon or carbon monoxide, has so far been unsuccessful. It is easy to prove that carbonic acid is acted upon in the plant by allowing plants to assimilate in a measured volume of air. It is then shown that carbonic acid disappears and the same volume of oxygen is given off by the plant—that is, just as much oxygen as was present in the carbonic acid which has disappeared. The assimilation coefficient $\frac{CO^2 \text{ (carbon dioxide)}}{O_2 \text{ (oxygen)}} = 1.$ Small deviations, especially the giving off of more oxygen, are explained partly by sources of error, partly by the nature of the plant substances built up with the help of the carbonic acid, partly perhaps, by an, in any case small, breaking down of the carbonic salts taken up by the roots, with the liberation of oxygen.

The gas exchange of assimilation proceeds in just the opposite direction to that of **Respiration,** which involves the taking in of oxygen and the giving off of carbon dioxide. The burning of the carbon-containing compounds which are gained by assimilation is the immediate source of energy for the life machinery of the plant. In many bacteria alone, does the burning or oxidation of mineral substances perform the same service. Germinating seeds respire not much less rapidly than man.[1] They produce within 24 hours almost 1 per cent. of their fresh weight of carbonic acid, whilst man, in the same time expires about 1.2 per cent. of his living weight of that gas. The rate of respiration increases with every increase in the rate of height-growth and becomes weaker as this falls off. There is therefore a great period of respiration which goes hand in hand with the great period of height-growth. Resting seeds give off only a very small, but nevertheless measurable quantity of carbonic acid (1 kilogramme cereal grain with 9 per cent. of water, 0.07–0.12 gramme carbonic acid in 4 months), whilst the respiration of the twigs of our woody plants[2] during winter is only about one-third less than during the growing period. Simon found the respiration in cut beech twigs small at the beginning of May in spite of the breaking of the buds. The greatest drop in respiration appears to set in just before cambium activity begins, at least in branches more than one year old. After strong growth in thickness had begun it rose and remained

[1] Handwörterbuch d. Naturwissensch. Bd. I; Atmung. Jena, 1912, G. Fischer.
[2] Simon, Jahrb. f. wiss. Bot., Bd. XLIII, 1906, p. 1.

high up the close of diameter growth at the end of August. A fall set in in *Fagus*, *Quercus* and *Aesculus* at the end of October, in *Tilia* only in December. Then, throughout the whole winter, respiration remained constant and was in fact only one-third to one-quarter less than during the period of most rapid diameter growth. It varied periodically during the course of the day and frost was followed by an increase in respiration.

De Saussure [1] found that the 24-hourly requirement of oxygen of the leaves of broad-leaved trees was 3–8, of juniper needles and other evergreen leaves (*Ilex*, *Buxus*) 0.86–2.6 (*Juniperus sabina*) parts of their volume. It should be noted that in the latter the proportion of the mass of cell walls to the volume of the leaf is greater and the mass of protoplasm smaller than in the former. Mangin [2] found the quotient $\frac{CO_2}{O_2}$ in winter buds of trees and shrubs almost always less than 1, and in fact, almost invariably 0.8–0.9. In the autumn it was smaller in leaves than in buds and shrank again considerably at leaf-fall.

Respiration does not completely stop at temperatures under 0 degrees C. When the temperature approaches zero, however, it rises rapidly so that, for example, pine needles at 0 degrees respire 25 times as strongly as at −12 degrees.[3] Between 0 degrees and 40 degrees respiration increases like other chemical processes (Van't Hoff's law), twice to three times for every rise of temperature of 10 degrees. Above 40 degrees respiration falls off rapidly until the death of the plant. Small quantities of poisons such as ether vapour may temporarily increase respiration and are employed in forcing. A content of more than five volume per cent. of carbonic acid in the air hinders respiration if it is not made harmless by assimilation. How the burning or oxidation processes of respiration are carried out has not yet been quite clearly made out in detail. According to Palladin's [4] theory, enzymes contained in the plasma are involved in it. These transfer the atmospheric oxygen to bodies which have the property of becoming coloured under its influence (respiration chromogens: blue coloration of *Boletus* species, formation of indigo, darkening of plants on drying, orange coloration of alder wood), but in the living plant, as a rule without becoming coloured, pass oxygen on and so co-operate in the burning of the consumable substances, which are not in a condition to combine with atmospheric oxygen without these intermediate bodies. The substances which are consumable in respiration are carbohydrates, fats and their derivatives and, in case of necessity, proteids.[5]

The rise of temperature associated with respiration is not generally observed, because the distribution of the strongly respiring cells and the great surface development of the plant favour too greatly the dissipation of the heat produced. If, however, living parts of plants are collected in a well isolated vessel, *e.g.* in double-walled, glass Dewar flasks with a vacuum between their walls, it is quite easy to demonstrate

[1] Czapek, Biochemie, 1. Aufl., Bd. II, 1905.
[2] Rech. sur. les bourgeons. Bull. soc. bot., T. XXXIII, 1886, p. 185.
[3] Maximow, Journ. bot. soc. imp. Nat. St. Petersburg, 1908.
[4] Palladin, Ber. d. D. bot. Ges., 1908, 1909; the same, Jahrb. f. wiss. Bot., 1910; the same, Pflanzenphysiologie. Berlin, 1911, J. Springer.
[5] Deleano, Jahrb. f. wiss. Bot., LI, 1912, p. 541.

a by no means inconsiderable evolution of heat. In Molisch's [1] experiments of this kind, leaves of *Carpinus betulus*, with an air temperature of 28 degrees attained 51.5 degrees within 15 hours, and lime leaves with an air temperature of 18 degrees, 50.8 degrees in 27.5 hours. Conifer needles and ivy leaves only warmed up very little.

The loss of matter naturally associated with respiration becomes clearly apparent when, as in experiments in the dark, it is not compensated by assimilation. When life activity is great, however, it may also even surpass the gain in material resulting from assimilation. Thus young tree plants suffer a serious loss in weight on the sprouting of the shoots in spring,[2] as some of the reserve materials stored up in the previous year are decomposed and consumed in respiration. Lammas shoots may also be associated with loss in weight. Ramann and Bauer found in 1-4-year-old pedunculate oaks, a loss in weight of 4 per cent. with the spring shoots and as much as 15 per cent. with lammas shoots, though at that time a great number of active living leaves were present.

The most easily recognisable product of carbonic acid assimilation in the body of the plant is starch, which appears in the form of lustrous granules in the interior of the chloroplasts and is coloured blue by aqueous iodine solution. It forms, with the sugars, cellulose and a number of other substances composed only of carbon and the elements of water, hydrogen and oxygen, the group of carbohydrates whose members represent the most important non-nitrogenous constituents of the plant body. In the leaves of most trees inosite [3] is present. On the assumption that only sugar, and in fact glucose, results from assimilation, the chemical reaction may be expressed by the equation:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2$$

From this it is seen how the quantity of oxygen liberated in the formation of sugar is, as far as regards volume, the same as that of the carbon dioxide decomposed. For a long time it was believed that starch was not only the most easily recognisable but also the first product of the activity of the green cells. It is now known that sugar is produced first and that starch only appears when the concentration of sugar has reached a certain height—in one case 6.8 per cent.[4] In the form of solid starch the mass of carbohydrate takes up little room and does not hinder the formation of further quantities of carbohydrates as a high concentration of sugar solution would do. Leaves in which the sugar is not converted into starch, so-called sugar leaves, such as are found especially in the monocotyledons, are surpassed by starch forming leaves, among which are those of our broad-leaved trees, in total production of assimilates per day, and the maximum is reached sooner by the former than by the latter.[5] Starch first appears in the needles

[1] Bot. Ztg., 1908, p. 211.

[2] Ramann u. Bauer, Trockensubstanz, Stickstoff und Mineralstoffe von Baumarten während einer Vegetationsperiode. Jahrb. f. wiss. Bot., Bd. L., 1912, p. 67.

[3] Meillère, Contribution à l'étude biochimique de l'inosite. Soc. biol. Paris, Nr. of 18. Oct., 1907.

[4] Schimper, Über Bildung und Wanderung der Kohlenhydrate in den Laubblättern. Bot. Ztg. 43, 1885.

[5] Müller, Arno, Jahrb. f. wiss. Bot., XL, 1904, p. 443.

of our conifers,[1] according to the temperature, at the end of February[9] after their having been almost entirely free from starch during December and January. From April to July the needles of almost all years are very rich in starch; it then begins to disappear. The average starch content and the course of starch transformation differ according to the species.

Naturally the accumulation of starch in the chlorophyll granules reaches its limits. The starch does not, however, remain in the leaves; rather is it, in part even while it is being formed, re-dissolved by conversion into sugar by means of diastase, which is formed in the leaves especially in the dark, and in this form migrates to the places in the body of the plant where it may be utilised in the formation of cellulose or other carbonaceous compounds or, converted anew into starch, be afterwards stored.

It is as a result of this process that the leaves are found in the early morning to be empty of starch which again accumulates in them in the course of the day. The completeness of the nightly emptying will depend on the proportion between assimilation and evacuation, the latter of which may be slowed down on cold nights. Starch disappears more quickly from leaves when they are wilting [2] somewhat, also from severed leaves from which it cannot be conducted away. This is due apparently to increasing concentration of diastase. In the guard cells of the stomata things are reversed. Salt solutions act in the same sense, *e.g.* application of $CaCl_2$ and KCl promotes the demolition of starch in the mesophyll but hinders it in the guard cells. To be sure Iljin found many plants to behave differently.[3] That still other substances besides carbohydrates are formed in the leaves, has been emphasised by Saposchnikoff,[4] who was convinced that part of the carbon of the carbonic acid taken up by the leaves was utilised in the formation of protein substances. Leaves of horse chestnut and elder were found to be richer in nitrogen in the evening than on the following morning [5] and the more starch moves out of the leaves at night the more nitrogen passes out also.[6] That light acts as the immediate source of energy for the formation of proteins is not yet proved by these observations.[7] Protein accumulates in the chloroplasts when saltpeter is supplied to leaves which are suffering from nitrogen hunger.[8] The proportion of nitrogenous substances in the increase in weight of the leaves of 15–20-year-old specimens of *Acer negundo* during a day, is shown more accurately in the following table of Schultze and Schütz,[9] in which the

[1] Kirchhoff, Fr., Über das Verhalten von Stärke und Gerbstoff in den Nadeln unserer Koniferen im Laufe des Jahres. Inaug.-Diss. Göttingen, 1913. The leaves are the richer in tannin the older they are. Seasonal variations seem to be small.

[2] Molisch, Ber. Dtsch. Bot. Ges., 39, 1921; Ahrns, Bot. Archiv. 5, 1924; Strugger u. Weber, Ber. Dtsch. Bot. Ges. 43, p. 431, 1925.

[3] Iljin, Stud. plant. Labor. Prague 2; *comp.* also Ahrends, Planta, Archiv. f. wiss. Bot. 1, 1925.

[4] Saposchnikoff, Ber. d. D. bot. Ges., 1890.

[5] Otto u. Kooper, Beiträge zur Abnahme bzw. Rückwanderung der Stickstoffverbindungen aus den Blättern usw. Landwirtschaftl. Jahrb. XXXIX, 1910, p. 167.

[6] Suzuki, Bull. univ. Tokio, Coll. of Agric., Vol. III, 1897, 241.

[7] Zaleski, Ber. d. D. bot. Ges., XXVII, 1909, p. 56.

[8] Ullrich, H., Ztschr. f. Bot., 16, 1924.

[9] Landwirtschaftl. Versuchsstationen, LXXI, 1909, p. 299.

raw fibre, *i.e.* cell-wall substance, which may be counted in with the non-nitrogenous substances, and the ash are given also:

	Protein.	Non-nitrogenous substances.	Raw fibre.	Ash.
May	50%	20%	15%	23%
June	27%	48%	11%	7%
July	33%	70%	20%	3%
August	25%	80%	20%	6%
September	20%	33%	5%	13%

It will be seen that in the young leaves the formation of protein substances preponderates. Not so much sugar appears in the leaves as could be produced out of the carbonic acid actually decomposed and their total increase in weight during assimilation sometimes exceeded their increase in carbohydrates by 50 per cent.

Carbohydrates will hardly originate in the leaf directly out of carbonic acid and water. There must be simpler intermediate substances present about which, however, nothing certain has been proved. Wislicenus [1] envisages the first stage of CO_2 reduction as the formation of **formic acid** by the action of hydrogen peroxide which is always to be detected in pure air, especially forest air. The reduction of CO_2 would proceed thus far without the addition of energy. For the further reduction of formic acid to **formaldehyde**, which has always been supposed to be an intermediate product, and said to have been detected,[2] a supply of energy by light and the activity of the chlorophyll is necessary. The third stage, from formaldehyde to sugar again requires no supply of energy. Wilstätter and Stoll,[3] however, with the most delicate reagents, have not succeeded in proving the presence of formaldehyde in the leaves of plants of the most diverse kinds. Klein and Werner [4] claim to have detected small quantities of formaldehyde in the assimilating tissue. The chemist Von Baeyer has expressed the formaldehyde hypothesis in the following equation:

$$\underset{\text{(Carbonic acid)}}{H_2CO_3} = \underset{\text{(Formaldhyde)}}{HCOH} + O_2$$

Sugar may be formed from formaldehyde by the linking up of a number of molecules:

$$6HCOH = C_6H_{12}O_6$$

The nature of the first sugar recognisable by analysis in assimilation varies and the question has not yet been completely cleared up. Gast and Kylie [5] always found cane sugar with few exceptions. Sugar leaves contain more cane sugar than starch leaves. *Tilia* forms an exception which has starch leaves with much cane sugar. That assimilation proceeds in the chloroplasts themselves has been disputed, although starch always appears in their interior. With the help of mobile

[1] Wislicenus, H., Ber. d. D. Chem. Ges. LI, H. 10, p. 942, Berlin, 1918.
[2] Curtius u. Franzen, Ber. chem. Ges., 1912.
[3] Willstätter u. Stoll, 1918, *loc. cit.*
[4] Klein, G. u. Werner, O., Formaldehyd als Zwischenprodukt bei der Assimilation. Biochem Zeitschr. 168, 1926, p. 361. Quoted from Bot. Zentralbl.
[5] From ref. in Zeitschr. f. Bot. 10, 1918, H. 8.

bacteria, which in a drop of water collect wherever the minutest quantity of oxygen is produced, it has been shown that chloroplasts, liberated from the cell, still go on assimilating for some time in the light. The assumption that in general the chlorophyll content like the number of chlorophyll granules (Haberlandt) in a green plant-part is proportional to the quantity of carbonic acid decomposed in a given time, has not been generally confirmed. According to Willstätter and Stoll no simple relationship exists between chlorophyll content and the amount of assimilation. The **Assimilation Number,** *i.e.* the hourly rate of assimilation expressed in grammes of CO_2 utilised per 1 gramme of chlorophyll, undergoes great variations according as normal or etiolated, young or old, spring or autumn leaves or leaves of yellow varieties were examined. From this it is to be concluded that some other agent besides the chlorophyll in the chloroplasts, perhaps an enzyme, determines the rate of the assimilatory process. In normal leaves the values varied between 6 and 9. The assimilation number decreases with the growth of the leaves, *e.g.* in the oak from 10.9 to 7.8 from May 11 to June 20. In proportion to their chlorophyll content, yellow varieties, poor in chlorophyll, functioned more rapidly than normal ones.

Nevertheless relationships between chlorophyll content and activity are in many cases unmistakable, as is shown especially by a comparison of light- and shade-leaves (*q.v.*). Light demanding species like pine, birch, larch and robinia have a small chlorophyll content and require for this reason a larger amount of light for carbonic acid decomposition than shade-bearing ones like beech, silver fir, *Taxus* and lime.

In the former—Lubimenko calls them ombrophobous [1] or sciaphobous (shade avoiding)—the assimilation curve rises up the upper limit of natural radiation; in the shade-bearing trees it sinks before reaching this limit or remains constant from a certain light-intensity onwards (*Taxus*), perhaps because there is too great a heating and consequently hindering of the activity of the chlorophyll associated with the great absorption in the highly concentrated chlorophyll of these plants. According to Lubimenko, the dry substance of green seedlings increases with increasing light-intensity to a maximum which lies below the strength of light of a clear summer day, and then finally diminishes. In this respect also various species of plants behave differently. In Stone pine seedlings, for example, the maximum coincides with the intensity of undiminished daylight, while in seedlings of the larch a certain weakening of the illumination apparently favours the increase of dry weight.[2]

The conifers, *Pinus*, *Picea*, *Abies* and *Larix* contain far less chlorophyll to the same dry weight of leaves than, for instance, *Fagus*, *Betula* and *Robinia*.

In seedlings [3] growing in various strengths of illumination, the quantity of chlorophyll is at its maximum at a light intensity which

[1] Wiesner used the same word in the sense of "rain-shy." Antiseptic properties of ombrophilous leaves *see* Haböck, Österr. bot. Zeötschr., LX, 1910.

[2] Lubimenko, Sur les variations du poid sec chez les végétaux supérieurs aux différentes intensités lumineuses. Compt. rend. Acad. d. sc. Paris, 1907; p. 1192.

[3] Lubimenko, Compt. rend. Paris, 1905, 1906, 1907.

lies below that of daylight. In the spruce [1] this increase of chlorophyll concentration with decreasing illumination goes on down to the weakest perceptible light intensity. In all other cases increase of chlorophyll with diminution of light comes to a halt at a certain degree of light intensity which lies below that of daylight and a decrease sets in with further weakening of the light. Wiesner [2] found the lower limit for greening to be a light intensity of $\frac{1}{10}$ normal candle power. In complete darkness, with etiolation, almost no chlorophyll at all is formed. The light-optima for the formation of chlorophyll are different for different species, and change with temperature for the same species of plant.

The colour changes [3] which are noticeable in the individual leaf during the course of the growing season go hand in hand with the increase and destruction of the chlorophyll. In the robinia, and in many cases also in the beech, the leaves are at first yellowish green or almost golden yellow, a colour which is retained and is conspicuous for a longer or shorter time in spring according to the weather. In Lund [4] (Sweden) the amount of chlorophyll increases until August, whilst in Vienna a falling off in the green colour is noticeable in sun-leaves even in June, in shade-leaves in July. There then appears, especially in the leaves struck by the direct rays of the sun, a characteristic brown-green which owes its origin to some extent to a coloration of the membranes.[5] Leaves undergoing autumnal colour-changes assimilate so long as the chloroplasts have not disintegrated (*see* below). The behaviour of leaves of different ages is well demonstrated by Curboni's [6] investigations, according to which the starch content in consecutive leaves of a *Vitis* twig, beginning with the youngest, was as 4 : 5 : 8 : 9 : 10 : 8 : 5 : 2 : 0. It is true that the example does not mean only one thing, because the appearance of starch depends not on the activity of assimilation alone, but also on the amount of sugar withdrawn from the leaves, which is not necessarily the same in different parts of the twig. Plester [7] investigated the chlorophyll-content and the amount of respiration and assimilation in differently coloured leaves of the variegated varieties [8] of *Populus*, *Corylus* and other shrubs and trees, and found that the chlorophyll-content of the pale green varieties amounts generally to less than 50 per cent. of that of the typical green form; it varies between 27 and 54 per cent. The amount of assimilation is only 34–59 per cent. but does not fall off in the same proportion as the chlorophyll-content. The chlorophyll-content of the red-leaved forms is sometimes smaller and sometimes greater (54–125 per cent.) than that of the related green form. Their assimilation is always less, as the leaf-red (anthocyanin) acts as a

[1] Lubimenko, Compt. rend. Acad. d. sc. Paris, 1907, p. 1192.

[2] Wiesner, Sitzungsber. a. K. Akad. Wiss. Wien, 1893; Jahrb. wiss. Bot., 1895.

[3] Wiesner, Lichtgenuss der Pflanzen. Leipzig, 1907.

[4] Jönsson, Farbenbestimmungen des Chlorophylls bei verschiedenen Pflanzenformen. Bihang till k. svens. Vet. Akad. Handl., Bd. 28, III, Nr. 8, 1902.

[5] Stahl, Biologie des Chlorophylls. Jena, 1909, G. Fischer.

[6] Quoted from Czapek, Biochemie.

[7] Kohlensäureassimilation und Atmung bei Varietäten derselben Art, die sich durch ihre Blattfärbung unterscheiden. Beitr. z. Biologie der Pflanzen, XI, 1912.

[8] White flecking, variegation of Malvaceae, *Ligustrum*, *Laburnum*, is an infection disease (E. Bauer). Variegation and grafting, *see* Timpe, Jahrb. d. Hamburgischen wissenschaftl. Anstalten, XXV, 1906.

light-screen and only allows assimilation to begin above a certain intensity of light. The poor assimilation in both kinds of varieties is partially compensated by a reduction of respiration with its consumption of matter. Red-leaved beeches and maples have more starch, red-leaved *Prunus*, more fat, in the pith than the green forms.[1] Red-leaved beeches also still thrive in Dorpat (Jurjew), where green beeches no longer maintain themselves.[2]

9. Assimilation and Light.—The formation of formaldehyde from carbonic acid, like every process by which a substance poorer in oxygen is produced from carbonic acid, is endothermic, *i.e.* heat is necessary to carry it out. Exactly the same amount of heat as is liberated by the burning of carbon to produce carbonic acid is required to again sever the connection between carbon and oxygen.

The source of this heat for the plant is the energy of the sun, which is, therefore, the first external requisite for the function of assimilation. The dependence on light of the colouring green of plants [3] by the accumulation of chlorophyll has been already mentioned. Only the seedlings of conifers and many life stages in lower plants become green in the dark.

Much more solar energy is used up by plants for the evaporation of water than for assimilation. With a total sunlight intensity of 600,000 cal. per square metre of leaf surface per hour, on a clear August day, sun-flower leaves, according to experiments by Brown and Escombe, utilised :

106,800 cal. = 27.5 per cent. for evaporation of water.
3,200 cal. = 0.5 per cent. for the formation of starch.

In diffused light 95 per cent. of the energy supplied was utilised but only 2.7 per cent. (according to Zederbauer,[4] indeed, hardly 1 per cent., by light-demanding trees even less, 0.4–0.5 per cent.) was employed for the formation of products of assimilation. In general, of the amount of light falling on a leaf, seldom more than 1.5 per cent., often much less (0.6–0.7 per cent., in *Acer platanoides*, 1.3 per cent.[5]) serves for assimilation. We shall see later which rays are effective for assimilation; only 4 per cent. of the total radiation is capable of supporting assimilation. Hornbeam leaves, according to Kreussler,[6] utilised 13.7 milligrammes CO_2 an hour per square centimetre of one-sided leaf surface in dull daylight (seven times the respiration); in electric light of 100 candle power at a distance of 31 centimetres, 28.5 milligrammes, equal to fifteen times the respiration. At a distance of 1–1.5 metres, the assimilation was hardly or not sufficient to neutralise the effect of respiration.

[1] Tischler, Bot. Zentralbl. XVIII, 1, 1905.
[2] Bot. Zentralbl., 101, 1906, 248.
[3] Monteverde u. Lubimenko, Untersuchungen über die Chlorophyllbildung bei den Pflanzen. Biol. Zentralbl., XXXI, 1911. Leipzig, Thieme. (The chemical process of chlorophyll formation and the green colouring do not completely coincide, which, however, does not concern us.)
[4] Quoted from Czapek.
[5] Puriewitsch, Jahrb. f. wiss. Bot. 53, 1914.
[6] Methode zur Beobachtung der Assimilation und Atmung der Pflanzen. Landw. Jahrb., 1885. Ref. Just's Bot. Jahresber, 1886, XIV, 1, 87.

The limits of the assimilatory efficiency of light are not the same for different plants. The lower limit lies quite deep. With the aid of luminous bacteria, which are caused to light up by any trace of oxygen, it has been shown that even the evening twilight brings about a little assimilation. If, in the beech and other densely foliaged trees, the leaves exposed to the minimum amount of light in the interior of the crown do not assimilate at all or only extremely little, this is not due only to the paucity of illumination as such, but also to the alteration in the constitution of the light in the interior of the crown by its passage through the outer leaves (*see* p. 203). The passage through a leaf may rob light of the rays which are effective for assimilation, and in the light-foliaged birch at mid-day, a distinct difference in the starch-content of the leaves according to their position in the crown is recognisable. The upper limit of assimilation in general appears to be only reached when the chlorophyll colouring matter suffers under too high an intensity of light. Reinke showed that the water weed (*Elodea canadensis*) still continued to assimilate with undiminished vigour under an illumination 800 times as strong as sunlight.

According to Stalfelt[1] the light requirement of pine and spruce needles, in which even mutual shading reduces assimilation, is very high. In one-year-old spruce needles and 1–2-year-old pine needles assimilation waxes with the increasing strength of the light and hardly reaches its maximum value in full sunlight. In older needles, however, the rise ceases at an intensity of 30 per cent. of full light.

The degree of assimilatory activity attained in a given strength of light depends on a whole series of circumstances. When, for example, Muntz found assimilation under a dull sky five times as poor as in full sunlight, it may have been due to the stomata being closed in the former case or to the temperature having fallen.

Assimilation is depressed especially by shortage of water, which results in the closing of the stomata long before wilting is visible. In the pine and spruce maximum assimilation takes place only during a few, up to 4, hours a day (10–12 noon) and only then when the previous night has been rainy and the sky in the morning overcast. In prolonged summer drought (1921) assimilation is almost completely quiescent (Stalfelt *loc. cit.*). In nature, a limit to the effect of light appears in fact only in shade plants in their first stages of development (seedlings of forest trees).

Which parts of the solar spectrum are absorbed by the plants is indicated at once, as Stahl[2] has shown, by the green colour of the leaves. If all parts were absorbed and no rays reflected from the green leaves they would appear black. The green of the leaves is composed of the green and orange-yellow rays of the spectrum with small fractions of the red and blue regions. The rays of these last colours are absorbed by the leaf green to a specially great extent. The chlorophyll spectrum has several absorption bands, whose distinctness and breadth increases with the thickness of the chlorophyll layer penetrated and the strength

[1] Stalfelt, Mitteil. d. Forstl. Versuchsanstalt Schwedens, 1921, 1924.

[2] Zur Biologie des Chlorophylls. Laubfarbe und Himmelslicht, Vergilbung und Etiolement. Jena, 1919, G. Fischer.

of the light. Absorption is greatest in the indigo-blue, violet and red. Rays of the infra red and the green regions of the spectrum remain unweakened. The broad band in the red belongs, as to its dark left half to chlorophyll a, and as to its lighter right half to chlorophyll b. In the spectrum of the living leaf the bands are shifted somewhat towards the red, as compared with the spectrum of a solution of chlorophyll, in consequence, as Iwanowski assumes,[1] of reflection effects. If green leaves are examined by transmitted light in 4–5 layers, they appear deep red, because, according to Kolkwitz, only the deep red part of the spectrum, at the upper side of the rainbow, is not absorbed but allowed by the chlorophyll to pass through.[2]

It was long thought that the red rays almost alone, were concerned in assimilation, because plants raised in blue light developed badly. When, however, the blue rays, which are more strongly refrangible and consequently more scattered in the spectrum, are brought to the same light intensity or strength as the red rays, they show about the same assimilatory activity.[3] It may thus be concluded, although all difficulties have not yet been removed, that the activity of the rays in assimilation corresponds with their absorption by the chlorophyll. Variations are explained by the alterations which the light undergoes in its passage through the cells and by the difficulty of producing the individual spectral colours quite pure for experiment. The efficiency of the different coloured rays is not the same in all the phenomena of nutrition.[4] The fluorescence of chlorophyll which causes both solutions and living chlorophyll granules to appear blood-red in light falling upon it, is associated by Molisch with the effect of the red rays. The fluorescence arises from the chlorophyll converting light of other colours into red. It is thus, Molisch considers, a manufacturer of rays of assimilatory power.[5]

The light for the enjoyment of which plants are adapted is less the direct rays of the sun than diffused light such as is reflected from the " clear sky." It is in conformity with this that plants have come to utilise just the red and the blue, and rejected the green part of the spectrum. It is precisely in the green that the maximum energy of undiminished sunlight lies. As the plant partly reflects and partly transmits the green rays, it avoids excessive heating when the sun is high, which makes the chlorophyll inactive and may lead to scorching of the leaves. Leaves may absorb 67–86 per cent. of the heat radiated to them [6] and *Sempervivum* species, in an air temperature of 28–31 degrees C., may warm up to 49–51 degrees C.[7] Leaves of hedge plants (*Corylus, Carpinus*) grown in the shade are scorched when by clipping they are brought into direct sunlight. The light of the sun, weakened

[1] Ber. d. D. Bot. Ges. XXV, 1907.

[2] Kolkwitz, Chlorophyllstudien mit dem Diaphanoskop. Mitt.Dt sch. Dendrol. Ges., 1924, p. 136.

[3] Kniep und Minder, Ztschr. f. Bot., I, 1909, p. 619. The plant examined is *Elodea*.

[4] Rev. générale de Bot., 1911.

[5] Wissenschaftliche Ergebnisse d. internat. Botaniker-Kongresses in Wien, 1905. Jena, 1906, G. Fischer.

[6] Mayer, A. G., The radiation and absorption of heat by leaves. Am. Jour. of Sc. III, Vol. XLV, 340. Temperatur des Blattinnern ; Smith, Bot. Zentralbl. 114, 1910, p. 5.

[7] Askenasy, Bot. Ztg., 1875, 441.

by its passage through thick layers of the atmosphere, is especially rich in red rays, the diffused light of the sky in blue rays and so it is these two colours which are most at the disposal of the plant in the light useful to it. We owe this train of thought to Stahl, who annexed to it Goethe's verse :

" Blutrot geht die Sonne unter,
Blau erstrahlt das Himmelszelt.
Fragst du nach der Gegenfarbe
Jedes Blättchen sie enthält."

10. Assimilation and Carbonic Acid.[1]—As almost the whole mass of dry matter in wood, generally over 99 per cent., consists of organic substances, the carbonic acid of the air from which these substances are formed is, in quantity, by far the most important food-stuff of plants, and in order to understand the life of a tree special consideration must be bestowed on assimilation in its relation to the carbonic-acid-content of the air.

It has long been proved that an increase in the supply of carbonic acid to the leaves results in a corresponding increase in carbonic acid assimilation and recent researches by Lundegardh,[1] R. Harder and others have shown that the production of matter by the plant depends on the carbonic acid at its command, in the same way as on any other food-stuff and growth factor. If the air supplied to a plant in a nutrition experiment is completely freed from carbonic acid all production of material naturally ceases. If in parallel cultures carbonic acid is supplied in increasing doses, all other growth factors remaining constant, the formation of material increases rapidly, with small doses of carbonic acid almost in proportion to the quantity of carbonic acid, with stronger doses the increase is less and less up to a definite maximum figure (Fig. 108). The curve of production, as a function of carbonic acid concentration in the air, approaches asymptotically a maximum value which is determined by the abundance of the other growth-factors, *e.g.* light. It is the same if carbonic acid is kept constant and any other growth-factor, *e.g.* light is varied. When light is plentiful the carbonic acid, and when carbonic acid is plentiful, the light, is better utilised. Light and carbonic acid may replace one another up to a certain point in their action on plant growth and the same holds good for the other growth-factors such as heat and the individual soil nutrients. So much is certain, that the ordinary carbonic acid concentration of the air, 0.03 per cent., is far from representing a limiting value of utilisability ; far rather may great shortage of carbonic acid prevail with this concentration.[2] Nevertheless the laws of optimum and maximum apply to the carbonic acid factor. Excess results in no further increase of the yield but may act injuriously, like excess of every other growth-factor; heat, light, nutrient salts, etc. Even at a concentration of 1 per cent.

[1] Lundegardh, H., Der Kreislauf der Kohlensäure in der Natur, Jena, 1924. Almost the whole extensive literature is collected ; *ibid.*, Klima und Boden in ihrer Wirkung auf das Pflanzenleben. Jena, 1925 ; Reinau, E., Kohlensäure u. Pflanzen, Halle, 1920 ; Bornemann, F., Kohlensäure u. Pflanzenwachstum, Berlin, 1920.

[2] Stalfelt, M. G., Unters. z. Ökologie d. Kohlensäureassimilation der Nadelbäume. Meddelanden fran Statens Stogsförsöksanstalt H. 21, Nr. 5, 1924 ; *ibid.*, the same, 5, 1921.

carbonic acid in the air, poisoning phenomena and checking of growth make their appearance.[1]

Thus, by increased supply of carbonic acid, plant yield can be considerably increased and this not only in glass chamber experiments but also in the greenhouse,[2] and, which was formerly not believed, also in the open ground. In the greenhouse, growth and yield have been raised to double and even more by carbon dioxide " manuring " of the air, *e.g.* in one of Lundegardh's experiments by increasing the carbonic acid concentration by 51 per cent. the yield was raised by 77 per cent. Great increases in yield in the open ground were brought about by

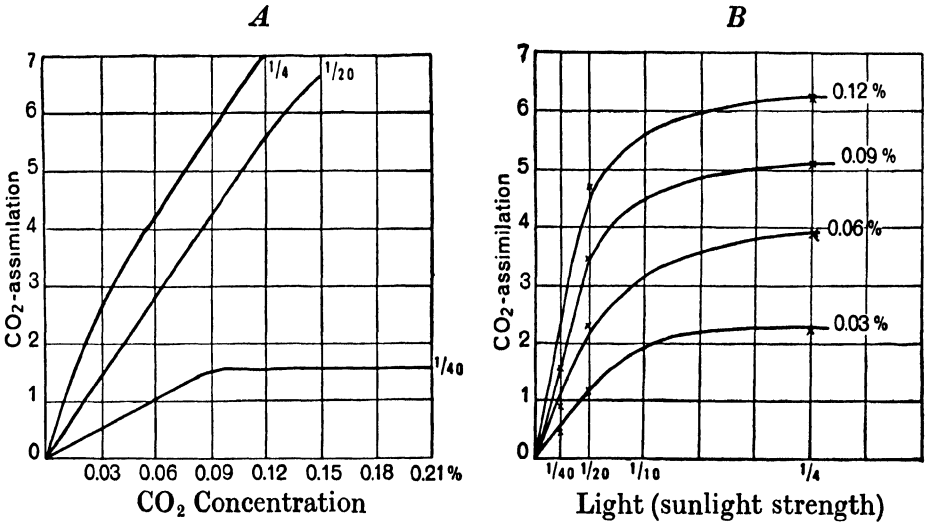


FIG. 108.—Carbonic acid (*A*) and light (*B*) curves of the assimilation of *Oxalis acetosella*. The CO_2 curves were determined for light intensities of $\frac{1}{4}$, and $\frac{1}{20}$ and $\frac{1}{40}$, the light curves for the CO_2 concentrations 0.3, 0.6, 0.9 and 0.12 per cent. After Lundegardh.

supplying carbonic acid from industrial waste gases, distributed over the fields by pipes.[3]

The concentration of carbonic acid in the open air is very small; it amounts, with small variations, to 3 parts by volume = 5 parts by weight of carbon dioxide in 10,000 volumes of air. The concentration is somewhat greater at night (by about 10–14 per cent.) than by day and somewhat greater in winter than in summer. Great quantities of carbonic acid are withdrawn from the atmosphere over the whole earth by the assimilation of green plants and stored up as organic matter. The carbonic acid locked up in this way in land plants has been estimated at 1,100 billion kilogrammes, and thus at one half the carbonic acid content of the atmosphere. Of this 1,000 billion kilogrammes would fall to the share of wood alone.[4] To some extent

[1] Lundegardh, *loc. cit.*, p. 164.

[2] Fischer, H., Gartenflora, 1912, 1913; Jahresber. Ver. f. angew. Bot. XI, 1913.

[3] Fischer, H., Gartenflora, 1919.

[4] The total forest surface of the earth amounts to 45 million square kilometres. The above figures are arrived at if the stock of timber per hectare, including root, branch and fallen wood, is taken as on the average 500 cubic metres with a specific dry weight of 0.5. To this are to be added 20–30 billion kilogrammes of foliage and a very large amount of carbon in the humus.

carbonic acid is permanently stored in peat deposits and in the mud of waters, especially of the sea. Further quantities of carbonic acid are lost from the air by the carbonic acid weathering of siliceous rocks Carbonates and easily soluble bi-carbonates are formed which are carried with spring water to the rivers and in them into the sea. Large quantities of carbon dioxide from the air dissolve in sea water which contains far more carbonic acid than the atmosphere.

Against these losses the following sources of carbonic acid stand on the receipt side. A part of the assimilated carbon is again respired and reaches the air out of the shoots and roots, and at night also out of the leaves. Dead plants and portions of plants pass over again into carbonic acid by the respiration of the heterotrophic organisms, especially man, animals, fungi and bacteria, which live upon them. Very considerable quantities of previously stored carbonic acid are returned to the atmosphere by the burning of hard and brown coal and wood, and the atmosphere is also enriched in carbonic acid from the interior of the earth by volcanic eruptions, carbonic acid containing springs and apparently also from other fissures in the rocks. Dissolved carbonic acid escapes from waters when the atmospheric pressure falls. The ocean acts in this way in a high degree as a carbonic acid regulator.[1]

Of special importance for plant nutrition, as older [2] and more recent [3] researches show, is the carbonic acid resulting from "soil respiration"; the respiration of the humus-forming and humus-decomposing soil organisms. The leaves and dead twigs falling annually and the dying roots nourish innumerable fungi, bacteria and animals which, in respiration, break down part of these organic remains directly to carbonic acid and supply it to the forest air. The remains of these decomposition processes and the soluble substances of the dead leaves, reach the soil in rain water and there form the humus which likewise undergoes decomposition by organisms and is converted into carbonic acid. For this reason soil air contains relatively far more carbonic acid than free air—in spruce forest, according to Vageler,[4] on the average 0.8 per cent., at the maximum, 2 per cent. at a depth of 15 centimetres. In cultivated soil Lundegardh found mostly about ½ per cent. The content of carbonic acid in the soil air increases with the depth in the soil. It depends very much on aeration, and when this is bad the limit of 1 per cent., at which poisonous effects may set in, is reached even at a depth of 15 centimetres. At depths of 0.5–1 metre concentrations of several units per cent. are frequent.

By diffusion, much less by changes in temperature or atmospheric pressure or by being driven out by percolating rain water, the carbonic acid from the soil gets into the layer of air adjacent to the ground [5] and

[1] On the carbonic acid balance of the earth *comp.* also Arrhenius, Sv., Das Werden der Welten, 1906. Ramann, Bodenkunde, 3 Aufl, 1911. Lundegärdh, *loc. cit.*

[2] Ebermayer, E., Die Beschaffenheit der Waldluft, Stüttgart, 1885.

[3] Lundegardh, *loc. cit.*; Oelkers, J., Kohlensäureversorgung des Bestandes. Forstarchiv 1, 1925, p. 177.

[4] Vageler, Mitteil. d. bayr. Moorkulturanstalt, Bd. 1, 1906.

[5] Romell, Die Bodenventilation als ökologischer Faktor. Mitteilungen forstl. Versuchsanstalt Schwedens, 1922, H. 19.

thence by means of air currents to the free atmosphere. In close crops of plants, however, this interchange with the open air proceeds very slowly, so that in the lowest strata of air a concentration of carbonic acid is often found which is double that of free air. The forest especially, produces, by the decomposition of its substantial debris, large quantities of carbonic acid which may be detected even at a fairly considerable distance from the forest by the higher carbonic acid content of the air. Warmth and moisture favour soil-respiration and by the changes in these factors great variations, up to 100 and more per cent., occur from day to day in the carbonic acid concentration of the layers of air near the ground.

Soil respiration, according to Lundegardh, Oelkers and Meinecke,[1] produces in the summer on the average about 0.4 grammes of carbonic acid per hour per square metre; under special circumstances when the decomposition of organic debris is rapid, even many times this amount.

This important supply would almost alone suffice to cover the total carbonic acid requirements of the forest trees. It does not do to generalise too much from these figures, however, as it must not be overlooked that only so much carbonic acid can in the long run be produced by decomposition as is supplied to the soil in the form of organic debris. As, however, at least half of the soil carbonic acid originates at night or in the period of vegetative rest when it cannot be or can only in part be utilised,[2] and as in the cultivated forest the greater part of the produce of the trees is removed from the forest in the stem timber, and as undoubtedly also during the day much of the soil carbonic acid escapes unutilised into the open air; only a small part of the carbonic acid required for the annually falling and decaying material, the leaves and a part of the twigs and roots, can be permanently supplied through the soil and the covering of litter. The forest owes its existence in the main to the carbonic acid of the free atmosphere. Nevertheless, the favorable influence of shelter from wind and the calmness of the air in the forest on tree growth, which is observable especially in windless valleys and hollows,[3] appears to be due partly to the locally produced carbon dioxide not being carried away by the wind and thus falling to the benefit of the forest itself. Doubtless also an improvement of the supply of carbonic acid and with it of tree growth may be temporarily, or even for a long time, produced by a rapid decomposition of the soil covering and the humus. The ground flora, the underwood and the lower, overshaded parts of the crowns, which with the normal supply of carbonic acid would no longer be capable of survival, will especially profit by soil respiration.

11. Arrangement of Leaves in Regard to Light.[4]—Most plants possess the faculty of bringing their leaves into the most favorable

[1] Meinecke, Kohlenstoffernährung des Waldes. Diss. Giessen, 1924, quoted from Oelkers.

[2] In the absence of wind the carbonic acid produced at night partly remains in the forest air and is also partly absorbed by the leaves to be assimilated during the day.

[3] Münch, Tharandter, Forstl. Jahrb. 75, 1921, p. 238. Forstl. Wochenschrift Silva 11, 1923, p. 1.

[4] Oltmanns, Über die photometrischen Bewegungen der Pflanzen. Flora, 1892, 183.

position as regards light, partly by growth-movements of the shoot [1] and partly by movements of the leaves themselves.

The bendings of the shoot induced by light have already been mentioned (*see* heliotropism). The light-movements of leaves differ from those of the shoot in accordance with the nature of these organs. They are dorsiventrally constructed, *i.e.* an upper and an under side can be distinguished.

Such dorsiventral structures, in so far as they are movable, are wont to orientate themselves towards the light that suits them so that the rays fall upon their upper side; they take up a **surface position.** If the action of the sun is in excess of the amount that the leaves can stand, they endeavour to present their edges to the source of light; they take up the **profile position.** These conditions can be beautifully observed in the acacia (*Robinia pseudacacia*). The leaves of this tree are imparipinnate, *i.e.* they consist of a midrib with about seven oval leaflets on each side and one at the tip. On passing through an avenue of acacias in bright sunshine, all the leaflets which are exposed to the sun's rays are seen to be arranged so that the rays strike their edges and as it were shine past the leaf surface. If a cloud passes over the sun or the whole sky is obscured, the same leaflets place themselves so that they present their full surface to the open sky. On such days the tree crown presents an appearance quite other than in sunshine. The leaflets may show various degrees of folding and spreading according to the position of the sun and the strength of the light. Often only one of the longitudinal halves of the leaflet stands with its edge towards the sun while the other remains horizontal. Oltmanns on sunny days in autumn found the leaflets spread out, *i.e.* the opposite leaflets of a pair standing at an angle of 180 degrees with each other, until 8 a.m. As the sun rose higher this angle diminished. It measured 40 degrees and less at about 12 to 1 o'clock and from 3 p.m. onwards again underwent a marked increase. Every cloud that covered the sun for barely half an hour caused an enlargement of the angle in question and a hazy atmosphere did not permit of its fall to under 90 degrees even during mid-day. Thus the most varied intermediate stages between the full surface and profile arrangements occur, by virtue of which the acacia leaf can provide a definite grade of radiation for each of its parts. All the movements necessary for this, except the folding of the leaflet along its own midrib, are carried out by means of joints which are to be found at the place of attachment of the leaflets to the common midrib. The leaves of other trees possess the power of regulating their position according to the strength of the light only so long as they are still in process of growth. In this juvenile stage they can alternate between the surface and profile arrangement according to the lighting conditions, by bendings and twistings of the leaf-stalk and the twig which cause them finally to remain in a position determined by the average brightness of their situation. In our climate this position is that in which the leaves take up a surface arrangement towards that portion of the open sky from which they receive light.

[1] Kölbl, Versuche über den Heliotropismus der Holzgewächse. Vorgelegt von Wiesner. Anz. d. k. Akad. Wien, 1909, XLVI, p. 273; Wiesner, Lichtgenuss der Pflanzen., Leipzig, 1907.

This is quite independent of the arrangement of the leaves on the twig. Whether they stand in spirals, in two ranks or in decussate pairs, whether they spring from the upper side, the lower side or the flanks of the shoot which bears them, they always spread their upper sides towards the open sky. If its light reaches the leaf not from above but from one side they direct their upper surface towards that side. The direct rays of the sun are often avoided. Thus leaves on the south and south-west sides of the tree often do not spread out flat but exhibit an infolding along the midrib and direct the hollow side towards those parts of the sky. The direct rays of the sun do not then meet the greater part of the leaf-blade at right angles and their effect is thus moderated. It also often happens that, of two leaves situated on the upper and under sides of a horizontal twig, the upper one arranges itself horizontally towards the base of the twig and the under one towards the tip, so that both present their upper sides towards the sky without their shading each other (*compare* p. 203).

Wiesner [1] has called leaves which place themselves in the most favorable position towards the diffused light of the open sky but ward off direct sunlight, **panphotometric leaves.** The leaves of the outer parts, especially the tops of thickly foliaged woody plants, behave in this way. The leaves of the interior of the crown, like the twigs of poorly illuminated shrubs, are more sensitive. They are **euphotometric** and place their surfaces at right angles to the strongest diffused light. **Aphotometric** leaves show, as a rule, no definite attitude towards the incident light. Among such are the pine needles which, being almost of the same structure all round may present any side that is convenient to the light. They do not need to practise economy in light because they live in sunny situations where they obtain a sufficient amount of light in every position.

Though no doubt may exist that the photometric arrangements serve for the utilisation of the light to the best advantage, this does not mean that they are all brought about by the action of light itself.[2] Research shows rather that, at least in the silver fir, the photometric arrangement of the leaves is apparently also conditioned by gravity. If a pectinate, dorsiventral shade twig of the silver fir (*see* Chap. VIII, 6) is twisted through 180 degrees so that the stomatiferous side, which is normally the lower, is turned upwards and the twig held fast in this reversed position, it is true that the needles already present continue to retain this position, but the newly developing twigs arrange their needles so that the stomata are below. The anisophylly, on the other hand, first undergoes a corresponding reversal in the twig of the next year but one; it is thus already prepared in the bud. Tschermak [3] describes such an occurrence on a large scale. (Silver firs bent over by snow had carried out exactly similar needle torsions on the branches turned out of their natural positions.) If, in these processes, differences in lighting between the upper and lower sides are also not excluded, it still appears that gravity plays a part in the arrangement of the needles.

[1] Biologie der Pflanzen, 102, Wien, p. 1902.
[2] Kny, Bot. Ztg., 1873, p. 433.
[3] Tschermak, Zentralbl. f. d. ges. Forstwesen, 1925, p. 351.

We may have here a case similar to that of the eccentricity of branches, which undoubtedly contributes to strength, but equally surely can be produced by the gravity stimulus alone.

That besides this, light also forms a factor in the casual complex of the photometric arrangement of the needles of the silver fir, is shown by an experiment by Wachter.[1] Horizontally growing dorsiventral side twigs of *Abies nobilis* developed almost radially in the dark, *i.e.* with needles standing out on all sides. On vertical side shoots, the needles turned towards the light falling from one side by twisting and bending in a sickle form. Wiesner [2] connects phyllotaxy also with the photometry of leaves. Photometric leaves are so placed, either originally or by means of bendings or twistings of the leaf stalk, that the strongest diffused light of the locality may fall to the benefit of each individual leaf. In upright shoots with many spirally-arranged leaves this favorable arrangement is $\frac{3-\sqrt{5}}{3}$ (*see* p. 6). The most unfavorable arrangement would be the two-ranked one, in which each leaf was overshaded by the one above it. On lateral shoots, however, this disadvantage vanishes as in this case the leaf surfaces are brought into a plane at right angles to the incidence of the light by torsion of the leaf-stalks.

12. Utilisation of Light by Plants.[3] Photometry.[4]—A leaf can only remain permanently living if it receives enough light to be able to produce at least as much material as it loses by respiration ; thus when the proportion, assimilation: respiration = at least 1. The position in the scale of light intensities of the " point of compensation," [5] *i.e.* the smallest quantity of light which the leaf must enjoy in order to maintain itself alive, depends on many factors ; first of all on the species of plant, then on warmth, nutrition with root nutrients and, as has already been stated, on the particular structure of the leaf, as light- or shade-leaf, mature or juvenile leaf. Species of trees whose shade-leaves remain alive even in a very low intensity of light are called **shade-bearing** species, in contradistinction to the **light-demanding** species. If the quantity of light in the interior of a close wood is determined, the light-value of the point of compensation for shade-leaves in the particular locality is obtained, because every species of tree produces in close canopy just so much shade as nourishes some and causes the death of others of its lowest leaves and makes it impossible for the same species to succeed In the underwood. On this depends the " self-pruning " and " crop cleaning," the dying off of lower branches and of the overshaded suppressed stems of the secondary crop. With regard to this, it must

[1] Ber. d. D. bot. Ges. XXI, 1903, p. 390. Geotropism acts in the same way on dorsiventral spruce and silver fig twigs, which lose their dorsiventrality in the centrifugal apparatus in the dark. *Taxus* seems also to develop radially in the dark even without centrifuging.

[2] Ber. d. D. bot. Ges. XX, 1902, and Biol. Zentralbl. XXIII, 1903.

[3] Wiesner, Der Lichtgenuss der Pflanzen. Leipzig, 1907.

[4] Zon, Rand, Graves, Light in relation to tree growth. U.S. Dept. of Agric. Forest Service Bull. 92, Washington, 1911.

[5] Harder, R., Bemerkungen ü. d. Variationsbreite des Kompensationspunktes beim Gaswechsel der Pflanze. Ber. d. D. Bot. Ges. 41, p. 194, 1923. Lundegardh, D., Kreislauf d. Kohlensäure, Jena, 1914.

be taken into account that the leaves nourish not only themselves but also the branches and twigs that bear them, so that a certain excess must be produced and supplied for these. The point of compensation must therefore be higher for the whole leafy twig than for the isolated leaf.

The position of the point of compensation in the light scale is best given, in Wiesner's process, as a percentage of the full light of the sky. It expresses the minimum enjoyment of light under which the twig is still capable of life. As it depends on a series of other factors besides the species, consonant statements of the minimum light requirements of species of trees and the degree of shade in dense woods are not to be expected. Well nourished crops bear and produce deeper shade than weakly growing ones, young crops deeper shade than old ones.

Wiesner has shown numerically that in nature the leaves of a plant, as a rule, benefit by only a limited part of the light which is radiated to a particular spot on the earth's surface from the whole vault of the sky during a day. For leaves shone upon by the sun a large percentage of this " total daylight " is destroyed by absorption into the surround ings ; only a small part of it reaches the leaves in the inner and lower parts of the crown and even of this, still a part is lost by reflection at the leaf surface.

Anyone who has taken photographs in the forest knows that it is necessary to expose very much longer under the leaf canopy—under beeches about 60 times, under pines about 20 times as long, as under the open sky.

When the leaves are first opening and in the case of lightly foliaged trees, the strength of the interior light of the tree is proportional to the strength of the total daylight. In closely foliaged trees a minimum occurs as a rule at mid-day, *i.e.* the strength of the interior light of the tree often falls off at the time of the sun's greatest altitude, because the light-position of the leaves presents the greatest obstruction to the entrance of light from the zenith. In trees which arrange their leaves, when taking up their fixed position with regard to light, partly according to lateral and partly according to overhead light (birch), the mid-day minimum is preceded and followed by maxima. Finally in trees whose leaves avoid the light from the zenith by a profile position (*Robinia*), a mid-day maximum may be set up. In the case of plants, green only in the summer, the strength of the interior light of the tree crowns shows an annual periodicity. From the time when leaf formation begins until it is finally complete, the mid-day minimum falls. The final minima of the interior light of trees are constant on the average for the various species, within definite limits determined by variations in the species and the locality. Thus for Vienna (June) the proportion of interior light to the total daylight is, in the box tree 1 : 108 ; in the beech (forest form) 1 : 60 ; in *Acer campestre* 8 : 48 ; in *Pinus laricio* 1 : 11 ; in the birch (*B. verrucosa*) 1 : 9 ; in the larch 1 : 5 ; in the pedunculate oak 1 : 26 ; in an isolated beech 1 : 60. One and the same species of tree has different strengths of light in the interior of the crown according to the locality.

Thus the minimum absolute amount of light required by *Acer platanoides* is:

In Vienna	$\frac{1}{55}$
In Drontheim	$\frac{1}{218}$
In Tromsoe	$\frac{1}{5}$

The further the locality lies towards the north the thinner becomes the crown and, Wiesner concludes, the greater the light requirement of the tree. The light requirement of a plant sinks and rises, in fact, with rising and falling warmth. By far the greater part of the light present in the interior of a tree crown has not passed through the leaves but has shone through the gaps in it. This is of the greatest importance for the life of the tree, because light which has passed through only two [1] leaves is not in a condition to decompose as much carbonic acid in a third leaf as will cover the loss by respiration. It is still, however, sufficient to effect green coloration, *i.e.* the formation of chlorophyll.[2] Griffon found the energy of assimilation of light after passing through a leaf of *Acer negundo* reduced to $\frac{1}{2}$, one of *Hedera ilex* to $\frac{1}{20}$th. Behind a leaf of the wild vine (*Ampelopsis*) it fell to $\frac{1}{12}$th when direct sunlight was used, to $\frac{1}{24}$th with diffused light.

The greater part of the light [3] which does pass through the leaves of trees goes through the veins which are poor in or destitute of chlorophyll. The light green, spring leaves allow far more of the light acting on the lamina to pass through than do the deep green summer leaves of the same species. The greater permeability of shade-leaves to light is, in the lime, exhibited especially towards the green rays. Sun-leaves allowed 8 per cent., shade-leaves 25 per cent. of these rays through, whilst the remaining rays were absorbed almost equally strongly by both types of leaves. Light-leaves of hazel and beech let through only one half as much of the light of the whole spectrum as shade-leaves—of the red even much less.

In direct sunlight 10–100 times as much light passes through as in diffused light.

Light which had penetrated two superimposed leaves was only measurable in the case of the lime and hazel besides the shade-leaves of the beech. No measurable light passed through four leaves in direct sunlight, or through three in diffused daylight. Light which has passed through leaves, whether coming direct from the sun or not, shows an increase in the brightness of the yellow-green part of the spectrum of the forest light as compared with the other regions of the spectrum.

Cieslar [4] has sought to supply a numerical expression for the light-conditions in woods. As with all Wiesner's [5] published figures, so here it is the rays affecting silver chloride which are dealt with and the strength of light is determined by means of a simple apparatus. He

[1] Griffon, Compt. rend., T. CXXIX, p. 1276; Rév. gén. de Bot., XII, 1900.

[2] Bonnier, Compt. rend., T. CXV, 1892; Kreussler, Methode zur Beobachtung der Assimilation und Atmung der Pflanzen. Landwirtschaftl. Jahrb., 1885.

[3] Knuchel, Spektrophotometrische Untersuchungen im Walde. Mitteil. d. schweiz. Zentralanstalt f. forstl. Versuchswesen, hrsg. von Arnold Engler, XI, 1, Zurich, 1914.

[4] Einiges über die Rolle des Lichtes in Walde. Mitteil. a. d. forstl. Versuchswesen Österreichs, XXX, 1904.

[5] Der Lichtgenuss der Pflanzen. Leipzig, 1907.

determines the time taken by silver chloride paper, in the light of the place in question, to assume the colour of a normal paper which was formed by a mixture of zinc oxide and lamp black. If the normal black tint was reached in 2, 3 or 4 seconds the strength of the light was a half, a third or a quarter and so on. The unit of light intensity is thus the blackening to the normal tint in one second. The proportion of the light intensity in a particular place to that of the total daylight measured in the open, is called by Wiesner the **specific light supply** (lichtgenuss) of that place.

Cieslar determined by Wiesner's method the amount of light kept back by the crowns and found that it amounted, in a thinned silver fir wood to 80 per cent., in a thinned beech wood to 80–90 per cent., and in a thinned Austrian pine wood to 60 per cent. of the total light.

From the quantity of light kept back in the common canopy and the number of stems per hectare, Cieslar calculated the shade effect or " the coefficient of shading " of the individual trees, which, in order to obtain a more convenient figure, is multiplied by 100.

Examples of " Coefficients of Shading " :

	Thinned.		
1. BEECH.	Lightly.	Moderately.	Heavily.
No. of stems per hectare = Z . .	2,208	1,216	876
Light-intensity in wood on June 3 = J .	0.032	0.038	0.059
Quantity of light kept back by the crowns in percentage of the light in the open = i, (1 — J) 100 . . .	96.8	96.2	94.1
Coefficient of shading $\frac{i}{Z}$. 100 . .	4.4	7.9	10.7
In unfoliaged condition (Apl. 24) $\frac{i}{Z}$. 100	3.2	5.3	6.4
Differences	1.2	2.6	4.3
II. *Pinus austriaca.*			
No. of stems = Z	8,296	6,071	3,476
Light-intensity in May = J . . .	0.17	0.23	0.31
Quantity of light kept back i . .	83	77	69
Coefficient of shading $\frac{i}{Z}$. 100 . .	1.0	1.3	2.0
Ground flora of experimental area	10 species	20 species	30 species

Boysen Jenson [1] has made similar determinations in Denmark. Percentage of daylight let through by :

	Isolated trees.	Forest.		Isolated trees.	Forest.
Picea excelsa . .	—	1.0	*Quercus pedunculata* .	3.9	11.0
Fagus sylvatica . .	1.2	1.8	*Fraxinus excelsior* .	8.5	13.6
Acer pseudoplatanus .	2.0	7–20	*Alnus glutinosa* .	12.6	18.5
Ulmus montana .	3.7	4.1	*Betula verrucosa* .	17.2	25.7

[1] Boysen Jensen, Über das Verhalten der Waldbäume gegen das Licht. Tidskr. for Skovvaesen, XXII, p. 1. Kopenhagen, 1910. His own German Bot. abs.: Zentralbl. Bd. 116, 1911, p. 595.

If the power of bearing shade of young plants is measured by their rate of growth compared with growth in full daylight, the following series is obtained: 1. *Abies pectinata*; 2. *Ulmus, Fagus, Acer pseudoplatanus*; 3. *Fraxinus, Quercus*; 4. *Alnus glutinosa*; 5. *Betula verrucosa*. Assimilation experiments show that the power of growing in the shade is connected with the power of utilising even low intensities of light. The assimilation curve of beech and maple rose, with increasing strength of light, more rapidly than that of ash, oak and alder.

The distinction in forestry between shade-bearing and light-demanding trees is based on the light-conditions in older woods. Many species when left to themselves form light, others dark woods. Among the latter are yew, beech, silver fir, spruce, Douglas fir, hemlock spruce; among the former are larch, birch, oak, pine, poplar and willow. The following are described as half shade-bearers: maple, ash, elm, alder, lime, Weymouth pine, Robinia. The degree of lightness of a wood is the result of the density of the individual crowns and the number of stems growing on a unit of area. Both of these are conditioned, however, not only by the light requirements of the individual species but also by the competition between the individuals in the crop for the water and food materials in the soil. That this is the case is brought out by Fricke's [1] observations and also follows from the experience that the "light-demand" of a species is the greater, its power of bearing shade the less, the cooler, poorer and drier the locality. On good, especially fresh soil or in a warm climate, a species which under average conditions is associated with much light, bears so much shade as to appear to disown its light-demanding character. Conversely a shade-bearing species requires so much light under conditions of locality which lie at the lower limit of its requirements, on poor dry soil, or in northerly or cold elevated situations, that it can hardly any longer be described as a shade-bearing species.[2]

The power of an old tree to bear shade is much less than that of a young plant because the relation between assimilating surface and consumption of material is less favorable than in the latter. It is also to be noted that young plants bear the most pronounced shade-leaves, which, as had already been said, are able to make the best use of reduced light.

Owing to the strong influence on the compensation point exerted by soil, climate and age, forestry observations of the light requirements of the species and the order of their power of bearing shade in the lists of different teachers of silviculture do not exactly agree with each other. Great variations are shown by the ash especially, whose seedlings, in the best soils, maintain themselves for a long time in the deepest shade, whilst older trees and plants on poorer soils are extremely sensitive to the withdrawal of light.

Two defects are associated with Wiesner's method of measuring light in the forest: first of all, it is difficult to determine exactly the

[1] Fricke, Licht-und Schattenholzarten, ein wissenschaftlich nicht begründetes Dogma. Zentralbl. f. d. ges. Forstwesen 30, 1904.

[2] Handbuch der Forstwissenschaft, 4 Aufl.; Bühler, Der Waldbau, 1. Teil, Stuttgart, 1918. Contains also further experiments with artificial deprivation of light. Also the Text-books of Silviculture of Gayer, Mayr, Ney, etc.

instant when the silver chloride paper has reached the normal tint ; [1] and secondly photometry with silver chloride only deals with a part of the spectrum, especially the violet rays which strongly affect silver chloride, whilst the red rays, so important for assimilation, are left out of account. In broad-leaved trees whose leaves greatly alter the quality of the light passing through them, this source of error is marked, not however in conifers, with which the light of the wood consists only of the unaltered daylight which falls through the gaps.

With careful attention to all difficulties, Oelkers [2] has carried out ray measurements in spruce and beech woods of different grades of density by the aid of a radiometer. A suitable filter made possible the separation of the dark and the luminous heat rays and enabled it to be recognised that the same crown-canopy altered the content of daylight differently in dark and in luminous rays. In all the woods examined the radiation of heat increased in proportion to the reduction of the density of the crop, and the rate of decomposition of the soil covering and the breadth of the annual ring increased in the same way. About the same amount of heat radiation struck the tree stem as the soil but reflection was greater from the light coloured beech stem than *e.g.* from the spruce. Oelkers attached to his investigations the practical conclusion that the most favorable grade for the utilisation of the heat rays for the decomposition of the layer of litter on the soil of the woods in his experimental areas, lies in the removal of about a third to a fourth of the existing volume in the beech areas and of a fifth in the spruce areas. Consideration for the full utilisation of the heat rays for the annual ring, requires the clearing of at most a fifth to a quarter of the existing volume in the beech woods and a seventh to a sixth in the spruce woods.

For the measurement of light in the forest, Ramann [3] utilised selenium cells whose electrical resistance alters with illumination. Instead of the comparison of the strength of light or of colours by the eye, the more certain reading of the galvanometer is employed. The usefulness of this method is diminished by irregularities in the sensitiveness of the selenium cells according to the wave-length and strength of the light. Knuchel [4] has made specially exact observations with an improved spectrophotometer. Rieckert [5] employed an apparatus in which an oil spot on paper was illuminated artificially. When this became invisible to the eye the external light was of equal strength with the artificial.

The colour-composition of forest light was first investigated from a forestry point of view by Max Wagner [6] with the aid of an improved spectralphotometer which brings out the polarisation phenomena.

[1] On self-registering photometer *see* Samek u. Jencic, Anz. d. k. Ak. Wiss. Wien, 47, 22.

[2] Jahresring und Licht. Zeitschr. f. Forst- u. Jagdwesen, 1914, 1917–18 ; *s.* a. Zederbauer, Zentralbl. f. d. ges. Forstwesen, 1907 ; Knuchel, *loc. cit.*

[3] Allgem. Forst- u. Jagdzeitung., 1911, p. 401 ; *comp.* also with Pfund, Physical. Zeitschr. XIII, 507.

[4] Knuchel, Mitteil. d. schweiz. Zentralanst. f. d. forstl. Versuchswesen, XI, 1, 1914.

[5] Rieckert, Forstl. Wochenschr. Silva, 1926, p. 241.

[6] Die Sonnenenergie im Walde. Allgem Forst- u. Jagdzeitung, 1913. Ein neues Spektralphotometer mit Savartschem Polariskop. Zeitschr. f. Instrumentenkunde, 1913 ; Pflanzenphysiologische Studien im Walde. Berlin, 1907.

Data as to the local and seasonal variations in light are to be found in the works mentioned and are also to be seen in the useful exposure tables for photographic purposes. Thus the Perutz Exposure-meter prescribes for subjects in the interior of open woods, 204 times the exposure necessary for shore landscapes, which strikingly demonstrates the great light-ecological importance of locality.

The following results may be cited from the works mentioned: The intensity of the diffused light decreases rapidly with increasing altitude above sea-level, whilst the direct radiation by the sun increases in a still greater degree. The total light is more intense therefore at high elevations. Because of the diminution of diffused light, the influence of position with regard to the direction of the sun's rays (exposure, aspect) in high elevations is of special importance to the forest. Cloudiness causes a diminution of the total brightness, to the extent of, on the average, 30 per cent. when the sun is concealed by clouds, by about 50 per cent. when there is a uniform grey covering. White clouds which do not obscure the sun increase the brightness. If the crowns are shone upon by the sun, the intensity of light in the interior of young and middle-aged woods is only about double as great, in old woods only imperceptibly greater, than under those not shone upon. From this it is evident that a very great part of the direct rays is reflected back into the atmosphere at the surface of the leaves.

13. Assimilation and Heat.—The maximum of assimilatory activity, besides being dependent on the presence of a sufficient quantity of carbonic acid and on light, is also dependent on heat.

Matthäi,[1] to whom we owe a clear presentation of the mutual relations of the three factors mentioned, states that at 18 degrees C., for example, only 39 per cent. of the possible light-activity was attained, at 22 degrees C. 50 per cent., at 28 degrees 70 per cent. Increasing one of the three factors increases the activity of assimilation always only up to a certain amount. It remains unchanged at the height then reached so long as the other factors are not also raised. For every carbonic acid concentration of the air and for every temperature there exists a maximum action of light which is not exceeded so long as the supply of carbonic acid and the temperature remain the same. Carbonic acid, heat and light behave with regard to assimilation like the mineral substances do with regard to nutrition through the roots. The total activity depends mainly on the factor which is not available in favorable quantity. (*Compare* the laws of action of growth-factors.) With regard to the effect of heat on assimilation in particular, Matthäi has shown by experiments with cut twigs, that at −5 degrees no further decomposition of carbonic acid takes place, that at 0 degrees feeble assimilation begins and that it then increases, to fall off rapidly above 37.5 degrees, completely disappearing at about 45 degrees. The heat curve thus presents the form of an optimum curve which rises to a peak and then sinks again far more rapidly. Only at low temperatures does assimilation remain for hours at the same height, above 23.7 degrees it diminishes from hour to hour. Thus the maximum efficiency

[1] Phil. Transactions, London, 1904, Vol. CXCVII, p. 47.

of heat is found to differ according to the duration of its action at various temperatures. The activity of assimilation, as a chemical process, must rise with the temperature in accordance with the law established by Van't Hoff also for other chemical processes, in such a way that it is doubled to trebled for every rise of temperature of 10 degrees.[1] The law finds expression in assimilation, however, only during the first period of the action of heat and ultimately not at all, because high temperatures make the chlorophyll inactive. The optimum curve therefore comes into being through the influencing of a Van't Hoff chemical curve by another running in the opposite direction which represents the injuring of the chloroplasts by higher temperatures.

At higher temperatures respiration rises much more rapidly than assimilation with rising temperature. The consequence is that beyond a certain limit the excess of assimilation over the consumption of material becomes less and less. This is of the greatest importance ecologically. By it is determined the ecological optimum temperature for assimilation and consequently also to a great extent the optimum climatic warmth for plants. Therein, according to Lundegärdh,[2] may lie the reason why many plants are confined to colder climates.

Mention may be made of an experiment by Harder [3] in which plants, accustomed by long maintenance at different temperatures to cold or to warmth, reacted quite differently towards temperature as to their assimilation. The assimilation of the "cold plants" was not promoted to the same extent by a rise of temperature as that of the "warm plants." Should these regularities, found in water plants, be proved also for trees, it would be of the greatest ecological and plant-geographical importance. The adaptability of species and races of trees to climate and restricted habitat and much else could then be much better assessed.

14. Energy of Assimilation.—Something has already been said in Section VIII, 6, on the specific energy of assimilation of light- and shade-leaves. A series of data exist for plants other than trees [4] which are mostly derived from assimilation experiments in the laboratory and judge of the greater by the less. Such methods of investigation are always uncertain because, under the conditions of a glass experiment, unmeasurable alterations, such as movements of the stomata, easily occur and the natural conditions are not exactly imitated. Determination of the amount of leaf activity is more easily and certainly reached by starting with the total production of matter by the crop in the unit of area and time. It is true that what is obtained is not the true assimilation but the production of material less what is lost by respiration. Such experiments have been already carried out by Becquerel [5] and Liebig [6] also for forest trees. Their results are, however, less useful

[1] Literature *see* Jost. Vorlesungen über Pflanzenphysiologie, 3 Aufl., 1913, p. 160.
[2] Lundegärdh, Der Kreislauf der Kohlensäure. Jena, 1924, S. 110.
[3] Harder, Über die Assimilation von Kälte- und Wärmeindividuen der gleichen Pflanzenspezies. Jahrb. f. wiss. Bot. 64, 1924.
[4] Weber, Inaug.-Diss Würzburg, 1879, also in Arb. d. Bot. Inst. in Würzburg 2, 346, 1879.
[5] According to the Handwörterbuch d. Naturwiss. Bd. VII, 798. Jena, Fischer.
[6] V. Liebig, Die Chemie in ihrer Anwöndung auf Agrikultur, 5. Aufl., p. 14 u. 15.

because at that time the working capacity of the forest was not yet sufficiently known. Ebermayer's [1] calculations are more accurate. According to them the dry matter produced annually per hectare amounts to :

	Total timber, inc. thinnings and rootwood.	Annual fall of litter.	Total dry matter.
Beech	3163 kg.	3331 kg.	6494 kg.
Spruce	3435 kg.	3007 kg.	6442 kg.
Pine	3233 kg.	3186 kg.	6419 kg.

Thus the specific energy of assimilation calculated on the unit area of the wood was, according to this, almost exactly the same for the three species. As however volume production varies very greatly according to the quality of the locality the comparison is unsafe. Weber [2] has therefore extended the comparison to the various yield classes. His results supported Ebermayer's statement: that our principal tree species, in equally favorable localities, all produce the same quantity of material when the yield is measured not by volume but by weight. He estimates the mean quantity of material produced annually on one hectare of the best quality class at 9–10 tons (of 1,000 kilogrammes) in which is 100–250 kilogrammes of ash. This cannot however be applied to all species, for the pine falls behind this rate of working even in the best localities because it opens up earlier. Perhaps the difference is only an apparent one, because the pine generally occupies poorer localities. The North American Douglas fir produces with us on the same area more than double as much as the spruce—up to 22,000 kilogrammes per pectare per annum, namely 30 (–35) cubic metres stem timber of 0.5 gravity specific, approximately 6 cubic metres root wood and about 3–4,000 kilogrammes of leaves.

From these data we can calculate the work done by the leaves according to other scales of measurement. The leaf-surface of a beech crop of the best growth amounts to about three times the growing space and thus to 30,000 square metres per hectare. Calculated on an annual production of 9,000 kilogrammes, the annual productivity of 1 square metre of leaf-surface of the beech amounts to 300 grammes, with 150 growing days, to 2 grammes per day ; calculated on the dry weight of the leaves, to about 3 kilogrammes assimilate per kilogramme of leaf or 20 grammes per day, or with a daily activity of 10 hours to 2 grammes per hour. For the spruce, which retains its needles for about six summers, an annual production of ½ gramme per gramme of leaf substance or a daily one of 3.3 grammes per kilogramme of leaf substance is found from the same figures. As however assimilation is very unequal according to the season of the year and the weather, it may be assumed that these average figures may be very considerably exceeded so that, in times of very favorable conditions for assimilation, the values of about 0.4–0.8 gramme per square metre, found from the

[1] Ebermayer, Die gesamte Lehre der Waldstreu, Berlin, 1876, p. 67 and 68.

[2] Weber, R., Lorey's Handbuch der Forstwissenschaft, 1 Aufl. I, Bd. 1. Abt. p. 68–71 ; the same, Lehrb. d. Forsteinrichtg., Berlin, 1891.

physiological side, may be approached.[1] Stalfelt also found the activity of pine and spruce needles, compared with needle weight, needle area or quantity of chlorophyll, considerably less than the activity of the leaves of other plants. The increment of pines, silver firs and spruces is also, according to Schwappach,[2] not proportional to the number or the weight of the needles.

Ebermayer [3] puts the carbon stored up in one hectare of forest at 3,000 kilogrammes per annum and in the whole area of the Bavarian forests at about 8 milliards of kilogrammes. R. Hartig took as the approximate measure for the quantity of leaves on a tree, the weight of the youngest twigs which bear them, the so-called fine faggot wood (Feinreisig). The quantity of wood which various trees produced per kilogramme of fine faggot wood then gave a measure of the approximate energy of leaf-activity. For example for oaks in the Spessart, the sample stem gave on the average per 1 kilogramme fine faggot wood:

At the age of	33	years	0.753	1.	wood per year.
,, ,,	90	,,	0.275	1.	,, ,,
,, ,,	246	,,	0.262	1.	,, ,,
,, ,,	400	,,	0.230	1.	,, ,,

From this it may be deduced that the feeding activity of the leaves is greater during the youth of the tree. Further:

In a good locality 1 kg. fine faggot wood produced in stems of different size classes.		In a poor locality 1 kg. fine faggot wood produced in stems of different size classes.	
I.	1.405 1. wood.	I.	0.259 1. wood.
II.	1.200 1. ,,	II.	0.335 1. ,,
III.	0.813 1. ,,	III.	0.270 1. ,,
IV.	0.538 1. ,,	IV.	0.283 1. ,,
V.	0.303 1. ,,		

It is recognisable that the same quantity of leaves with the same lighting, worked very much more energetically in the better locality than in the inferior one.

The productive activities of some agricultural crops are quoted for comparison [4] and the maximum activity of the hardwood forest appended, the carbon content of wood being taken as one half of the dry matter.

Amount of production of Carbon per hectare per annum:

	Kg. Carbon.	Leaf area in times the soil area.	Grams C. per sq. m. leaf-surface.
Clover . . .	6124		
Sugar beet . .	4715	4.7	100.2
Potatoes . .	4117	3.25	136.2
Oats . . .	4114		
Beech 1 class locality .	4750	3.0	158
Beech 2 class locality .	3300	2.4	138

[1] Giltay, Annales Buitenzorg 15, p. 43, 1898; Brown, Proc. Roy. Soc. Vol. 79, p. 29, 1905; and others.

[2] Schwappach, Zeitschr. f. Forst- u. Jagdwesen, 1893, 664; Bertog, Forstlich naturwiss. Zeitschr., 1895, 178.

[3] 1885. [4] Gohren, Landw. Versuchsstat. 9, 1867, p. 298. Quoted from Reinau.

Since, as a rule the best beech crops would flourish on arable soils which give these yields, the figures should be comparable, and show that the forest fixes about the same quantity of carbon, for the leaf-surface perhaps a somewhat larger quantity than agricultural plants, which benefit, it is true, by manuring, but are handicapped as against forest trees by their shorter growing season.

15. Death and Fall of the Leaves.—The natural duration of life of tree leaves is among the phenomena of the individual nature or specific structure of the plants but, like the duration of life of the whole plant, is dependent on external influences. Just as there are long-lived and short-lived plants, so there are leaves that only live for a few months and others that remain capable of work for years. These two kinds of leaves occur both in equable and extreme climates, although in the former long-lived, evergreen, in the latter, short-lived, summer-green or rain-green species predominate. This is partly due to the fact that the greater number of woody plants are generally endowed with long-lived leaves. Where, as in the perpetually moist tropical regions, the number of woody plants is especially large, the evergreen leaf preponderates for this reason. Obviously however the duration of life as well as the form and structure of the leaf is also an expression of the possibilities of the different climates (*see* pp. 1 and 2).

Within the limits set by the individual nature of each plant, the duration of life of the leaves is influenced by the relationship to other parts of the plant body (correlation) and by deviations of the light and water supply from that usual in the locality. Darkening and the shortage of water especially may bring about the fall of the leaves.[1] Pruning may prolong the life of leaves.[2] Leaf-fall need not be preceded by wilting, so far as by wilting is understood drooping and eventual withering. This is always the result of injurious influences especially the shortage of water, as has been fully worked out by Briggs and Shantz.[3]

The duration of life of evergreen leaves varies greatly.

For *Ilex aquifolium*	it was found to be	25	months.[4]
„ *Ilex nobilis*	„ „ „	53	„
„ *Vaccinium vitis idaea* . . .	„ „	29	„
„ *Hedera ilex*	„ „ „	28	„
„ *Prunus laurocerasus* . . .	„ „ „	15	„

The following figures for the duration of life of the needles of some of the conifers are given by May [5]:

[1] Wiesner, Sommerlaubfall, Treiblaubfall, Hitzelaubfall, Frostlaubfall. Ber. d. D. bot. Ges., XXII, 1904, XXIII, 1905; Dingler, *ibid.*, 1905 and 1906 (Cutting, topping); Hoffmann, H., Zentralbl. f. d.ges. Forstwesen, Wien. IV, 7; Furlani, Österr. bot. Zeitschr., 1906.

[2] Dingler, *loc. cit.*

[3] Flora, hrsg, von Goebel, 1913, p. 224; *see* also Caldwell, 1913; Brown, 1912.

[4] Hoffmann, Bot. Ztg., 1878.

[5] Die Lebensdauer der Nadeln bei einigen ummergrünen Nadelhöltzern (Zeitschr. f. Forst. u. Jagdwesen, Bd. XXVI, 1894. There further literature. *Comp.* also Döbner-Nobbe, Botanik für Forstmänner, 4 Aufl., 1882).

Pinus laricio Poir.	2½–4½ years and over, generally 3½–4½ years.
Pinus montana Mill.	In youth the age limits are between 4½–8½, mostly 5½ years; in age 5½–10½, mostly 7½ years.
Pinus cembra L.	3½ years. 4½ year-old needles are exceptional.
Pinus strobus L.	1½–4½, mostly 2½ years.
Tsuga canadensis Carr.	1½–3½, mostly 2½ years.
Pseudotsuga Douglasii Carr.	On the main shoot, 2½–4½ years, mostly 2½–3½ years; on the lateral twigs, 3½–6½, rarely 7½; mostly 3½–5½ years.
Abies pinsapo Boiss.	On middle shoot 3½, on side shoots, 9½–12½ years.

According to existing data the needles of the Scots pine usually attain 2–3 years, of *Taxus* and the common juniper 4–5, of the spruce usually 6, of the silver fir 5–7 years. Needle-fall does not take place all at once like the fall of broad leaves, but the needles of a twig gradually diminish in number, but in such a manner that, *e.g.* in the Scots pine, a larger number of them detach themselves in the September and a smaller number in the October and November of each year. The needles of the spruce fall throughout the year, most plentifully however in May. Large falls of needles in other months are indeed induced by insects and other pests.

The duration of the needles varies according to the external conditions. Thus insufficient light accelerates their fall, which can be understood in view of what has been said above on the dependence of leaves on their assimilative activity. The duration of evergreen needles is conditioned in a high degree by the climate of the locality and the physiological peculiarities of races. The spruce in the lowlands retains its needles for 4–5 years, at the upper tree limit for 10–13 years, the pine has 2–3 years of needles in the German lowlands, 5–8 years' at 1,500–2,000 metres elevation in the Engadine. In Engler's [1] cultivation experiments at high elevations, pines from every source possessed 3–4 years' needles, the plants originating in the warmer lowlands nevertheless losing their needles somewhat earlier than the alpine and northern pines. Zederbauer [2] found that, when transplanted into another climate, plants from the north and from high mountains retained the duration of life of the needles adapted to the climate of their origin. Shade-needles live longer than sun-needles.[3]

The **change of colour** of leaves which commonly precedes their fall, has no necessary connection with the latter, for, on the one hand, many leaves, such as those of the alder, privet, sometimes also the elder and the ash,[4] fall green, and on the other hand leaves which are not

[1] Engler, Mitteil. d. Schweiz. Zentralanstalt f. d. forstl. Versuchswesen, X, 1913.
[2] Zederbauer, Beitr. z. Biol. d. Waldb. II, Lebensdauer der Blätter, Zentralbl. f. d. ges. Forstwesen, 1916.
[3] Schreiber, *ibid.*, 1924, p. 137.
[4] Kolkwitz, Über das Schicksal des Chlorophylls bei d. herbstl Verfärbung. Ber. Dtsch. Bot. Ges. Bd. 37, 1919.

falling, such as the needles of many conifers, also undergo an autumnal colour change. This change in colour of evergreens is induced by the combined action of sunlight and low temperature. It becomes therefore especially evident on the sunny side of the tops of conifers and in ivy leaves exposed to the sun. These become a very dark red-brown, whilst pine needles assume a more yellow-brown tint. Red colour tints are due to the appearance of red colouring matters in the cell-sap, as occurs when assimilates are accumulated through transport out of the cells being hindered.[1] It is possible that they are useful as light-screens for the chlorophyll, or, as they absorb much heat, as heat storers for promoting the movement of carbohydrates out of the leaves, which in the red condition may be richer in diastase. The brown winter coloration of the evergreens (conifers, ivy) arises from the conversion of the chlorophyll into a brown-green substance. Both colorations disappear again through the warmth of spring and may also be removed in winter by bringing the coloured twigs into a room. The winter colour-change of pine needles becomes the more pronounced the higher the latitude of the locality.[2] It is greatest in January and is retained in the descendants of east-Russian and Scandinavian pines, also in other climates. Engler regards the colouring matters in question as respiration ferments, the formation of which in winter and in northern climates promotes respiration which is hindered by low temperatures.

The autumnal change of colour of falling leaves is due to the appearance of red colouring matters in the cell sap and the decomposition of the chloroplasts with the formation of small yellow drops or granules and larger colourless oil drops. Here again the sun favours the appearance of the red colour which is now and then sharply defined by the edge of a shadow. Anthocyanin, the autumn red of leaves, arises through the enrichment of the cells with food materials, whereupon a condensation of certain substances (carbohydrates, tannins) sets in, the end product of which is anthocyanin. Low temperatures, insect punctures and other wounds may be the cause of this enrichment.[3] Red colouring is shown especially by various plants introduced from North America such as the Virginia creeper, American oaks (*Q. rubra* and *coccinea*) and the tanning sumach (*Rhus typhena*), also by the Norway maple, barberry, dogwood (*Cornus sanguinea*), spindle tree, pear, the two viburnums, the aspen, cherry and others, *i.e.* by representatives of quite different families. Leaves which only turn yellow are those of the field maple (*Acer campestre*), sycamore, ash, birch, lime, Spanish chestnut, and those of robinia, which may also fall green, the walnut and several others. The leaves of the horse chestnut generally become yellow but may also occasionally turn red. The red coloration of the Virginia creeper affects mainly but not exclusively the better lighted epidermis and palisades.

How greatly the yellowing of the leaves is hastened by drought is striking and to be seen in every street. Nördlinger [4] states that in the

[1] Koning u. Heinsius, Bot. Zentralbl., 98, 1905, p. 142.
[2] Engler, Mitteil. d. schweiz. Zentralanstalt f. d. forstl. Versuchswesen, X, 1913.
[3] Schander u. Schaffnit, Landw. Jahrb. 52.
[4] Forstbotanik.

abnormally dry summers of 1834 and 1842 our trees had assumed their autumn clothing even in July and August, first on the south and then on the western sides. According to the same observer, there runs through the broad-leaved forest along the whole length of the northern slope of the Schwabian Alps, a narrow strip with shallow underlying rock, on which the foliage colours several weeks earlier than above and below.

The colouring matters which make their appearance on the fading[1] of leaves are not the same in all plants. They are not the same xanthophylls as those contained in the chlorophyll, but new formations of the autumn. Their further oxidation may lead to the complete whitening of the leaves. The red colouring matters appear when no decomposition of the chlorophyll is observable. A precondition of their formation is the accumulation of sugar in the cell-sap, such as occurs in ageing leaves when the nights become cold and assimilation has not yet ceased. The finest red colouring therefore appears when, in the autumn, cold nights alternate with sunny days. Before red coloration commences, an accumulation of starch[2] becomes evident in many leaves (not for example in *Sorbus torminalis*). Following this the sugar content rises to a maximum, and this may also happen when the accumulation of starch does not take place. Then follows the emptying of the leaf of carbohydrates. In many evergreen leaves, the starch disappears in the autumn (end of October), to reappear in March.[3]

A tannin maximum is also found in the already somewhat yellowed or reddened leaves which disappears again or is retained till their fall. The withdrawing starch remains longest in the neighbourhood of the vascular bundles. That starch may still be present in completely yellowed leaves[4] is explained by its evacuation from the leaf being hindered by low temperatures.

The movement of nitrogen and other mineral nutrients varies according to the species of tree and the conditions.[5] The loss of nitrogen should be general, as it depends on the impoverishment of the protoplasm whose remains including the nucleus are otherwise, still present in the faded leaves.

Schultze and Schütz[6] state that, in the leaves of *Acer negundo* after an increase in the relative and absolute content of nitrogenous constituents, from May to June, a constant diminution occurs from July onwards. Otto and Kooper[7] find a constant decrease from the maximum in April and May until death. Apparently the ageing leaves no longer possess the power of forming protein to replace that which is destroyed in respiration or transferred to the stem.

[1] Swart, Die Stoffwanderung in ablebenden Blättern, Jena, 1914, G. Fischer. Here the literature. *Comp.* also Czapek, Biochemie.

[2] Schmidt, Beiträge zur Kenntnis der Vorgänge in absterbenden Blättern. Inaug.-Diss. Göttingen, 1912.

[3] Mer, Bull. de la Soc. bot. de France, XXIII, 1876.

[4] Harter found 9.89% of starch in fallen leaves of *Platanus occidentalis*. Plant World, XIII, p. 144.

[5] Leaves to be comparable must be collected at the same time of day.

[6] Landwirtschaftl. Versuchsstationen LXXI, 1909, p. 299.

[7] Landwirtschaftl. Jahrh. XXXIX, p. 167, 1909 (*Aesculus, Sambucus*).

As a rule the leaves as they become yellow, besides losing nitrogen also lose phosphoric acid and potash, the amount of which varies between wide limits. The iron and magnesium contents remain fairly constant Calcium, silicon, sulphuric acid and chlorine may even increase to some extent. According to some of Ramann's [1] figures the following passed out from the leaves into the stem, the content of the green leaves being put at 100 :

	N.	P_2O_5	K_2O	
Beech	35.0%	26.5%	great increase	Fading leaves from Eberswalde
Oak	25.6%	31.9%	remains the same	
Hornbeam	25.6%	33.9%	31.5%	
Hazel	26.8%	—	11.9%	
Birch	50.6%	20.2%	44.3%	Quite dead leaves from Bernau.
Oak	45.4%	41.9%	56.8%	
Maple	71.1%	18.4%	26.6%	
Robinia	49.4%	35.4%	5.2%	

The content of the green leaves (put at 100) relative to the content of the faded and dead leaves was :

	CaO	SiO_2	
Beech	100 : 109	100 : 128	Fading leaves from Eberswalde.
Oak	100 : 209	100 : 213	
Hornbeam	100 : —	100 : 134	
Hazel	100 : 135	100 : 173	
Birch	100 : 108	100 : 263	Dead leaves from Bernau.
Oak	100 : 191	100 : 281	
Maple	100 : 97	100 : 110	
Robinia	100 : 228	100 : 121	

In *Populus canadensis* potassium passes out long before fading, to fulfil an important function elsewhere or perhaps to be accumulated in the bud. Phosphorus and nitrogen decrease during fading by leaps and bounds because removal is no longer compensated by supply. It is not so much the loss of the power of forming protein as the cessation of the supply of raw materials that is responsible for the processes in the autumn leaf. That fading is postponed by checking the removal of material (cutting through the veins) (Stahl) is not incompatible with this.[2] Stahl [3] sees in the falling leaves organs for getting rid of superfluous mineral materials.

When leaves are prematurely frozen [4] a reduction, though slight, of potash and phosphoric acid (not however of nitrogen) may nevertheless take place, so that it may be assumed that a rapid movement of materials proceeds during the few hours between freezing and drying up.

The materials carried to the soil by the falling leaves are not lost to the tree. On the decay of the leaves they are transformed again

[1] Wanderungen der Mineralstoffe beim herbstlichen Absterben der Blätter. Landwirtschaftl, Versuchsstationen, LXXVI, 1912, p. 161.

[2] Richter, Landwirtsch. Versuchsstationen, LXXIII, 1910, p. 457.

[3] Stahl, Flora, 1919.

[4] Ramann, Landwirschaftl. Versuchsstationen, LXXVI, 1912. Schander u. Schaffnit Landwirtsch. Jahrb. 52, 1918.

into mineral compounds which may be taken up again by the roots. The well-known injury caused to trees by the repeated raking off of the litter, depends on the removal of valuable food substances as well as on the injury done to the physical properties of the soil. Ramann found a shortage of potash and lime in the leaves of back-going trees on soil from which the litter had been removed over a long period.

The period of fading of the leaves during which the loss of materials is essentially completed, lasts about 2–3 weeks and occurs mostly in October. It may begin earlier and be shortened in exceptionally dry or cold, wet years. The decomposition of the chlorophyll during the period of fading may be delayed by separating the leaf from the shoot or severing the conducting tissues of the leaf. From this Stahl concludes that it is dependent on the removal of the products of decomposition.

Though the faded leaf soon detaches itself from the twig it is not yet dead, and even leaves lying on the ground are not necessarily dead. Leaf fall is initiated by a slow diminution of the supply and the evaporation of water. The stomata lose their power of opening and in the vascular bundles tylose formation and the closing of the sieve tubes by callus sets in. Prepared by their own life processes the fall of the leaves finally follows as the result of small shocks from without. The whole process is an example of **chorism,**[1] the normal throwing off of organs no longer capable of functioning, such as is presented by the fall of floral leaves and stamen filaments, the dwarf shoots of *Taxodium* and pines, the shedding of twigs (*q.v.*) and also in pathological processes when, *e.g.* pine needles are attacked by the needle-shedding disease (*Lophodermium pinastre*) and are then thrown off. (The shedding of the dwarf shoots of the pine occurs through the medium of a thin-walled cork layer at the boundary between the dwarf and the long shoot.) The ageing of the organs concerned brings with it stimulus effects which cause the shedding, just as in cases of premature leaf fall, all sorts of other stimuli do. There is still a good deal in this connection which is puzzling. According to experiments by Neger and Fuchs,[2] in cut branches of Douglas fir lying in the air, it is mainly the needles of the older years that detach themselves; if, however, twigs, previously somewhat dried, are placed in water, it is mainly the young needles that detach themselves smoothly. In the same species needles killed by sulphurous acid fall off; not so in the spruce. Prolonged darkness, shortage of water, damming back of assimilates and other disturbances of the transport of materials,[3] the action of tobacco smoke [4] and other impurities in the air may also cause young leaves to fall.

The preparations for leaf-fall consist of the loosening of the connection between the leaf and the twig, often also between the blade and the leaf-stalk, and in the closing up of the wound formed by the shedding. The cells of a layer of parenchyma at the base of the leaf-stalk round themselves off from each other and become separated from each other

[1] Fitting, Jahrb. f. wiss. Bot., XLIX., 1911; Varga, Österreich. bot. Zeitschr., LXI, 1911. The disposition to leaf fall is evoked by reduction of assimilation and transpiration in consequence of lowering of temperature.

[2] Untersuchungen über den Nadelfall der Koniferen. Jahrbuch f. Wiss. Bot. LV, 1915.

[3] Pfeiffer, H., Ber. D. Bot. Ges. 42, p. 291, 1924.

[4] Molisch, Pflanzenphysiologie.

by the dissolution by a ferment [1] of the so-called middle lamella—a middle membrane layer differing chemically from cellulose which is never absent where two mature cells adjoin one another. No more violent rupture of the cells takes place at the point of separation than in the separation of the pollen grains from each other or in the scaling off of the root cap. In all such cases the individual cells loosened from each other remain quite undamaged. The vascular bundles entering the twig from the leaf-stalk are already specially thin and poor in tough-walled elements at the place of separation; according to Wiesner they may indeed consist in many cases only of cambium cells.[2] Their rupture consequently requires no particular application of force, and in fact, leaves may even fall by their own weight. Leaf-fall is naturally accelerated by wind and also by the formation of ice in the place of separation. If the lime tree is observed on an October morning after a frosty night it is seen that in the same measure as thawing proceeds under the rays of the sun from the top to the base to the crown, so do the leaves fall, so that in quite a short space of time the hitherto richly foliaged tree has lost its coloured attire.

The formation of the parenchyma layer within which the separation of the cells proceeds, occurs, according to Mohl,[3] only a few weeks before the fall of the leaf, thus at the beginning of October, without previous preparation. In the beech it proceeds only after the leaf fall, often only in the following spring.

Tison and Lee [4] have closely studied the **occlusion** of the wound left behind by the falling leaf. They distinguish a protective layer under the remains of the layer of separation, whose cell walls are lignified and suberised. This protective layer arises either by the conversion of the cell walls of already existing cells (*Castanea, Ligustrum, Acer pseudoplatanus*, etc.) or the conversion is preceded by division in all directions (*Tilia, Carpinus betulus, Betula verrucosa, Fraxinus*). It may also be formed by a cambium which develops lignified and suberised cells towards the surface of the scar and in winter, to the outside a layer of cells with cuticle like the normal epidermis, towards the other side one or two layers of living cells (Willows, Poplars). The single-layered cambium may repeat its work in the following spring, to end it with a second cuticularised cell layer. These cork layers below the protective layer finally gain connection with the cork of the supporting shoot and with this the healing of the wound is complete. Strangely enough the first of these cork layers, *e.g.* in Robinia, may originate months before the appearance of other autumn changes in the leaf, so that it cannot possibly be the cause of its death. Exchange of substances and the supply of water proceed by means of the vascular bundles which pass through the cork layer. In other cases the cork layer arises after the fall of the leaf, in the following spring or even, as Magnus [5] observed in the oak, some (3) years later.

[1] Molisch, Laubfall. Sitzungsber. d. Wiener Akad., Bd. XCIII, 1886, Abt. I.

[2] Sitzungsber. d. Wiener Akad., math.-nat. Kl., Abt. I, Bd. LXIV, 1871.

[3] v. Mohl, H., Über die anatomische Veränderungen des Blattgelenkes, welche das Abfallen der Blätter herbeiführen. Bot. Ztg., 1860.

[4] The morphology of leaf-fall. Ann. of Botany, Vol. XXV, 1911, p. 51.

[5] Magnus, Werner, Physiologischer Atavismus der Eichen und Buchen. Biol. Zentralbl. XXXIII, 1913; Lakon, Jahrb. f. wiss. Bot., 1916, p. 378.

Fruits from the cupule (chestnut, beech, oak) and the fruit stalk on ripening are also shed by means of similar layers of separation.[1] In such cases there occurs a swelling of the cell walls and the dissolution, not only of the middle lamellae, but also of the secondary parts of the walls in the layer of separation.

In the Abietineae [2] the separation of the needles takes place at the boundary between a layer of hard cells and one of thin-walled cells, the former of which adheres to the leaf-cushion and is designated by Neger the separation layer. Except in *Pinus* it is already begun at a time when the remaining tissues of the needle are not yet fully formed. The formation of a periderm in the supporting twig may play a part in the shedding of the needles. According to Neger, the shedding is brought about, purely mechanically, in the spruce by tension differences set up at the base of the needle when water is lost, through different degrees of shrinkage in thick- and thin-walled cell layers adjoining each other. If drying out does not occur long-dead spruce needles may continue to adhere. The difference in contraction of the cell layers lying on each side of the surface of separation may amount to 7–9 per cent. As in the dicotyledons, the closing of the wound is effected by cork, the formation of which follows mostly 2–6 weeks after the fall of the needle.

Beech and oak, especially the sessile oak, tend to retain their withered, dried-up foliage in the winter. The phenomenon is most pronounced in young, strongly-growing, specimens, in beeches especially in the lower parts, in young plants not exposed to full light, and on the lower, large branches of older trees whose upper branches are quite bare. Oaks of considerable age may remain fully foliaged. The foliage tends to remain long on heavily clipped hedges. The mode of occurrence of the phenomenon suggests that external circumstances, according to Lakon [3] better supply of nutrient salts and water to the twigs that do not shed their leaves, are the immediate cause. The cause may also be the leaf-base being surprised and killed by frost before the separation tissue is formed.[4] Young plants and stool shoots are especially prone to it as they tend to grow on too long into the autumn. It also sometimes happens however that the dead foliage of our trees remains hanging in frost free tropical regions when they are transplanted there.[5]

As in other cases, *e.g.* in adaptation to light, reaction to changed

[1] Fehér, Unters. ü.d. Abfall der Früchte einiger Holzpfl. Ber. d. D. bot. Ges. 43, p. 52, 1925.

[2] Tison, Mém. soc. linnéenne d. Normandie, XXI. Caen, 1903; Neger u. Fuchs, Untersuchungen über den Nadelfall der Koniferen. Jahrb. f. wiss. Bot. LV, 1915, p. 609.

[3] Über den rhythmischen Wechsel von Wachstum und Ruhe bei den Pflanzen. Biolog. Zentralbl. XXXV, 1915; Varga, Österr. Bot. Zeitschr., LXI, 1911. Abs. Bot. Zentralbl. CXVII, 1911, p. 24; Molisch, Radiumemanation verfrüht den Laubfall. Author's abstract. Bot. Zentralbl., CXX, 1912, p. 389.

[4] Claussen, P., Über die Wirkung der Frühfröste auf den Laubfall. Mitteil. Dtsch. Dendrol. Ges. 29, p. 343, 1920.

[5] Dingler, Periodizität in den Tropen. Sitzungsber. d. bayr. Akad. d. Wiss., 1911; Volkens, Laubfall und Lauberneuerung in den Tropen. Berlin, 1912, Borntraeger; Klebs, Biolog. Zentralbl., XXXII, 1912; Lakon, *ibid.* XXXIV, 1914, p. 161; Kniep, Über rhythmische Lebensvorgänge bei Pflanzen. Würzburg, 1915, Kabitzsch. (From: Verh. d. Phys.-med. Ges. zu Würzburg, N.F., XLIV.) Kamerling, Periodische Laubfall in den Tropen. Ber. d. D. Bot. Ges., XXXI, 1913, p. 324.

conditions requires time, it is so also in leaf-fall. Peach trees,[1] grown from European seed, became nearly evergreen within a period of 20 years in the equable climate of Reunion, by standing bare for a shorter time in each successive year. Seedlings of the plants which became evergreen were evergreen even when they were sown in the mountain land where peach trees from European seed shed their foliage periodically.

[1] Bordage, A propos l'hérédité des charactéres acquis. Bull. scient. de la France et de la Belgique, 7e sér. T. LIV, Paris (also Kniep, p. 2).

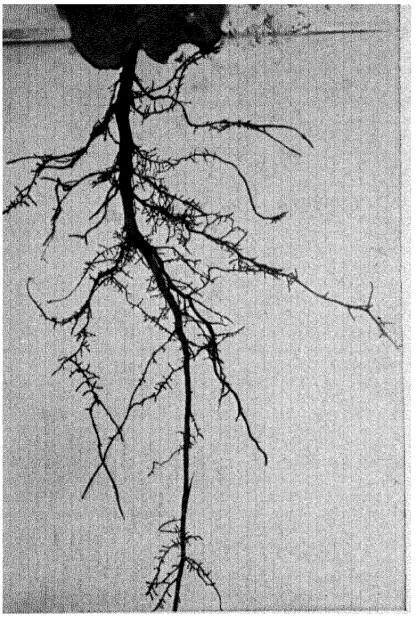


FIG. 109.—Root system of a 2-year-old Silver Fir (tap root). About half natural size.

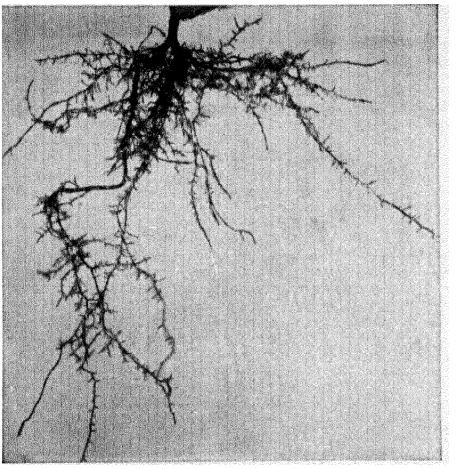


FIG. 110.—Root system of a 2-year-old Spruce. The upper lateral roots begin to surpass the main root (flat root). About half natural size.

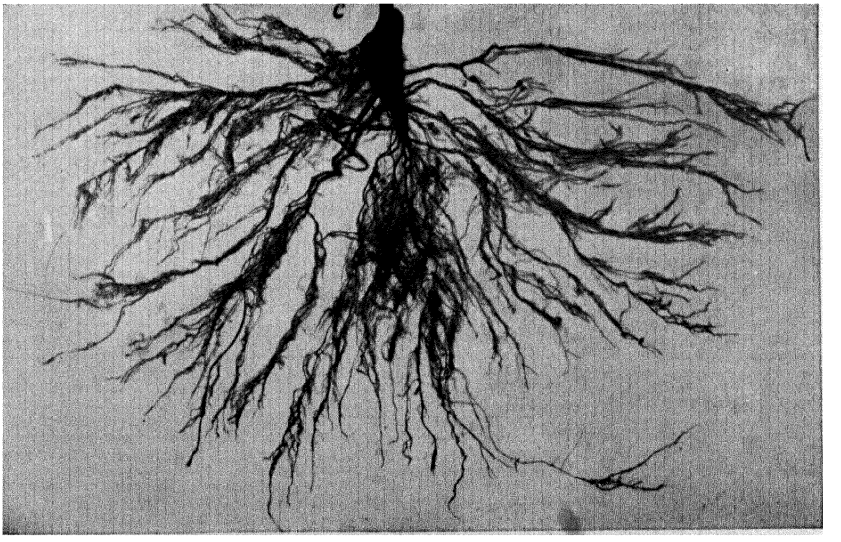


FIG. 111.—Root system of a 2-year-old Alder.

[*To face p.* 269.

CHAPTER IX

THE ROOT

1. The Form of the Root System.—In Chapter I we learnt to recognise the part of the tree above ground as an aggregate, built up of individual constituents, the annual shoots, assembled with strict regularity which finally, under the influence of external forces acting on the tree, escapes the confines of that regularity and develops into a structure which derives its form less from the original plan than from the adaptations to light and gravity. The same is the case to an even greater extent with the root system. The practical distinction **tap root, heart root** and **flat root** thus gives pretty well the only architectural characteristics of its individuality which a root system taken as a whole retains. Almost all others—number, direction and size of the root branches—express first of all, adaptations to the environment. Even the characters distinguished by the above terms are not always retained. In oak, pine and silver fir (Fig. 109), it is true, there is always found, at least in young plants, the deep-going tap root, in the spruce, (Fig. 110) and poplar the flat roots stretching out horizontally under the surface of the soil; though there are, as we shall see, very many exceptions to this rule according to the external conditions. In the young alder a tap root often runs straight downwards like that of the oak, or again, several roots of about equal size thrust out in a rather more oblique direction; or finally, a horizontal side root, running just under the surface of the soil, appropriates the nourishment to such an extent that it equals or even surpasses the main root in size. The root system of very young beeches also exhibits varying forms, though it generally possesses a pronounced vertical main root; on the other hand, in unfavorable soil, it may spread out as flat as a table. The roots of young birches very commonly show a pronounced crook close under the surface of the ground. Th. Hartig [1] ascribes to the birch root generally, a tendency to bend sideways out of the vertical. According to him, it occurs in all less vigorously growing plants without recognisable cause, whilst strong growing plants in free soil possess a tap root running fairly straight down and having a length equal to that of the shoot above ground, as well as a plentiful development of lateral and fibrous roots. Older birches have, like the beech (Fig. 121)

[1] Naturgeschichte der forstlichen Kulturpflanzen, etc. Gives details of the root systems of individual trees.

and alder (Fig. 111), heart roots, *i.e.* several side roots of about equal size proceed from the so-called root knot, and, in a 50-year-old tree, may be traced stretching horizontally up to 8 metres away. The mountain pine (*Pinus pumilo*), just as it possesses no upright stem, also forms no single, long, tap root but many root strands which produce a flat spreading structure. The parts of the stem which rest on the soil root themselves as layers (Th. Hartig).

The wealth of branching and the whole appearance of the root system are governed in a striking manner by the nature of the soil into which the root penetrates. In loose sand or humus or in water the roots always develop much more plentifully than in heavy, compact soil. Mechanical obstacles seem to affect this more than do conditions of nutrition. Heaps of leaves or compost may be very thoroughly permeated and exhausted within a year by tree roots penetrating into them. The roots of neighbouring trees quickly make their way into the loose soil of well cultivated and manured forest nurseries and fields, withdrawing nutrient substances and water from them. At the margins of woods, tree roots are not seldom to be met with at a distance of 20 metres in the adjoining fields. For this reason cultivated ground near woods must be protected from the roots of trees by means of trenches. Young spruces and pines in open soil may send out side roots a metre long even in the first two years, and masses of raw humus heaped into banks on planted areas are thickly permeated by roots within a few years. In such cases, besides the openness of the soil, the better nourishment and the absence of competition from other tree roots are responsible for the great extension of the roots. In other cases, however, it is certain that the absence of mechanical obstacles is the determining factor. When the roots of trees penetrate into water drainage pipes they develop there so thickly and plentifully in the flowing drainage water as to completely block up the pipes. In drift sand pine roots reach very great lengths though they are in such cases only sparsely branched. Schwarz [1] found that the root system of the pine developed the quicker in proportion as the sandy soil was poorer in salts.

Undoubtedly, however, better nutrition may also promote luxuriance in the development of the roots if at the same time mechanical hindrances, as in rich clay soil, are not present. Better nutrition in a particular part of the root area exerts a favorable influence on the production of side rootlets and, in soils minerally very poor, side roots already started may die off again. As the roots consist for the most part of organic substances which, together with the converted nutrient salts, are supplied by means of the descending sap stream from the leaves, this local promotion of root growth cannot be explained simply by better soil nutriment alone. Some kind of stimulus must proceed from the roots which attracts the building materials by preference to those parts of the root which are better supplied with soil nutrients. Everything in this connection is not yet satisfactorily explained and the observations are not yet completely in agreement with one another or with those made in the laboratory.

[1] Schwarz, F., Zeitschr. f. Forst- u. Jagdwesen, 1892.

Muller-Thurgau [1] observed that, of two lateral roots of the same main root, the one immersed in a nutrient solution rich in nitrogen developed better and produced more rootlets than the sister root immersed in a nitrogen-free solution. Even when the supply of oxygen is ample, a plentiful supply of water [2] hinders the growth of the radicle in land plants, whilst it promotes it in water plants. Tunker and Seelhorst [3] determined by observations on pot plants of oats, that whilst the mass of plant substance above ground increased with increasing water supply in the soil, the weight of the roots was greatest in plants grown in the soils poorest in water. The materials utilised for the increased formation of roots in the soils poor in water were withdrawn from the mass above ground, without the enlarged root mass being able to supply sufficient to replace them. In the most copiously watered pots the favorable conditions increased the weight both of the roots and the yield and also, with a medium amount of soil moisture, even a poor amount of root was able to supply a large quantity of water and food material to the organs above ground. In young spruces also, as Oberlandforstmeister Matthes in Eisenach pointed out to me, the root mass is smaller in well watered soil than in dry soil, both absolutely and relatively to the mass above ground. In unmanured and one-sidedly manured (potash, nitrogen) soil,[4] the plant endeavours to make up for the paucity of nutriment by great root development, without however being able to do so entirely. When the supply of food stuffs is abundant, the mass of the roots and the amount of substance above ground grow simultaneously.

Very important for the form of the roots, are the conditions for the supply of oxygen. Roots cannot penetrate into subsoils which are wet, compact, poor in oxygen or rich in carbonic acid, or they occasionally die off again in such soils. In soils of this kind, such as former arable land, clay consolidated by exposure or puddled, and especially in wet peat soils [5] the humus acids of which absorb much oxygen and the water drives out the air, all trees are shallow rooted. Even the pine, which in deeply aerated soil can send down its long tap root and large sinker roots apparently as far as diminishing oxygen and increasing carbonic acid content permit, possesses a true plate root on wet soil. In old heath soil [6] the tap root of the pine only penetrates as far as the iron pan or other compacted layer and then goes off at right angles, extending horizontally for long distances. Even more variable is the root form of the spruce, the roots of which appear to be specially oxygen-requiring. On heavy, wet or otherwise "physiologically shallow" [7] soils it forms extremely flat root plates and is then very

[1] Einfluss des Stickstoffs auf das Wurzelwachstum. VI. Jahresber. d. deutsch-schweizer. Versuchsstationen usw. in Wädensweil. Ref. Bot. Zentralbl., Bd. 80, 1899, p. 74.

[2] Wakker, Beeinflussung des Wachstums der Wurzel durch das umgebende Medium. Jahrbücher f. wiss. Botanik, 1898.

[3] Journal f. Landwirtschaft, 1898, 52; Beih. z. Bot. Zentralbl., 1898, p. 530.

[4] Tunker u. Seelhorst, *loc. cit.*; Langer, *ibid.*, 1901, 209.

[5] Kokkonen, Beob., ü. d. Wurzelsystem d. Kiefer auf Moorboden. Acta forestalia Fennica, 25 1923.

[6] Aaltonen, V. T., Über d. Ausbreitung u. d. Reichtum d. Baumwurzeln in den Heidewäldern Lapplands, *ibid.*, 14, 1920.

[7] Bernbeck, O., Beitr. z. Physiologie d. Bodens. Forstwiss. Zentralbl., 1914.

subject to wind-throw. On the other hand, in deeply disintegrated, porous or well aerated soils, it grows numerous sinker roots up to over a metre long [1] which afford the tree great stability and enable it to withstand periods of drought better than on shallow soils exposed to all sorts of variations in moisture. Root forms of this sort only rarely come to sight because such spruces hardly ever have their root masses lifted from the soil by storms. The famous oaks of the Spessart have, strangely enough, no deep tap root such as the oak has elsewhere, but rather shallow root plates.

The malformations which are often induced in roots by transplanting should also be considered here. If pine roots are bent or twisted in planting, deformations and malformations arise which are still visible at the root-stock even after some decades. Many foresters ascribe great importance to these malformations for the future development of the tree and seek to explain by them all sorts of defects in the later years of the crop. A very detailed investigation by Wibeck [2] gave the surprising but absolutely certain result, that, at least up to the 15th year, the more the root stocks were bent and deformed the better the stems grow. Evidently the building materials, which are saved in the formation of the roots in consequence of the bending of the root system, fall to the benefit of the stem above ground. Whether the result obtained in young pines can be applied to all localities, species and ages has not yet been investigated. Wibeck presumes that the crops will suffer damage later owing to their stability being reduced.

Attention has already been given (*compare* Chap. I) to some relationships between the form of the crown in some trees and the inborn nature of their root system. Others originate from the mutual dependence of root and crown on each other for nutrition. The nutrient solution supplied by one portion of the roots benefits first of all the branches on the same side of the tree, so that, for example, an apple tree which stands between cultivated garden ground and grass land, develops its branches more strongly on the side towards the former than on the opposite side. If, conjectures Vöchting,[3] such a tree which has three main roots and three main branches corresponding to them, had one of the roots severed, the branch belonging to it would fall behind the others in development without however perishing. The same rule—that the exchange of substances between crown and root proceeds best in a vertical direction—is equally well shown by the Lombardy poplars mentioned by Vöchting, which, growing on the verge of a steep slope, formed stronger branches on the side away from the slope which naturally afforded the roots a greater opportunity for development, than on the other, although the latter was better lighted. By cutting the root system right round a fruit tree at a distance of several inches from the stem (10 in the first year, 14 in the second and 18 in the third), at the same time removing the main root, the formation of long shoots was hindered in favour of the production of dwarf shoots, the bearers of flowers and fruit (Rivers, see Vöchting, *loc. cit.*).

[1] Wiedemann, E., 1925.

[2] Wibeck, E., Über Missbildungen des Wurzelsystems der Kiefer bei Stieleisenpflanzung Mitteil. a. d. forstl. Versuchsanstalt Schwedens 20, 1923, p. 300.

[3] Vöchting, E., Über Organbildung im Pflanzenreich, II, 1884.

In consequence of the close exchange relationship between the nutrition and formation of root and crown and the stimulus effects on growth already mentioned, the amounts of crown and root always stand in a definite proportion, so that both the regular water requirements of the evaporating crown and the mechanical requirements of the tree for stability are satisfied and, on the other hand, the roots are assured of sufficient nourishment by organic substances from the leaves. Broad-crowned, deeply branched, isolated trees have therefore much larger masses of roots than those confined in a dense wood. According to Zederbauer,[1] the root system of the spruce is more regularly formed when the growing space is larger than in close stand. He found the proportion between the weight of the roots and that of the above-ground parts always the same, about 1 : 4. Weber [2] gives the proportion by weight between the underground and above-ground mass in crops as 30–35 per cent. It is less in tall slender crops and greater in open, short-stemmed ones. Pines grown in the shade have much weaker roots, especially lateral ones, than those fully lighted.[3]

That, according to Engler,[4] the roots on the valley side on steep slopes are more strongly developed than those on the upper side, may also be due to exchange relations between the roots and the corresponding parts of the crown.

Long and short shoots [5] may also be distinguished in the roots. The former are the so-called **main** or **pioneer roots,** which, endowed with great and prolonged growth in length, effect the extension of the root system. They produce, at a distance varying from a few millimetres to several centimetres from the tip, lateral roots which may all again become long roots but also may remain short and perish later. Main roots alone, or at least no sharply defined short roots, are found, for example, in the currants, elders (*Sambucus*) and ash. Short roots, which like the dwarf shoots in the crown of the birch, soon die off, are possessed by the beech and the birch. They bear the name of absorbing rootlets and effect the complete utilisation of the region penetrated by the main roots.

In the beech, for example, the 1.5 millimetres thick radicle grows rapidly down 10–15 centimetres deep into the soil. At the end of the seedling's first year of life those of the lateral roots which are not destined to live long may already be distinguished from others which are to become permanent members of the root system (Fig. 112). The root system undergoes a " cleaning " just like the stem. At the end of the second year 7–8 generations of roots are found, the last members of which reach a thickness of only a fraction of a millimetre. These thin rootlets are present in great numbers and are well adapted for penetrating between the minutest particles of the soil and depriving

[1] Zederbauer, E., Ein Beitrag zur Kenntnis des Wurzelwachstums der Fichte, Zentralbl. f. d. ges. Forstw., 1920.

[2] Weber, R., In Handbuch d. Forstwissenschaft, 1. Bd., *loc. cit.*

[3] Wiedemann, 1926, *loc. cit.*

[4] Engler, A., Tropismen u. exzentrisches Dickenwachstum, 1918, *loc. cit.*

[5] Büsgen, Flora, 1905, Ergänzungsband ; and Büsgen, Kupuliferen : in Lebensgeschichte der mitteleurop. Blütenpflanzen, hrsg. v. Kirchner, Loew u. Schröter, Bd. II, 1. Stuttgart, Ulmer ; Noelle, Vergleichende Anatomie und Morphologie der Koniferenwurzeln mit Rücksicht auf die Systematik. Bot. Ztg., 1910. V. Alten, Wurzelstudien, Bot. Ztg. 1909.

them of their last covering of water. It appears therefore that the root system of the beech is designed for intensive water economy not for extensive working like the root system of the ash, which consists merely of moderately thick root branches which extend far but are poorly provided with rootlets.[1] (Fig. 122.) Rootlets are developed in especial abundance in the humus of the upper layers of the soil and among the decaying leaves. The thickness and method of branching of the outermost roots are characteristic for whole families of plants. The other Cupuliferae, the Moraceae, and many Leguminosae behave like the beech, other Oleaceae, Caprifoliaceae and Cornaceae like the ash.

At my request Herr Geheimer Forstrat Dr. Vater has very kindly placed at my disposal the following results of the investigations carried out by himself and his co-workers, and by Herr Forstmeister Graser, on the root-development of the pine, spruce and beech and the variation of each according to age and locality, and also the Figs. 113–121.[2] The conclusions are based upon exact investigations of the locality, determinations of age, description of the whole tree and especially on observations and photographs of the natural position of the roots in the soil, which in older trees can only be obtained by scraping away bulky soil coverings and carefully laying bare the root system. The investigations extended only to mineral soils with a horizontal or only slightly inclined surface, and also in general only to dominant and co-dominant trees. The branches of a number of roots were investigated by counting the annual rings in several places after the manner of stem analyses. During the life of the tree, parts of the roots, more or less large, die off and completely disappear by decomposition, their former places of attachment covering themselves with rind. The newly-formed parts of the root may possess a different form to the dead ones. This is least striking with the pine, more so with the spruce and very much so with the beech. The power of trees to alter their root form in the course of time is also the reason why planted trees generally possess normal root systems in later years even when the roots, immediately after planting, were to a great extent bundled together or otherwise deformed. The lateral roots lying nearest the surface of the soil reach by far the greatest length. The extent of their spread, *i.e.* the horizontal distance of their extremities from the centre of the root-stock, is greatly influenced by the closeness of the stand; it may be double as great at

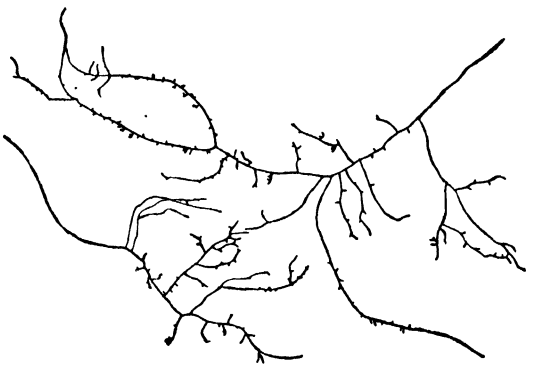


FIG. 112.—Long roots of Beech clothed with short roots, from the humus of the forest soil. About half natural size.

[1] *See* note 5, p. 273.

[2] A detailed account will follow in the Tharander forstl. Jahrbuch.

the margins of woods and in gaps, as in the close crop. On the other hand, in dense woods, the nature of the soil was not found to have any great influence on the spread of the lateral roots. The idea that a soil of poor fertility leads to a more extensive rooting does not appear to be absolutely correct. Contrary to a widespread idea, no direct influence of the depth of the roots on the height of the tree could be proved. The height of the tree is determined by the total possibilities of nutrition. The roots of a tree usually incline away from each other, though the opposite also occurs for reasons unexplained. In no case was penetration of the roots into subsoil water observed.[1]



FIG. 113.—Old Pine with tap-root in deep sandy soil. After Vater.

In the pine, in contradistinction to the spruce and beech, the lateral roots attain their greatest amount of spread in youth.[2] A 14-year-old pine in a dense crop had a spread of 6.47 metres. Only in 7 cases did the root-spread of 38 pines, 14-year-old and upwards, exceed 6.47 metres. The greatest measurement was 8.75 metres (tree 59 years old). The smallest spread, 2.80 metres, was found in an 80-year-old and in an 87-year-old tree. This phenomenon is due to extensive dying off of the ends of the roots and the replacement of the dead parts by lateral roots of higher order. The rooting in depth of the pine takes a different form according as to whether the roots, on the one hand, can penetrate easily and without great resistance, as in sand or soils derived from it, or, on the other hand, find penetration impeded, as by coarse gravel, shale or stones, perhaps also by the tenacity of the soil. In the

[1] *Comp.*, however, Hesselman, H., Über Sauerstoffgehalt des Bodenwassers und dessen Einwirkung auf die Versumpfung des Bodens und das Wachstum des Waldes. Mitteil. der. Schwedischen forstlichen Versuchsanstalt. 7. Heft, 1910, p. 91.

[2] Also, according to Liese (Beitr. z. Kenntnis d. Wurzelsystems der Kiefer. Habilitationsschrift, Berlin, 1926, enlarged reprint from Zeitschr. f. Forst- u. Jagdwesen, 1926, H. 3), already in the first two decades, the length of the lateral roots of the pine very closely approaches the ultimate length. The main lateral roots are all traced back to the branchings of the main root in the first year.

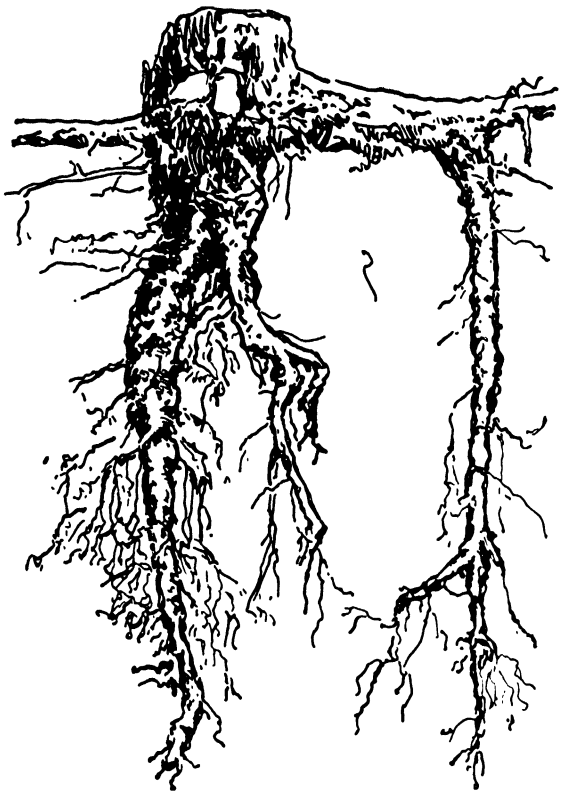


FIG. 114.—86-year-old Pine in sandy soil, with tap-root and sinker roots. After Vater.

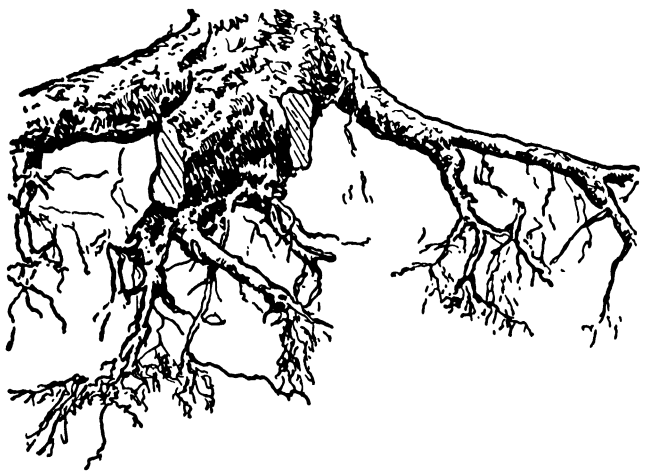


FIG. 115.—Old Pine in gravelly, stony soil. Irregular roots up to about one metre deep. After Vater.

former case appears the well - known tap - root (Fig. 113). Besides the tap-root, several other roots, which may be termed sinkers or sinker roots, go vertically downwards from the lateral roots, at a greater or less distance from the root stock (Fig. 114). The deepest tap-root, deeper than 4.80 metres, at which depth excavation had to be stopped, was found in sand. A 66-year-old pine had a tap-root 2 metres long, whilst the deepest sinker roots reached 4.6 metres. In dry, pure sand the depth of rooting did not generally exceed 2 metres. On felspar of the Elbsandstone region pine roots reached down to a depth of 7 metres. In gravelly or shaly soils the original tap-root is quickly lost and more or less numerous roots from the uppermost layer of lateral roots descend irregularly, mostly to a depth of less than 1 metre (Fig. 115). In the neighbourhood of subsoil water a brushlike root system was observed (Fig. 116).[1]

As a seedling the spruce possesses a tap-root which, however, disappears

[1] *Comp.* also, for the pine, Tolsky, Beitr. zur. Kenntnis des Wurzelsystems von *Pinus silvestris*. Petersburg, 1907, and Aaltonen, Über die Ausbildung und den Reichtum der Baumwurzeln in den Heidewäldern Lapplands, Helsinki, 1920.

later. In spruces over 30 years of age, the spread of the roots varied from 2½–5½ metres, increasing irregularly with age. The maximum was found in an 81-year-old spruce with a spread of 9.33 metres. On wet or at least moist soils, shallow-running lateral roots are found exclusively, which possess none but accessory roots which descend only a few centimetres (Fig. 117). In windfalls, spruces of this kind have the well-known root-plates. The lateral roots are also in these cases covered with rind on the under side like the stem. On fresh, gravelly, weathered soil, on the other hand, the descending accessory roots are much longer and stronger, so that 30-year-old spruces acquire a root system of considerable depth (generally 1–1½ metres to 2.10 metres observed) (Figs. 118 and 119).

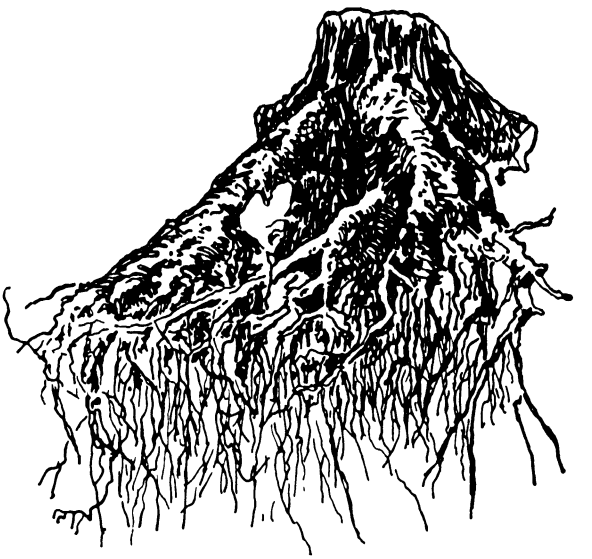


FIG. 116.—Brushlike root system of an old Pine above the subsoil water. (After Vater.)

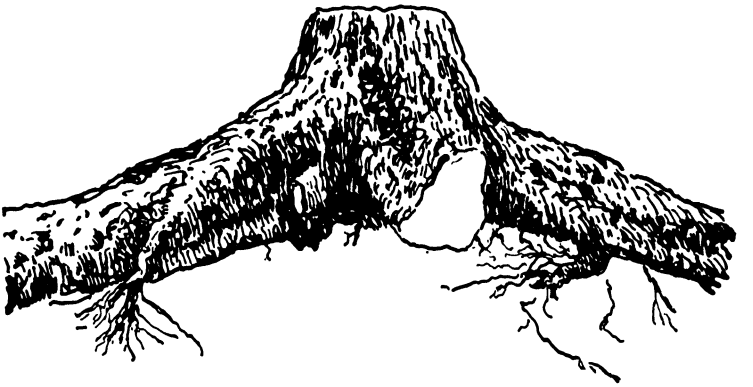


FIG. 117.—Shallow roots of Spruce over wet, heavy soil. After Vater.

Where root growth is not hindered, the beech has, in the first years of its life, a very marked tap-root (Fig. 120 *a* and *b*). (Representations of young beeches in the literature have also a tap-root.[1]) According

[1] Büsgen, Studien über die Wurzelsysteme einiger dikotyler Holzpflanzen. Flora, 95, Ergänzungsband zum Jahrgang 1905, p. 58 (beech two years old). Metzger, C., Dänische Geräte zur Bodenbearbeitung in Buchensamenschlägen. Berlin, 1908, p. 28 (beeches 1, 4 and 10 years old). Garthe, Praktisches Mittel zur Erhaltung der von den Mäusen geschälten Buchenpflanzen. Zeitschr. f. Forst- u. Jagdwesen, 1892, 24, p. 335 (beech 20–30 years old). Zielaskowsky, Standortsuntersuchungen. Zeitschr. Forst- u. Jagdwesen, 1898, 33, p. 139 to p. 145 (beech 60 years old).

to Graser's account, the tap-root is retained up to the 45–60th year in the gneiss soils of Zoblitz Revier, but then disappears (*e.g.* Fig. 120 *c* for sandy soil). During this process and after it, a mass of side roots



FIG. 118.—Old Spruce with deep-going root fibres on sedentary soil. After Vater.

develops which spring from near the root knot and penetrate obliquely into the soil. In this way the tap-root transforms itself into a heart-root (Figs. 120 *d* and 121). The place in the root knot where the tap-root previously originated is covered by rind. The greatest breadth of spread of a beech, which stood on fresh, shaly, stony ground, was found to be 6.20 metres, the greatest depth 1.23 metres. The latter was surpassed by a beech standing on moist, fine-grained diluvial formations with 1.80 metres.



FIG. 119.—Deep roots of the Spruce (81 years old) on sedentary soil. After Vater.

The very widespread idea that the spruce is shallow- the beech deeper- and the pine the deepest-rooted is not generally true. Of the trees chosen at random for investigation, especially in fresh, shaly, stony soil, the older pines and beeches were as a rule rooted about 1 metre deep, the older spruces about 1½ metres. Thus far, Vater.

G. Krauss [1] points out that in considering tree roots, not only the

[1] Forstwiss. Zentralbl. 1926, p. 469 ff.

spread of the root system but also the permeation by roots of the *intervening areas* must be included, as, in the older crops, these make up a great part of the total area and are the source of the differences between individual species and localities which have most effect in water- and food-economy.

No regularity in the arrangement of the accessory roots is to be found by casual observation. Only when they are sought at the youngest root tips is it recognised that they emerge from the mother root in two, three, four or more longitudinal rows. This is associated with the position of the vascular groups in the interior of the mother root, as the accessory roots are formed in their immediate neighbourhood. Later, when the ring of thickening has developed, the appearance of new lateral roots (adventitious roots) is governed by external circumstances and the position of the medullary rays. Their angle of divergence generally approaches a right angle. For the rest, gravity at first exerts an influence on the direction of the roots. Just as in the shoot system it is this force that causes the main root—growing, it is true, in the opposite direction—to place itself in the vertical and retains the accessory roots in an oblique position. Its influence falls off in the later root generations so that they can follow unhindered any other directive agencies. Among such is above all to be mentioned the presence of moisture to one side of the root. This causes a bending of the latter towards the source of moisture



FIG. 120.—Development of the Beech root. *a* (3 years) and *b* (27 years) tap-root. *c* (53 years) the tap-root is suppressed. *d* (80 years) formation of heartroot. After Vater.

which even the main roots, so sensitive to gravity, do not escape. If seed is germinated on the underside of a wet clay plate or in a wet sponge the whole of the rootlets apply themselves to these wet bodies instead of growing vertically downwards. In many plants the growing root turns away from the light, in others it does not. Further, it is observed that roots to which solutions of mineral substances are supplied from one side, turn towards or away from that side according to the nature and strength of the solutions (chemotropism). The roots appear in this way to seek out many substances and to avoid others, and it is certain that the faculty of carrying out bending movements as the result of such influences often appears of advantage to the roots; whether there is actually present an adaptation to particular chemical stimuli or whether the bending movements owe their origin to other causes, has not yet been made out.[1] The power of root tips in running water to carry out bending movements which present their concavity towards the side from which it comes and which are perhaps not independent of the composition of the liquid, may belong to the same category.[2] When gases [3] such as oxygen, carbonic acid, hydrogen, and also the vapours of alcohol, ether and ammonia reach the roots from one side, the roots first bend towards the source of the gas, though they bend away again afterwards, *e.g.* from carbonic acid.



FIG. 121.—70-year-old Beech with fully developed heartroot. The side roots have been removed. After Vater.

All these bending movements belong to the stimulation phenomena more fully illustrated in Chap. I, 11–13. In most of them it is obvious that they assist in bringing the root into the conditions most favorable for its existence and it can be easily understood how the many-sided sensitiveness of growing root-tips might remind Darwin of the functions of our brain.

The comparison cannot be carried through, but it has at least been proved that the greatest sensitiveness to the stimulus of gravity actually has its seat in the root-tip, whether or not it be due to the mobility of starch grains in the interior of the root cap (*see* below), as Haberlandt [4] will have it. Some of the stimuli exercised by

[1] Porodko, Über den Chemotropismus der Pflanzenwurzeln. Jahrb. f. wiss. Bot. 49, 1911, p. 307.

[2] Hryniewiecki, Schriften d. Naturforscherges. b. d. Univers. Jurjeff, XIX, 1908.

[3] Literature in Jost, Vorlesungen über Pflanzenphysiologie, 3. Aufl., p. 642.

[4] Physiologische Pflanzenanatomie, 4. Aufl. Leipzig, 1909, Engelmann.

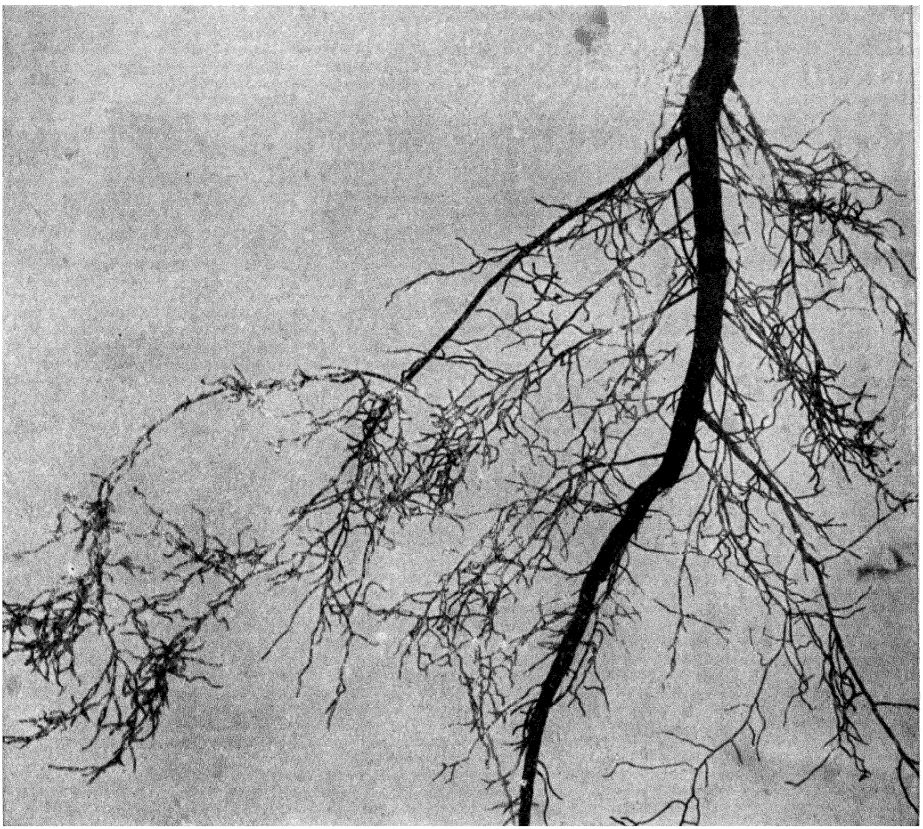


FIG. 122.—Root system of a 2-year-old Alder. Long roots and short roots not sharply differentiated. Natural size.

[*To face p.* 280.

different chemical solutions and the stimulus of galvanic currents are also taken up by the root-tip.[1]

Noll [2] observed that the lateral roots strove to keep to the direction of the radius of their mother root and thus to remain always as far as possible from others in the same horizontal plane. When diverted, the growing tip always turns back again to the corresponding direction, especially in accessory roots of higher order in which the directive action of gravity is no longer so disturbing. The phenomenon pointed out by Noll, that when roots are bent spirally or in one plane, accessory roots appear mainly on the convex, outer side, which is probably connected with the tension of the tissues at the place of bending, answers to the same requirement for the separation of the individual roots from one another.

2. Functions of the Root System and Structure of the Root Tip.—Of the two functions in the life of the tree which are assigned to the root, the first—the firm anchoring of the tree in the soil—is performed by the whole of the root system. The second function, which alone will be discussed here—the taking up of water and mineral food materials—is assigned exclusively to the root-tips, which are provided with a remarkable osmotic apparatus for the purpose.

The small quantities of water which the tree takes in through the leaves, and in winter through the bare twigs and buds, may be of consequence at times, but in general recede in importance before that which must be provided through the roots. The most important source of water for the tree is thus the moisture found between the solid particles of the soil. This is composed of easily and difficultly moved water particles. To the former belongs the water which drops from a sample of soil when it is squeezed, to the latter, the water which may still be present even in an apparently dry soil, held fast by the soil by virtue of the surface action of its constituent parts or in loose chemical combination. Part of this water, hardly detectable by us, the plant is still able to withdraw from the soil; a final residue, which, according to Sachs, may amount to 1, 5, 8, and even 12.3 per cent., is no longer available even for it. The mineral content of the soil-water seldom amounts to more than one thousandth, but the roots have the power of drawing to themselves (*see* below) the store of nutrients distributed in very great quantities of water and even to absorb food materials from the solid constituents of the soil. This last may be done with the aid of carbonic acid [3] which forms a saturated solution in the mucilagenous coating of the root-hairs. In this matter the micro-organisms of the soil, bacteria in arable soils and fungi also in forest soils, are of service to the plant roots in the decomposition of difficultly soluble mineral substances, by reason of the great amount of carbonic acid

[1] Cholodny, Abstract of the Russian work *see*: Bot. Zentralbl., Bd. 110, 1909, p. 131 (Chemotropism); Rothert, Zeitscher. f. allgem. Physiologie, VII, 1907, p. 142 (Galvanotropism); Porodko, *loc. cit.*, p. 368.

[2] Eine neue Eigenschaft des Wurzelsystems (Exotropy). Bot. Zentralbl., LX, Jahrg. XV; Nordhausen, Jahrb. f. wiss. Bot., 44, 1907, p. 557.

[3] Aberson, Jahrb. f. wiss. Bot., 42, 1906, p. 372. *Ibid.* 47, 1909. Stoklasa und Ernest, *ibid.* 46, 1908.

liberated by them in respiration.[1] Other acids also, such as formic, oxalic and lactic acids, have been observed outside the root-hairs. Certainly their appearance is often the consequence of a poor supply of oxygen or of an injury to the root-hairs; Schulow [2] has, however, observed the presence of malic acid and sugar on the roots of maize and peas which he raised free from bacteria, and Pfeiffer and Blanck,[3] from the great utilisation of phosphorite, concluded that the plant did not work with carbonic acid alone. In very dilute nutrient solutions the root generally tends to excrete organic and mineral substances.[4] If the solutions are made stronger the absorption of substances by the roots increases at first more rapidly than the concentration, then becomes proportional to it and finally independent of it. The cell wall of the root-hairs, moreover, possesses the faculty of liberating acid from soil minerals by absorbing colloidally the basic constituent from soil salts.[5] Finally, substances set free by the regular dying off of the cells of the root-cap (*see* p. 292) and the shortlived root-hairs, assist decomposition of the soil. It must be presumed that there are differences in the root secretions according to the species of plant and the soil conditions.[6] Leguminosae, for example, decompose the soil more strongly than grass roots.[7] The acid reactions given by the excretions of beech and oak are marked, those of pine, spruce and silver fir would lie below the limit of sensitiveness of litmus paper.

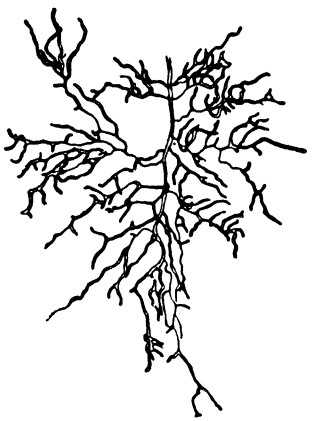


FIG. 123.—From the root system of a Maple. Slightly reduced. The osmotic apparatus at the root-tips is thicker than the older parts of the root on which it is situated. After Büsgen in Flora.

The working efficiency of a root increases with the number of its active tips. The more such tips a tree possesses the better will it be able to utilise the soil. Thus Nobbe [8] ascribed the so-called non-exacting character of the pine, as compared with the silver fir and spruce, to the advantage it enjoys through its better developed root system. In youth the pine possesses twenty-four times as many root fibres and eight times as large an absorbing surface as the silver fir. It surpasses the spruce in the same properties twelve and five times respectively.

[1] Stoklasa, Über Resorbtion d. Ionen durch d. Wurzelsyst. der Pflanzen aus dem Boden. Ber. Dtsch. Bot. Ges. 42, p. 183, 1924.

[2] Ber. Dtsch. Bot. Ges., Bd. 31, 1913.

[3] Landwirtschaftl. Versuchsstationen, 77, 1912, p. 217.

[4] Ponget et Chouchak, Compt. rend., Paris, 1912, p. 1709.

[5] Baumann u. Gully, 1910; Wieler, Ber. Dtsch. Bot. Ges., Bd. 30, 1912. The Acidity of Cell-membranes; Hansteen Cranner, *see* below, p. 285.

[6] Raciborski, 1902. Bot. Zentralbl., Bd. 90, p. 122: Leptomin in the root secretion; Schreiner and Reed: Oxidising power of the roots. Bot. Gaz., 1909; Prianischnikow, Bot. Zentralbl. Bd. 96, 1904, p. 349; Mazé, Ann. de l'Institut Pasteur, XXV, 1911, p. 705; Pfeiffer u. Blanck, 1912, Landwirtsch. Verschsstationen, 77, p. 217: Slight diastase secretion in maize roots; Wohlleb, Inaug.-Diss., Leipzig, 1911; Ponget et Chouchak, *loc. cit.*

[7] Kuntze, G., Jahrb. f. wiss. Bot., Bd. 42, 1906, p. 372.

[8] Beobachtungen und Versuche über die Wurzelbildung der Nadelhölzer. Landwirtschaftl. Versuchsstationen, 18, 1875, p. 279.

The pine, therefore, succeeds in places where the silver fir and spruce would simply starve, because it is better able to utilise the sparsely distributed food materials and water from a large body of soil. In Nobbe's one-year-old experimental plants, the area of the underground organs exceeded that of the aboveground ones, in the pine by about five times, in the spruce about three times, in the silver fir only twice, whilst in all three genera the root mass formed only about half of the total material produced. The total length of all root fibres amounted to 1 metre in the silver fir, 2 metres in the spruce and to 12 metres in the

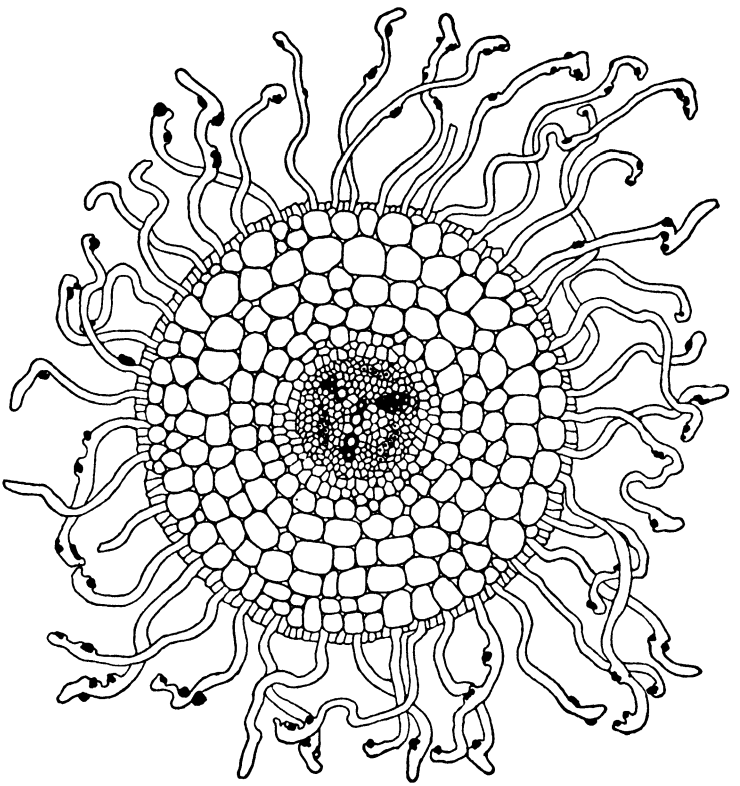


FIG. 124.—Cross section of a root-tip of *Robinia pseudacacia*.

pine. In a one-year-old beech I found 136 tips on a piece of root not quite 3 centimetres long; in a Norway maple (Fig. 123) and lime, on root branches 6 centimetres long, 60 and 46, respectively. The rapid increase in the activity of the root system from the first to the second year of a young plant is shown by the total length of roots being as follows:

	At the end of 1 year.	At the end of 2 years.
In a birch . . .	153 cm.	941 cm.
In an alder . . .	184 cm.	2,000 cm.

The osmotic apparatus of the root-tips is recognisable in the forest of **hairs** which clothes their surface, sometimes beginning close behind the extremity of the root, sometimes beginning further back. These

hairs are mostly shortlived, and may shrivel up and die off soon after they appear. Active hairs are then only to be seen on a short length of the root. In other cases, however, hairs cover whole branch systems for a stretch of some centimetres, as in the roots of the Austrian pine and the maple. These hairs are generally outgrowths of the cells of the epidermis. Only in conifers do they originate, when they are developed at all, from cells of the second or third layer from the surface of the rind.[1] They are tubes a few hundredths of a millimetre wide and of varying length, up to several millimetres, which are outgrowths of the cells of the epidermis of the root. In dry habitats they are more strongly developed than in moist or wet ones, where they may even be absent altogether. High temperatures and moisture are prejudicial to the formation of root-hairs [2]; shortage of oxygen and hindrances to the growth of the root tips are accompanied by the increased formation of root-hairs. The task of the root-hairs consists in enlarging the surface of the root tips and by penetrating between the soil particles, multiplying infinitely their contact with the latter. The contact becomes such a close one that even a powerful jet of water is unable to wash away the soil particles adhering to the hairs. In addition, a tactile and nutritive stimulus proceeding from the soil particles influences the growth of the hairs in a special way so that their ends press against the particles as tight as wax with the formation of widenings and claw-like curvings (*see* Fig. 125). The cell membrane of the hair has properties which differ from those of ordinary cellulose walls. It does not give the cellulose reaction with iodine and sulphuric acid, but is easily permeable by water and aqueous solutions. The cell content of the root-hair consists of a protoplasmic body covering the inner side of the solid membrane as a thin layer, with a large vacuole enclosed in it.

In this cell content is to be sought the seat of the forces which effect the absorption of the soil liquid. They are found in the osmotic properties of the protoplasm and the substances dissolved in the cell sap. The absorptive power of the root cells rises in the same measure as water is withdrawn from the root cells by evaporation in the above-ground parts (*see* Chap. II, 1) and the entrance of soil water follows, if such is present in sufficient quantity. If, however, soil water is scarce, the root cells lose at last so much water that their cell wall relaxes and the total absorptive power corresponding to the osmotic value of the cell sap and the swelling energy of the protoplasm may come into play which, to a certain degree, tears away also the water held firmly to the soil particles by capillarity and adhesion. The epidermis of the root cells is so far permeable to dissolved substances that they take up with the water of the very dilute soil solution, mineral substances, and also certain organic substances. In doing this the roots can, within certain limits, make a choice among the substances offered, apparently according to their requirements: a phenomenon which is still not fully explained but may have to do with changing permeability of the plasma

[1] Noelle, Stud. z. vgl. Anatomie und Morphologie d. Koniferenwurzeln mit Rücks. auf d. Systematik. Bot. Ztg., 1910; v. Tubeuf, Die Haarbildungen der Koniferen. Forstl. naturw. Zeitschr., München, 1896.

[2] Hesse, Inaug.-Diss., Jena, 1904; Snow, Bot. Gaz., XL, 1905.

and also of the cell walls.[1] The absorption of substances is, however, in a large measure determined by what is offered to the root. When the supply of any particular manurial substance is very plentiful a luxury consumption may take place and when there is shortage of a individual substances their place may be taken to a certain extent by others.

The surface layer of the root tip which bears the root-hairs, is bounded on the inner side by a many layered sheath of large roundish cells (Figs. 124 and 126) which must also be included in the osmotic apparatus. Like the root-hairs, they possess only a thin protoplasmic wall lining and a large vacuole filled with a water-clear liquid. The outermost and innermost of these cells join on to each other without gaps, whilst the middle layers are traversed by narrow air passages in the direction of the length of the root which permit of the exchange of gases associated with respiration. The whole sheath of cells bears the name of **primary root cortex,** and is destined to serve as the first place of reception for the fluid absorbed by the root-hairs.



FIG. 125.—Tip of a root-hair concrescent with soil particles.

It has been sought to explain the taking up by the roots by preference, within certain limits, of just those substances which the plant requires and consumes, by an especially steep concentration and diffusion gradient being set up through the consumption of a substance, that is to say, by its separation out of the solution of the plant juices. Under this assumption the difficulty arises in the case of the tree, that the nutritive salts are mostly first consumed in the leaves and thus at such a distance from the soil that there can be no question of an effective diffusion gradient. It is necessary to take into consideration that the composition of the descending sap-stream, which extends down into the root tips from the leaves, depends on the quantity of root nutrients supplied to the leaves and worked up in them. In this manner, for example, a superfluity of a substance not consumed in the leaves will, in a roundabout way through the circulation of the sap, again appear at the root tip and stand in the way of further absorption of the same substance. In this way, in fact, an absorption of materials graded according to requirements might be attained by purely physical means.

Thoroughly saturated with water, the cell walls permit of its passage from cell to cell without difficulty. Only when they adjoin air passages are they covered with a material less permeable to water, as in other similar cases in the plant body, so that water is not squeezed out into the passage. The cortex of the root represents a living reservoir for the liquid taken up by the root-hairs, in which larger quantities are accommodated than in the narrow cavities of the epidermal cells. The water channels leading upwards, which draw upon the

[1] Hansteen Cranner, Über das Verhalten der Kulturpflanzen zu den Bodensalzen. III. Beitr. z. Biochemie u. Physiologie der Zellwand lebender Zellen. Jahrb. f. wiss. Bot., 53, 1914. Also 47, 1910.

reservoir, become in this way to a certain extent independent of the irregularities to which the activity of the hairs is exposed.

The innermost layer of the root cortex (**endodermis** or protective sheath) (Fig. 126) has a special character. It consists of parallelopiped-shaped cells somewhat elongated in the direction of the length of the root and often having their inner walls thickened, which are also so closely bound together that air passages can never appear between them. The access of gases to the central parts of the roots from the intercellular spaces of the root cortex is thus prevented.[1]

The passage of dissolved substances from the root cortex into the conducting channels of the central cylinder and thence to the other parts of the plant is also regulated by the endodermis. The plasma of the endodermis allows only certain substances through and is more or less impermeable for others as also for organic substances. Thus the access of undesired substances from the soil into the conducting tissues and the exit of nutrient substances from the central cylinder is precluded. According to A. Meyer and Ziegenspeck [2] a similar function is performed by the Casparian Strips, a lignified thickening of the radial walls of the endodermis which allows only such substances through as can pass the plasma of the endodermal cells, and thus prevents the access to the interior of dissolved substances by going round the plasma membrane through the radial walls. At some distance behind the root tip, the endodermis becomes suberised and often much thickened at the places opposite the bast, generally only on the bast side, whilst at the points of the xylem star, unthickened passage cells are left. This hinders or prevents the entrance of water into the leptome of the conducting channels in those parts of the root further back, where it serves not only for water absorption but also for the transmission of material to the growing tip. According to Münch, this is important for the undisturbed conducting of assimilates to the growing root tip. (*Compare* XII, 2.)

The great impermeability of the endodermis for certain substances is connected with its having, as A. Meyer [3] assumes, apparently no plasmodesms in the tangential walls through which dissolved substances could reach the central cylinder without passing through the plasma membrane.

The layer of the root cortex lying under the epidermis [4] (Exodermis) also consists of cells closely joined to each other, whose membranes exhibit suberisation in parts. The innermost portion of the young root, enclosed by the endodermis, is called the **central cylinder.** Its ground tissue consists of delicate-walled parenchyma cells between which are found the sieve tubes and vessels which very early traverse

[1] Strasburger, Leitungsbahnen, 407.

[2] Ziegenspeck, H., Über die Rolle des Casparyschen Streifens . . . , Ber. D. Bot. Ges. 39, p. 302, 1921.

[3] Rumpf, G., Bibliotheca botanica, 1904, 62. H.

[4] For more details of this *see* Mylius, Das Polyderm. Eine entwicklungsgeschichtliche Untersuchung über die physiologischen Scheiden, Polyderm, Periderm und Epidermis. Inaug.-Diss., Marburg, 1912 (Bibliotheca botanica); Alterations in the anatomical structure of the root during the winter *see* Plaut, Jahrb. f. wiss. Bot., Bd. 48, 1910, p. 143; Kroemer, Wurzelhaut, Hypodermis und Epidermis der Angiospermenwurzel. Stuttgart, 1903 (Bibliotheca botanica, Bd. 59); Noelle, Koniferenwurzeln. Bot. Ztg., LXVIII, 1910.

the young root longitudinally.[1] The arrangement of the vessels in radial bands (Figs. 124, 126 and Chap. III, 4) gives them the advantage of close contact with the root cortex from which the liquid they have to conduct upwards flows to them. The number of bands of vessels varies with the species of plant and the size of the root. Thus in lime roots 4 or 5 are found, in the roots of the Norway maple, spruce, larch and silver fir 2, in the wild plum 4, in the robinia 3, in the beech 5 or less, in the birch 3, in the black elder (*Sambucus nigra*) 5, etc. In the juniper and its allies the short roots have generally three bands of

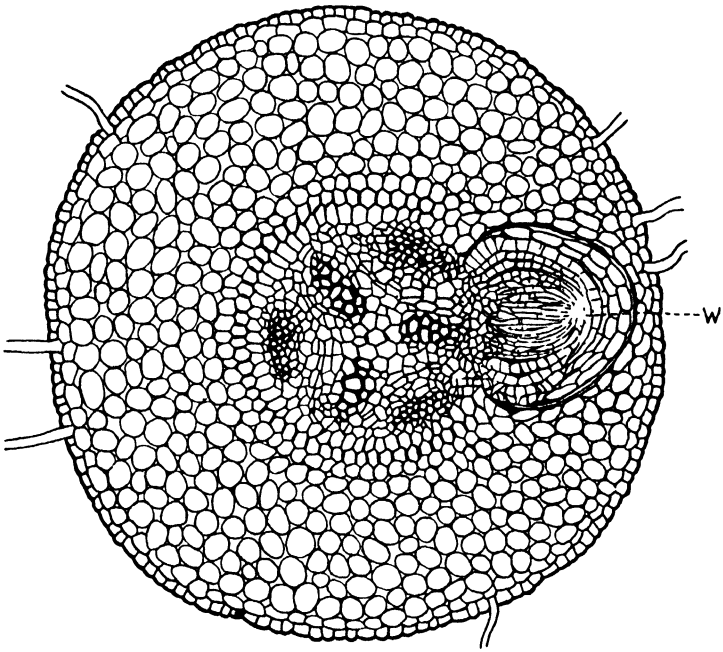


FIG. 126.—Cross section of the root-tip of the Pea with the rudiment of a lateral root. The endodermis of the mother root marked by thicker radial walls. Highly magnified. *W* root cap of lateral root. Under the endodermis the thin-walled rhizogenous layer (*s.* below 4.). H. W.

vessels ; in the long roots two bands of vessels are present at first, two more being added later (Noelle). The pine root has at the beginning generally 3, more seldom 4 bands of vessels, later, in the deeper layers, only 2.[2] In the robinia, the bands of vessels extend to the centre of the root, finishing off with a particularly large vessel, whilst in the ash something of a root-pith is present.

3. Bleeding.—The excretion of liquid from the living cells of the central cylinder into the vessels causes the latter to be filled with watery solutions during the times when the consumption of water is small. This occurs especially in the spring when the roots have already begun their work but the evaporation of water through the leaves has

[1] Plant, Morphol. u. mikroskop. Merkmale u. Periodizität d. Wurzel sowie v. d. Verbreitung d. Metakutisierung d. Wurzelhäute. Festschrift Gehenheim, 1918.

[2] Liese, Zeitschr. f. Forst.- u. Jagdwesen, 1926.

not yet reached great dimensions. If the vessels are then opened by boring or by cutting off branches or stems, the sap exudes from them—a phenomenon which is widely known under the name of "**Bleeding.**" Several litres of sap may exude from a bore hole in the stem of a birch in the course of a day, and if a suitably bent glass tube is inserted in the tree, it can be seen that the excretion of the liquid still continues under a certain counter pressure. The sap flowing from a stem was able to support columns of mercury 100, 300, 930 (old birch) and even over 1,000 millimetres high.

In the warm, moist atmosphere of the tropics [1] exudation pressures of 8 atmospheres and bleeding when in full foliage have been observed. The exudation pressure appears first at the base of the stem and then rises higher in the stem, that at the base becoming constantly greater. Miyoshi [2] found in a species of *Cornus*, the pressure almost constant in the morning hours up to 7 o'clock. As soon as the crown of the tree is shone upon by the sun and the wind rises, oscillations set in, which, in American birches, followed an alternation between sunshine and shade with surprising rapidity.[3]

Variations in pressure of 2.5 centimetres of mercury in one minute have been observed in connection with a variation in temperature of less than 1 degree C. on the black-bulb thermometer in the sun. When night comes on the pressure again becomes constant and then rises slowly throughout the night until morning. Watering causes an immediate rise of the pressure. In the maple (*dasycarpum ?*) the pressure may become visible first in the branches; but in whatever part of the tree it first appears it always tends to rise in the morning hours and to fall in the afternoon.

The exudation saps consist of aqueous solutions of carbohydrates as well as protein substances and inorganic salts. Their composition alters during bleeding and varies with the height of the bore hole in the stem. In the birch, for example, Schroeder [4] found that the lower down the stem the bore hole was placed, the richer was the exuded sap in sugar, whilst in a Norway maple the opposite condition obtained. The sap of a birch stem tapped immediately above the ground contained 0.69–1.40 per cent. of sugar, that of a Norway maple tapped in the same way 1.76–3.06 per cent., under other conditions even 3.57 per cent.; thus as much as the sap of the American Sugar Maple, which according to Clark contains 3.57 per cent. of sugar, but, according to a statement in Tschirch's "Applied Plant Anatomy," 8 per cent.[5] (?). One litre

[1] Figdor, Sitzungsber. d. Akad. d. Wiss. Wien, CVII; Molisch, Ann. Buitenzorg. II, Suppl.; the same, Bot. Ztg., LX, 1902, p. 45.

[2] Bot. Zentralbl., 83, 1900, p. 347.

[3] Merwin and Lyon, Sap pressure in the birch stem. Bot. Gaz., Vol. XLVIII, Chicago, 1909, p. 442; Chamberlain, Réch. sur la sève ascendente. Original abstract, Bot. Zentralbl., 79, 1899 (Bull. du bot. gén. de l'université de Genève, Vol. II, 1897); Bleeding of the Vine: Meissner, Jahresber. d. Vertr. d. angewandten Bot., III, 1906, p. 22 (Sugar maximum, 0.359 per cent.).

[4] Die Frühjahrsperiode der Birke und des Spitzahorns. Landwirtschaftl. Versuchsstationen, XIV, 1871. *Also*: Pfeffer, Handbuch der Physiologie, I, 1881; Wieler, Das Bluten der Pflanzen in Cohn's biol. Beitr., VI, 1–120. Here and in Strasburger, Bau und Verrichtungen der Leitungsbahnen in den Pflanzen, more details about bleeding.

[5] 1889, I, 122. Recent literature: Handwörterbuch der Naturwissenschaften, X, 544. Article: Wasserversorgung der Pflanzen by Renner.

of birch sap contained 0.0068–0.033 gramme of protein, one litre of maple sap 0.0079–0.0344, there thus being no great difference between them in this respect. Finally the ash content of one litre of sap varied, in the birch between 0.29 and 1.14 gramme, in the Norway maple between 0.93 and 1.32 gramme; the former being richer in lime, the latter, on the other hand, three times as rich in potash as the other tree. Two analyses of the ash of a litre of sap are appended for comparison.

One litre of sap exuded from a bore hole low down in the stem in April contained, according to Schroeder, in the Birch:

Potash.	Soda.	Magnesia.	Lime.	Iron oxide.	Phosphuric acid.	Sulphuric acid.	Chlorine.
0.0848	0.0109	0.0403	0.1527	0.0011	0.0252	0.0104	0.0062 g.
In the Maple:							
0.2708	0.0096	0.0584	0.2404	0.0050	0.0968 g.	Very small quantities or not determined owing to shortage of material	

Finally it should be mentioned that both saps contained malic acid, which in a litre of birch sap amounted to 0.2340–0.4493 gramme.[1]

According to Richter [2] the exuded sap of the birch contains 0–1 per cent., that of the hornbeam, 0.3–0.7 per cent. of invert sugar, that of the maple, 1–2 per cent. of cane sugar. The exudation saps contain in addition colloidal gums and protein substances.

With regard to the utilisation of sugar maple sap it may be mentioned that in 1893 sugar gardens with 2,000–5,000 trees existed in Delaware and Otsego, from which 25–60 hectokilograms of sugar or the corresponding amount of syrup was obtained in favorable years In many old sugar gardens, trees may be found which have been tapped annually for a hundred years. In all about 25,000 tons of maple sugar were obtained.

The exudation sap of 1-year-old plants was investigated by Ulbricht [3] in the Sun Rose (*Helianthus annuus*). Its sap contained 0.8 gramme per litre of organic dry matter and 1.360 gramme of ash. The composition of the latter was as follows:

18.15% potash.	12.50% phosphoric acid.
1.72% soda.	6.99% sulphuric acid.
24.62% lime.	11.58% silica.
0.20% iron oxide.	1.77% chlorine.

One litre of sap gave, in addition, 48 milligrammes ammonium oxide. Ulbricht concluded from his analyses that, even in 1-year-old plants, the exudation sap is not the raw nutrient solution which is taken up from the soil by the roots, and that soil, manuring, and the stage of life of the plant are not without influence on its composition.

Among trees the birch and maple bleed with special freedom and after them the hornbeam and beech. In the robinia, alder, willows, poplars, silver firs and larches Th. Hartig observed at least a marked

[1] Lenz, Ber. d. pharmazeut. Ges. XIX., 1909, p. 332.

[2] Richter, Neue Unters. ü. d. Bluten u. d. Blutungssaft d. Laubh. Mitt. D. dentrol. Ges., 1925, p. 138.

[3] Landwirtschaftl. Versuchsstationen, 1865, Bd. V und 1866, Bd. VII.

wetting of the cut surface, whilst in the pine, spruce, oak, lime and horse chestnut no such phenomenon was detected.

Reinders [1] criticises pressure measurements made with manometers affixed to the tree. Such measurements gave the actual pressure in the wood only during the first few days and the results then become useless owing to the stopping up of the vessels. It should also be noted that the water channels in the wood are only incompletely connected radially and tangentially and that therefore the trains of vessels constitute a number of water channels, to a certain extent independent of one another.

Root pressure only suffices to raise water to a certain height in the stem and to make up in the spring the store of water which has fallen in the summer; it is, however, not able to keep the vessels full of water when consumption by the leaves reaches certain dimensions. This explains the cessation of bleeding in the summer months, during which the vessels even suck in water supplied to them. In variations of pressure consequent on temperature changes, expansion and contraction of the air present in the wood co-operate.[2] The amount of exudation increases with the temperature. It is less dependent on atmospheric humidity (Richter).

In the same class of phenomena as the bleeding of branches and stems, is guttation, the excretion of liquid at the buds, in the hornbeam, black poplar, oak and also less freely in the ash, lime, hazel, birch and maple, and from the fully unfolded leaves of trees (*see* p. 206). According to Strasburger,[3] the water at the buds comes from the scars of the supporting leaves in whose axils the buds in question stand. On the young leaves in the interior of swelling buds drops of water are found which originate from the leaves themselves. All these excretions result from the same cell activity which brings about bleeding and cease as soon as water consumption becomes greater owing to increasing evaporation by the leaves. The power of producing exudation pressure is not the exclusive prerogative of root cells; for cut pieces of twig also bleed at one cut surface, if the other is tightly sealed up, the cortex and if necessary also the wood laid bare, and the twig dipped in water, or if young leafy twigs are placed with their foliage in water.[4]

As regards the mechanics of bleeding, this much is certain: it depends on the osmotic activities of living cells in root and shoot. Something more than this, however, is required for the cell to be in a condition for it, because osmotic pressure alone cannot result in the squeezing of water out of the cell, or in particular in the movement of water in one direction. For this certain conditions must be fulfilled about which several hypotheses have been set up. Pfeffer conceives that the content of the cell exercising exudation pressure may have osmotic power of a different magnitude in opposite parts of its vacuole.

[1] Reinders, Das Manometer in der Saftsteigungsfrage. A. d. bot. Lab. d. Univers. Groningen. Trav. bot. Néerlandais, Vol. X, 1, 1913.

[2] Merwin, Causes of sap pressure variations in the birches. Bot. Gaz., XLVIII, Chicago, 1909, p. 447.

[3] Leitungsbahnen, p. 841.

[4] Pfeffer, Pflanzenphysiologie, 2. Aufl. Bd. 1, 1897, p. 237.

If, for instance, the cell sap in the lower part of a cell has a higher concentration than in the upper part, water flows in below and is pressed out above. Ursprung [1] speaks in such cases of unhomogeneous or polar absorption and claims to have found such polar variations in the endodermis by means of plasmolysis. Nothing can be brought against Pfeffer's theory from a physical standpoint. The difficulty lies in explaining the setting up and maintenance of such concentration differences, for the flow of water in one direction inside the cell works towards the equalisation of the differences. It might, for example, be considered that the endodermal cells often thicken their walls on one side only, to the inside of the shoot, and by a one-sided consumption of dissolved substances set up for some time an unequal concentration of the cell sap. Only very small quantities of water, however, could be set in motion by this. Above all, however, it cannot be proved or even made to appear likely, that the endodermis is supplied with materials from the rind side alone, because there are no transmission channels for organic substances present there. Another hypothesis assumes a one-sided permeability of the plasma membrane, though in this way, not pure water, but only call sap can be pressed out and provision must be made for its renewal by supply from one direction, which is impossible in a simple physical way. Even less satisfactory is Janse's hypothesis, according to which plasma streamings in the medullary rays might move on water under pressure out of one trachea into another, for according to Dixon and Marshall, the rapidity of the plasma streamings is not nearly sufficient for this. The pulsation theory recently advanced by Bose [2] also could not be made acceptable. Pulsations alone do not lead to a movement of water in one direction. Here also polar differences in the cell must be assumed. Pulsations are, therefore, not necessary as an osmotic apparatus works continuously. Moreover, Dixon [3] was not able to confirm Bose's experiments on a re-test.

An attempt is made to avoid the deficiencies of the earlier hypotheses by the sap-stream theory of Münch,[4] more fully detailed in Chap. XII, 2, which applies the unequal concentration of the cell sap, assumed by Pfeffer for the single cell, to the whole symplast (*see* Chap. III, 1). If the dissolved substances in the cambium are converted into wood, and thus made osmotically inactive, water must, according to Pfeffer's theory, here pass out into the xylem. It is replaced by the streaming in of solution out of the sieve tubes, which is pushed in under pressure through the plasmodesms or even through the rest of the plasma if it is permeable to dissolved substances. The solution in the sieve tubes, thus partially emptied, is replaced by an inflow from the storage cells of the cortex, which bring their reserve materials into solution and take up the necessary solvent water from the endodermis. The water expressed into the wood out of the growing cambium is the exudation sap.

It is in accord with this that only such species bleed as exhibit

[1] Ursprung, Jahrb. wiss. Bot., 1926.
[2] Bose, The Physiology of the Ascent of Sap.
[3] Dixon, The Transpiration Stream, London, 1924.
[4] Münch, Dynamik der Saftströmungen. Ber Deutsch. Bot. Ges., 44, 1926, p. 68.

root-growth during the period of maximum bleeding, early spring, and the pressure of the exuded sap rises with the temperature, because the rate of such reactions must increase with the temperature. The bleeding of rootless shoots observed in experiments is explained in a similar way by the excretion of water by growing cells.

It is a presupposition for the correctness of this explanation that the passage of material from cell to cell takes place in such a way that not the dissolved substances in themselves, but whole solutions as such, pass over. There is, however, no doubt of this, even when the plasmodesms are not regarded as the sap channels (*see* Chap. III, 1), but the osmotic penetration of the solute through the whole plasma membrane is assumed, for the plasma membrane and the cell wall are probably everywhere completely permeable to water. When there are pressure differences, therefore, a corresponding quantity of water must always pass over with the solute, held fast as solvent water by the solute and taken along with it.

As the activity of living cells is the cause of bleeding, it is not surprising that stimulation effects are in evidence. Among these is the raising of the pressure and promotion of the exudation of sap from living tissues, by wound stimulus, such as assists in the extraction of palm wine.[1]

The period of functioning of the osmotic apparatus is only a short one; a root hair can hardly last in an efficient condition longer than a year. Whilst the root tip grows forward and new hairs are formed the old ones shrivel up and at the same time the whole root cortex dies, dries up and is finally lost. With this the first stage in the life of the root is closed. After the loss of the osmotic apparatus it is now no longer an organ of absorption but serves only for the transmission upwards of the substances taken in, the fastening of the tree in the soil, and just like the stem of the tree, as a place of storage for building materials formed in excess, for use in cases of necessity and in mast years.

4. The Growth of the Roots in Length and Thickness.—As the seasonal changes only make themselves felt in the depths of the soil slowly and in a moderate degree, the growth of the roots does not show in all species the marked periodicity of that of the above-ground portions of the plant. It may proceed also in winter, in mild weather. When the roots are at rest they are usually covered by a brownish layer of cells from which, in the spring, the growing tip emerges white. Longitudinal growth [2] of the roots and the formation of new roots usually takes place in the spring, the early summer and in the autumn into November, whilst in July and August a slackening or cessation occurs, which is not dependent only on the great consumption of water by the parts above ground. A stoppage of the development of the roots in late summer also occurs in the conifers, which may be afterwards followed by a new period of formation. The time of un-

[1] Molisch, Pflanzenphysiologie, 5. Aufl., Jena, 1922, p. 60 f.

[2] Engler, A., Untersuchungen über das Wurzelwachstum der Holzarten. Mitteil. d. schweizer. Zentralanstalt f. d. forstliche Versuchswesen, Bd. 7, 1903, p. 247–317.

folding of the buds is not dependent on root growth.[1] The growth in length of the roots, like that of the shoot, is effected by the multiplication of cells at the extreme tip—the growing point—and the elongation of the new cells in the region lying immediately behind it.

Just as the growing point of the shoot is protected against drying out and mechanical injury by the young leaves bending together over it, so the leafless root possesses a covering which ensures that the tender conducting tissue of its apex does not come into direct contact with its surroundings. This is the **Root Cap**, a membranous structure which is constantly renewed from within outwards at the extreme point of the root tip in the soil and at the same time disintegrates somewhat further back, giving rise to a mucilagenous mass, which facilitates the sliding forward of the root tip in the soil [2] and is also active in the formation

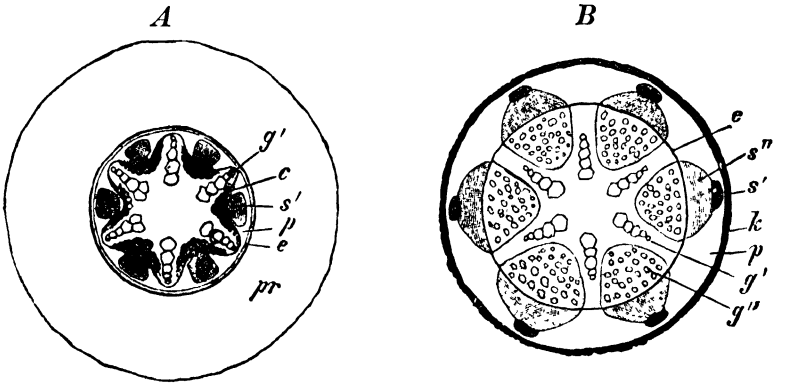


FIG. 127.—Diameter-growth of the root. Transverse sections. *pr* primary cortex, *c* cambium, *g'* the first groups of vessels, *s'* primary phloem, *p* rhizogenous layer, *g''* wood derived from the cambium, *s''* phloem derived from cambium, *e* endodermis, *k* outer rind, formed from the endodermis in place of the primary cortex. *A* at the time when the cambium is originated, *B* after the cambium has been active for some time. After Strasburger.

of rock-dissolving acids by the colloidal adsorption of bases. Similarly, it may be owing to the absence of protective leaves, that lateral roots do not, like lateral shoots, originate in the outer surface of the mother axis but arise in the interior of the mother root (Fig. 126, p. 287). They originate by local cell multiplication in the outermost layer of cells of the central cylinder, which directly adjoins the endodermis, and which for this reason is called the rhizogenous layer, and then break through to the outside, through the root cortex, by pushing off or loosening the cells of the latter. A part of the tissue of the mother root in many cases takes part in the growth of the young root and encloses it during its passage through the cortex as a kind of pocket, which, according to Van Tieghem and Douliot [3] co-operates in the loosening of the cortical cells by secreting a ferment. Lateral roots arise on young roots only at the points of the xylem star; they are therefore, according to Liese, arranged in two, three or four ranks according to the number of points in the star. The growth of the root in thickness begins approximately

[1] Wieler, Forstwissenschaftl. Zentralbl., 16, Jahrg., 1894.

[2] Hunger, Inaug.-Diss., Leiden, 1899.

[3] Recb. comp. sur l'origine des membres endogènes dans les plantes vasculaires. Ann. d sc. nat. 7e. Sér. T. VIII, Paris, 1888.

with the dying off of the osmotic apparatus. It proceeds from a cambium, which, just as in the shoot, runs along the boundary between the primary wood elements and the sieve tube bearing tissue (*see* Chap. III, 4 and Fig. 127).

The root cortex and the epidermis are replaced, as in the shoot, by cork or even a kind of bark, the formation of which proceeds from a cork cambium. That root wood, in spite of this, is usually easily distinguished from stem wood, is due to the pith in the former being scarcely visible or absent all together, the annual rings (Fig. 87) in some places only attaining a very small thickness and to wide and comparatively thin-walled vessels predominating in the root wood which thus appears particularly porous. In poorly lignified roots, tyloses serve to stiffen the vessels but are often absent on other cases.[1] Schütze found the proportion of medullary rays a certain means of distinguishing between root and stem timber in the spruce.

The transition from the vascular bundles of the seedling root to the bundles of the seedling stem may be effected with the disappearance of the primary xylem plates and the division or also the shrinkage of the primary phloem. At the same time new xylem and new phloem appear, in the arrangement characteristic of stem and twigs.[2] External influences also affect the anatomical structure of the roots.[3] Pioneer roots or long roots which open up new regions of the soil, develop the xylem late and only to a small extent; in the feeding roots (absorbing rootlets) the xylem is specially furthered.[4] The nature of the soil may indeed change the development of the root parenchyma; the water content of the soil and the resistance offered by it to the growth of the root being more effective in this respect than its chemical properties. Unfavorable conditions for nutrition may produce a diminution of the vessels and fibres and also of the xylem plates and the pith (Flaskämper). It should be observed, in making investigations in this direction, that parts of the root of different order and of different age do not quite resemble each other. Dry nutrient media produce larger and more numerous vessels as well as greater lignification with smaller diameter (Wildt).

As in stem wood, so in the wood of the root, the formation of conducting and strengthening tissue depends on the requirements.[5] Root wood forms the more wood fibres and the fewer vessels, the more it is required for strengthening, owing to its position with regard to the stem. In the pine root the length of the tracheids also depends on this; it increases with the distance from the stem—in an extreme case, from 1.44 millimetres to 9.9 millimetres at a distance of 10 metres from

[1] V. Alten, Inaug.-Diss., Göttingen, 1908; Losch, Inaug.-Diss., Göttingen, 1913.

[2] Chauveaud, Tissus transitoires, etc. Ann. d. sc. nat., 9e sér., XII, 1.

[3] V. Alten, Wurzelstudien. Bot. Ztg., 1909; Büsgen, Kieselpflanzen auf Kalkboden. Bot. Jahrbücher f. Systematik usw. hrsg. v. Engler, Bd. 50, Suppl. (Festband f. Engler). Leipzig, 1914, Engelmann; Wildt, Experimentelle Erzeugung von Festigungselementen in Wurzeln und deren Ausbildung in verschiedenen Nährböden. Inaug.-Diss. Bonn, 1906; Flaskämper, Abhängigkeit der Gefäss- und Sklerenchymbildung von äusseren Faktoren und über Heterorhizie. Flora, N.F., I, 1910, p. 181.

[4] V. Alten, Inaug.-Diss., Göttingen, 1908; Losch, Inaug.-Diss., Göttingen, 1913.

[5] Liese, Ber. d. D. bot. Ges., Bd. 42, 1924; Generalversammlungsheft, p. (93), also; Ztschr. f. Forst- u. Jagdwesen, 1926. *Comp.* also Omies, Forstl. naturw. Ztschr., 1895.

the stem. That it is external influences which cause the special structure of root wood is shown by Wieler's [1] experiments, in which portions of stem, placed under water or under soil and thus in the life conditions of roots, produced wood of the same open structure as roots.

Tension in a longitudinal direction, according to other experiments,[2] brings about an increase in the mechanical tissues and other alterations, such as an increase in the width of the vessels.[3] The root wood of the robinia, likewise also that of the beech and oak, compared with the stem wood, has, according to Liese, very few wood fibres and, on the other hand, many more vessels and parenchyma cells, which are developed to a larger size. Libriform fibres are formed in roots only in tension wood. The medullary rays do not lie radially but at an acute angle to the surface. The formation of tyloses and heartwood is absent in the root wood of the robinia even in the 20th annual ring, whereas in the stem wood of the same tree seldom more than three annual rings are without tyloses. These peculiarities of the wood are favorable to the functioning of the roots as organs serving almost exclusively for conducting water and for storage, and less on the other hand for strengthening. When roots accidentally emerge from the soil or when above-ground parts of the roots are again enclosed in a covering of moss, anatomical changes are set up which correspond to their new functions.

That the form of section of the root corresponds in some cases with its mechanical requirements was explained in Chap. VI, 3 (Fig. 87).

5. Mycorrhiza.[4]—It has been long known to truffle hunters that the growth of the valuable fungus is closely bound up with the presence of living tree roots. In the year 1880 Rees submitted this remarkable connection between tree and fungus to closer investigation in the Stag Truffle (*Elaphomyces granulatus*) and recognised that the mycelium of the fungus is bound up with the root tips of the pine as closely as a parasite alone can enter into union with its host plant. The roots of the pine appeared not to suffer in the least from the presence of the fungus. They only began, when it settled itself on them, to branch unusually, so that the developing, roundish, fruit bodies of the fungus were ultimately completely embedded in ramifications of the roots as in a nest. His attention having been aroused by these and similar phenomena, Frank,[5] in connection with his researches, undertaken for the benefit of Prussian truffle culture, submitted the already long observed root fungi of our most important forest trees [6] to a more detailed examination. He found that the roots of the beech, oak, birch and their relatives, as well as the conifers and many other woody plants, quite regularly harboured fungus mycelia on their absorbing rootlets. In *Taxus*, *Ulmus* and *Acer* the fungal hyphae penetrated into the cells of the root cortex

[1] Wieler, Tharandter Forstl. Jahrb. 41, 1891, p. 143.

[2] Hibbard, Influence of tension on the formation of mechanical tissue in plants. Bot. Gaz., XLIII, p. 376; Jaccard, Racines hypertendues. Rev. gén. de Bot., XXV bis, 1914, p. 359.

[3] Pohl, F., Vgl. Anatomie von Drainagezöpfen, Land- u. Wasserwurzeln. Beih. z. Bot. Zentralbl. 42, 1, p. 229.

[4] Collection of the whole of the literature up to 1913 by Burgeff in Handwörterbuch d. Naturwiss. Bd. IX (Mycorrhiza). Jena, G. Fischer.

[5] Ber Dtsch. Bot. Ges., III, 1885, p. 128.

[6] Sarauw, Mycorrhiza des arbres forestiers, etc. Rev. mycologique, XXV, 1903, p.157; Jaccard, Journ. for. suisse, 1904.

itself. In the other conifers, the Fagaceae, Corylaceae, Betulaceae and Salicaceae, also, according to Frank the lime, they cover the whole surface of the youngest absorbing rootlets with a compact integument (Figs. 128, 129) and penetrate between the cells as well. The fungal hyphae, closely crowded together, form a kind of net within the cell wall which has received the name **Hartig net,** from that of its first discoverer, Theodore Hartig. In the same root the fungus may penetrate into the interior of the cells of the cortex. Hartig net and hyphae in the interior of the cells have been described in the case of the juniper. The ash and *Sambucus* are as a rule without fungus. In the horse chestnut the fungus lives intercellularly in special dwarf roots and may also be present in the cortical cells of all rootlets. In the mycorrhiza of the spruce and pine, Peklo [1] has recognised, in the interior of the cells of the growing point, and the cells in process of elongation lying behind it, hyphae which later break up and disappear, so that the cells which have been invaded by the fungus and those which have not, can no longer be distinguished. These observations wipe out the difference between **endotrophic** and **ectotrophic** mycorrhiza and favour the idea that the fungus is used by its host for nutrition. In the pine (Fig. 129*a*) the mycorrhiza are short branchlets, dichotomously forked once or several times, and may be aggregated into small tufts or, as in *Pinus cembra* and *P. montana*, into small nodules; other mycorrhiza are likewise short, thick, branchlets but are without the regular forking (Figs. 128*a*, 130). The parts of the root surface which are in association with the fungus bear no root hairs, but hyphae of different forms or bunches of hyphae may radiate from them into the surroundings so that it looks as if the fungus were providing the nutrition of the tree from the soil. Mangin [2] has described these mycelia more in detail. He distinguishes fungal sheaths with a smooth surface, as well as those which possess a loose, flocculent constitution at their surface of contact with the soil, and those which form striking, more or less stiff, or woolly or finally, pear-shaped (*Pinus sylvestris*) hairs in that region. The flocculent mycelia now and then (*Fagus sylvatica, Quercus robur*) show

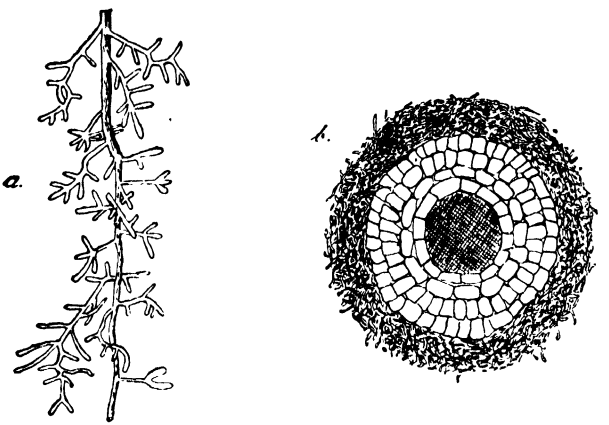


FIG. 128.—*a* Fungus-infected root (Mycorrhiza) with characteristic branching. After Frank. *b* Cross-section of a fungus-infected root. The fungoid sheath almost as thick as the root cortex.

[1] Zeitschrift fur Gärungsphysiologie, II, Heft 4, 1913.

[2] Introduction à l'étude des Mycorrhiza des arbres forestiers. Nouv. archivs du Museum d'hist. nat., V. 2, Paris, 1910.

the clamp connections widespread in the hymenomycetes. In most mycelia the colour is not characteristic, though yellow, rose-red and bluish mycelia are found.

The importance of root inhabiting organisms for the supply of nitrogen to the alder has been proved by cultural experiments extending over many years.[1] This tree produces small nodules on its roots, which on growing for some years, may become masses several centimetres in diameter, composed of short roots much branched (Fig. 132). The nodules are formed by the activity of fibre shaped **bacteria** which penetrate through the root hairs and, apparently utilising atmospheric nitrogen, produce in the cells of the nodules peculiar roundish bodies which are dissolved by the alder and so contribute to its supply of nitrogen. Peklo succeeded in producing nodules by infection on alder plants previously free from them. He called the oft-investigated parasite: *Actinomyces alni*, and placed it among the relatives of the

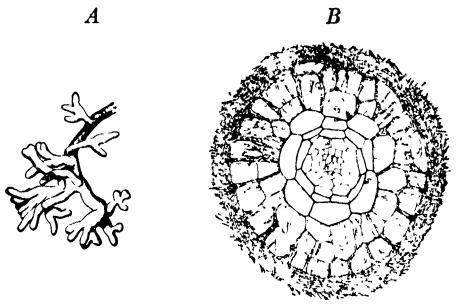


FIG. 129.—Mycorrhiza of *Pinus sylvestris* from the outside and in cross-section. *A* Slightly, *B* highly magnified. After Kirshner, Loew, etc.

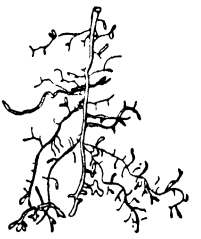


FIG. 130.—Fungus-infected part of a Beech root. Rootlets partly dead. Slightly reduced.

tubercle bacillus. Its behaviour is reminiscent of the bacteria of the root nodules of the leguminosae, whose activity in collecting nitrogen has become the basis of green manuring and soil inoculation. That the single leguminous species of our woods—the robinia or false acacia, imported from North America [2]—has the power of working up atmospheric nitrogen, like the black and white alders and the oleaster (*Eleagnus*), has been proved by cultural experiments. Four seeds of the robinia, sown in quartz sand entirely free from nitrogen, while seedlings were developing from them, increased their original nitrogen content from 0.0024 gramme to 0.092 gramme, between May 1 and September 10; thus not far short of forty times. The dry weight of the plants raised without bacteria increased by 22 times as a result of infection by the proper leguminosa bacterium, their nitrogen content by 150 times; an effect more powerful than that produced by plentiful

[1] Peklo, Die Pflanzlichen Aktinomykosen. Zentralbl. f. Bakteriol.- u. Parasitenkunde, 2· Abtlg., Bd. 27, 1910.

[2] Nobbe, Schmid, Hiltner u. Hotter, Landwirtschaftl. Versuchsstationen, XXXIX, 327; Nobbe, Hiltner u. Schmid, *ibid.*, XLV, 1894, p. 1; XLVI, 1895; Frank, Ber. d. D. bot. Ges., Bd. VIII, 1890, 331; Landwirtschaftl. Jahrb., Bd. XIX, 1890, 523-640; *ibid.*, 1892; Nobbe u. Hiltner, Landwirtschaftl. Versuchsstationen, XLV, 155 (on oleaster, alder and others); LII; Kochs, Jahresbericht über die Lehre von den Gärungsorganismen und Enzymen. Leipzig; Summary by A. Koch in the Handwörterbuch der Naturwissenschaften, Bd. I, 1912, p. 808. Jena, G. Fischer.

manuring with ammonia or nitric acid (Fig. 131). Outside the leguminosae the nodule bacteria fix no considerable quantities of nitrogen. In contact with the protoplasm of the cells of the roots of leguminous plants they undergo a transformation into branched or swollen rods (bacteroids), the protein of which is apparently appropriated by the host plant, whether it be that the bacteroids are thereby completely consumed or are only stimulated by the deprivation to constantly renewed nitrogen fixation. Sub-microscopic organisms (bacteriophagi),[1] which also live in arable soils, may take part in the dissolution of the bacteria in the nodules.

On the question of which fungi are involved in the mycorrhiza of forest trees, certainty has for the first time been provided by the recent comprehensive researches of Melin.[2] Melin raised pines, spruces, larches, birches, etc., in pure culture from sterilised seed in fungus-free, closed glasses, and inoculated them with pure cultures of soil fungi and mycelia which he had obtained in pure cultures from soil fungi and from mycorrhiza after sterilising their surfaces with sublimate. One difficulty consisted in the spores of mycorrhiza fungi not germinating in artificial cultures. The mycelia have to be raised from fragments taken from the interior of the fruiting body with the exclusion of foreign fungal germs. With the greater number of fungi the inoculations resulted in true mycorrhiza soon developing. It appeared that it is mainly the large-fruited hymenomycetes, which only occur in the forest, that are involved in the formation of mycorrhiza, especially the fleshy *Boleti* and many Agaricineae. A number of such fungi are in nature usually or exclusively confined to the root region of particular species of trees; thus *Boletus elegans* and *viscidus* only occur under larches, *Boletus luteus*, *variegatus*, *bovinus* and *granulatus* almost exclusively under pines, *Boletus scaber*, *Lactaria torminosa*, *Tricholoma flavobruneum* and *psammopus* under beeches, *Boletus rufus* under birches and aspen, and *Boletus Boudieri* exclusively under five-needled pines, especially the Weymouth pine. Other polypori and agarics are confined, it is true, to living trees but are less particular as to the species, and others again flourish without trees, in meadows, etc. The obligate forest-soil fungi disappear after the clearing of a wood and only reappear sometime later in the growing crop. The adaptation of such fungi to the tree roots is so close that their spores do not germinate in artificial cultures, their mycelia in such cultural media grow only slowly or generally not at all, and in nature their fruiting bodies, and perhaps also the mycelium, do not develop unconnected with living tree roots.

In addition to most of the above mentioned fungi, Melin obtained mycorrhiza in pure cultures by artificial synthesis with the following species of fungi and trees: on larch, *Amanita muscaria*, *Cortinarius*

[1] d'Herelle, Der Bacteriophage und seine Bedeutung f. d. Immunität. German translation, Braunschweig, 1922.

[2] Melin, E., Unters. ü d. *Larix*-Mykorrhiza, Svensk. Bot. Tidskrift 16, H. 2, 1922; the same, Exper. Unters. ü. d. Birken- und Espenmykorrhizen und ihre Pilzsymbioten, *ibid.*, 17, H. 4, 1923; the same, Zur Kenntnis d. Mykorrhizapilze von *Pinus montana* Mill., Botaniska Notiser, 1924, p. 69; the same, Über den Einfluss d. Wasserstoffionenkonzentration auf. d. Virulenz der Wurzel-pilze v. Kiefer u. Fichte, *ibid.*, 1924, p. 38; the same, Exp. Unters. ü. d. Konstitution u. Ökologie d. Mykorrhiza v. *Pinus silvestris* L. u. *Picea Abies* Karst. in Falck, Mykol. Unters. u. Ber., Kassel, 1923; the same, Unters. über d. Bed. d. Baummykorrhiza, Jena, 1925.

camphoratus; on birch, *Amanita muscaria;* on *Pinus montana: Cortinarius mucosus, Lactarius deliciosus, Russula fragilis, Thicholoma virgatum;* on pine, *Amanita muscaria, Cortinarius mucosus, Lactarius deliciosus, Russula fragilis;* on spruce *Amanita muscaria* and *Lactarius deliciosus.*

It was found as a rule that the mycelium of the ectotrophic fungoid sheath also penetrates into the interior of the cells and is there finally dissolved and digested. The tree mycorrhiza are thus ectendotrophic.

As to the physiological significance of the mycorrhiza, every conceivable hypothesis has been previously put forward by numerous authors. We can now pass them over, since through Melin's work systematic cultural experiments [1] of many years are before us. According to Melin the mycorrhiza fungi only thrive in acid media,[2] best with a p_H of about 4–5, and thus a degree of acidity to be found in acid forest soils. This explains why mycorrhiza are formed most plentifully in acid, raw-humus soils and are feebly developed or not at all in neutral or basic ones. The mycelial growth of the mycorrhiza fungi is greatly promoted by the phosphatides; that is phosphorus- and nitrogen-containing substances which are excreted from the roots. The mycelia, therefore, grow better in contact with the root than without it. They grow badly in humus extract. A supply of glucose favours growth. According to this, the mycorrhiza fungi live, at least to a large extent, on the root excretions and on carbohydrates which they extract from tree roots.

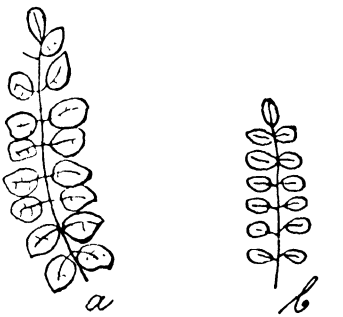


FIG. 131.—*a* Leaf of a *Robinia* plant which was raised in a pot and infected with *Robinia*-bacteria. *b* Leaf of a similar plant but infected with pea-bacteria. From drawings of the plants by Nobbe. The whole specimens are just as different in size as these leaves.

Pine and spruce plants in pure culture assimilate complex organic nitrogen compounds less well than nitrates, ammonium salts or asparagin. The mycorrhiza take part in the absorption of ammonium salts and facilitate that of organically combined nitrogen. They do not assimilate free nitrogen. They are of special importance in those acid and poor soils in which nitrogen is combined in organic humus substances, and not rapidly broken down to nitrates or ammonium compounds by bacteria, as in less acid or neutral, rich, humose soils. On acid raw-humus soils, where nitrification is absent, the tree roots could not supply their nitrogen requirements, as the small quantities of ammonia compounds available have been previously appropriated by the numerous fungal hyphae present. The mycorrhiza make it easier for the tree to compete with the fungi for nitrogen. When conditions for nitrogenous nutrition are favorable, as in rich, well nitrified soils, the mycorrhiza are unnecessary and generally only sparsely developed. Apparently the mycorrhiza also supply the tree with carbon compounds from the soil,[3] just as the chlorophyll-free, mycotrophic *Monotropa*, the

[1] Melin, *loc. cit.*, 1925. [2] Melin, Bot. Not., 1924, *loc. cit.*
[3] Falck, R., Mykologische Untersuchungen und Berichte 2. Kassel, 1923.

Yellow Bird's Nest, receives the whole of its carbon through the fungal symbiont. These sources of carbon cannot, however, be very important for trees; certainly they have never been shown to be so.

Melin and others conceive the symbiosis of mycorrhiza as mutual parasitism, in which that symbiont for which the locality is best suited retains predominance and, under certain conditions, may become injurious to the other. If the higher plants are for any reason feeble whilst the fungi are vigorous, the fungi become, according to Melin, one-sidedly parasitic, and in favorable conditions for the trees alone, the fungus attack is thrown off or the fungus which has gained entrance is digested. Between lies the usual case of mutual symbiosis from which both symbionts gain advantage.

Root fungus infestations which are altogether injurious (Pseudo-mycorrhiza) such as were found by Melin, being purely pathological phenomena, are not discussed here.

NOTE.—A full account of the work of Melin and others appear in: Rayner, N. C., "Mycorrhiza," London, 1927, Wheldon and Wesley. (Tr.).

CHAPTER X

WATER ECONOMY OF THE TREE

1. The Water Consumption of Trees.[1]—Among the conditions of the habitat which decide whether trees will flourish one of the most important is the water supply. Not only does it determine the number of plants which thrive side by side on a particular spot, but it also plays a part in determining which species finally gain the victory in the struggle for existence. The experience of foresters teaches how varied are the requirements of the different species of trees with regard to the humidity of the locality: "The pine is the tree of dry sandy areas and sunny arid slopes, silver fir and spruce thrive best in the moist hallows of mountains rich in springs, the ash also seeks these or wide river valleys with their water-percolated detritus and pebble deposits, whilst the birch is confined to soil with a low average degree of moisture and the beech is able to share the habitat of the alder as well as that of the pine."

Variations of this kind are connected with the life processes of the plant as a whole and cannot be derived simply from one anatomical peculiarity or another. Experience has taught, however, that plants of localities constantly or periodically dry, possess contrivances which give them the power of diminishing the consumption of water to a greater or less extent. Such plants may, nevertheless, consume large quantities of water in favorable seasons. Small leaves with thick cuticle, often covered with wax, and stomata sunken or capable of being closed are very commonly characteristic of such plants. The possession of these characteristics does not, however, of necessity justify the conclusion that the tree in question requires but a small amount of water.[2] In the case of pine needles, the characteristics mentioned are indeed associated with the power of survival in a dry habitat; not so in the spruce and silver fir, for these species have a very high water-requirement. In them, as also in other evergreen woody plants (ivy, holly, etc.), the ecological importance of the xeromorphic leaf structure evidently lies in the checking of evaporation by closed stomata in winter when the supply of water is often stopped by the freezing of the wood, whilst evaporation, especially in sunshine and wind, does not entirely cease. Plants which are satisfied with little water, and have, therefore, the advantage of others in arid localities, are called **xerophytes**, those

[1] Burgerstein, Die Transpiration der Pflanzen, 3 Bände.

[2] Kamerling, Welche Pflanzen sollen wir Xerophyten nennen? Flora, N.F. XI, 1914.

of an opposite nature **hygrophytes**, whilst between them stand the **tropophytes** (*see* Chap. I, 1). The xerophytic mode of life is by no means only made possible through protection against evaporation; equally important are contrivances for facilitating water absorption, such as high absorptive power, wide-spread root system and the power of bearing considerable desiccation without perishing.[1]

Part of the water absorbed is decomposed and assists in the building up of cellulose, wood, proteins and other constituents of the plant substance. In order to form 100 grammes of cellulose, for example, some 55 grammes of water at least must be destroyed. A larger portion of the water taken in remains in the conducting channels, in the living cells as a solvent for the assimilata, or, as imbibition water in the cell walls. The amount of water used in these ways, in itself considerable, is, however, far surpassed by the water consumed in transpiration.

Von Höhnel [2] determined the water consumption of a number of young woody plants by careful experiments extending over three years. He cultivated them in pots which could be made water-tight and watered them regularly. He then determined the daily loss of water by weighing. At least two experimental plants were employed for each species of tree. Von Höhnel obtained in this way the mean figures for the water consumption of each tree during the three growing seasons, calculating it per 100 grammes of leaf substance. The following gives in kilogrammes the average consumption of water per 100 grammes of leaf substance for the respective species in the three growing seasons:

Ash	85.614	Pedunculate and sessile oaks	54.572
Birch	81.433	Norway maple	53.063
Beech	74.858	Spruce	13.501
Hornbeam	72.973	Pine	9.426
Elm	66.170	Silver fir	7.178
Sycamore	58.595	Austrian pine	6.734

In judging of the water consumption of whole trees and crops of trees from these figures, it is to be noted that the experiments were carried out on young plants which would consequently have juvenile leaves of less marked light-leaf character. The transpiration of such leaves, calculated on the kilogramme of leaf mass is, however, as we have seen, greater than that of sun-leaves such as are formed on old trees. Besides this the plants were copiously watered and thus represented only the conditions of crops well supplied with water. Above all, however, it is to be borne in mind that the leaf-mass varies enormously according to species, vigour of growth and the quality of the crop and the locality. The spruce, which generally retains its

[1] Renner, Xerophyten in Handwörterbuch der Naturwissenschaften. Huber, B., Die Beurteilung des Wasserhaushaltes der Pflanze, Jahrb. f. wiss. Bot. 64, 1924. Walter, Der Wasserhaushalt der Pflanze in quantitiver Betrachtung, H. 6. d. Sammlung Naturwissensch, u. Landwirtsch., Freising-München, 1925; the same, Anpassung der Pflanzen an Wassermangel, *ibid.*, 1926, H. 9, with literature. *Comp.* also the profound researches on the water economy of bog plants by Montfort, Jahrb. wiss. Bot. 60, 1921, and Zeitschr. f. Bot. 14, 1922. Stocker, O., Zeitschr. f. Botanik 15, 1923, p. 1.

[2] V. Höhnel, Zentralbl. f. d. ges. Forstwesen, X, Wien, 1884; Über d. Transpirationsgrössen der forstlichen Holzgewächse, Mitt. a. d. forstl. Versuchswesen Österreichs II, 1, 1879; further researches, *ibid.*, II, 3, 1880.

needles 5–6 years, has twice as great a needle mass per acre as the pine and 5–6 times as much as the beech, the latter again far more than the birch and other light-demanding species. Von Höhnel himself made some determinations of leaf weight, but the values he obtained were apparently too high, as he judged of the greater by the less. From these he calculated the annual consumption of water of 1 hectare of close wood (if we convert his figures, calculated in kilogrammes of water per hectare, into depth of water covering the soil of the crop area) as 272 millimetres for 115 year-old beech and 233 millimetres for 50–60 year-old beech. Vater [1] calculated from Von Höhnel's transpiration figures and the probably unreliable data of Ebermayer as to leaf weight (*see* p. 199), an annual consumption of water per hectare of 290 millimetres for the beech, 255 millimetres for the spruce and 103 millimetres for the pine. Burger [2] obtained in the same way, using however other figures for the leaf-mass, 210 millimetres for the beech, 170–180 millimetres for the spruce, 120 millimetres for the oak, 47 millimetres for the pine.

We now come to a method of evaluating water consumption, which, though only an estimation, is in many cases more accurate. It is based on the following considerations. On good, not too permeable soil and with small to medium amounts of precipitation, the forest, when growing unchecked, consumes the whole of the precipitation which falls during the growing season, so that the soil becomes more and more dried out as the summer advances and during that period lets through little or none as drainage water. It appears from experience in lower and medium elevations in the mountains of mid-Germany, that the highest yields of all our chief species are obtained, even without the supply of subsoil water, when there is an annual precipitation of 600–700 millimetres of which half falls during the months of growth, May to September. With smaller precipitations the yield is less, and the forest, especially spruce, in order to give the best growth is dependent on the supply of subsoil water. According to forest-meteorological measurements in broad-leaved trees 20 per cent., in conifers over 30 per cent. of the summer rain remains suspended in the crowns, at least 30 per cent. evaporates from the soil and soil covering and thus at the most a half is absorbed by the roots and evaporated or stored by the tree. The amount of winter moisture, which at least in lighter soils is only small, may be set off against water flowing off the surface and occasionally, in heavy rain, percolating through. Thus, on the average 150–175 millimetres vegetation water = 1,500–1,750 cubic metres per hectare suffices, but is also necessary, for the best growth of all our species of trees, although the spruce, according to experience, is somewhat more, and the sessile oak and the pine somewhat less exacting, in water requirements. From this and from the leaf-mass according to Burger (*see* Chap. VIII, 1) the consumption of water per kilogramme leaf dry-weight works out at 63–78 l, for the spruce 12–14 l.

[1] Vater, Der Wasserverbrauch von Buche, Fichte und Kiefer. Tharandter Forstl. Jahrb. 74, p. 47; *see* also: the same, Wasserabgabe aus dem Walde, Ber. ü. d. 49. Vers. d. Sachs. Forstverein, Tharandt, 1905.

[2] Burger, Die Transpiration unserer Waldbäume, Zeitschr. f. Forst- u. Jagdwesen, 1925. p. 473.

If the leaf surface of the beech amounts, as in the best woods, to three times the area of the crop, *i.e.* 30,000 square metres per hectare, the water consumption of the beech amounts to 50–58 l per square metre per annum.

This excellent agreement with the figures for transpiration calculated by Von Höhnel in quite a different way, only proves first that leaves regulate their emission of water according to the supply, and secondly that the tree naturally does not evaporate more than it takes up, but within certain limits, uses up completely the quantity of water at its disposal. We can, therefore, regard Von Höhnel's figures as a means for estimating the water consumption of other species in woods, if we take account of the quantity of leaves, which varies with the species and the quality of the crop. Unfortunately sufficient comparable data of the leaf mass of various species and localities are not yet available. The local climate (especially the atmospheric humidity), the amount and distribution of the precipitation and the kind of soil (especially the lime content) caused deviations from the values given. According to agricultural determinations, a certain quantity of water is necessary for each kind of plant to produce a given quantity of dry substance. This quantity may indeed be many times greater in some species and varieties of plants than in others and it also undergoes certain variations within the species, as ample supplies of water induce luxury consumption, though it remains in general fairly constant. According to Hellriegel,[1] this " relative water consumption " is, for example, for barley 310, oats 376, horse beans 282, red clover 310, summer rape 329 kilogrammes of water per kilogramme of dry matter produced.[2] For our forest trees, if we take the annual production in the best yield classes as 10,000 kilogrammes of dry matter (*see* p. 258), the relative water consumption works out at 150–175 l, and is thus only half as large as that of the agricultural crops mentioned. The extent to which the water consumption of forest trees changes with the quality of the locality and rate of growth, has not yet been sufficiently investigated. As, however, leaf mass varies remarkably with the quality of the locality—according to our account in Chap. VIII, 1, it is 4–5 times as large in the best locality as in the poorest—and as badly nourished leaves will never transpire better than well nourished ones, it can certainly be assumed that flourishing crops consume many times as much water as those which are growing badly.

The water consumption of the individual species depends not only on the factors hindering or promoting transpiration, such as temperature and air movements, and opening of the stomata in light, but also on the supply of water, because this also influences the amount of opening of the stomata. With the least possible watering the ash consumed 56·689, with the most copious 98·305 and 101·850 kilogrammes of

[1] Hellriegel, Grundlagen der Landwirtschaft.

[2] Further determinations of relative water consumption *see* Briggs and Shantz, The water requirement of plants, U.S. Dept. of Agric. Bur. Plant Indust. Bull. 284; Pilaski, Wasserverbrauch der Kulturpfl., Bot. Archiv. XV, 1926. According to this the relative water consumption varies very much with the species of plant, being in some only half, in others up to four times as high as in those quoted above.

water per 100 grammes of leaf substance; the pine, in the first case 5·802, in the last 12·105 kilogrammes. These and corresponding figures for other trees are the best illustration of what was said about the automatic regulation of transpiration. That the difference between the loss of water in broad-leaved trees or conifers in the shade and broad-leaved trees or conifers in the sun is small, and even varies in the opposite sense to the radiation which promotes transpiration, is to be ascribed to the same phenomenon, as well as to differences in leaf structure and, as Von Höhnel assumes, to wetting by dew and rain.

Loss by transpiration per 100 gramme, leaf dry matter:

	In the shade.	In the sun.
Broad-leaved trees . .	44·472	49·533
Conifers	4·778	4·990

Mean amount of transpiration per 100 grammes air-dry weight from April 1 to October 31, 1879:

	Shade specimen.	Half-shade specimen.	Sun specimen.
Broad-leaved tree	94·350	88·783	62·683

In seedlings of the Weymouth pine, the transpiration of the fully shaded was to that of the half-shaded and unshaded specimens, as 1 : 8 : 21, the ash content as 1 : 3 : 5.[1]

Among the physical factors affecting evaporation from the leaves in still air, the most important is the relative humidity of the air, of which the psychrometer difference, *i.e.* the difference in temperature between a dry and a wet bulb thermometer, is a measure.[2] In general, everything which results in the closing of the stomata [3] checks transpiration very greatly, because when the stomata are closed only the much smaller cuticular evaporation is active. (This effect is produced in many plants even by the wind, which, from a purely physical standpoint, enormously promotes evaporation.[3]) Livingston [4] calls the proportion between the giving up of water from the leaves and the evaporation from a free water surface, the **relative transpiration.** It falls off in a surprising manner on sunny days, while the absolute transpiration rises. Livingston sought the cause of this in the incipient drying of the cell walls. This purely physical giving up of water is, however, according to Renner,[5] only small. In the living plant the transpiration is in the main regulated by the stomata. According to Huber,[6] the amount of transpiration falls off greatly with increasing height on the stem, so much so that the transpiration of the lowest twigs under otherwise similar external conditions is up to sixteen times as large as that of twigs at 12 metres high. The cause of this lies in the greater difficulty of supplying water to the upper parts of the tree, in consequence of the resistance offered to the water current by the amount

[1] Burns, Plant World, XVIII, 1915.
[2] Huber, B., Ber. d. D. Bot. Ges. 42, p. 19, 1924.
[3] Wiesner, Sitzungsber. Akad. Wiss. Wien, 1887. Bernbeck, Der Wind als pflanzenpath. Faktor. Diss. Bonn, 1907, Stuttgart, 1907, *comp.* also Gradmann.
[4] Livingston, Botanical Gazette, LIII, 1912, and LII, 1911. The relation of desert plants to soil moisture and evaporation, Carn. Inst. Wash. Publ. 50, 1906.
[5] Renner, Jahrb. wiss. Bot. 56, p. 617, 1915.
[6] Huber, Zeitschr. f. Bot. 15, 1923, p. 465.

of lift and by friction. If the amount of transpiration of a leafy twig is determined immediately after its severance from the tree it is always found to be much greater than a few hours later. It falls off rapidly at first, then more slowly and approaches a constant value which apparently corresponds with the purely physical cuticular evaporation, in contradistinction to the physiologically regulated transpiration through the stomata at the beginning.

Even in the depth of winter the giving off of water through twigs and needles is not completely at a standstill. According to Iwanoff,[1] the needles of the evergreen conifers are in fact better protected against loss of water than the hibernating one-year-old twigs of deciduous trees, but the large surface of the needles still causes a not inconsiderable emission of water even in deep frosts of 13–20 degrees. The amount of the daily loss of water in winter, in his experiments in the moist climate of Leningrad, varied round about 0.4 per cent of the fresh weight of the needle-covered twigs and, for the pine, about 1 per cent. of the fresh weight of the needles. Compared with the transpiration in summer, the transpiration in winter is 300–400 times smaller. As the transmission of sap is much checked in winter and in frozen wood completely stopped, the water content of the needles gradually diminishes in winter, although the activity of the roots is not completely interrupted. Among deciduous trees the larch evaporates least, the broad-leaved trees up to nine times as much. Woody plants from southerly regions evaporate more in winter than those from northerly ones, one-year-old twigs more strongly than older ones.

Some help in the study of leaf evaporation, and in particular of cuticular evaporation, is afforded by the results of measurements by Ebermayer,[2] who determined the rate of wilting of the freshly gathered leaves of various trees.

In addition to its importance as a building material of plant substances and as a means of maintaining the turgor of the cells endangered by transpiration, water acts as means of transport into the plant body of the mineral food materials and makes possible their migration as well as that of dissolved organic building materials from place to place within it. This fact has afforded Ebermayer an opportunity of determining the water consumption of trees in still another way. Every drop of water taken in through the roots contains mineral substances which are carried with it into the leaves and, in part at least, remain there after the evaporation of the drop of water that brought them. Ebermayer, therefore, conceives that a greater supply of water may be deduced from the presence of a greater ash content of the leaves. Ebermayer's experiments actually gave as a result that the leaves of those woody plants, which according to experience demand most water (ashes, willows, alders, maples, elms), contained the most ash (7–10 per cent.), whilst beech, hornbeam and oak leaves showed only 4–5 per cent., silver fir, spruce and larch 2.9–3.5 per cent., the least water-demanding Austrian pine as little as 2 per cent. and *Pinus sylvestris* 1.3–1.8 per cent. pure ash.

[1] Iwanoff, L., Ber. Deutsch. Bot. Ges., 42, p. 44 and 210, 1924.
[2] Ebermayer, Forstl. naturw. Zeitschr. II, 1893.

A similar if not exact parallelism between the amount of transpiration and the ash content of the leaves and twigs, was found by Huber (*loc. cit.*) on comparing *Sequoia* twigs at various heights in the stem. The lowermost, strongly evaporating twigs were also relatively richer in ash than those from the upper crown. Difference in the amount of transpiration is, however, by no means the only cause of the difference in ash content. Muenscher [1] found, for example, no kind of connection between ash content and the amount of transpiration in barley seedlings which were caused to transpire at different rates by cultivation in dryer or moister atmospheres. The selective action of the plasma of the water absorbing root cells undoubtedly contributes greatly to regulating the absorption of nutrient salts ; the distribution among the twigs of the substances once absorbed will depend on the amount of their transpiration. It is also to be noted that a great part of the mineral substances is again transported out of the leaves and carried in the descending sap stream to other parts of the plant.

2. The Water-Content of Trees.—The water-content of a tree is to be distinguished from its water consumption and its water demands. The first does not run by any means parallel with the two last. Thus the water-content of the timber of the ash, which consumes so much water, is smaller throughout the year than that of the elm and beech, while the easily satisfied Scots and Austrian pines are characterised by the high water-content of the wood.

For the determination of its water-content, a stem is cut up into equal sized pieces, which are weighed, then made air dry or absolutely dry in a hot oven, and again weighed. The difference of the two weights gives the water-content, which is most conveniently expressed in percentage of the green weight. In an examination of 30 different species of timber, Robert Hartig [2] found a variation of the water-content between 30 and 60 per cent. from species to species and somewhat smaller variations in one and the same species according to the season of the year. On the average of the whole of the species the greatest water-content, 50.5 per cent., occurred in the beginning of the year, whilst at the time of " bleeding " (March and April) it was generally less (47.5 per cent.). The best representation of the changes in sap-content in the course of the year is given by the data published by Hartig of the water-content of oak, beech, birch, spruce and pine.

If we consider the curves (*see* Fig. 133) in which R. Hartig set out his results, we find a striking similarity between the lines of the beech and the pine. Both show a maximum water-content in December (beech ca. 60 per cent., pine ca. 52 per cent.) and also large amounts in June (beech 50 per cent., pine 43 per cent.) which in both trees remain below the December maximum. An important difference is shown in the minima of the two curves. In the beech the water-content sinks greatly from July to October, while the curve of the pine hardly sinks at all during this period.

The rise of both curves from October to December is due to the

[1] Muenscher, Amer. Journ. of Bot. 9, 1922, p. 311.
[2] Hartig, R., Untersuchungen a. d. forstbotan. Institut zu München, II.

activity of the roots still continuing whilst evaporation is greatly diminished, in the beech by leaf fall, in the pine by the autumn closing of the stomata and by the weather. From December the increased cooling down [1] and final freezing of the soil—perhaps also a periodic resting of the absorbing rootlets—brings about the stoppage of the supply of water. As the transpiration still goes on, though in a diminished degree, the water-content of both trees sinks, until the rising soil temperature sets the roots working again.

Among the other curves, those of the spruce and oak show similarity. Both show a maximum water-content in July and a minimum in winter,

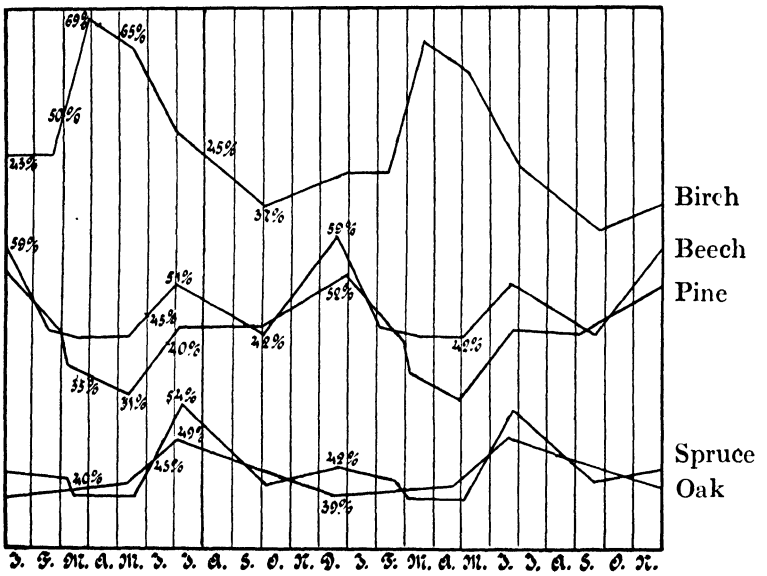


FIG. 133.—Changes in the water-content of certain species of trees in the course of the year. After Hartig, R.

but in the spruce alone a slight rise from October to December. The curve of the birch differs from the rest by the maximum being already reached in March, and, after a great fall to October, being followed by a second, lower, maximum in December. The early occurrence of the maximum is connected with the early awakening of vegetative activity in the birch, the rapid fall with its great consumption of water. It is obvious that the dates given above will vary according to climate and locality; thus Tonkel's [2] figures show the maximum of the birch already in February and the early summer maximum of the pine is not in general so clear. Besides these two species Tonkel also investigated the aspen, and states that there is an increase of the water content in early winter up to December, but then a fall lasting, with unimportant interruptions, into September, and probably into October, which was not taken into account. His percentage figures are as follows. The specimens were dried at 100–120 degrees.

[1] Kosaroff, Beihefte z. bot. Zentralbl., XII, 1902, p. 293.

[2] Mitteil. d. land- u. forstwirtschaftl. Akademie zu Petrowskoe, 5 Jahrg., Heft 2. Moskau, 1882. According to Bot. Jahresber., 1883, I, 6.

	Birch.		Aspen.		Pine.	
	Stem.	Twigs.	Stem.	Twigs.	Stem.	Twigs
November . . .	41.39	32.73	49.1	33.5	50.0	48.3
December . . .	42.39	44.4	51.0	49.3	61.9	51.2
January . . .	45.59	44.4	50.0	47.5	62.7	56.1
February . . .	46.23	42.7	50.5	50.2	61.3	53.7
March . . .	44.8	39.2	49.6	46.2	58.5	61.3
June . . .	38.1	51.3	42.2	50.5	55.2	60.1
July . . .	41.3	49.9	41.6	50.8	52.0	60.2
August . . .	39.1	44.8	42.7	53.1	55.1	56.6
September . .	38.4	38.7	41.3	46.0	50.5	52.3

Finally, Gelezn off[1] found the following percentage of water in the wood of the pine and Norway maple:

Pine.	Norway Maple.
In winter up to 64.5%.	In spring, 44.4% (maximum).
In spring and autumn, 62.2–63.3%.	In winter, 37.1% (minimum).
In summer, 59.5%.	

Investigations on bore chips and small splinters of hornbeam, ash, Norway maple, Weymouth pine and larch, taken in conjunction with all the other relevant observations, proved to Büsgen and Olkers [2] that great variations in water-content occur in summer, which are due to the combined action of the variations in moisture of the air and soil and the condition of the organs of the tree which absorb and part with water. Even between morning and evening marked variations occur. The low water-content in autumn and the increase in winter up to the time of leafing, as well as the great fall in April and May, also appear in Büsgen and Oelkers' observations. Great individual deviations occur which may be due in part to accidental variations in the bore chips, which as a material are not all that could be desired.

The mean water-content of fresh leaves was found by Ebermayer [3] in percentages:

Lombardy poplar	70.49
Ash and horse chestnut	65.90
Black alder and acacia	64.10
Oak, elm, white alder and lime . . .	63.32
Birch, rowan, sycamore	61.66
Willow, Norway maple, aspen . . .	69.48
Beech, hornbeam, field maple, white poplar	57.02

3. The Movement of Water in the Tree.[4]—As a result of transpiration at the surface of the leaves, water is constantly being

[1] Sur la quantité et la répartition de l'eau dans les organes des plantes. Bull. de l'Acad. de St. Pétersbourg, XXII, Nr. 3. Abstract: Bot. Jahresber., 1876, 708; the same: Rech. sur la quantité et la repartition de l'eau dans les tiges des plantes ligneuses. Ann. d. sc. nat., 6e sér., Bot., T. II, 1876, p. 344.

[2] Studien über den Wassergehalt einiger Baumstämme. Zeitschr. f. Forst- u. Jagdwesen, 1911. Berlin, Springer.

[3] Ebermayer, Forstl. naturw. Zeitschr. II, 1893.

[4] Renner, Wasserversorgung der Pflanze; in the Handbuch der Naturwissenschaften, Jena, 1915. Bachmann, F., Das Saftsteigen der Pflanzen; in Ergebn. d. Biologie 1, p. 343, 1926. Walter, *loc. cit.*, 1925 and 1926. Dixon, The transpiration stream, London, 1924. Historical; the same, Progr. rei botanicae III, 1909, p. 1.

withdrawn from the upper parts of the tree and must be replaced from below. This necessitates a constant movement of at least a part of the water in the body of the tree.

That this upward water current proceeds in the xylem and not in the rind has been long known, as a simple and incontrovertible proof of it can be obtained at any time by ringing. If a stem or branch has the rind removed right round in not too broad a band, no wilting of the foliage situated above the place of ringing sets in. The tree or branch continues to live on until its wood has lost its water conducting power through atmospheric influences or the action of parasitic organisms at the wound or until the roots are too badly injured by insufficient nourishment from the leaves, the assimilates from which, as we shall see, move in the rind. Girdled branches may go on vegetating for years and grow normally in thickness above the ring, whilst whole trees perish more rapidly unless adventitious shoots below the ring supply nourishment to the roots for a time. Slight injuries to transmission of sap do, however, often occur after ringing, because the outermost parts of the wood, which normally conduct most of the water, finally die off, become stopped up or dry out. That the rind absorbs and conducts water supplied to it only very slowly, so that it cannot by itself maintain the evaporating twig in a fresh condition, is shown especially by experiments by Birch-Hirschfeld.[1] It has been known for a long time that the upward movement of water does not proceed by any means in the whole of the xylem but only in the outer annual rings. This indeed became apparent by the everyday observation that in stem cross sections it is only the outer zone of sapwood that appears moist.

Strasburger [2] supplied proofs of it. When he placed a branch of *Robinia pseudacacia*, 4 metres long and 22 millimetres thick, in a solution of the red dye eosin, he found after a certain time that the coloured fluid had risen in the outermost rings to a height of 50 centimetres. At height of 1.5 metres only 2 annual rings and at 2.5 metres only 1 were coloured. The eosin solution had risen more rapidly in the outermost ring than in the others. In a sweet chestnut branch the eosin rose in the 5 outer rings, though in a lesser degree in the innermost of them.

Wieler [3] found in the twigs of the robinia, of 2 annual rings 1½ conducting, in *Quercus sessiliflora* of 6 rings, 2, in *Acer platanoides* of 5 rings, almost the whole wood, in *Fagus silvatica* of 6.9 rings, 3.6 conducting. In stem wood of *Betula alba* from August 9 to 16, of 15 annual rings the innermost had transmitted the dye to 15 centimetres above the cut surface, only the 3 outer rings to 30 centimetres above it, and only the outermost ring to 48 centimetres. If, however, the normal path of the water is interrupted, annual rings lying further inside may take part in the conducting of water by assisting and replacing. They can obviously do this only in so far as they have not become impassable by the stopping up of the conducting elements through access of air, the formation of tyloses or otherwise. Molisch found in the English elm

[1] Birch-Hirschfeld, Jahrb. wiss. Bot. 59, 1920.

[2] Bau und Verrichtung der Leitungsbahnen. Jena, G. Fischer; Water transmission in conifers *see* Stopes, New Phytologist, VI, 1907, p. 46.

[3] Jahrb. f. wiss. Bot. XIX.

2–10, and in *Quercus alba*, 10 annual rings free from obstructions. The inner sapwood forms a kind of water reservoir which is drawn upon only in case of necessity.

The reason for the water normally moving only in the outermost sapwood rings is to be sought in the fact that in them the water ways are less interrupted by air and that they alone provide a direct longitudinal connection between the vessels or tracheids of the absorbing rootlets and the leaf veins from which the transpiring leaves draw their supplies. The new wood structures of each year at the upper and lower ends of the plant naturally find their direct continuation in the cambium products of the same year. Older water channels can only draw on the youngest root vessels by the aid of transverse connections and can only permit water to reach the leaves in this indirect way, which offers a correspondingly great resistance. Lateral water conducting connections at the place of contact between the wood of a young shoot or root and the wood of the previous year are provided by pits between the last elements of the previous year and the first of the current year's growth; in the pine by transversely directed tracheids which are in contact with the medullary rays. As is well known, pits in the tracheids of conifers are found in the greatest numbers on the radial walls, so that the exchange of water between laterally adjoining elements of one and the same annual ring proceeds with ease. The vessels run (in willow wood) in such a way that they come into connection with several neighbouring ones,[1] so that in special circumstances lateral movement of water across the length of the shoot is possible.

The rapidity of movement of the ascending water in the plant was found by Sachs, with lithium nitrate, to be 18.7 centimetres to 206 centimetres per hour according to the species. Strasburger found a rate of one metre in 50 minutes in the robinia in June and July at about 20 degrees C., 3 metres, in one case in 4 hours, in another case, in 5 in the Norway maple at 20–24 degrees C., thus 60–75 centimetres an hour. In a lime branch 3 metres high, well furnished with twigs, the coloured solution reached the tip in 5 hours, in the shade at 24 degrees C. *Vitis vulpina* gave a rate of 90 centimetres, *Clematis vitalba* in dull weather at 14 degrees C., 80 centimetres per hour. As to the greatest rate, Strasburger found an ascent of 6 metres in the hour in *Bryonia dioica* in July and August at 20–26 degrees C., in the pumpkin even somewhat more. Groom [2] found in larches a rate of ascent up to 240 centimetres in the hour, in the beech up to 223 centimetres. It thus appears that the transpiration stream in conifers may move just as fast or faster than in broad-leaved trees. In another conifer (Silver fir) hourly rates of 120 centimetres were reached. Ewart and Rees found rates of 6–10 metres an hour in Australian eucalypti. Mercury injections showed vessels several metres long in these trees.[3]

The difficulties in the study of the movements of water in trees began with the question as to the actual paths of travel of the water and the contrivances by means of which the very great amounts re-

[1] Zimmermann, A., Ber. d. D. Bot. Ges., 41, p. 401, 1923.
[2] Ann. of Botany, XXIV, 1910.
[3] Bot. Zentralbl., Bd. 123, 1913, p. 107.

quired are conveyed up into the crowns of the highest trees. Assuming that a 60-year-old beech in full foliage evaporates 18 l of water a day, the supplying of a tree 20 metres high would require an expenditure of 360 metre-kilogrammes of work daily, or 0.004 metre-kilogrammes per second, if all that was to be done was to lift the water to the height mentioned. A steam engine of one horse-power would, under this assumption, be able to supply 18,750 crowns. In practice, however, a much greater amount of work is necessary, because, besides the weight of the water, the resistances in the interior of the tree have to be overcome. These alone require 3–4 times the work that has to be expended in overcoming the height of lift. The obvious thing was to proclaim as the active cause of the movement of water in the tree, that same force which causes water to flow out from the stumps of felled trees in spring—an upward pressure produced by the activity of the root cells. This " exudation pressure " (*see* Chap. IX, 3) is not, however, able to replace the water consumed in summer sufficiently fast. The presence of spaces in the wood almost empty of water and air, cannot be avoided during great summer evaporation. The stump of a tree newly felled at that time does not bleed but actually sucks in water poured upon it. Besides this, water absorption may take place also through dead roots and through the cross section of sawn off stems.[1] It is necessary, therefore, to look round for other sources of power. Molecular forces operating in the cells walls of the wood elements, capillarity, co-operation of external air pressure with air rarefaction present in the interior of the tree, life manifestations of the cells of the medullary rays and parenchyma, processes of distillation in the interior of the vessels and finally—in all seriousness !—the pressure of the soil weighing on the roots, were one after another and in part simultaneously, claimed to be the driving force of the water movement. But neither the hypotheses which have been known as the Imbibition Theory (J. v. Sachs, 1862–1882), Air Pressure Theory (J. Böhm, 1889), Gas Pressure Theory (R. Hartig, 1882), Climbing Theory (Westermaier, 1883), Distillation Theory (Scheit, 1886), Polarity and Enzyme Theory (Janse, 1908–1913), Condensation Theory (Baker, 1915), Pulsation Theory (Bose, 1924) nor the attempts at explanation by Godlewski (1884) and Janse (1887) operating with a one-sided filtration resistance of the medullary ray cells, were able by sufficient actual proofs to disarm all objections and obtain for themselves general acceptance. As permanent gain from all these and other efforts we may look upon the facts—proved especially on the one hand by R. Hartig,[2] Boehm and Elfving, on the other hand by Strasburger—that the water does not, as the long and widely held imbibition theory would have it, move in the lignified membranes but in the inner cavities of the wood elements, and that the ascent of water can continue for some time without the help of the living cells. Strasburger supplied the proof of this last named fact by sawing off trees up to 21 metres high and immediately standing them in poisonous liquids. The leaves of the trees went on

[1] Strasburger, Leitungsbahnen, and Hansen, Arbeiten des bot. Instituts zu Würzburg, III, 308, also Böhm, Ber. d. D. bot. Ges., XIII, 1889.

[2] Hartig, R., Unters. a. d. forstbot. Inst. zu München II, 1882; III, 1883.

transpiring and the liquids ascended up to their tips, although every living cell with which they came into contact immediately died. For example, a 75-year-old oak 21.9 metres high was fastened to adjoining trees by ropes and then sawn off horizontally 10 centimetres above the soil, rapidly lifted by tackle and placed suspended in a tub containing water, which later, after the cut surface had been cleaned and smoothed, was replaced by a saturated solution of picric acid. After three days the liquid had already reached the leading shoot, as could be recognised by the changed appearance of the leaves. Now although picric acid is known to be a poison which is rapidly fatal, the experiment does not so far exclude the possibility that the living cells might have fulfilled one of their ascent-producing functions before the liquid reached them. In order to meet this, Strasburger, after the poison had reached the top, now offered the tree picric acid coloured by fuchsin. This fluid also reached the top of the tree, although when it entered the whole tree was already dead.

In a similar manner, of recent years, solutions of dyes which for industrial purposes have been led into the lower parts of the stem through bore holes by means of pipes, are made to ascend as far as the twigs and leaves (Tree Colouring process). Sapwood trees, such as beeches, hornbeams and birches whose " ripewood " is also conductive, become coloured through and through in a few days. Slender poles can be easily impregnated in this way by cutting them off in full leaf and setting them in tubs of the impregnating fluid.

Such experiments have afforded proof that plants, at least for a short time, can raise water in the shoot far above the height of atmospheric pressure, and thus meet the requirements of transpiration, without the assistance of living cells. In this way the problem of the ascent of sap has been removed from the difficult region of life processes into the realm of simpler, purely physical explanations. The water channels of the wood are in fact dead organs without plasma, which can act after the manner of a mechanical apparatus. Strasburger's conjecture that physical causes, as yet unobserved, may be in play, should soon be confirmed. The English investigators Dixon and Joly [1] and the Heidelberg scientist Askenasy [2] were able, by bringing in the **cohesion of water,** to set up a theory of the mechanics of the transpiration stream which was, it is true, at first not sufficiently supported at all points by inductive proofs but was free from physical and from anatomical and physiological objections. Later Renner [3] and his students [4] further expanded the theory and supplied the still missing proof of

[1] Dixon and Joly, On the ascent of Sap. Phil. Trans. of the R. Soc. of London (B), 186, 1895.

[2] Askenasy, Über das Saftsteigen. Verh. der Naturhist. u. med. Ver. in Heidelberg 5, 1895, Beitr. zur Erklärung des Saftsteigens, *ibid.*, 1896.

[3] Renner, O., Experiment. Beitr. z. Kenntn. d. Wasserbew., Flora 103, 1911. Ber. Deutsch. Bot. Ges. 30, pp. 576 and 642, 1912. Wasserversorgung der Pflanzen. Handwörterbuch d. Naturwissenschaften, Jena, 1915. Theoretisches u. Experimentelles z. Kohäsionstheorie. Jahrb. Wiss. Bot. 56, p. 617, 1915. Vers. z. Mechanik d. Wasserversorgung. Ber. Deutsch. Bot. Ges. 36, p. 172, 1918. *Ibid.* 43, p. 207, 1925. Flora 118–119, p. 402, 1925 (Goebelfestschrift).

[4] Holle, H., Unters. über Welken, Vertrocknen und Wiederstraffwerden. Flora 108, p. 73, 1915. Bode, H. R., Beitr. z. Dynamik d. Wasserbew. in d. Gefässpfl. Jahrb. wiss. Bot. 62, p. 92, 1923.

the facts. The following representation of the transpiration stream and its driving force is given from these and other publications [1] in the very extensive literature.

The ascending water stream moves almost exclusively in the tracheae and tracheids of the xylem, and in fact in their lumena. Absorbed dye solutions are observed to ascend rapidly in them and only to spread from them later into neighbouring parts. The narrow lumened wood fibres take very little part in the conducting of water.

The tracheae form tubes directed longitudinally, sometimes several metres long, open or with pierced transverse walls. The tracheids are, it is true, only a few millimetres long, but they are connected together, especially near their ends, by numerous bordered pits whose closing membranes are traversed by fine pores and are therefore easily permeable to water. All these conducting organs are united together so as to form continuous conducting channels running longitudinally in the xylem either in straight lines or with slight lateral deviations.[2]

We have, therefore, to picture the water in the wood in the form of a great number of continuous threads which extend from the extreme terminations of the leaf veins down to the root tips and are connected together laterally through pits and medullary rays. The dividing up of the conducting channels into chambers in the tracheids makes it possible to ensure that the continuity of the water threads shall remain, when one or even many of them are excluded from water conducting by the penetration of air or some other accident.

The continuity of the water channels is most complete in the outermost annual rings of the sapwood which are almost entirely filled with water and contain little air. The cambium cells from which the young wood originates are completely free from air bubbles; they contain cell sap alone in the vacuoles and even after the disappearance of their plasma and the lignification of their cells they are always at first filled with liquid. Robt. Hartig always found only small quantities of air in the youngest sapwood of trees.[3] For example he found the average water and air content of the last ten annual rings of the spruce [4] (parts by volume in 100 parts of fresh wood, the rest is made up of wood substance) as follows:

Height in the tree	1.3	5.5	9.7	13.9	18.1	22.3	26.5	30.7 m.
Water volume %	90	69	70	70	73	72	72	67
Air volume % .	9	8	7	7	6	7	6	10

Thus the water channels in the last annual rings are very little interrupted by air.[5]

From this almost solid column of water in the outer annual rings the leaves withdraw water upwards by transpiration and arrangements

[1] Dixon, Transpiration and the ascent of sap. Progr. rei Botanicae 3, p. 1, 1909. Bachmann, F., Das Saftsteigen der Pflanzen; Ergebn. d. Biologie 1, p. 343, 1926 Gives all the latest literature.

[2] Zimmermann, Ber. Deutsch. Bot. Ges. 41, p. 401, 1923.

[3] Hartig, R., Unters. a. d. Forstbotan. Inst. zu München, II and III, Berlin, 1882–1883.

[4] Hartig, R., Das Erkranken und Absterben der Fichte . . . Forstlich- naturwiss. Zeitschrift, 1, 1892.

[5] *Comp.* also Strasburger, Leitungsbahnen, p. 677 ff.

must be made for replacing this from the roots. As we know, there exists no pressure from below even approximately adequate for this. If the stem of a plant in leaf is cut off immediately above the soil [1] the stump always exudes much less water than is absorbed by the leafy stem if it is placed in water or than is consumed by it in undisturbed connection with the root. If the stump is connected to an air pump and water sucked out from it the exudation of water does indeed increase somewhat, but it never becomes so great that the needs of transpiration could be met by it alone without stored water. In conifers there is no exudation of sap at all, and even in species which do bleed, such as birches, maples, beeches and hornbeams, root pressure is confined to the lower part of the stem and in transpiring trees of these species also an absorption tension alone is to be detected.

Besides the inadequate root pressure from below we must consequently take into consideration a lifting force which has its origin in the leaves.

The process of transpiration in the leaves consists of the evaporation of water which soaks through the outer walls of the cells of the leaf tissue, especially where, unprotected by cuticle, they abut on the intercellular spaces. These walls absorb or " imbibe " an equal quantity of new water from the interior of the cell with a force similar to that with which plastic clay retains its moisture.[2] Just as it would require an extraordinarily great pressure to squeeze out the water from the latter, so the moisture contained in the cell walls can only be forced out with great difficulty. The greatness of the absorptive power of the cell walls is also shown by their generally being able to draw their imbibition water from the interior of the cells, although it is very firmly held there by osmotic forces.

The withdrawal of water from the interior of the cell reduces the volume of sap [3] and provides room for the taking of new water into the cell lumen. The tension of the cell wall—the wall pressure—which in the fully turgid cell opposes a resistance to the osmotic absorption of water, falls off, and the absorptive power of the cell increases in proportion to its " saturation deficit " (Renner, 1911). The absorptive power in fact increases up to the full value of the osmotic absorptive force of the cell sap, if the loss of water leads to wilting—*i.e.* the loss of tension and the relaxing of the cell wall. The cell now absorbs water osmotically out of the water channels in the leaf veins until the cell wall, once more made tense, again sets a limit to the further increase of the cell contents. (In reality these processes are carried out, not in rhythmical alternation, but continuously and simultaneously.) The evaporating leaf cells thus exert a constant sucking action on the water in the wood and the absorption tension thus produced propagates itself along the continuous water channels through the whole xylem of the leaf veins and the shoots down to the root tips, actually by virtue of the **cohesion** of the water particles, which under the conditions present in the water passages in the wood may reach extraordinarily high values.

[1] Jost, Zeitschr. f. Bot. 8, 1916.

[2] Schermbeck, Tätige Kolloidstruktur der Membranen, Wageningen, 1910.

[3] Measurements of the alterations of leaf volume with physical explanations, *see* Bachmann Jahrb. wiss. Bot. 61, p. 372, 1922.

At the lower end these strained threads of water are in contact with the living cells of the roots and there the tensile strain is again converted into osmotic force. Just as in the leaves evaporation withdraws water from the cells bordering on the intercellular spaces, so this tensile strain brings about the extraction of water from the cell walls in the neighbourhood of the vessels of the root. The force of imbibition of the unsaturated walls makes good the deficiency from the contents of the living cells. Their wall pressure thereby sinks and their absorptive power rises so that they, for their part, replace the loss by absorbing water from the soil by means of their osmotic force.

Every emission of water from the leaves, in so far as storage water is not used to replace it, immediately results in an equal absorption of water by the roots. Water emission, water absorption and rate of flow, place themselves automatically and almost simultaneously in a dynamic equilibrium, as in the simple exhaust pump. Stimulus effects and stimulus transmissions, such as must be required between leaf, wood and root if the pumping action of living cells alone is assumed, are not in play. They would be improbable because of the long distances over which they would have to be transmitted in high trees.[1]

Transpiration itself provides the driving force for covering its requirements. The driving force of the transpiration stream is ultimately to be traced back to the energy of the rays of the sun, which produce the heat and the water vapour deficit in the air and leaves necessary for evaporation. The heat of the leaves themselves, arising from the destruction of assimilates in respiration, promotes evaporation. It has, however, only a very small share—according to Huber,[2] only about 1 per cent.—in the total work of transpiration.

Askenasy has described a simple experiment to illustrate the cohesion theory. If a well-cleaned glass tube a metre long is filled with air-free water and one end closed by a gypsum stopper, the latter may be considered to represent a cell with its walls permeable to water but not to air, drawing water from a leaf vein. The column of water may represent a water thread in the tree. If the tube is placed with its open end in mercury, while water evaporates from the outer surface of the gypsum stopper the mercury rises in the tube at a corresponding rate and does so, far above the barometric height for the time being, from which it is clear that it is not atmospheric pressure that causes it to rise. Copeland [3] has constructed a similar artificial tree 12.4 metres high out of glass tubes which he filled with plaster of Paris. That the leaves are actually able to develop as great an absorptive power as theory requires, is proved by the experiments and measurements mentioned below.

The propagation of the tension in the wood water above the height of lift corresponding to the pressure of the atmosphere (10.33 metres) is the starting point of the "cohesion theory." The cohesive power of

[1] Renner, Jahrb. wiss. Bot. 56, 1915.

[2] Huber, B., Die Beurteilung des Wasserhaushalts der Pflanze. Jahrb. wiss. Bot. 64, p. 79, 1924.

[3] Copeland, Bot. Gazette, 34, 1902. Gives the older literature.

water which makes this propagation of tensions possible was formerly not sufficiently noticed by botanists. Before Dixon, Böhm alone had rightly recognised its importance for the ascent of sap, though he had not brought it into correct connection with the other forces of the movement of water. Water has the property that its particles, in spite of their great mobility, can only with difficulty be separated from each other by pulling. To compress liquids very great forces are necessary and no smaller one are required to tear their particles apart. This great cohesion of water only comes into effect when the water cannot avoid the pull by altering its shape, as by forming drops, and thus only in narrow tubes where the adhesion of the water to the walls prevents such change of form. Especially in the narrow water conduits of the wood is it difficult for water to be separated from the walls, as they hold fast the imbibed and adherent water and therefore also the liquid water in the lumen of the vessel which coheres with it. The lignification of the membrane, which is found in all the water channels of plants of every family from ferns to trees, appears to be adapted to fulfil the task of preventing the rupture of the water threads. (Porsch.[1])

Even in glass tubes, in which the adhesion of water to the walls is much less than in the capillaries of the wood, high cohesion forces have been proved. Steinbrink [2] found values of 2–5 atmospheres, according to the rate of flow and the width of the glass tubes, Dixon and Joly up to 150 atmospheres, and by using wood sap, actually over 200 atmospheres. Renner [3] proved that the liquid in the cells of the annulus of fern sporangia only ruptured at a tension of 300 atmospheres and Ursprung [4] obtained similar figures. The cohesion in the conducting channels of spruce wood appears, however, according to Holle, to be considerably smaller.

A prerequisite for the maintenance of cohesion is the absence of gas bubbles in the liquid. Dissolved gases tend to separate in the form of bubbles on reduction of pressure ; a process which can be seen when a bottle of liquid charged with carbonic acid gas is opened. Cohesion experiments are only successful with very pure water free from dissolved gases. The water of the wood, however, always contains in solution, air—partly already dissolved from the soil and partly from the intercellular spaces—and carbonic acid, which arises through respiration. It was therefore long held to be impossible for the cohesion of the wood water to be maintained under great tensions, and this idea hindered the acceptance of the cohesion theory. In actual fact, however, no gas bubbles separate from the solution in the wood sap within the conducting channels. Small gas bubbles making their appearance would have to overcome the cohesion of the water, which actually far surpasses the tensions which occur in plants and thus would have to break down exceedingly high resistances. If the wood water comes under tension the dissolved gas separates in the places of least resistance, and therefore, not in the inside of the liquid channels but on the outside

[1] Porsch, O., Zur physiolog. Bed. d. Verholzung. Ber. D. Bot. Ges. 44, p. 137, 1926.
[2] Steinbrink, Jahrb. wiss. Bot. 42, p. 579, 1906.
[3] Renner, Jahrb. wiss. Bot. 56, p. 617, 1915.
[4] Ursprung, Ber. Deutsch. Bot. Ges. 33, p. 153, 1915.

of the imbibed membrane, which it can easily traverse by diffusion in a dissolved state, and passes into the intercellular and other air spaces. The fact is, that even under high tension no air bubbles appear inside the wood channels for a long time. Holle and Bode have directly proved this microscopically in isolated vascular bundles and leaf veins. The experiments of Strasburger,[1] V. Höhnel[2] and Lindner,[3] according to which gases under pressure-differences of less than 1 atmosphere diffuse through the imbibed wood-walls into the vessels and may be pumped out from there in gaseous form, did not take into consideration the resistance of cohesion to the formation of gas bubbles and so failed to reveal the actual condition of things. Their observations are only valid for cell walls which are bounded by gas on both sides, and for vessels empty of water.

Cohesion also makes it possible to cause mercury to ascend in narrow tubes and in wood, far above barometric height (Askenasy, Copeland, Ursprung,[4] Strasburger). In wide tubes, as in the ordinary barometer or exhaust pump, this is, as is well known, impossible. Here the liquid, in consequence of its great mobility, separates from the cell wall and leaves behind a Toricellian vacuum. Thus an exhaust pump acts with very narrow tubes quite otherwise than with wide ones. It is the microscopic narrowness of the conducting channels which makes possible the maintenance of the cohesion in wood and the great heights of ascent in high trees under the sucking action of the leaves. Against this advantage must be set the large increase in the resistance to filtration in narrow passages[5]—inversely proportional to the fourth power of the diameter of the tube. Cohesion will maintain itself longest in the narrowest conducting channels, the tracheids; the wide lumened organs, according to Holle, serve as reservoirs, which give up their store of water in time of need and replace it by air. The tracheae are consequently often filled with air. That the width of the tracheids in coniferous wood, according to Groom,[6] is governed according to the plentifulness of the water supply, is in consonance with this. Trees in arid regions have, on the whole, narrower tracheids than those in wet climates.

A result of the negative cohesion tension in wood-water is that the conducting channels of the wood become demonstrably narrower as soon as transpiration leads to tensions. Friedrich[7] showed, by measurements with a delicate apparatus, that the circumference of the tree-stem exhibits variations in the course of the day which run exactly parallel with the atmospheric forces producing evaporation, especially the humidity of the air. Bode[8] measured directly with the microscope

[1] Strasburger, Leitungsbahnen.
[2] V. Höhnel, Jahrb. wiss. Bot. 12, p. 47, 1879.
[3] Lindner, Cohns, Beitr. z. Biol. d. Pfl. 13, p. 1, 1917.
[4] Ursprung, Ber. Deutsch. Bot. Ges. 34, p. 475, 1916.
[5] Huber, *ibid.* 43, p. 410, 1925.
[6] Groom, P., A preliminary enquiry into the significance of tracheid-caliber in coniferae, Botanical Gazette 42, No. 4, 1914.
[7] Friedrich, Über den Einfluss der Witterung auf den Baumzuwachs. Mitt. a. d. forstlichen Versuchswesen Österreichs, 22, 1897. Also MacDougal, D. T., Reversible variations in volume, pressure and movements of sap in trees. Carnegie Inst. Publ. 365, Washington, 1925.
[8] Bode, Jahrb. wiss. Bot. 62, p. 92, 1923.

the contraction of vessels on the setting up of transpiration. Under prolonged drought the shrinkage of wood may proceed so far that gaping seasoning cracks (heat cracks) appear in living spruce stems, which close again on renewal of the water supply and relief of the sucking tension. As such trees go on living it may be assumed with certainty that liquid water is still present in the lumena of the wood during the shrinkage.

In spite of this resistance to the penetration of air, bubbles do finally appear in the water channels and displace the water, especially in the older wood and when there is great consumption of water. The sapwood of most trees contains a quantity of air which increases towards the interior of the tree, and the heartwood of conifers, as we have seen, generally no longer contains any liquid water. According to Renner,[1] this air can only have penetrated through pores. The closing membranes of the bordered pits are pieced by fine pores which are, it is true, stopped up with water by capillarity but allow of the passage of gases when the tensions are sufficient to overcome the capillary forces. Besides these, the pores of the plasmodesms originally present pass through the closing membranes of the pits leading from the vessels into the parenchyma cells and from these into the intercellular spaces. So long as the plasma of these cells is alive it prevents the entrance of air through such pores, but after its death air may be let through. Under ordinary circumstances, however, so many conducting channels remain free from air in young wood that sufficient continuous passages remain to ensure the regular supply of water.[2]

In conifers only a small part of the wood-water is driven out by air even in case of extreme shortage of water. In spruces whose sapwood was sawn through, Hartig [3] found the sapwood in the upper parts of the stem for the most part full of water up to 75 per cent. of the free space, after 4 and 10 weeks, when the crown had already dried up. Even the powerful sucking force of the needles was not sufficient to withdraw all the liquid water from the conducting channels, when the pushing up of water from below was made impossible. On the other hand, the continuous conducting channels of broad-leaved trees under similar conditions, had been, to a great extent, emptied of water from the cut surface upwards and filled with air.

When the wood-water is under great cohesion tension every air bubble which has penetrated into a vessel must fill the whole lumen immediately and drive out the water from it, because air will expand to an unlimited extent under a tension. Each air bubble also forms a nucleus for the further separation of dissolved air in gaseous form. Every air bubble therefore cuts out the whole vessel in which it appears from the conducting of water. In the conifers where the short tracheids divide the conducting channels into small chambers, the entrance of air only affects a very small part of the conducting passages; if, however,

[1] Renner, Die Porenweite der Zellhäute in ihrer Beziehung zum Saftsteigen. Ber. d. D. Bot. Ges. 43, p. 207, 1925.

[2] Friedrich (*loc. cit.*) proved, however, that the water content even in the youngest sapwood of the spruce varied within a day in accordance with transpiration. He found 65% of water in the youngest sapwood in the morning, 57.3% at noon and 59.6% in the evening.

[3] Hartig, Unters. a. d. forstbot. Institut in München, III, 1883.

an air bubble penetrates into a trachea of a broad-leaved tree, the vessel empties itself throughout the whole of its length, often more than a metre, so far as an open connection exists between its constituents. This difference between hardwoods and conifers can be easily followed macroscopically (Münch).[1] If, in summer, the rind is stripped off a tree without injuring the wood and the sapwood is stabbed with a knife across the fibres, a white strip running up and down the wood immediately originates from the wound, of the same width as the latter, indicating that the air has penetrated into the previously saturated wood. In a broad-leaved tree this air strip can be followed for a length of several decimetres, but in a conifer for only a few millimetres. Here also, however, the aeration proceed gradually for the length of several tracheids, proving that the tracheid walls in these circumstances do not permanently resist the penetration of air.

On the grounds of such observations and especially of physical considerations, the cohesion theory assumes that in the transpiring tree, only entire tracheae and tracheids, not parts of them, may be filled with air. Accordingly, for example, in young spruce wood with an air volume of 6–10 per cent., only 6–10 per cent. of the number of tracheids are excluded from transmitting water, the remainder are fully efficient. This number would be amply sufficient to establish continuous water channels throughout the whole sapwood, even if the distribution of the air-containing tracheids were unfavorable. The inductive proof of the absence of small air bubbles has, however, only been given in a few cases. Under the microscope the air is generally found distributed in the form of minute bubbles (Strasburger),[2] often in whole chains of them (Jamin's chains) which must oppose great resistance to the movement of sap. This arrangement of air in preparations may arise from the equalisation of the tensions after cutting the shoot, through the penetration of air and liquid with the consequent contracting of the air present into bubbles. In addition, according to Bode,[3] in the process of preparation small bubbles of water vapour may appear in the vessels. These are formed by the mere touching of the wall of the vessel with a needle in consequence of its deformation, and soon disappear again of their own accord.

Whether the water can move between the air bubbles and the wood wall,[4] and also what forces would be required for the movement of Jamin's chains,[5] have been investigated. These questions, formerly very much in the foreground, have by this time lost a great deal of their importance.

The extent to which surface forces are involved in the formation and demolition of water-vapour bubbles in the water of the wood was investigated by Bode.

As regards the magnitude of the driving forces of transpiration,

[1] Münch, Naturw. Grundl. d. Kiefernharznutzung. Arb. d. Biol. Reichsanst. f. Land- u. Forstw. X, H. 1, p. 105, 1919.

[2] Strasburger, Leitungsbahnen, p. 677 ff.

[3] Bode, Jahrb. wiss. Bot. 62, p. 92, 1923.

[4] Vesque, La séve ascendente. Rev. génér. de. Sciences, 1891. Ann. agronom., T. XI, 1885. Strasburger, Leitungsbahnen, p. 703 ff.

[5] Schwendener, 1886, Sitzungsber., Berlin, p. 561 (Ges. Abh. 1, 207).

there is no doubt that the power of transpiration would be equal to the greatest demands. Even the evaporation caused by the reduction of the relative humidity of the air from 100 per cent. to 93 per cent. produces a sucking force of 100 atmospheres.[1] The great forces of evaporation are not, it is true, fully utilised in the plant. The water does not evaporate immediately out of the conducting channels but out of the leaf parenchyma, whose delicate walls, on giving up water, collapse and consequently cannot transmit cohesion tensions directly. Between the force of evaporation and the cohesive force of the water channels is interposed the osmotic absorptive force of the leaf cells, whose maximum, the osmotic power of the cell sap at threshold plasmolysis—*i.e.* with fully relaxed cell wall—limits the absorptive power of the cell.

Renner [2] determined the absorptive force of transpiring parts of plants and at the same time the resulting cohesion tensions in the following way. He measured the rate with which a leafy shoot sucked water through a glass capillary (a potometer); then cut off the leafy end of the twig and connected the stump to an exhaust pump of known power. By comparing the suctions so obtained with those of the leaves, he was able to assess the magnitude of the sucking power of the leaves. If then the resistances of the shoot thus treated were artificially raised by pinching, squeezing, notching, stopping up, etc., or by osmotic resistances induced by supplying rooted plants with salt solutions, maximum sucking actions and sucking forces could also be determined. Negative pressures which could raise water above the height corresponding to one atmosphere, generally to many atmospheres, were always found, even in plants in the open. Nordhausen,[3] who repeated Renner's experiments with somewhat different methods, obtained fundamentally similar, though as a rule somewhat lower results, which may be considered minimum values. The absorptive powers of various tissue constituents were investigated by Ursprung, Blum and Hayoz,[4] by plasmolytic means. Their troublesome and difficult procedure consisted in the main of determining the concentration of a sugar solution in which the volume of the cells neither increased nor diminished by exchange of water with the solution. The absorptive power of the cell is then equal to the osmotic absorptive power of the sugar solution. In this way absorptive forces were found in the leaves which corresponded, in general, with the requirements of the cohesion theory. They are greatest in the palisade parenchyma, less in the spongy parenchyma and in the epidermis. Within these kinds of tissue the absorptive powers are the greater as the distance from the leaf veins which supply water increases. The osmotic values of the stomata are fairly independent of those of the surrounding cells. Higher absorptive powers prevail in the upper leaves than in those growing lower down or

[1] Renner, Jahrb. wiss. Bot. 56, 1915.

[2] Renner, *loc. cit.*, 1911, 1912, 1925.

[3] Nordhausen, Ber. D. Bot. Ges. 34, p. 619, 1916. Jahrb. wiss. Bot. 58, p. 295, 1919, 60, p. 307, 1921.

[4] Ursprung und Blum, Ber. D. Bot. Ges. 34, pp. 525, 539, 1916, 36, p. 577, 1919; 37, p. 453, 1919; 39, p. 70, 139, 1921. Biol. Zentralbl. 40, p. 193, 1920. Jahrb. wiss. Bot. 63, p. 1, 1924. Ursprung und Hayoz, Ber. D. Bot. Ges. 40, p. 368, 1922. Ursprung, Ber. D. Bot. Ges. 41, p. 338, 1923. Flora 118–119, 1925 (Goebelfestschrift), p. 566. Hayoz, Beitr. z Kenntn. d. Saugkraft des Efeublattes, Diss. Freiburg (Schweiz), Passau, 1923.

in the shoots and roots. In the root cortex absorptive powers diminish from within outwards. Values of over 40 atmospheres were found in the leaves.

The limiting value of absorptive power—the osmotic value at threshold plasmolysis—does not always run parallel with the effective absorptive powers found, as the latter depend in a great measure on the water saturation. According to detailed analyses by Ursprung and Blum,[1] the osmotic value in the beech is highest in the palisade parenchyma; it varies with the time of year and the time of day. In the leaves of trees it amounts generally to over 20 atmospheres, but often to over 40, and in the highest instance hitherto observed, in mangroves, which have to absorb against the osmotic resistance of salt sea water, to 205 atmospheres. According to comprehensive data obtained by Korstian [2] by the measurement of the depression of the freezing point in expressed cell sap, the osmotic value during the growing period is always higher in woody plants than in herbaceous plants and higher in dry localities than in moist ones.

If the walls of the evaporating leaf-cells are so stiff that they oppose a considerable resistance to the shrinking of the cells on loss of water—as is to be assumed, for example, for epidermis cells and the green cells of pine needles which are strengthened by resilient ridges—cohesive forces may also become effective in the leaf parenchyma and raise the absorptive power of the leaf cells above their osmotic limiting value (Holle, *loc. cit.*).

In any case the absorptive powers of the leaves easily suffice to overcome the weight of water and the height of lift even in the highest trees. Forces must also be available, however, to overcome the frictional resistances to the water current and to extract the water from the soil to whose particles it clings by adhesion or capillarity.

The frictional resistances increase in simple proportion to the rate of flow and diminish in proportion to the fourth power of the diameter of the conducting channels. Resistances also arise owing to the penetration of the sap stream through the closing membranes of the bordered pits. That these resistances, at least when the rate of flow is low, are remarkably small, is obvious from the "drop experiment" described by Th. Hartig. If a piece of stem, fully saturated with water, is cut off—best in the spring at the time when the sap is flowing—and a few drops of water applied to the upper cut surface, an equal quantity of water very soon exudes from the lower surface. The water applied fills up the menisci by which the water threads are suspended at the upper end and thus destroys the capillary adhesion which retained the water in the wood. Shoots with very wide vessels (Lianes) and long stems allow water to flow out even without the applying of drops. With greater rates of flow the frictional resistances are, however, greater and exceed that of the weight of water raised by many times.

[1] Ursprung und Blum, Über die Verteilung des osmotischen Wertes in der Pflanze; Ber. D. Bot. Ges. 34, pp. 88, 115, 123, 1916.

[2] Korstian, C. F., Density of cell sap in relation to environmental conditions in the Wasatch Mountains of Utah. Journ. Agric. Research, 28, p. 845, 1924. With references to literature.

Ewart [1] declares that high resistances are improbable. Huber [2] estimates the resistances to be at most 0.2–0.4 atmospheres per metre of the conducting passages with high rates of flow—values which correspond well with the differences in absorptive power at various heights in the tree,[3] actually measured by Ursprung and Blum. It is also to be noted that the resistances apparently become proportionally smaller as the height of the tree increases, as the lumena of the vessels in older trees and in the higher parts of the stem are wider than in young ones.[4] The proportion between the cross section of the conducting wood and the evaporating surface of the leaves should be the same on all parts of the plant, though this has still to be completely investigated, because Jaccard's data [5] are by no means sufficiently supported and experiments by other authors on other plants, to some extent fail to confirm the existence of such a condition of affairs. According to Hartig-Weber, however,[6] it is true that correlations exist in the beech between the amount of evaporation and the number and size of the vessels, and that in the beech the conducting capacity of the sapwood appears to be the same throughout the whole branchless stem, since the number of the vessels of an annual ring above and below is always the same in spite of differences in ring-breadth.

The anatomy of the conducting channels is in closest accord with the cohesion theory. The great stiffening of the conducting channels, of the wood by annular, spiral, reticulate and scalariform thickening or general thickening with the exception of the bordered pits, is necessary to sustain the great tensions to which the vessels of transpiring plants are exposed. The protective sheaths of thickened sclerenchyma fibres by which the vascular bundles are as a rule enclosed, serve to support the sucking tensions in the wood-water. The structure of the bordered pits, which are found exclusively on the walls of water-conducting channels but are never absent from these, is only understandable in this connection. If air has penetrated into a vessel the contents come under higher pressure, since the pressure of gases can only be positive even though smaller than atmospheric pressure, whilst the neighbouring vessels, containing water only, may be under strong negative tension. The closing membrane of the bordered pit is pressed against the wall of the water-containing vessel by this difference in pressure, so that the torus actually closes up the pore. In this way the rupture of the tender closing membrane and the passing of air from one vessel into the other are avoided. If both vessels contain water both stand under an equal negative pressure, the closing membrane remains in a middle position and allows water to pass through its very delicate marginal portion which is pierced by fine pores.

According to all this, the mechanics of the transpiration stream

[1] Ewart, A. J., The ascent of water in trees. Phil. Trans. of the Roy. Soc. of London, 198, p. 41, 1905. Proc. Roy. Soc. of London, 74, p. 524, 1905.

[2] Huber, B., Ber. D. Bot. Ges. Bd. 42, p. 27, 1924.

[3] Janse, Jahrb. f. wiss. Bot. 18, p. 36, and Strasburger, Leitungsbahnen p. 779, obtained varying values, in part similar to Huber's.

[4] Huber, B., Transpiration in verschiedener Stammhöhe. I. *Sequoia gigantea*. Zeitschr. f. Bot. 15, p. 465, 1923.

[5] Jaccard, Naturwiss. Zeitschr. f. Forst. u. Landw. 11, p. 241, 1913; 13, p. 321, 1918.

[6] Hartig-Weber, Das Holz der Rotbuche, Berlin, 1888, p. 69 ff.

appears to be amply explained by the cohesion theory. Even if it wants supplementing on the quantitive side, in respect of resistances to flow and the sucking forces in high trees, there can be no hesitation in acknowledging that the nature and magnitude of the forces depicted are sufficient to provide the water which is given off in transpiration.

All the water movements in plants are, however, not yet explained by it. It is obvious that evaporation by its own power can only cover its own requirements. There are, however, other requirements besides those of transpiration. There is, as we have seen, a quantity of water, small it is true, which remains in the plant as water of vegetation and of constitution, and in addition a very considerable quantity required to refill emptied water channels and water storage organs. If the water current were driven solely by suction forces, every vessel, once emptied, would be precluded from containing water for the rest of its life, the water content of the tree could at best only remain constant and never increase again from time to time and the long and short periodic variations in the water content of the xylem, already mentioned, which, especially in the bleeding species of broad-leaved trees reach considerable dimensions, would be impossible. Within the sphere of action of root pressure the filling up of water storing organs is done by the exudation sap and to a small extent by capillary forces. The action of these forces is, however, confined to the lower part of the stem and still other forces must be sought for the upper part of the tree.

Renner and other supporters of the cohesion theory assume that living cells in the conducting channels also take part in some way in the ascent of sap, though the mechanics of this co-operation could not be made comprehensible by the many attempts at vitalistic explanation.

The sap-stream theory of Münch, with which we have already made partial acquaintance in our discussion of exudation pressure, and shall discuss further in the chapter on the circulation of sap, seeks to close this gap.

CHAPTER XI

THE MINERAL NUTRIENTS

1. General.—It is easy to understand the importance of mineral substances in the economy of plants and animals, when they occur in the form of actual stones which act mechanically, such as the calcium phosphate and carbonate in the bony skeleton of the higher and the shells of the lower animals, and the calcium oxalate in leaves, the rinds of trees, and young fruit perithecia,[1] where, in many cases, it forms stony sheaths round the leaf veins and also stony walls or arches which, like the clumps of needle-shaped crystals [2] (raphides), are especially useful as a means of protection against the attacks of animals and also against mechanical pressure. Less easily recognisable is the chemical rôle played by mineral substances in the organism. The protoplasm with the nucleus has sulphur and phosphorus as never-failing constituents; iron is indispensable for the formation of chlorophyll. Magnesium is present in chlorophyll and in the stored material in seeds; moreover, mineral substances play a part in the conversion of soluble into insoluble compounds and as agents in many other chemical processes, and finally as constituents of the cell walls and in the setting up of osmotic actions in the cell sap. It is only a small number of elements whose compounds are indispensable for green plants: four metals: potassium, calcium, magnesium and iron, and three non-metals: sulphur, phosphorus and nitrogen. To these are added water, with its two elements, hydrogen and oxygen. The supplying of these nine simple substances through the roots forms just as necessary a condition of life for green vegetation as does the obtaining of the carbonic acid through the leaves. They are, however, not the only elements which the plant absorbs. Besides them, chlorine, silicon and manganese are almost never-failing constituents of the body of the tree. It is remarkable that aluminium, the universally distributed metal of clay, is only rarely found in large quantities in the plant. In the club mosses it may form a quarter of their ash, and Ramann [3] was able to find it in considerable quantities in the robinia. The ash of the lime,[4] for

[1] Baccarini, Intorno ad una probabile funzione meccanica dei cristalli di ossalato calcico. Ann. d. R. istit. bot. di Roma, I, 1, 1884.

[2] Stahl, Pflanzen und Schnecken. Jena, 1888, G. Fischer. Separate reprint from Jenaische Zeitschr. f. Naturwiss., Bd. 22.

[3] Zeitschr. f. Forst- u. Jagdwesen, XIV, 497.

[4] Compt. rend. Acad., Paris, T. CXX, 1895, 288.

example, however, contains only 0.0025 per cent. of alumina. According to Rothert,[1] all plants can absorb aluminium if it is offered in a suitable form; it is, however, for the most part retained in the roots.

The form in which the elements are offered to the plant is that of such salts as are found in the rock-forming minerals and their decomposition products. As sources of potassium, Mica and Felspar are especially important. Calcium is available for plants in combination with silica in the calcareous Felspars (Plagioclase), Augite and Hornblende as well as their derivatives, but also especially as carbonate in Limestone and Dolomite and as sulphate in Gypsum and Anhydrite. Another calcium salt, calcium phosphate, forms in Apatite, widely distributed in small quantities, the most important source of phosphorus, another being, perhaps, Vivianite (iron phosphate). Magnesium is available as a carbonate in Dolomite, as a silicate in Magnesia-mica, Augite, Hornblende, Olivine, Chlorite, Serpentine and Talc, whilst the universally distributed iron may occur in all the compounds and minerals mentioned and in many others. Finally, as sources of sulphur, Gypsum is to be mentioned and any other sulphates which may be formed by the weathering down of the widely distributed Iron Pyrites.

Two methods of investigating the behaviour of trees towards mineral substances are open to us: **ash analysis** and **cultural experiments.** It will be conjectured that the absorption of those substances which are never absent from the ash of plants is necessary for the plant, whilst the tendency will be to regard those which are sometimes present and sometimes absent, or which vary very much in quantity, as only accidental elements in plant nutrition. These questions are decided by the cultivation of plants in water or pure quartz sand to which quantities of nutrient substances are added, now one and now another of the nutrients mentioned being omitted. From the varying success of the plants so cultivated it is possible to decide which substances are necessary and which are not. It is even possible to judge of the quantities in which the individual substances are demanded. It is very difficult, however, to carry out such cultural experiments with trees in an adequate way, because of their slow development (which allows, for example, the decomposition products of the glass walls of the culture vessels to exert an influence), their subsequent increase in size and the demands they make on the physical condition of their culture medium. Hence in this sphere we have hitherto had to depend on ash analyses and the cultural experience of foresters. Ash analyses may, however, teach us about the content of the tree and its parts in mineral substances, and thus about its actual consumption; consumption, however, is not always the same as requirement. We know from the researches of agricultural chemists, that plants may exhibit a certain prodigality with mineral substances. When supplies are ample they are able to absorb large quantities of them without giving a correspondingly increased yield of organic substance. It will also be the same with trees. According to Weber,[2]

[1] Bot. Ztg., 1906, Bd. LXIV, p. 43. (Quoted from Jost.)

[2] Allgem. Forst- u. Jagdztg., 1886, and R. Hartig u. Weber, Holz der Rotbuche. *See* Büsgen, Kupuliferen.

for example, the calcium content of the silver fir increases with the calcium content of the soil and the manganese content of the beech is influenced by the condition of the soil. G. Krauss [1] closely investigated the variations in calcium content of beech foliage in light-leaves (of the autumn fall, 1923) and proved a far-reaching dependence of the absorption of lime on the soil conditions. Here also the exchange relationship between the absorption of calcium and that of silica, already previously observed,[2] could be further followed out. By determining, not the total calcium content but only (approximately) the calcium for the time being combined with oxalic acid, a fairly regular silicification of the beech leaf manifested itself when the habitat made the absorption of calcium difficult. The differences in ash content between wood of different ages in similar localities are much greater than those of wood of the same age grown in different localities. Especially in the case of the phosphorus content is the influence of age greater than that of the character of the soil.

2. The Time of Absorption of Mineral Substances.—It is important for the life of trees in communities, that the different species, at least in youth, supply their requirements for minerals at different periods in the growing season.[3] Thus larch and pine take up most of their potassium in late summer (mid-June to mid-September), whilst the spruce supplies itself with this element in early summer (mid-May to mid-July) and the silver fir mainly in spring (February to mid-May). The absorption of calcium occurs, with the larch and spruce chiefly in late summer, with silver fir uniformly from spring to late autumn; with the pine exclusively in late summer and autumn (mid-September to November). The absorption of magnesium by the larch is regular up to September, when it ceases, whilst in the case of spruce, pine and silver fir it lasts only from mid-May onwards. The larch shows a slight absorption of phosphoric acid in early and late summer, very great absorption in autumn, whilst the pine absorbs phosphorus exclusively and strongly in late summer, the spruce only moderately in early and late summer, the silver fir also only moderately and exclusively in spring and early summer. Ramann and Bauer,[4] who discovered these facts about the behaviour of young trees by the investigation of 50–100 specimens of 3–4-year-old plants of each species, and proved corresponding behaviour with regard to the absorption of nitrogen (*see* below), find in them a reason for the success of mixed forests composed of several species, in which also the whole condition of the soil is more favorable and lastingly so, than in woods which consist only of a single species.

Among broad-leaved trees, ash,[4] pedunculate oak [5] and beech [6]

[1] Forstw. Zentralbl., 1926.

[2] Ebermayer-Weber, Lehre von der Waldstreu.

[3] Ramann u. Bauer, Trockensubstanz, Stickstoff und Mineralstoffe von Baumarten während einer Vegetationsperiode. Jahrbuch. f. wiss. Bot., Bd. L, 1912, p. 67; Bauer, Stoffbildung und Stoffaufnahme in jungen Nadelhölzern. Inaug.-Diss., München. Separate reprint from the Naturwiss. Zeitschr. f. Land- u. Forstwirtsch., 1910.

[4] Bauer, Naturwiss. Zeitschr. f. Forst- u. Landwirtsch., 1911.

[5] *Ibid.*, *loc. cit.*, 1912.

[6] Kübler, *loc. cit.*, 1912.

were investigated. They make greater demands on the soil nutrients than the conifers, at least in youth, because they produce much more organic substance. In 2-year-old ash transplants even before the opening of the leaf, considerable quantities of potash, lime, silica and nitrogen were absorbed, but little magnesium and apparently no phosphoric acid. The absorption of all mineral substances reaches a maximum in early summer and falls off rapidly in late summer, absorption of calcium, least.

The pedunculate oak takes up only extremely little from the soil from March 15 to May 24. Potash absorption, like that of silica, reaches its maximum in the last weeks of June and during July, but also continues later. Magnesium is absorbed mainly between May 24 and June 25, calcium in greatest quantity in August and the first half of September. The absorption of phosphoric acid proceeds comparatively regularly from May 24 up to September 19 (close of the experiment).

Kübler's experiments on young beeches give an insight into the influence of manuring with basic slag, kainite, meat manures, dung, and compost on the absorption of mineral substances. The following excesses or deficits, in percentages of the material originally present in each case, were found :

	Dry matter	K_2O	CaO	MgO	P_2O_5	N
1. Before leaf-break—						
Unmanured	− 21	− 30	− 32	− 15	− 38	− 21
Manured	− 19	+ 1	− 14	− 30	+ 0	− 17
2. During period of leaf-break (in May)—						
Unmanured	+ 14	+ 43	+ 24	+ 8	+ 28	+ 22
Manured	+ 4	− 20	+ 1	+ 21	+ 15	+ 9
3. First part of the main growing season (mid-May to mid-July)—						
Unmanured	+156	+235	+216	+183	+107	+ 70
Manured	+193	+220	+199	+195	+177	+143
4. Second part of the main growing season (July to mid-September)—						
Unmanured	+164	+113	+ 81	+ 62	+155	+113
Manured	+683	+406	+587	+645	+521	+499
5. Close of vegetation (mid-September to mid-November)—						
Unmanured	− 14	− 84	−111	+ 31	+ 88	+ 23
Manured	−281	−191	−331	−316	−385	−290

In the first period there is to be recognised a falling off in the dry weight which is connected with respiration (*see* page 284). In no case have the mineral substances increased. Their apparent diminution in fact points to moving back into the soil, in so far as it is not perhaps explained by dissimilarities in the plants examined at the beginning and the end of the period. At the time of leaf-break the unmanured beeches were already absorbing potash, lime, phosphoric acid, and nitrogen, whilst in the case of the manured ones, leaf-formation, though it was much greater than with the former, was supplied by existing stores. The smallness of the increase in dry weight shows that here the development of the leaves (33 per cent. of the total dry weight as against 16 per cent. for the manured plants) drew chiefly upon the reserve materials of the previous year. In period 3 also (up to July 9)

the manured beeches have still scarcely surpassed the unmanured ones in the formation of dry matter or in the absorption of nutrient materials. The absorption of nitrogen alone is considerably greater, potassium is not at all, and phosphorus very little affected. In period 4 the influence of manuring at last becomes very evident. The decrease in dry matter and in mineral salts in period 5 is explained by leaf-fall.

It is noteworthy that the proportion of the root in the dry weight was the same at the end as at the beginning of the growing season and considerably greater in the unmanured plants than in the manured ones (*see* page 270 in the Chapter on Roots).

Conditions similar to those in trees are met with in the absorption of nutrients by agricultural plants. Schreiner and Skinner [1] grew large numbers of wheat seedlings for 24 days in nutrient solutions renewed every three days, with various amounts of calcium phosphate, sodium nitrate and potassium sulphate. During the first three three-day periods after germination, only very little phosphoric acid was withdrawn from the solution; in distilled water, the seedlings even gave up phosphoric acid to the water. The mean amount withdrawn during the time mentioned was: 10 per cent. phosphate, 39 per cent. nitrate, 52 per cent. potash. During the five following periods it was 21 per cent. phosphate, 44 per cent. nitrate, 35 per cent. potash. The withdrawal of phosphoric acid had thus increased and that of potash fallen off. The greatest withdrawal of nutrients as a whole, but the smallest alteration in the composition of the nutrient solution, took place on growth in the most favorable solution (10–30 per cent. phosphate, 30–60 per cent. nitrate, 30–60 per cent. potash). The more the composition of the solution differed from the optimum in the proportions of its constituents, not in the total concentration, the more it altered during the experiment, an attempt by the plants to withdraw the nutrients in the proportions of the optimum being thereby evinced. On the other hand it was also shown that the plants absorb the more of a nutrient substance the greater the quantity of it present in the solution, without, however, growing any better. Barley, summer wheat, peas and mustard [2] had already absorbed the maximum amount of nutrient substances at the time of flowering and the beginning of fruit setting, potatoes only by the final harvesting. Part of the materials in the first-named plants moved back into the soil at the time of ripening.

3. Mineral Content of the Leaves.—A tree's annual consumption of mineral matter includes everything that is laid down in the growing roots, the year's product of the cambium and the foliaged shoots; three aggregates of which the last is usually the greatest. Just as the greatest consumption of water takes place in the leaves through

[1] Bot. Gaz., Vol. L, 1910. Very effective presentation of the results in the triangle: Schreinemacher, Zeitschr. f. phys. Chemie, II, S. 81, 1893; Bancroft, Journ. f. phys. Chemie, VI, p. 178, 1902.

[2] Willfarth, Römer u. Wimmer, Über die Nährstoffaufnahmen der Pflanzen in verschiedenen Zeiten ihres Wachstums. Landwirtsch. Versuchsstationen, LXIII, p. 1, 1906; Biennials (Carrots) *see* Deleano, Univ. d. Genève, Inst. d. bot., 8 ser., fasc. 2 and 3, 1908; Bot. Zentralbl., 1910, Bd. 113; Olschowy, Zeitschr. f. d. landwirtschaftl. Versuchswesen in Österreich, 1899, II, Course of the nutrient-absorption of flax. (Ref. Beihefte z. Bot. Zentralblatt, 1900, p. 230); Tobacco and Maize: Sigmond, Journ. f. Landwirtsch., 1900, p. 251.

evaporation, so, in their cells the mineral substances which travel with the water, are deposited in the greatest quantities.

The following are some figures determined by Ramann [1] and Pässler [2] of the mineral content of the leaves, in percentages of the dry weight:

	Ramann.	Pässler.	
		Spring.	Summer.
Weymouth pine	1.31		
Pine, spruce, silver fir	2.11–3.59		
Hornbeam	5.21 (July) to 3.81 (Sept.)	5.38	6.30
Beech	5.14 (July)	4.58	5.78
Norway maple	—	7.04	7.46
Sycamore	—	6.66	8.23
Large-leaved lime	—	7.70	9.88
Small-leaved lime	—	7.55	8.40
Black alder	3.79 (Sept.)	5.68	5.55
White alder	—	3.84	4.69
Goat willow	—	5.90	6.36
Aspen	8.87 (July)	6.29	7.40
Common birch	—	4.49	4.90
Field elm	—	11.27	13.83
Wild cherry	6.70 (July)	7.54	8.37
Hazel	6.65 ,,	6.66	7.21
Pedunculate oak	4.51 ,,	4.79	5.58
Ash	7.0 (July) to 8.72 (Sept.)	8.47	10.66
Mountain ash	—	7.70	8.39
Black elder	—	11.46	15.01
Red elder	—	11.12	13.61
Horse chestnut	—	7.05	7.53
Acacia	9.11 (Oct.)	—	—

The figures show that great variations occur. Generally speaking the leaves which are poor in ash are those of the unexacting conifers, birch and white alder, the richest, those of the elders, elms, limes, and ashes—those of the most exacting species. The other broad-leaved trees lie between these extremes, whilst the needles of the conifers are less rich in ash than the leaves of any of the broad-leaved trees. The consumption of mineral substances in the annual formation of leaves naturally increases with the expansion of the crown, and the following figures by Ramann serve to show the quantities of minerals withdrawn from the soil by the roots and transmitted to the leaves in the different periods of life.

Annual consumption of the beech for leaf production in kilogrammes per hectare:

[1] Ramann, Zeitschr. f. Forst- u. Jagdwesen, 1883, 65.

[2] Pässler, J., Über den Futterwert der Blätter, Triebe und schwächsten Zweige verschiedener Laub- und Nadelhölzer, Tharandter Forstl. Jahrb. 43, p. 212, 1893. Contains further analyses of organic and inorganic constituents.

Beech I—III Yield Classes.

	Nitrogen.	Potash.	Lime.	Phosphorus.	Pure ash.	
21–40 yrs.	46.9	10.4	86.2	11.0	265.2	kg.
41–60 ,,	53.3	12.5	103.4	13.2	318.2	,,
61–80 ,,	61.6	13.5	112.8	14.3	345.5	,,
81–100 ,,	57.0	14.9	123.1	15.7	378.8	,,
over 100 yrs.	60.3	13.4	110.8	14.1	340.9	,,

Schroeder [1] has published analyses of the consumption of nutrients by young plants.

With regard to the behaviour of the leaves in the different months of the growing season, the analyses show that their mineral content rises so long as water is evaporated in them. If, therefore, comparable analytical results are desired, the material must be collected from the various trees at the same time. The ash-content of sun-leaves is somewhat lower than that of shade-leaves.[2] In the conferences at Eberswalde in April, 1896, between the heads of the Chemistry Departments of the Forest Research Institutions of Eberswalde, Munich and Tharandt, the month of August was fixed. At the same time it was laid down that care should be taken that only light-leaves and only leaves in the same stage of development should be used. In spruces and silver firs, needles in the autumn of their second year of growth, in the pines, in the autumn of their first year, are to be employed.

An example of the composition of a leaf-ash may be afforded by Rissmüller's [3] analyses, which have become famous by reason of Wehmer's [4] showing, by comparing the results expressed in percentages of the total ash and the absolute figures, that conclusions as to the movement of the mineral substances may not be drawn simply from representations in the first form.

I. Percentage of potash and phosphoric acid in the ash of beech leaves in the various months:

	Potash %.	Phosphoric acid %.
May	31.23	21.27
June	21.47	8.43
July	11.85	5.24
August	9.81	4.53
September	10.53	4.24
October	7.67	3.22
November	5.78	1.08

[1] Schroeder, Über die Düngung d. Saatkämpe u. Forstgärten mit spez. Berücks. d. Nährstoffbedarfs junger Fichten. Thar. Forstl. Jahrb. 43, p. 129, 1893; *comp.* also Vater, D., Kalkgehalt d. Bodens und der Rotbuche, *ibid.* 71, 1920, p. 319.

[2] Leiningen, Graf zu, Naturw. Ztschr. f. Land- u. Forstwirtsch. 3, p. 207, 1905.

[3] Landwirtschaftl. Versuchsstationen, B. XVII, 1874, 17.

[4] Landwirtschaftl. Jahrb., 1892; Ber. d. D. bot. Ges. X, 1892. Further literature *see* Swart, Die Stoffwanderung in absterbenden Blättern. Jena, 1914, G. Fischer. Pässler, J., Wanderung der anorgan. Bestandteile d. Rotbuche. Thar. Forstl. Jahrb. 43, p. 63, 1893; with analyses. Schroeder, Supplemente z. Tharandter Forstl. Jahrb. Bd. I, p. 173.

II. Content in grammes of 1,000 beech leaves :

	Potash %.	Phosphoric acid %.
May	0.77	0.53
June	1.20	0.46
July	1.28	0.56
August	1.19	0.66
September	1.14	0.45
October	0.87	0.36
November	0.74	0.14

Since the young May shoots and leaves are formed, in deciduous trees almost entirely, in conifers, very largely from the reserve materials of the older parts of the tree, the latter are to a great extent impoverished in mineral matter by the formation of shoots. The extent of this impoverishment is shown by Bauer's investigation of 4-year-old spruces. During the time of development of the shoots, up to May 22, the stem and root of the plant had lost and given up to the young shoots 13 per cent. of dry matter, of which 19 per cent. was potash, 27 per cent. phosphoric acid and 22 per cent. nitrogen. The roots were most impoverished in these substances. On the other hand, the newly-formed spruce needles were extraordinarily rich in the so-called valuable nutrients, especially nitrogen. The storing of potash and nitrogen in the roots and their diminution in the spring is also recognisable in analyses by Ramann.[1] In seed years, according to Weber,[2] the rind and the wood lose magnesium and nitrogen (*compare* also page 354).

According to analyses by Ramann,[3] the foliage of an old beech possesses very early, at least after the completion of leaf unfolding, the normal content of the important mineral nutrients—nitrogen, potash and phosphoric acid ; the quantity of these substances does not alter so long as the leaves remain in a working condition. Lime and silica increase continually or only become constant much later. The final conclusion which Ramann draws from the analyses—that retro-migration does not occur so long as the leaf remains alive—is to be understood to mean that the content of the leaf in mineral substances does not diminish. Retro-migration may take place in spite of this ; it only requires to keep pace with immigration.

Ramann [4] has investigated the mineral content of leaves (beech, oak, hazel, plane and maple (*Acer dasycarpum*) in the daytime and at night, and found that the lime content rises at night and falls again by day. Ramann concludes from this that calcium takes part in the passing out of assimilates from the leaves, since, during the formation of organic substances, this is more rapid in the daytime than in the night. The replacement of the calcium which has moved out during the day with the assimilates would take place at night. No migrations of other mineral substances which had led to a noticeable difference in the

[1] Ramann u. Gossner, Aschenanalysen der Esche. Landwirtsch. Versuchsstationen 76, 1912.

[2] Weber, Forstl. naturw. Zeitschr., 1892.

[3] Wanderungen der Mineralstoffe beim herbstlichen Absterben der Blätter. Landwirtschaftl. Versuchsstationen, LXXVI, Berlin, 1912, P. Parey.

[4] Jahrbuch f. wiss. Bot. Bd. L, 1912.

composition of the ash in the daytime and at night were found by Ramann.

The changes in the mineral content of the leaves which are to be met with on various kinds of soil are also of great importance in Forestry. The fallen foliage has quite different manurial effects on the forest soil according to its content in salts. The lime content of the leaves varies up to twofold according to the locality; with increasing difficulty of lime absorption, a strong silicification of the leaves occurs.[1] Beech litter, poor in lime, has a much less favorable effect for the micro-organisms of the soil than litter rich in lime, which maintains the soil in activity.[2]

4. Mineral Content of the Rind.—The ash content of stem structures is greater in younger organs than in older ones, greater in the tips of the twigs of large trees than in the stem and there also potash and phosphoric acid are most plentiful. The higher ash content of such shoots is due to their possessing a larger proportion of rind. The rind is always richer in ash than the wood belonging to it, but its ash content varies within wide limits. Ramann [3] gives values of up to about 0.75 per cent. of the dry matter in the rind of the pine and birch, 1.4 to 1.8 per cent. in the spruce, 2 per cent. in the silver fir, 3–4 per cent. in beech and oak and 8–9 per cent. in the field maple and elm. Bark is always poorer in ash than the living rind. For this reason the ash content of the rind of bark-forming trees falls off with age owing to the increasing formation of bark. Conversely, the ash content in smooth rind rises with the age of the tree, because the greater portion of it takes a continuous part in the physiological exchanges and thereby becomes enriched in insoluble compounds.

Analyses by R. Weber (Ramann, *loc. cit.*) demonstrate this very clearly for the oak and beech. Lime is specially prominent in quantity among the mineral substances in the smooth rinds, *e.g.* in the hornbeam (7.7 per cent. lime with 8.8 per cent. pure ash), the ash (3.3 per cent. lime with 4.1 per cent. pure ash) and the majority of the other species such as oak, alder, robinia, hazel, mountain ash, etc. Elm rind also possesses a high lime content (7.777 per cent.) along with 0.421 per cent. silica, which is found in even greater relative proportions in the rinds of beech and spruce. Potash occurs more plentifully in the rind than in the wood. The hard mineral materials in the rind may provide a certain protection against the gnawing of animals; though the calcium oxalate in the rind of trees is not entirely inactive in the physiological exchanges. Kraus [4] found that as a rule it diminishes in the rind at the time of the breaking of the buds, to the extent of 12 per cent., 42 per cent. or even 50 per cent. It may thus be dissolved and again drawn into the physiological exchanges.

[1] Krauss, Über die Schwankungen des Kalkgehaltes im Rotbuchenlaub. Forstwiss Zentralbl., 1926, p. 401.

[2] On the buffer action of lime in beech litter, *comp.* Ramann, Zeitschr. f. Forst- u. Jagdwesen, 1922, p. 4.

[3] Zeitschr. f. Forst- u. Jagdwesen, 1883, p. 4.

[4] Über das Verhalten des Kalkoxalats beim Wachsen der Organe. Flora, LXXXIII, 1897, p. 54.

5. The Mineral Content of the Wood.[1]—The mineral content of the wood is very small compared with that of the rind. In most species of trees it amounts to 0.3–0.4 per cent. of the dry matter, and seldom reaches, as in the ash-rich robinia, 0.5 per cent., but rarely falls below 0.3 per cent. as in the pine (0.22–0.24 per cent.) and Weymouth pine (0.19 per cent.). According to Daube's investigations (Forstliche Blätter VII, 1883, 177) on the larch, pine, spruce and oak, the ash content of the sapwood is greater than that of the heartwood, whilst sapwood trees, like beech and silver fir, according to Hartig and Weber (Holz der Rotburche, p. 143), exhibit the opposite condition. Especially does the ash of sapwood contain more phosphoric acid and potash than heartwood ash, though the latter is richer in lime.[2] The nitrogen content again, is greater in sapwood ash than in the heartwood. Daube sees the reason for the smaller content of the heartwood in the substances named, in a migration from it of the most important mineral substances.

R. Hartig and Weber, in their already oft-quoted work, gave detailed particulars of the distribution of mineral substances in stem wood. By analysis of wood sections which were taken from the trial stems at various heights, and the separate examination of the ash samples from groups of consecutive annual rings, they were able to form a picture of the variations in mineral content over the length and cross section of the tree.

The ash content of the xylem of the beech, in percentage of the dry matter, increased generally from the periphery of the tree to the centre and in each growth period from below upwards. The minimum content in the centre, found by Daube, only made its appearance when the formation of heartwood occurred, which, as previously remarked, in the case of the beech is of a pathological nature. The maximum ash content is found in the middle of the section of the tree in which the stem spreads out into the branches, often in the top timber.

The variations in the ash content of successive groups of annual rings in one and the same tree resemble, in the main, the variations recognisable in the proportion of ash to dry matter in different trees of the corresponding age classes. They are worthy of note, because they throw a gleam of light on the relation between growing space and the mineral nutrition of trees. The percentage of ash in the wood of the beech falls off regularly with the age of the tree up to the 60th year; it rises again in the age gradation 80–90 years and then falls. Weber explains this by the crowded stand in the sapling and pole forest periods of the beech forest bringing about the first diminution of the percentage of ash in the individual trees. Towards the end of the thinning period, the individual stems attain a greater growing space for nutrition, and free crown development, whereupon the ash percentage again increases.

[1] Mineral content of the Cambium, *see* above, p. 184. The magnesium content of the cambium rises and falls with its dry matter. The phosphoric acid content follows the magnesium rather than the calcium: Sieber, *loc. cit.*

[2] Weber, Forstl. Naturw. Zeitschr., 1892. Zimmermann, Zeitschr. f. angew. Chemie. Ref. Bot. Zentralbl., 1893, VI, 37. Molisch, Bot. Zentralbl., 1881, IV, 425, quoted from Zimmermann.

A few more analyses of wood may be given here [1]:

Spruce, 60 years. Inner wood . . .	48.63 C,	5.8 H,	45.18 O + N,	0.39 ash
Silver fir, 100 years without rind . . .	50.95 C,	5.91 H,	42.21 O + N,	0.93 „
Pine heartwood, 100 years	51.48 C,	6.11 H,	42.09 O + N,	0.32 „
Oak heartwood . .	48.80 C,	5.42 H,	44.88 O + N,	0.90 „

6. Mineral Content of Various Species.—Great differences exist in respect of ash content between the various species. I extract most of the following data from Ramann's oft-cited book, where the collected literature is to be found.

The pine is among the species poorest in ash and is surpassed by the spruce in potassium- and calcium-content, less so as regards phosphoric acid. The silver fir contains considerably more potassium than the pine and spruce, so that it is cited as a potash tree, and also somewhat more phosphoric acid, but falls behind the other two in lime content. The content of the larch in mineral nutrient materials is smaller than that of the spruce and silver fir, and that of the Weymouth pine is the smallest of all the trees investigated. A high content of magnesium in all parts of the tree is characteristic of the larch. Further, as an example of the variations that occur, it may be mentioned that J. v. Schroeter found over 33 per cent. of manganese protoxide in silver fir ash, whilst Councler only came across it in small quantities. The Douglas fir contains more potash and less lime in the wood than does the spruce.[2]

Among the broad-leaved trees, the oak differs from the beech by a smaller absorption of potassium and phosphoric acid and a greater absorption of calcium in the production of wood. Wild cherry, beech and hornbeam contain 0.134–0.195 parts of potash and phosphoric acid in 100 parts of dry matter; mountain ash, field elm, oak and field maple, 0.210–0.234 parts of the same substances; aspen, wild apple and hazel, 0.293–0.331 parts, and finally the ash, 0.4 parts. The robinia takes up very large quantities of mineral matter and contains an especially large amount of lime in the leaves and in comparison, less potash and phosphoric acid.

With regard to the importance of these facts for tree life, it should be remembered that, in the first place, they give information as to the extraction of mineral substances which the soil suffers through the trees mentioned. That this need not coincide with their needs and their demands as to soil quality is best shown by the behaviour of the wild acacia. It absorbs very large quantities of minerals and so extracts much from the soil; nevertheless it is to be called unexacting, because it can supply its needs also from poor soils, exhausting the latter, it is true, earlier than other species of trees. The conceptions: demands, needs and extraction are very well distinguished from each other in Ramann's book.

[1] Hartig, R., Zersetzungserscheinungen der Nadelholzbäume und der Eiche, Berlin, 1878.
[2] Hoppe, Zentralbl. f. d. ges. Forstwesen, Wien, 1900.

In conclusion, the mean percentage composition of the wood ash of a number of trees is appended.[1]

	No. of Analyses.	Ash.	In 100 parts ash.									
			K_2O	Na_2O	CaO	MgO	Fe_2O_3	Mn_3O_4	P_2O_5	SO_3	SiO_2	Cl.
Beech ..	9	0.46	30.86	2.01	28.85	11.83	1.07	5.26	14.72	2.87	2.42	0.09
Oak ..	13	0.48	34.78	2.36	22.44	16.54	0.62	2.69	16.98	2.75	0.71	0.32
Birch ..	6	0.33	23.60	2.27	29.03	16.48	0.90	8.66	14.71	1.69	1.99	0.66
Pine ..	7	0.30	14.31	0.99	53.64	10.69	0.11	3.34	6.05	3.51	2.61	—
Larch ..	6	0.17	33.57	1.70	45.14	13.20	3.04	—	7.68	2.05	3.23	—
Spruce ..	9	0.21	19.66	1.37	33.97	11.27	1.42	23.96	2.42	2.64	2.73	0.07
Silver Fir..	2	0.24	39.87	0.90	11.14	9.55	0.73	28.56	6.13	1.80	1.33	—

7. The Rôle of the Mineral Nutrients in Plant Life.—To rightly understand the rôle which the mineral substances mentioned play in plant life, it is necessary first of all to keep in the foreground the fact that the various salts, quite apart from their nutritive value, offer the best conditions for plant life in the form of a mixture with a definite proportion of each of them. A nutrient solution which contains the necessary salts in the right proportions is called an equalised or balanced one. In such a solution one salt may nullify the poisonous effects of another. Thus Hansteen Cranner has shown that if the ions of magnesium, sodium or potassium salts alone are at the disposal of plants, the kations of these salts, especially the magnesium ions,[2] set up a sickness of the roots. In suitable mixtures, on the other hand, potassium and magnesium ions in part mutually annul their poisonous effects and calcium ions render non-poisonous both potassium and magnesium solutions when they are supplied in the right proportions.[3] Such toxic actions may alter the properties of the cell membranes and so again affect nutrition. From this it is evident that, to the question of the importance of a mineral substance for the plant, no answer can be expected in the sense that each individual substance is alone responsible for a single definite life process. Nevertheless manuring experience does teach that certain activities of the plant are specially strongly influenced by the absence or predominance of definite mineral substances. The optimum proportion of calcium to magnesium[4] varies according to the nature of the salts and of the plants. For cereals it is stated to be one, for onions, spinach and cabbage two, for leguminous plants three. It is also to be kept in mind that the mineral substances influence transpiration. Plants raised in mixed nutrient salt solutions generally transpire less than those kept in distilled water. In very dilute (0.05–0.25 per cent.)

[1] Ebermayer, Physiolog. Chemie d. Pflanzen I, 737, Berlin, 1882.

[2] Hansteen Cranner, B., Über das Verhalten der Kulturpflanzen zu den Bodensalzen. I–III. Jahrb. f. wiss. Bot. XLVII, 1910, and LII, 1914; Poisonous action of Magnesium *see* also Loew Flora, XCII, 1903, and Landwirtschaftl. Jahrbücher, XXXII, 1903.

[3] Faack, Mitteil. d. Landwirtschaftl. Lehranstalt d. k. k. Hochschule f. Bodenkultur, Wien, 1913, 1914.

[4] Loew u. Aso, Bot. Zentralbl., Bd. 99, 1905, p. 56; Bernardini e Corso, Staz. sperim. agrarie, XLI, 1908, p. 191 (Bot. Zentralbl. Bd. 110, 1909, p. 476); Benecke, Ber. d. D. bot. Ges., Bd. 25, 1905. The poisonous effects of potassium and magnesium salts can be nullified by calcium salts in the alga *Spirogyra*; Loew u. Honda, Junge Pflanzen japanischer Koniferen. Bull. agric. coll. Imp. Univ. Tokio, Vol. II, 1896.

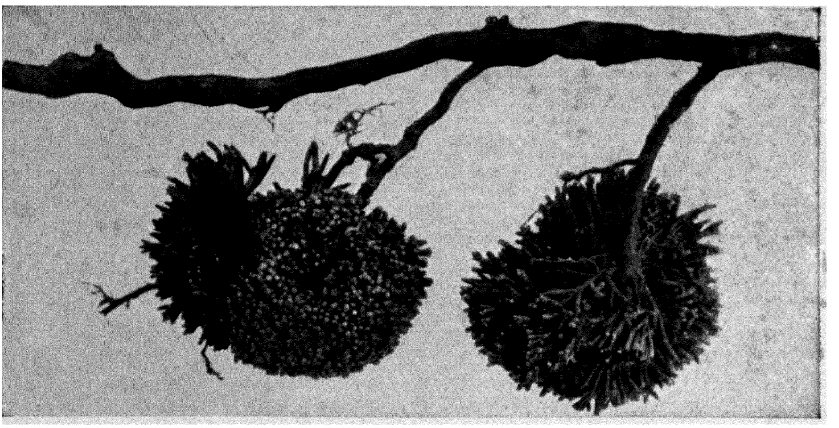


FIG. 132.—Nitrogen collecting root nodules of the Alder. Half natural size. (Mch.)

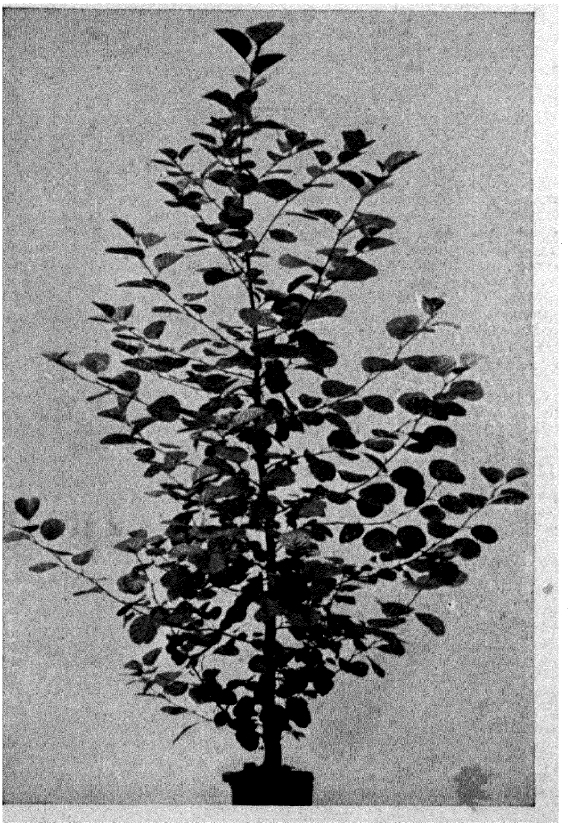


FIG. 134.—Alder several years old, raised by Nobbe in a nutrient solution free from nitrogen.

[To face p. 337

solutions of single nutrient salts, transpiration as compared with distilled water rises with the salt content of the solutions until it reaches a maximum at a certain concentration which, with alkaline salts, lies at a lower, with acid-reacting salts, at a higher percentage content than with salts of neutral reaction. With higher salt concentrations transpiration falls off and with 0.3–0.5 per cent. solutions becomes smaller than with distilled water.[1] Plants are not equally sensitive to over-manuring [2] with nutrient salts. The phenomenon that plants in solutions rich in potash appear dark green and turgid but in isosmotic lime solutions, pale green and limp, Hansteen Cranner explains by the influence of those salts on the supplying of water.[3] Shortage of nitrogen causes the loss of the full green colour in agricultural plants [4] and in one-year-old pines,[5] and the appearance in its stead of a light green or yellowish coloration. The needles remain small and weak. Pines plentifully supplied with nitrogen have strong, dark green needles. In the absence of sulphur, pine needles remain small and delicate and exhibit a palid green different from the coloration induced by the absence of nitrogen. Without phosphorus, pine plants become bluish red even in August and dull violet later. According to Vater's observations [6] also, young pines become bluer in colour with a shortage of phosphoric acid. Vater suggests that this may possibly be due to anthocyanin, which pigment appears red when the reaction of the cell sap is acid, and bluish red when it is alkaline.

Möller's pines developed much more vigorously in the absence of magnesium than when sulphur and phosphorus were excluded. The needles were yellow at the tip, red in the middle and remained green at the base. Mamelli also observed the scantiness or absence of green coloration in the absence of magnesium. Pine seedlings, in the absence of potash, became dull, pale green. When iron is excluded, plants do not become green, though chlorophyll contains no iron. However, as Vater [7] insists, no conclusions as to the chemical composition of the soil can be arrived at with certainty from these colorations because other factors also cause similar colour changes. A superabundance of lime causes a yellowing of the seedlings of plants averse to lime, such as the broom, sweet chestnut, maritime pine (*Pinus pinaster*) and many species of lupins, which it is sought to explain by the upsetting of the absorption of iron from the soil. It appears to be curable by iron,[8] and plants which, by means of acid excretions from their roots, dissolve the iron of the soil in spite of excess of lime, do not become yellow. Lime chlorosis disappears of itself, however, if once the plants survive the

[1] Burgerstein, Die Transpiration der Pflanzen, p. 142, Jena, 1904, G. Fischer.

[2] Warnebold, Zur Kenntnis der Wirkung starker Düngesalzgaben auf Entwicklung und Bau der Pflanzen. Inaug. Diss. d. Univ. Göttingen, 1916, Merseburg.

[3] *Loc. cit.*, 1914, p. 539.

[4] Möller, A., Karenzerscheinungen bei der Kiefer. Zeitschr. f. Forst- u. Jagdwesen 36, 1904; Willfarth u. Wimmer, Journal f. Landwirtschaft. 1903, p. 129; Mamelli, Bot. Zentralbl. 122, p. 200; Gerneck, Inaug-. Diss. Göttingen, 1902. (Maize, cress, oats, wheat.)

[5] Burgerstein, *Loc. cit.*

[6] Das Zulangen der Nährstoffe der Waldboden usw. Tharandter forstl. Jahrbuch, LIX, 1909.

[7] Vater, Naturwiss. Zeitschr. f. Forst- und Landwirtschaft. 8, 1910, p. 576–577.

[8] Mazé, Ruot u. Lemoigne, Chlorose végétale provoquée par le Carbonate de Calcium. Compt. rend. Acad. sc. Paris, CLV, 1912, p. 435.

sensitive juvenile stage.[1] Meanwhile investigations by Mevius [2] show that it is not the calcium ion in itself which causes the injury but the alkaline reaction induced by excess of lime. The low hydrogen ion concentration increases the permeability of the plasma for salts and the protoplasm becomes flooded with them.[3] Lime is indispensable even for the calcifugal plants. According to agricultural experience, excess of lime also hinders the absorption of potassium ; an injury which can be nullified again by heavy potash manuring (Ehrenberg's Lime-potash Rule).

On the degree of acidity of forest soil several researches have been made, from which it appears that the degree of acidity undergoes great variations according to the humus- and lime-content of the soil, that it changes with the depth in the soil and that it influences the composition of the soil flora. Forest trees appear, on the other hand, to be much less dependent on the acidity of the soil than agricultural plants, though it may be observed that the most exacting hardwoods, maple, ash, elm, have a preference for basic soils, whilst the conifers are, within wide limits, independent of soil acidity for their success. The fertility of forest soils is at any rate not so dependent on acidity as that of agricultural soils. It appears that most of our forest trees can make themselves independent of soil acidity to a great extent by means of their mycorrhiza (*q.v.*). Investigations into this matter are, however, not yet complete and have not yet adequately solved the question.

Sulphur and phosphorus are constituents of the living substance of the plant—the protoplasm and the nucleus. They cannot, therefore, be absent from any cell and are consumed especially where protoplasm and nucleus are multiplying, and thus in the formative tissues of the shoots and roots and in the cambium. The nucleins, characteristic of the cell nuclei, are phosphorus compounds the formation of which sets in strongly when flowering is over, in order to supply the seed.[4] According to their acid, neutral or alkaline character, phosphates have an influence on the solution and formation of starch.[5] Without phosphates, according to Noll,[6] development comes to a complete standstill. Life continues but the dividing tissues are quite quiescent. With a fresh application of phosphates abundant sprouting occurs. According to Schimper,[7] much potassium phosphate—a compound already produced in the body of the plant from the calcium phosphate absorbed through the roots—is decomposed in the places mentioned, with the consumption of the phosphorus, and is constantly produced by fresh supplies of calcium phosphate flowing in. From the latter new potassium phosphate is formed by the calcium salt of an organic acid. This explains the occurrence of crystals of calcium oxalate in the neighbourhood of the growing point and in the products of the cambium on the side towards the rind. To its power of forming with the oxalic acid this salt, which

[1] Büsgen, Kieselpflanzen auf Kalkboden. Bot. Jahrb., hrsg. von A. Engler, Bd. L. Supplementband, 1914. Engelmann, Leipzig u. Berlin.
[2] Mevius, Jahrb. wiss. Bot. 60, 1921.
[3] The same, Zeitschr. f. Bot. 16, 1924.
[4] Iwanowska, Bull. de. l'acad. d. sc. Cracovie, 1906.
[5] Fouard, Ann. institut Pasteur, 1907, p. 475.
[6] Bot. Zentralbl. 1895, III, 184.
[7] Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze. Flora, 1890.

is only soluble in the cell sap under special circumstances, calcium owes some part of its importance for the plant. Especially, however, does it appear indispensable for the normal formation of the cell walls. It also prevents the injuries which the cell walls of roots suffer in distilled water (*see* Hansteen Cranner, *loc. cit.*). Oxalic acid is a powerful poison for cells which is made innoxious by its combination with calcium. Schimper believed that he was able to detect poisoning phenomena as a result of the accumulation of oxalic acid, in plants which were raised without supplying calcium. Portheim puts down the sickening of plants raised without lime to formaldehyde poisoning.[1] It is true that, generally speaking, phenomena of this sort do not occur, because plants can regulate their physiological exchanges according to circumstances. When little calcium is present, the production of oxalic acid is restricted. That oxalate crystals may serve as a means of defence against the gnawing of animals [2] and against pressure has already been mentioned in the discussion of the rind. The calcium oxalate [3] present in the membranes of the green leaf-cells of the abietineae, except the larch and the two- and three-needled pines, also plays a similar part. In many cases, however, the calcium oxalate is again dissolved and the calcium given a new chemical rôle. Thus, for example, according to G. Kraus,[4] 50 per cent. of the calcium oxalate stored in the rind of the twigs of apple trees passes again into solution between the beginning of April and the beginning of May. The importance of lime for the physical condition and the acid content of the soil and for the conversion of the ammonia compounds in it, can only be briefly mentioned here.[5]

We know magnesium as a constituent of chlorophyll and the protein granules which occur as the storage form of nitrogenous substances and in the seed (Aleurone grains). It is also found very plentifully, together with potassium, in the formative tissues, in which calcium is absent, and in the green leaf-cells and the sieve-tubes. Loew,[6] therefore, ascribes to these two metals a rôle in the carrying over of phosphorus into organic compounds, as magnesium phosphate is more easily decomposed than calcium phosphate. In plants raised without potash, there is a diminution in the size of the leaves and in the thickness of the stalk and assimilation finally ceases.[6] Like calcium, magnesium is also to be found in the plant as an oxalate. Reed [7] found that potash is necessary for starch formation and nuclear division, phosphorus similarly for the conversion of carbohydrates and nuclear division, calcium for the growh and activity of the chlorophyll granules and for the formation of cell walls but not for nuclear division, magnesium for the action of chlorophyll.

[1] Sitzungsber. d. Wiener Akad. Math.-nat. Kl, CXV, 1906.

[2] Stahl, Pflanzen und Schnecken. Jena, G. Fischer; Räuber, Die natürlichen Schutzmittel der Rinden, etc. Jenaische Zeitschr. f. Naturwiss., Bd. 46, 1910. Against Stahl: Heikertinger, Biol. Zentralbl. XXXIV and the work quoted on p. 147 Note.

[3] Wilhelm, Tageblatt d. 94 Naturforscherversammlung.

[4] Über das Kalziumoxalat der Baumrinden. Halle, 1891; Bokorny, Bot. Zentralbl., 1895, II.

[5] Ramann, Bodenkunde, 3. Aufl. Berlin, 1911, Springer.

[6] Loew, Flora, 1892. A hypothesis of his on the employment of calcium in the formation of the chlorophyll granules and the nucleus *see* Bot. Zentralbl., 1895, III.

[7] Annals of Botany, XXI, 1907, p. 501: Value of certain nutritive elements to the plant cell (Fungi, *Spirogyra*); Stocklasa, Zeitschr. f. Landwirtschaftl. Versuchswesen, XI, 1908, p. 52.

Of the mineral nutrient substances which are apparently not indispensable but are nevertheless generally distributed in plants, chlorine and silica may be mentioned. The former is believed to favour the transport of carbohydrates in the plant. Silica place itself in line with calcium oxalate as a means of protection against damage by animals. In this character it is found, for instance, in the outer layers of the rind of the beech, which " often covers itself with a veritable coat of mail " (Ramann) and in the leaves of the hornbeam, in which Ramann and Will [1] found over 60 per cent. of the whole of the silica absorbed by the tree, though the mass of the leaves did not make up more than 3 per cent. of the whole tree. Attempts to raise plants quite free from silica have not yet been successful,[2] so that, while the great masses of silica found in nature, *e.g.* in grasses, are chemically unnecessary, small quantities may indeed be indispensable. Silicic algae (diatoms) do not thrive without silica. Many substances, unnecessary in themselves, may promote the growth of plants by satisfying their " salt hunger," the need for salts in general. With regard to manganese compounds, it is known that *Cryptomeria* plants watered with such, surpass the control plants in increment and in weight. Manganese salts are also found to raise the yield (of peas by 24 per cent., barley by 6 per cent., rice by one quarter, also sugar beet and potatoes; but not red clover and pot herbs). In the case of wheat, promotion of the formation of straw, the setting of the seed and the nitrogen-content of the seed is reported.[3] In oats (increase of yield 14–17 per cent.) manganese sulphate acts as a stimulus to the absorption of lime.

The whole relations of mineral substances to the development of woody plants has, following the precedent of agricultural chemists, been expressed in the " Law of Minimum." " It is the factor in plant nutrition present in minimum which determines the total amount of production." The rule implies that if only one single nutrient material falls below the necessary amount, the productivity of the plant suffers, even if all the other substances are present in the best possible quantities. Taking into consideration the fact that too large quantities of a nutrient substance may also be injurious, Helbig [4] has given the law the following form: " That growth-factor determines the production, the extent of whose activity lies furthest towards the maximum or the minimum from the optimum which is necessary for the greatest possible yield." The law has been extended from the ash constituents so as to include all the factors of vegetation such as water, light, heat and carbonic acid, and has received through Vater [5] the general form: " The fruitfulness

[1] Zeitschr. f. Forst- u. Jagdwesen, XV, 244.

[2] Literature in: Jost, Vorlesungen über Pflanzenphysiologie, 3. Aufl., p. 112, Jena, 1913, G. Fischer.

[3] Loew u. Honda (*Cryptomeria*), 1904; Nagaoka (Rice), 1903; Salomone, Staz. sperim. agrarie, XL, 1907, p. 97 (Wheat); Kakehi u. Baba, Bull. Coll. of Agric. Tokyo VII, 1907, p. 455; Loew, Flora, 1902, Bd. 91, p. 264; Fallada u. Greisenegger. Österr.-ungar. Zeitschr. f. Zuckerindustrie, XLIV, Wien, 1915; Sajfert (Bohemian), Bot. Zentralbl., 129, 1915, p. 376; Clausen, Deutsche Landwirtschaftl. Presse, 1913, p. 1217 (stimulating substances).

[4] Helbig, Düngung im forstlichen Betriebe. Neudamm, 1906, J. Neumann; Mayer, Landw. Versuchsstationen, LXXXIII, 1914, p. 397.

[5] Vater, Das Zulangen der Nährstoffe im Waldboden für das Gedeihen von Kiefer und Fichte. Tharandter forstl. Jahrb., LIX, 1909, p. 213; Müller, P. E. og Helms, Kunstdünger und Fichtenkultur. Det forstl. Forsöksvaesen i, Danmark, III, 1913.

of a locality is limited by its most unfavourable characteristic." Against this elastic conception no objections can be raised. On the other hand the earlier expressions of the effect of the minimum, according to later investigations, require limitation. To potassium, calcium and magnesium the law of minimum does not apply because, besides the absolute minimum quantities, the proportionate amounts of the salts have an influence on the success of the plants. Also for the other factors in production the law applies in so far that the factor present most in minimum has a greater influence than the others ; it has, however, been established that the factors of productivity, to a certain extent, mutually replace and interfere with each other. If any factor, *e.g.* heat, is varied, all the other factors remaining constant, from a minimum under which in general no growth is possible, up to the optimum of heat, at first an increase in growth almost proportional to the increase in warmth occurs. If the temperature is still further raised until the other factors, or one of them, becomes a minimum relatively to the heat, there is not, perhaps, that cessation of the further increase of the yield which one would expect from strict formulation of the Law of Minimum, rather does the yield go on increasing up to the optimum for heat, though at a continually slower rate. The same applies if any other factor is varied and the heat kept constant. Set out in the form of a curve the yield rises as a function of one factor at first rapidly, then at a constantly decreasing rate, finally approaching asymptotically a maximum value, as we have shown in Chap. VIII, 12, for the growth-factors light and carbonic acid. Mitscherlich,[1] to whom we owe the recognition of this regularity, has expressed it in the following mathematical formula: $y = A\,(1 - e^{-cx})$, in which y is the yield, A the maximum yield obtainable, the other factors remaining constant, x the variable factor and c a constant, the " Factor of Efficiency." This law of efficiency of the growth-factors implies, that the raising of the plant yield by the raising of the variable factor x is proportional to the defect in yield from the maximum yield A.

Experimental cultures by Vater in the Tharandt Instruction Forest showed that, in pine and spruce soils there, it is nitrogen which is the nutrient which is least sufficient for the nutrition of the forest trees. As mineral soils become continuously poorer in nitrogen with depth, this result is valid independent of the thickness of the layer examined. As will be shown in the following section, this decisive importance of nitrogen for the fertility of forest soils applies almost universally, mostly also for arable soils. For the layer 0–3 decimetres, the investigations described by Vater indicate that phosphoric acid, potash and lime, in varying quantities, suffice for success. Besides nitrogen, phosphoric acid alone was met with in minimum quantity. The important result of lime manuring in agriculture is explained for the most part, not by the lime-content before manuring being insufficient for the nutrition of the plants with lime, but by a series of indirect effects, among which the influence of lime on the physical properties of the soil, on its degree of acidity and on the microscopic soil flora of fungi and bacteria are involved. Vater points out that a very low lime-content in the soil

[1] Mitscherlich, Bodenkunde, 1920 ; Baule, B., Zu Mitscherlichs Gesetz der physiologischen Beziehugen. Landw. Jahrb. LI, p. 363, 1918.

does not allow of the immediate conclusion that there is not sufficient lime for the growth of the trees. In consequence of its great solubility in soil water, even small quantities of lime are easily accessible to the roots. On the other hand, it can be more readily concluded from the smallness of the potash- and phosphoric acid-content of the soil that a bare sufficiency of these substances is present, as they are found only in traces in soil water and are, in the main, obtained where the root hairs come into direct contact with potash- or phosphoric acid-containing soil particles. Hausrath [1] calculates, from the quantities of minerals contained in the timber of one rotation and from soil analyses, that, according to the yield class, exhaustion of pine soil may be expected, in potash, at the earliest after 32–51 rotations (4–7,000 years), in lime after 10–409 rotations (1,300–57,000 years), in phosphoric acid after 63–70 rotations (7,500–9,800 years).

8. The Nitrogen Supply of Forest Trees. Vegetation of the Locality.—As a never-failing constituent of protein substances, which on the average contain about 16 per cent. of it, nitrogen is among the absolutely necessary nutrient substances. It does not appear in the ash because it escapes in gaseous form on combustion.

According to Ebermayer the formative tissues, the young twigs and leaves and the seed are the richest in nitrogen. The dry matter of beech nuts contains, for example, 3.04 per cent., that of chestnuts 2.50 per cent. of nitrogen. In spring the young leaves of trees contain 4.0-4.6 per cent., older leaves 2–2.5 per cent. of nitrogen. Stem timber is poor in nitrogen, which amounts to only 0.17 per cent. of its dry weight. Fallen leaves contained the following percentages of nitrogen in their dry matter:

Beech leaf litter	1.34%
Spruce litter	1.06%
Pine litter	0.91%

Nitrogen-content of dried green leaves at the end of July:

White alder	2.84%	Large-leaved lime	2.21%	Ash	1.77%
Small-leaved lime	2.37%	Acacia	2.00%	Birch	1.75%
Sycamore	2.37%	Goat willow	1.97%	Beech	1.70%
Hazel	2.32%	Elm	1.87%	Aspen	1.61%
Oak	2.30%	Mountain ash	1.81%	Black alder	1.46%
		Hornbeam	1.24%		

Analyses by Ramann and Bauer gave per 100 spruces [2]:

1 year old plants	0.1439 g. nitrogen.
2 ,, ,, ,,	0.7240 g. ,,
3 ,, ,, ,,	4.6956 g. ,,
4 ,, ,, ,,	12.0318 g. ,,
5 ,, ,, ,,	36.0227 g. ,,

[1] Pflanzengeographie. Wandlungen d. deutschen Landschaft. Wissenschaft u. Hypothese, XIII; Schwappach, Die Kiefer. Neudamm, 1908.

[2] Jahrb. f. wissenschaftl. Bot., Bd. L, 1912, p. 75.

According to Ebermayer the nitrogen requirement per hectare per annum with average production is as follows:

In beech forest	about	51 kg.	nitrogen.
In silver fir forest	„	41 kg.	„
In spruce forest	„	38 kg.	„
In pine forest	„	34 kg.	„

The nitrogen-content of the leaves is due to the great amount of protein in them, the young May shoots being specially rich. In hardwoods, according to Pässler,[1] the content of the leaves in raw protein varies in spring between 18.84 per cent. (mountain ash) and 36.02 per cent. (black elder), in summer between 13.10 per cent. and 32.65 per cent., in pure protein between 17.18 per cent. and 27.23 per cent. and between 12.27 per cent. and 24.89 per cent. respectively of the absolute dry weight. The small twigs up to 1 centimetre contained in summer 9.49 per cent. (Mountain ash) to 24.07 per cent. (black elder) of raw protein.

It has long been an enigma and even to-day is not clear in all details, how the tree supplies its nitrogen requirements. There are no nitrogen containing minerals known which are so widely distributed that we could point to them as sources of nitrogen for trees. Birches and other forest trees, however, often grow well on raw mineral soil, as on the refuse heaps of stone quarries. They must, therefore, be ways of making the nitrogen from the unlimited stock in the atmosphere available directly or indirectly for the roots of trees.

That tree roots, either alone or in combination with fungi, as mycorrhiza, cannot assimilate atmospheric nitrogen, has been proved by Melin's experiments, already mentioned. A limited number of trees—the leguminosae, the alders (Figs. 132 and 134) and eleagnaceae—are, however, able, as we have seen, through their symbiosis with bacteria in root nodules, to absorb the gaseous nitrogen of the air through the roots and bring it into organic form.[2] Among the plants of the soil flora of the forest especially effective in this way as a collector of nitrogen, is the common broom *Sarothamnus scoparius*, one of the leguminosae, which often appears in dense masses on cleared areas. It supplies to the soil, by its decaying leaves and fragments of stem and roots, the nitrogen assimilated from the air by means of its nodules. The broom is, therefore, willingly suffered on clearings and like the similarly nitrogen-collecting white alder and lupins,[3] even introduced artificially for the purpose of gaining nitrogen. Other leguminosae, like clover and *Lathyrus* species, occur too sparsely in the forest to be able to enrich the soil with important quantities of nitrogen. More important is the gain in nitrogen through nitrogen-fixing micro-

[1] Pässler, Über den Futterwert der Blätter, Triebe und schwächsten Zweige verschiedene Laub- und Nadelhölzer. Tharandter Forstl. Jahrb. Bd. 43, p. 212. Contains numerous analyses of ash, protein, fat, etc.

[2] Nobbe, Schmidt, Hiltner u. Hotter, Landwissenschaftl. Versuchsstationen XXXIX, 327; Nobbe, Hiltner u. Schmid, *ibid.* XLV, 1894, p. 1; Frank, Ber. d. D. bot. Ges., Bd. 8, 1890, 331; Landwirtschaftl. Jahrb. Bd. 19, 1890, 523–640; *ibid.*, 1892; Nobbe u. Hiltner, Landwirtschaftl. Versuchsstationen, XLV, 155. (On *Eleagnus* and alder, among others.)

[3] Flander, Allgem. Forst- u. Jagdzeitg., 1912, 1913.

organisms, especially bacteria [1] (*Azotobacter* and *Clostridium*) and cyanophyceae. Whether nitrogen-collecting bacteria are also active in forest soil, and if so which, are as yet unsolved questions, on which Wittich [2] especially has been working. Certain soil fungi also appear capable of absorbing nitrogen from the air.[3] Further sources of nitrogen are the nitrogen compounds which reach the soil with snow and rain water, among which there is even some nitric acid and about 2–5 times as much ammonia. The total quantity of combined nitrogen conveyed to the soil in this way amounts, according to Ramann,[4] on the average to 10 kilogrammes (2.5–24 kilogrammes) per hectare per annum. In open vessels with acid exposed to the air, an absorption of 30.6 kilogrammes of ammonia per hectare per year and even as much as 63 kilogrammes was found. From this it appears that the absorption of ammonia from the air must be of great importance, at least for acid soils. Perhaps it explains the enrichment in nitrogen which Henry and Hornberger [5] obtained in leaf litter of broad-leaved trees, with unhindered access of air. It is true that the soil organisms mentioned are also concerned here.

Apart from these supplies against which are set great losses of nitrogen by denitrification and washing out, forest trees are dependent on the nitrogen which by circulation is again carried to the soil in the falling leaves and twigs. The main bulk of the nitrogen absorbed by the roots remains in the leaves ; only $\frac{1}{4}$–$\frac{1}{5}$ of the total nitrogen is stored in the stem timber and permanently removed in it from the forest. The nitrogen-content of the leaves is already considerable in itself and is further enriched relatively and absolutely by their decomposition into humus. The humus formed from the decomposed plant debris finally contains considerable quantities of organically combined nitrogen —according to Ramann,[4] in humid regions, 2–5 per cent.—the more the more regularly the decomposition proceeds, the less the more slowly it progresses. Humus formed from wood contains 1–2 per cent. nitrogen. Forest humus, and also the dry peat, often accumulated to a great depth, thus contain a great store of combined nitrogen, to retain which and make it accessible to the tree roots is the most important task of the art of Forestry, just as agriculture also has great problems in front of it in the better utilisation of the nitrogen in farmyard manure, which under ordinary treatment is for the most part lost.[6]

The nitrogen in the forest litter and humus, bound up in high-molecular organic compounds, is as a rule further broken down by micro-organisms—bacteria and fungi—and, with the complete decomposition of the humus, finally mineralised. In unfavorable, poor, dry and acid soil, this breaking down of the humus and often also the supplying

[1] On the bacterial flora of the soil *see* Benecke, Bau und Leben der Bakterien. Leipzig u. Berlin, 1912. Koch, A., Jahresber. ü. d. Lehre von den Gärungsorganismen und Enzymen. Appeared since, 1890, Leipzig. Handwörterbuch d. Naturwiss. I., p. 806, 810, etc.

[2] Wittich, Unters. ü. d. Einfl. intensiver Bodenbearbeitung, 1926.

[3] Ramann, E., Bodenkunde, 3. Aufl. Berlin, 1911.

[4] Ramann, *loc. cit.*

[5] Streu und Stickstoff, Zeitschr. f. Forst- u. Jagdwesen, 1905, p. 7 ; Henry, Bull. soc. d. sc. Nancy, ser. III, T. IV, 1903, p. 173 (Austrian pine and spruce also treated.)

[6] Krantz, H., Binnenversorgung durch Bodenkraftmehrung, Augsburg-Stuttgart. 1924.

of nitrogen is feeble, so that increasing surface coverings of raw humus collect. Such humus, according to the investigations of Süchting,[1] produces under certain conditions only very small quantities of easily absorbable nitrogen compounds. On felled areas and under the shelter of young crops, however, the raw humus covering accumulated during the later years of the old crop, disappears wholly or for the most part by decay and the quantities of nitrogen thereby set free offer an ample supply to the young plants. Heavy thinnings may, according to Hesselman,[2] in consequence of the greater atmospheric action, promote the decay of humus and nitrification, and thereby apparently raise the total increment, at least temporarily.

In many soils, only NH_3 appears as the end product of the breaking down of the nitrogenous compounds in the humus, in others it is further oxidised to nitrites and then to nitrates (Nitrification).

It is difficult to determine by experiment alone which of these substances are absorbed by the roots and worked up by the plant.[3] With artificial manuring with various nitrogenous substances, secondary reactions occur which may seriously influence the results. If only the acid radicle is absorbed by the roots from saltpetre and the kation left behind, there results, under certain conditions, an injurious change of the soil reaction in an alkaline direction ; the converse being the case with ammonium salts. Saltpetre is also very easily washed out, whilst ammonium salts are absorbed. In addition, unfavorable alterations in the structure of the soil may arise through heavy manuring with saltpetre. More especially, however, ammonium compounds in the soil are mostly very soon nitrified. Manurial experiments in the open ground [4] and ordinary nutrition experiments therefore lead to very uncertain results. According to Süchting, Möller's comprehensive manurial experiments,[5] with raw humus on the one hand and mineral salts on the other, also afford no proof, because far too great quantities of manures were employed. In order to determine which nitrogenous compounds are converted by the tree root, it is necessary to work with pure cultures, with the exclusion of micro-organisms, as Melin [6] did with spruces and pines. According to these experiments, tree roots can absorb both ammonium salts and nitrates, but organic nitrogenous compounds only with difficulty. They do so better, however, as mycorrhiza in association with fungi.

In nature, however, according to the thorough investigations of Hesselman [7] and others,[8] saltpeter proves the best source of nitrogen,

[1] Süchting, Der Abbau der organischen Stickstoffverbindungen durch biologische Vorgänge Forstwiss. Zentralbl., 1925.

[2] Hesselman, Mitt. d. forstl. Versuchsanstalt Schwedens, 1926.

[3] Ehrenberg, Die Bewegung des Ammoniakstickstoffes in der Natur. Berlin, 1907. Vater, Bemerkungen zur stickstoffaufnahme der Waldbäume. Tharndter forstl. Jahrb. LIX, 1909.

[4] Helbig, Forstwiss. Zentralbl., 1920, p. 262.

[5] Möller, Zeitschrift f. Forst- u. Jagdwesen, 1904. Möller und Albert, *ibid.*, 1916.

[6] Melin, E., Unters. ü. d. Bedeutung der Baummykorrhiza, Jena, 1925.

[7] Hesselman, H., Studien ü. d. Nitratbildung in natürl. Böden u. ihre Bed. in pflanzenökologischer Hinsicht. Mitt. a. d. forstl. Versuchsanstalt Schwedens, 1916–17, Bd. I, H. 13–14, p. 297, and XXXIII.

[8] Vogel von Falkenstein, Internat. Mitt. f. Bodenkunde, Bd. III, 1913. Wiedemann, E., Fichtenwachstum und Humuszustand. Arb. a. d. Biol. Reichsanst. f. Land- u. Forstw., 13 Bd., H. 1, 1924.

not only, as was already assumed, for agricultural plants, but also for forest trees. The " more exacting " broad-leaved trees and young growths in particular, are much forwarded by the nitrification of the nitrogen in the soil. The best forest growth, especially of hardwoods, is always found on soil with vigorous nitrification. Spruces and pines can, it is true, also thrive on humus which provides only ammonium compounds and no nitrate, but they also attain their most luxurious growth on nitrate soils. The more valuable hardwoods, elms, sycamore and ash, appear in nature to be confined entirely to nitrate soils ; this is perhaps connected with their having sparse mycorrhiza or none at all.

In spite of the high total nitrogen-content of humose forest soil, the nitrogen available for the trees is often one of the soil nutrients present in the minimum, and the problem of timber yield is to a great extent a problem of the uninterrupted setting free of humus nitrogen by nitrification. It is bound up with the presence of electrolytes or soluble salts and occurs therefore most plentifully in rich, basic " active " moulds, also in peat which is moistened by running water, especially in alder breaks. Worms and soil insects promote saltpetre formation as they mix up the soil, bring the mineral soil into closer contact with the humus and devour a great part of the leaf-fall and convert it into easily decomposed excrement. Nitrification may be stimulated [1] by the access of ample light and warmth, in gaps in the crop and on cleared areas, where layers of raw humus may also be nitrified and produce excellent manurial effects. Nitrification is also promoted by cultivation of the soil, which mixes the inactive surface humus with the mineral soil, again by ground fires and decaying fallen timber and branch-wood —which play a great part in remote primeval forests. Afforested arable lands also show, as a rule, strong nitrification. Nitrification is stopped if the humus cover becomes much dried out, and so especially where cleared areas lie bare for long periods. A single summer drought which completely dries out the humus cover and converts it into " coaly " humus may, according to Hesselman, confirmed by Wiedemann (1924), make the nitrogen of the humus useless to tree roots and so bring tree growth to a stop for many years. On soils with a thick, dry-humus covering the protection of the surface of the soil from drying out by means of suitable arrangement of the fellings, mixing with quick growing, shade giving nurse trees, etc., is an important task of the forester. In coniferous forests rich in moss, no nitrification takes place as a rule, the breaking down of nitrogenous compounds coming to a stop with ammonia.

Whether saltpetre formation is taking place in the soil is generally to be perceived from the characteristic nitrophilous soil-flora. Some of the most widespread nitrate plants may be mentioned here.

On felled areas with nitrifying soil the following appear mostly in thick crops : the willow herb, *Epilobium angustifolium*, the raspberry, *Rubus idaeus*, which may serve as indicator plants, further *Senecio sylvaticus*, *Atropa belladonna*, strawberry, etc. Besides these, especially

[1] Hesselman, H., Regeneration measures and the formation of saltpetre. Mitt. a. d. forstl. Versuchsanst. Schwedens, 1916–17, Bd. 2, H. 13–14, p. 923 u. XCI.

on nitrifying beech soil are found: *Stellaria nemorum, St. holostea, Asperula odorata, Oxalis acetosella, Arenaria trinerva, Lactuca muralis, Prenanthes purpurea, Dentaria bulbifera, Corylus* sp., *Luzula pilosa* (the best indicator of "Bodengare"[1]) *Galium sylvaticum, Viola sylvestris, Ranunculus ficaria.* On nitrifying soil of the more valuable hardwoods: *Geum rivale, G. urbanum, Viola sylvestris, Stachys sylvatica, Mercurialis perennis, Urtica dioica, Corydalis, Adoxa Moschatellina, Pulmonaria officinalis.*

On wet nitrate soils: *Senecio Fuchsii, Mercurialis perennis, Chrysosplenium alternifolium, Ranunculus repens, acris, ficaria.*

In wet alder woods: *Anthriscus sylvestris, Urtica dioica.*

Further nitrophilous plants are: *Impatiens noli tangere,* which appears only to occur when the nitrogen supply is favorable, *Lysimachia nemorum, Galeopsis tetrahit, Geranium Robertianum, Taraxacum officinale,* and of the shrubs, especially *Sambucus racemosa,* the red-berried elder and *Sambucus nigra,* and of grasses: *Festuca gigantea* and *sylvatica, Milium effusum, Melica nutans* and *uniflora*—in short, most of the exacting plants of our good forest soils.

The following, among others, point to the absence of nitrification: *Aira flexuosa,* a marked raw-humus plant, which nevertheless indicates still comparatively good humus conditions, then the bilberry (*Vaccinium myrtillus*), *Molinea coerula, Calluna vulgaris; Vaccinium vitis idaea* and especially lichens indicate the worst nitrogen conditions.

Where, with sufficient access of light, the most luxurious nitrate plants predominate, the best forest growth is to be expected, so that, according to Cajander,[2] the quality of the wood can be assessed in many cases according to the soil flora (Forest types).

The knowledge of such relations between the soil flora and the quality of the locality has reached a stage of great completeness in Finland through Cajander[2] and his school. For the more complex conditions of locality and crops in middle Europe the research into forest types is only in its initial stages. As a rule, it is true, tree growth is in accord with the soil flora, but too many cases are to be found in which such relationships are not immediately recognisable. There are also factors of the locality which influence tree growth to an even greater extent than they do the soil flora, such as the amount of the precipitation and the evaporation and, above all, in certain circumstances also the subsoil, for most of these "plants of the locality" indicate in the main

[1] This term, for which there is no English equivalent, is used by the German farmer to denote the puffed up or aerated structure of a soil in good arable tilth. It is supposed by some that the production of this aeration is analogous to that of the aeration by the evolution of CO_2 in the working of dough. This explanation has, however, been strongly controverted by many soil workers, who deny that the CO_2 produced by bacterial oxidation in the soil could produce a structure analogous to that of spongy dough. Tr.

[2] Cajander, Acta forestalia Fennica, 1909, 1921, 1923, 1924. Further works on soil flora: Lagerberg, Die Analyse der Bodenvegetation mit objektiver Grundlage. Mitt. forstl. Versuchsanstalt Schwedens, 1914. The whole literature in: Lönroth, E., Die Waldtypen u. d. innere Bestandsentwicklung, Mitt. Dtsch. Dendrol. Ges., XXXVI (Finnland Buch), 1926, I. Hartmann Grundlagen für die Analysierung der Bodenflora im Dienste bestandsbiologische Forschungen Forstw. Zentralbl., 1923; Zeitschr. f. Forst- u. Jagdwesen, 1923. Schwappach, Forstl. Rundschau, 1921, p. 113. Bornebusch, Unters, ü. Boden u. Flora dänischer Waldungen; Das forstl. Versuchswesen in Dänemark, Bd. 8, H. 1, 1923. Feucht, Die Bodenpflanzen unserer Wälder, Stuttgart, 1925, etc.

the goodness of the surface soil, especially the condition of the humus (Rubner).[1] Thus if poor sand is underlaid by marl at a considerable depth, but still within reach of the tree roots, the soil flora may be poor and unexacting and yet tree growth very good. The rich soil of basalt ridges generally carries a rich nitrate flora, whilst tree growth may be checked by strong winds. Again, the alternation of species which is the rule in many German forest regions makes the assessment of the locality according to the soil flora difficult. These and similar complications which are still to be cleared up restrict the application of Cajander's forest types. It might, however, be throwing away the good with the bad to deny, on this account, the high value possessed by the soil flora for locality investigations in forestry, for natural regeneration and other silvicultural measures. The way in which the botany of the soil flora in conjunction with geology and climatology is to be made of service in the investigation of locality cannot yet be reduced to a system. Nevertheless the following very common main forest types together with sub-types of Cajander (beginning with the best quality) may provide valuable assistance in the recognition and classification of localities.

1. *Oxalis*-type (OT.) with sorrel as indicating plant
   (*a*) *with Impatiens* (and *Asperula*)
   (*b*) with *Asperula*
   (*c*) with *Oxalis*
   (*d*) with *Oxalis* and *Vacc. Myrtillus*
2. *Myrtillus*-type (MT) indicating plant: Bilberry
   (*a*) with Raspberry
   (*b*) with Wavy Hair Grass (*aira flexuosa*)
   (*c*) with Bilberry
   (*d*) with *Calamagrostis Halleriana* (higher elevations).
3. *Calluna*-type (CT), indicator plant: Heather with sub-types with Feather Moss (*Hypnum*) Lichens, White Moss (*Leucibryum*).

As a means of indicating the forest types it is the vegetation of old open woods that counts. Under certain conditions, also, the indicator plant may be absent and be replaced by others of similar requirements.

In a moist, equable, climate, plant roots absorb almost every trace of the nitric acid formed in the soil, so that the latter cannot be discerned in forest soil. Nevertheless Weis [2] found in acid forest soil about 4 milligrammes of nitric acid to 1 kilogramme of soil.

Nitrophilous plants, especially in youth, store up saltpetre in the leaves when it is plentifully supplied, in such quantities that it is easily

[1] Rubner, Forstliche Standortsgewächse, Forstwiss. Zentralbl., 1920. The same, Die Bedeutung der Waldtypen für den deutschen Wald, Silva, 1922. The same, Die pflanzengeographischen Grundlagen des Waldbaues. 2. Aufl. Neudamm, 1925. *Comp.* also Graf zu Leiningen (Sammelreferat über Waldtypen), Zentralbl. f. d. ges. Forstwesen, 1922.

[2] Weis, Auftreten und Bildung von Salpetersäure in Humus und Moorböden. Det forstliche Versögsväsen II, Kjöbenhavn, 1908, p. 257; quoted from Vater.

detected and may be used as a proof of strong nitrification.[1] Nitrogen is only found in the form of nitric acid in the interior of tree stems when they have been grown in saltpetre-containing soils, *e.g.* arable land; generally, however, even on nitifying soil, saltpetre is not detectable in the tissues of trees.

[1] Hesselman, *loc. cit.*, 1926. Graf zu Leiningen, Über Stickstoffaufnahme verholzender Pflanzen, Forstw. Zentralbl., 1925.

CHAPTER XII

MOVEMENTS AND TRANSFORMATIONS OF SUBSTANCES IN THE BODY OF THE TREE

1. The Stem of the Tree as a Storehouse of Reserve Substances.—It is a widespread phenomenon in the botanical world that formative materials are not consumed immediately they appear. Just as in human economy, a supply of water is not led directly from the spring to the dwelling houses, but into a reservoir from which households can draw at need, so in the plant the carbohydrates and proteins are stored before they are used so as to make consumption independent of the productiveness at the moment of the process of assimilation. Storage of this sort may take place even in the assimilating cells themselves, as the appearance of starch in the green cells of the leaf and rind testifies. It also occurs in the vicinity of the places of consumption, as, for instance, just below the growing point. Finally, storage takes place in special receptacles for reserve materials, for which purpose, like store cupboards in somewhat compactly arranged houses, all sorts of parts of the plant are utilised. Tubers, bulbs and rhizomes are commonly such receptacles for reserve materials. In trees all the living cells may take part in the storage of substances which are for the time being superfluous. The places in which are kept materials which are to be stored for a somewhat longer time, however, are the living elements of the xylem of the stem and roots, namely the wood parenchyma and medullary rays, as well as, in certain cases, the pith. This last, however, in the greater number of broad-leaved trees, is, according to Alfred Fischer,[1] free from starch, but in others—for example in oaks, planes, birches and hawthorn, and, in isolated cells and chains of cells, also in the lime—is able to store up starch. Thus the stem of the tree as a storehouse of reserve materials, shows us yet another side of its importance in the life of the plant. It has been already recognised as the supporter of the crown which raises the leaves towards the light.

The reserve materials stored in the parenchyma of the shoot and root are, for the most part, dissolved in the spring, excreted into the water of the wood in the form of sugar, and carried with it to the opening buds, where they serve to build up the young shoot until it is

[1] Jahrb. f. wiss. Bot. XXII, 1890.

able to nourish itself. Ringing experiments by Th. Hartig [1] showed that, inside the ringed part, the starch in the parenchyma of the wood disappears and is carried away by the wood water. The reserve materials of the buds themselves would naturally not be sufficient to form the shoots.[2] That the nutrient materials for the unfolding of the buds do in fact come from the wood water and not from the bast is proved by ringing experiments. If buds are cut off from the bast by ringing before they break, they nevertheless develop into shoots.[3] Chlorophyll-free (etiolated) leaves are, however, nourished not through the wood, but through the bast, as has also been proved by ringing experiments.[4]

If the reserve materials pass in the form of sugar from the living wood parenchyma cells into the lifeless channels of the wood, they must do so through the closed plasma utricle, since no plasma connections lead in this direction, as we saw in Chapter III, 1. In plasmolysis experiments under the microscope, the living plasma proves itself to be very little permeable to sugar, especially to cane sugar, which is not seldom present in the wood water. Its permeability must therefore either become greater in spring, or if it remains very small, must be sufficient to allow considerable quantities of sugar to diasmose into the wood water during the long winter months. According to Schellenberg, transportable nutrients are also supplied to the wood sap by extracellular transformations such as the dissolution of part of the wood wall. Plasma membranes must again be traversed when the dissolved substances pass from the wood channels into the cells of the young shoot. The permeability of the plasma must be greater in this region, as considerable amounts of sugar must be absorbed in a short time into the plasma bodies of the cells of the growing point and young leaves in order to supply the great quantities of material consumed by the young shoots which are making their appearance. According to Osterhout,[5] the presence of sugar greatly increases the permeability of the plasma.

The young shoots of deciduous trees are entirely dependent on such material. Their wood sap also contains far more sugar in the spring than that of the evergreens. The excretion of sugar from the wood parenchyma into the wood water appears to take place throughout the whole length of the xylem, for the sugar concentration increases considerably from below upwards. Thus, for example, the following percentages of "sucrose" were contained in the wood sap of *Acer macrophyllum* and obtained by centrifuging [6]:

	Below.	Above.
13. X	0–0.6	0–0.5
25. II	1.0–3.0	3.0–5.5
14. IV	0.4–0.5	0.7–0.7

[1] Hartig, Th., Bot. Ztg., p. 338, 1858.
[2] Fischer, A., Jahrb. f. wiss. Bot. 22, p. 125.
[3] Strasburger, Leitungsbahnen.
[4] Weevers, Th., Ringing exper. with variegated branches. Proc. Akad. Wetensch. Amsterdam, 1923, 26, p. 755. Quoted from Bot. Zentralbl.
[5] Osterhout, Plant World, XVI, p. 129, 1913.
[6] Dixon and Atkins, Sc. Proc. of Roy. Soc. Dublin, XV, 1916, p. 51.

Reducing sugars could be detected in the wood sap only in traces or not at all. In these processes starch is converted into maltose and this by further hydrolysis into glucose. (Further details on the content of the spring sap, *see* Sect. IX, 3.)

It is thus the reserve materials which make possible the surprisingly rapid greening and the unfolding of flowers in the hardwood forest in spring and the rapid elongation of the shoots within the space of a few

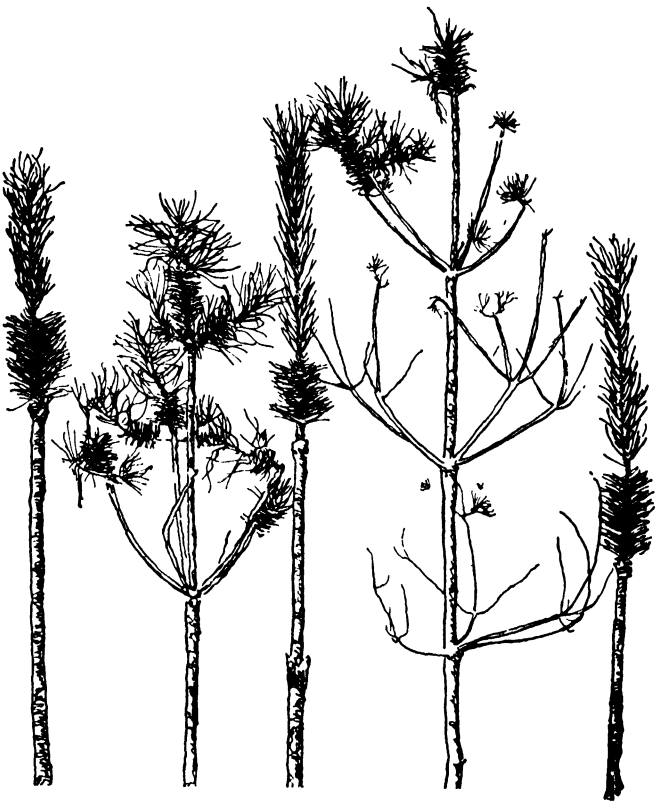


FIG. 135.—Pines, defoliated two years previously by the needle-shedding fungus (*Hysterium pinastre*), produced, in the summer following defoliation, short, brush shoots with the full number of needles, and in the second summer, comparatively long shoots with few needles. (Mch.)

days. The reserve materials are, however, not completely exhausted by the formation of shoots ; they suffice for the formation of a second, albeit more feeble crop of leaves if the first is lost through frost or insect attack. Trees do not stand a still further defoliation. Even the oak, which regenerates its foliage so easily and so completely, dies if the first crop of leaves is destroyed by caterpillars and the second crippled by mildew.

Whilst in broad-leaved trees the young shoots are formed almost entirely from the reserve materials stored up in the previous year, the reserve materials in conifers do not go so far. In them the needles of former years must co-operate in the building up of the spring shoots. Spruces completely defoliated by caterpillars in summer, invariably

perish. They can only form from their reserve materials, very weak shoots which are not sufficient to nourish the tree. Pines may retain their vitality better by means of substitute shoots, especially if defoliation occurs only late in the year, but if they are defoliated even in July they also die as a rule. Complete defoliation by the needle shedding fungus in early spring invariably results in the death of one-year-old pines. Older pine plants after defoliation, expand their buds by using up reserve materials, but only very feebly and require several years to recover themselves (Fig. 135). In the new shoot, it is true, all the needles laid down in the bud unfold, as we showed in Section II, 3, but they and the shoot remain very short—"**Brush Shoots**" are produced.

It has already been pointed out that there is a perceptible loss of weight in young trees on the development of the buds, because in the process of respiration, which must supply the energy for the increased life activity, more materials are consumed than the still scanty assimilation can supply. At the same time there is a migration of reserve substances out of the stem into the newly enlarging shoots, which makes itself evident in a loss in weight of those parts even when there is no loss in weight of the plant as a whole. Ramann and Bauer [1] give in the following table the loss in weight of stem and root in some 2–3-year-old forest trees, in percentages of the dry substance present before sprouting:

	Date.	Loss in weight in percentages. Stem.	Root.
Norway maple	2.5 to 21.5	47.0	44.4
Black alder	27.4 to 18.8	1.2	46.4
Ash	4.5 to 21.5	29.6	36.1
Beech	27.4 to 21.5	16.6	38.9
English elm	2.5 to 18.5	27.0	36.2
Larch	27.4 to 21.5	20.5	15.5
Spruce	27.2 to 22.5	6.0	23.0
Silver fir	22.5 to 14.5	7.1	5.9
Scots pine	11.3 to 22.5	19.9	

In general the roots are emptied more than the stem, which, especially in the alder and oak, is very little drawn upon. Most of the reserve materials present in the root disappear in the spring. Sugar is to be found in the root mostly during the growing season, whilst the shoot behaves in almost the opposite way.[2] The small withdrawal of material from the roots of the larch is explained, according to the authors, by the low soil temperature at the time when this species sprouts, as it wakes early from its winter sleep.

Observations made by Lutz on defoliated beeches and pines throw some light on the seasonal course of the accumulation and the method of utilisation of reserve starch. Beeches, 6–8 years old, disbudded and defoliated, in the middle of March, on May 20, June 15 and July 1 and 15, caused numerous preventitious buds to sprout, which when removed were constantly replaced by new ones. The tree defoliated in March

[1] Trockensubstanz, Stickstoff und Mineralstoffe von Baumarten während einer Vegetationsperiode. Jahrb. f. wiss. Bot. Bd. 50, 1912, p. 70.

[2] Leclerc du Sablon, Compt. rend., Paris, 1902; Bot. Zentralbl. 92, 1903, p. 123.

did not grow in thickness but remained sound and in autumn still possessed reserve starch. In the specimen defoliated on May 20, a certain amount of increment took place; in autumn, however, its twigs had begun to die and were quite without starch, which was present only in the first five annual rings immediately above the root collar. With defoliation on June 15, the starch of the little stem was consumed except for small remnants, while an increment of 25–50 per cent. of the previous year's ring was formed. Finally, defoliation in July and later had admitted of the completion of the annual ring and the accumulation of large quantities of starch. All the experimental trees therefore utilised the whole of their reserve materials for the forming of accessory buds and formed new wood only in proportion to the longer or shorter time the foliage was active, *i.e.* the newly-produced assimilates alone were available for the cambium. Things were different in experiments by R. Hartig.[1] Hartig had completely topped old beeches, mostly over 100 years old, no sprouting whatever taking place on them in consequence. In these trees a normal, though narrow ring developed in the first year at the expense of the reserve materials in the wood. No further growth took place in the second year. These materials may therefore be utilised for diameter growth as well as for the production of adventitious shoots; though the last named use seems to have the preference. In disbudded and defoliated pines, utilisation of the reserve materials for diameter growth preponderated, as these trees developed accessory buds only to a moderate extent. Finally, 100-year-old silver firs, 95-year-old pines and 120-year-old spruces, deprived of branches and leaders in April, showed after felling in October, that 0.36 (fir), 0.25 (pine) and 0.12 (spruce) of the ring breadth of the previous year had appeared without the assistance of new assimilates and at the expense of reserve materials alone.[2]

The reserve materials of the stem find yet further employment in the formation of the fruits. In old oaks and beeches, which apply a considerable part of their products to the forming of fruits, reserve materials even seem stored up mainly for that purpose. Hartig [2] says, with regard to the beech: "Before a mast year the outer rings, actually in older trees, the outer 20 rings, are so full of starch that all the parenchyma cells are packed with it. The inner 20–50-year-old rings contain only half as much granular starch or even less. The reserve starch of the tree does not dissolve in years in which no seed is produced but remains unaltered in a resting condition and only the last two rings, bordering on the cambium sheath, show, from mid-June onwards, a reduction of starch to a half or even less of their full content. In October these as well as the newly-formed ring refill themselves with starch grains."

Beeches felled after a seed year contained only traces of granular starch in the wood. They had applied their 8 years' accumulated stock to the production of seed. Nitrogen had also almost disappeared from the wood and rind of the seed beeches. Hartig therefore considers that

[1] Hartig-Weber, Holz der Rotbuche, 1888.

[2] Hartig, R., Holz der deutschen Nadelwaldbäume, 1885. The same, Lehrbuch der Anatomie und Physiologie usw., p. 252.

the recurrence of seed years depends on the time required by the tree to fill up its storage organs again. In elms and fruit trees one year of rest is necessary for this; other species require 3, 5, and even 10 years, according to their inherent character and the favorableness or otherwise of the weather for their assimilative activity. According to comparisons made by Tubeuf,[1] seed years recur in poplars, willows, robinias, birches, hornbeams, alders, maples, limes, ashes, larches and silver firs, almost yearly (every 1–2 years); in the sweet chestnut, hazel, elm, as in most fruit trees, every 2–3 years; in pine and oak, every 3–5 years; in the spruce, every 5–7 years. In the beech, von Tubeuf noticed a partial yield of seed every 3–4 years and a full one every 10–15 years (*see* below).

Nitrogen [2] often migrates at the time of the flushing of the shoots, even more strongly than the organic substances, and more than a half of it is not infrequently given up to the young shoots. Besides starch, fat, sugar and hemi-celluloses are also to be considered as non-nitrogenous reserve materials of the tree. Glucosides also may be consumed in the sprouting of the buds and the ripening of fruits. Thus salicin,[2] which appears in the leaves in the daytime, disappears from them at night, to increase in the rind at night, where conversely it diminishes by day. A winter accumulation of similar substances is observed in the neighbourhood of the buds of the ash.[3] In *Taxus*, the taxin, abundantly stored near the growing point, diminishes when the development of tissue begins there, while it continues to accumulate in the older organs.[4] In the stem it is most plentiful in the epidermis and bast. Reserve layers of cellulose (hemicellulose) which are accumulated in winter on the inner side of the cell walls of living wood fibres (libriform fibres) and disappear again in spring, were found by Leclerc du Sablon [5] in willows. They have also been reported in mountain ash, *Vitis* and robinia.[6]

If we examine an ash twig in autumn after growth has come to a standstill, we find the cells of the rind (with the exception of the sieve tubes and their companion cells), the medullary rays and the wood parenchyma closely filled with starch—the carbohydrate produced by the leaves in excess of the requirements of the summer. It is the same with other trees. From the time of leaf fall to the end of October or the beginning of November, the tissues mentioned are usually rich in reserve starch. They therefore contain quantities of material valuable for human nutrition but which is only available to the digestive juices when the wood elements are reduced to fine powder (Haberlandt, *see* page 178).

In evergreens, like *Pinus australis*, Leclerc du Sablon [7] found the

[1] V. Tubeuf, Samen, Fruchte und Keimlinge usw. der forstlichen Kulturpflanzen. Berlin, 1891.

[2] Weevers, Jahrb. f. wiss. Bot. XXXIX, 1903, p. 228.

[3] Russel, Siège d. quelques princ. act. d. végétaux pendant l. répos hibernal. Rev. gén. d. Bot., T. XV, p. 160.

[4] Russel, Rech. s. l. localisation de l. taxin chez l'If. Assoc. franc. Avanc. scienc. Congr. d. Montauban, 1903, p. 696. Ref. Bot. Zentralbl., 93, 1903, p. 402.

[5] Rev. gén. d. Bot. 1904, T. XVI, Nr. 189, 190.

[6] Schellenberg, Hemizellulosen als Reservestoffe bei unseren Waldbäumen. Ber. Dtsch. Bot. Ges., XXIII, 1905, p. 39.

[7] Compt. rend. Paris, 1905; Rev. gén. d. Bot. T. XVIII, 1906.

maximum carbohydrate content in root and stem in the spring. In the branches of most broad-leaved trees (oak, hazel, elm, plane, maple, *Prunus*, ash), also the softwoods,[1] starch, in so far as it is present in the wood, lies unaltered through the winter. In the cells of the rind, however, it appears that winter does not mean a period of complete cessation of physiological exchange. The starch of the rind even in late autumn is already again dissolved by conversion into sugar, pentosans and perhaps still other substances and partly migrates into the wood. In many trees, such as pine, lime and birch, even the whole of the starch present in the twigs is included in this conversion. The conversion of starch may be reversed by a rise of temperature. The lower the temperature, the more sugar and the less starch is present. The behaviour of beech twigs is similar to that of potatoes, in which, as is well known, cold produces sweetening.

Under certain external conditions these conversions may occur several times during the winter.[2] Lidforss [3] found in most of the winter green plants of southern Sweden, almost complete conversion of starch into sugar in cold weather and re-formation of starch in warm. Colville [4] conceives the formation of sugar to be brought about by the starch being brought by the freezing process into contact with the sugar-forming enzymes, through the plasma, which separates the starch from the enzymes, being made more easily permeable to the enzyme by freezing. A mechanical squeezing out of the enzymes by freezing is also conceivable, whereby they escape from the vacuoles in which they are enclosed and so reach the starch contained in the leucoplasts.

That the sugar content of the cell sap increases frost hardiness has already been mentioned on p. 1. Vandevelde traces the checking of the injurious effects of cold by the formation of glucose, to the sugar slowing down the freezing of the cell sap and thus hindering the precipitation of protein substances by the mineral salts of the cell, which must occur when water is frozen out. Metz [5] sees the value of the winter conversion of starch in the formation of thermically active sugar in the place of thermically passive starch. The conversion is according to him a storage of heat, which is reversed when heat is supplied from without. The connection between sugar content and frost-hardiness may not be so simple, for the lowering of the freezing point by the sugar solutions present in the tree is only small. According to the investigations of Dixon and Atkins (*loc. cit.*) and Korstian, it amounts generally to less than 2 degress as compared with distilled water. The protective action of the sugar solution against freezing is to be sought much more in the crystallising out of the solutions of only

[1] Prestonaud Philipps, Season. var. food reserves of trees. Forestry Quarterly, IX, 1911, p. 232; Mer., 1898.

[2] Mer, Compt. rend. Ac. Sc. Paris, 112, p. 964.

[3] Lidforss, B., Zur Physiologie u. Biologie der wintergrünen Flora. Bot. Zentralbl., 68, p. 33, 1896. The same, Lunds Univ. Arsskr. n. f. Bd. 2, 1907; *comp.* also Tuttle, G. M., Ann. Bot. 33, p. 201, 1919

[4] Colville, F. V., The influence of cold in stimulating the growth of plants. Jour. Agr. Res., 20, p. 151, 1920. Rigg, G. B. Some factors in evergreeness in the Puget Sound region. Ecology, 2, p. 37, 1921. Sinott, E. W., Factors determining the character and distribution of found reserve in wood plants. Bot. Gaz. 66, p. 162, 1918.

[5] Flora, 1905, p. 94.

part of the water on freezing so that a certain quantity of water remains in the plasma. In winter the interior of the stem often has a higher temperature than the surrounding air. With external temperatures of from –15 to –22 degrees it may be only –13 degrees.[1] According to Th. Hartig the temperature curve of the stem is similar to that of the soil and only trifling differences exist between the temperatures of the living and dead stem during the winter rest.

Berthold [2] is of opinion that the winter dissolution of starch is connected with the translocation of substances, such as a partial migration into the deeper lying parts of the twigs and of the stem.

A. Fischer [3] called those trees in whose wood starch remains in the winter: **Starch Trees,** the conifers and a few of the softwoods examined by him, whose starch disappears periodically out of the wood in winter: **Fat Trees,** because he found fat in their wood at this time. How far this fat originates through the conversion of the starch does not clearly emerge from the existing investigations. Suroz [4] observed the formation of fat from starch with the microscope; on the other hand, Vandevelde,[5] by macroscopical investigation, found the content of fat and protein substances in beech twigs approximately constant throughout the year (Fig. 136), in spite of considerable variations in starch and sugar content in summer as well as winter. Prestonaud Philipps found no notable increase in fat in late autumn and early winter in most trees, though it did occur in others. *Salix alba* contained little starch but much fat in winter. Antevs [6] detected in young twigs of broad-leaved fat trees (*Salix*, *Prunus*, etc.) during the winter, either alone (*Alnus*) or in addition to fat and starch, a fat like substance which did not give all the fat reactions and at the time of the re-formation of starch went over partially into fat and starch. He found the dissolution of fat and re-formation of starch in spring so dependent on the weather that unfavorable spring weather after sunny days brought a part of the starch into solution—the process, in *Pinus* and *Picea*, coinciding with an increase in the fat content. At the time of the starch maximum (when the breaking of the buds was beginning), starch and fat were present in equal quantities and on the whole remained so later when the fat and starch were being dissolved. Niklewski [7] came to the conclusion that the appearance of fat has nothing directly to do with the conversion of starch. In lime wood in December the re-formation of starch, brought about by a temperature of 19 degrees, went hand in hand with an increase of fat (from 6.42 per cent. to 8.46 per cent.). The fat-content of the rind increased from 7.87 to 8.78 per cent. With the fall of temperature in January, fat and starch diminished simultaneously.

[1] Leick, Temperaturzustand verholzter Achsenorgane. Mitteil. d. naturwiss. Vereins f. Neuvorpommern u. Rügen, 44. Jahrg., 1912, Greifswald, 1913.

[2] Untersuchungen zur Physiologie der phlanzlichen Organisation II, 1, p. 222, 1904.

[3] Beiträge zur Physiologie der Holzgewächse, Jahrb. f. wiss. Bot. XXII, 1890.

[4] Beihefte z. bot. Zentralbl., 1891, p. 342.

[5] Bijdrage tot de scheikundige physiol. van d. stam d. boomen. Gent. 1895 and Chem. Zentralbl., 69, 1898, I, p. 466; Lidforss, Wintergrüne Flora, Bd., 1907; Jonescu: January to April much starch, 20th May much oil, in beech twigs. Ber. d. D. bot. Ges., 12, 1894, p. 129.

[6] Zur Kenntnis der jährlichen Umwandlungen der stickstofffreien Reservestoffen der Holzpflanzen. 1916. Ark. Bot. K. svenska Vet. Acad., XIV, 1916. Authors abstract. Bot. Zentralbl. Bd. 131, 1916, p. 313.

[7] Beihefte z. bot. Zentralbl. 19, Abt. I, p. 68, 1905.

In winter the fat-content of the trees at first increases and then diminishes, quite independent of the temperature; at most the increase of fat proceeds more rapidly with higher temperatures. I quote a few of his figures:

Fat-content of the Lime.			Fat-content of the Birch.		
Date.	Wood.	Rind.	Date.	Wood.	Rind.
December 30 .	6.42%	7.87%	August .	1.74%	1.91%
January 14 .	7.07%	8.35%	October .	2.16%	2.10%
January 22 .	9.16%	10.28%	January 14	2.29%	2.40%
January 29 .	7.68%	8.91%	February 9	1.64%	2.40%

Weber [1] finds that there are considerable amounts of fat in Fischer's fat trees also in the summer and that the formation of fat in the stem of the conifers is not confined to the autumn. In the spruce, according to Fabricius,[2] the conversion of starch in the spring only proceeds in the youngest twigs. By it are formed substances, such as sugar, capable of being transported which are utilised in the breaking of the buds. Simultaneously, in the older parts of the stem, the replacement of starch by fat begins, apparently by conversion, and this formation of fat continues throughout the whole summer. During this period starch is not stored up in the wood. Only from the end of September onwards, is the fat of the wood mostly reconverted into starch. Then, in the spring, occurs the starch maximum also described by Fischer, which is maintained only for a short time. In the rind, the fat present is consumed during the summer. There occurs besides an accumulation of starch proceeding from above downwards. This may, however, at least in the younger parts of the stem, be again consumed. The assimilates formed after the growth of new wood has ceased, from about mid-August onwards, produce the main bulk of the reserve materials. The rind of the root, according to Fabricius, contains fat so long as the root is growing, but during the resting periods in August and September and in winter, fat is entirely or almost entirely absent. The rind starch does not, however, completely disappear in summer. The winter period of higher fat- or sugar-content, according to Coster,[3] completely disappears when our trees are raised in the equable, warm climate of the tropics. Temporary artificial cooling also results in no increase of the fat-content in such trees. Few species of tropical trees contain fat in the stem.

To facilitate the choice of material for further investigation some data of Schmidts'[4] may be given. He cites as **fat trees**: *Salix* species, *Betula nana* and *humilis*, *Castanea sativa*—as **starch trees**: *Carpinus* species, *Juglans* species, *Carya porcina* and *Ostrya*, and found no starch and only very little fat in *Alnus incana*, *Populus balsamifera*. Substances which give the potassium bichromate reaction of tannins, show

[1] Bot. Zentralbl., 113, 1910, p. 166 (Abstract from the original work in Anz. d. K. Akad. d. Wiss. Wien, XLVI, 1909, p. 286.

[2] Untersuchungen über Stärke- und Fettgehalt der Fichte auf der oberbayerischen Hochebene. Naturwiss. Zeitschr. f. Forst- u. Landwirtsch., III, 1905, p. 137.

[3] Coster, Ch., Die Fettumwandlung im Baumkörper in den Tropen. Annales du jardin Bot. Buitenzorg 35, p. 71.

[4] Bot. Ztg., Abteil. II, LXVII, 1909, p. 129.

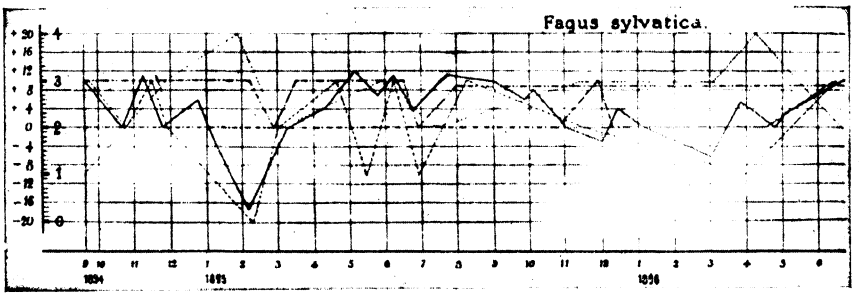


FIG. 136.—After Vandevelde. *Fagus sylvatica*. Content of starch, sugar, fat and protein substances during the year. The figures on the right of the temperature scale denote the quantities, the horizontal row of figures the months. ——— Temperature, – – – –Starch, ····· Sugar, ·–·–·–·– Fat, –··–··–··– Protein substances.

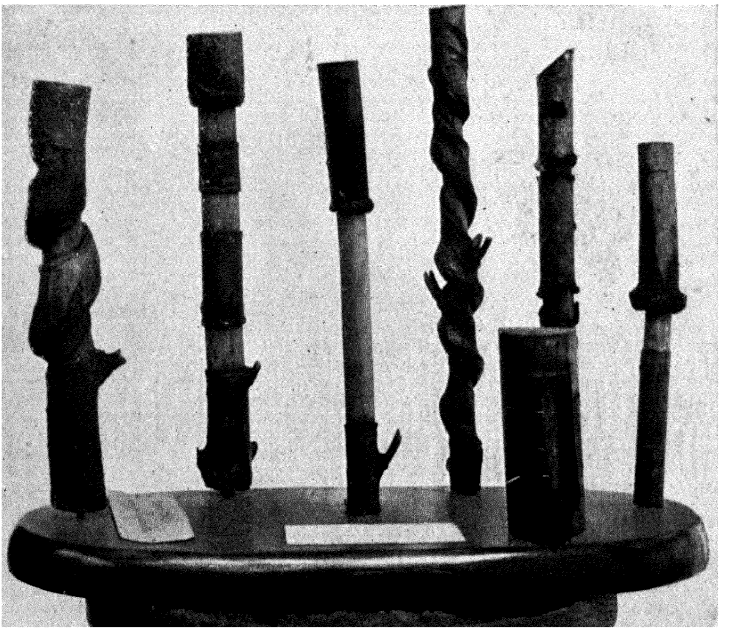


FIG. 137.—Original preparations of Heinrich Cotta, 1806, on the Circulation of Sap. From the collection of the Botanical Institute of the Forest High School in Tharandt. (Mch.)

[*To face p.* 359.

no relation to the course of the winter conversion of starch (*Acer*, *Betula*, *Aesculus*).[1] The want of harmony among the existing data is explained by the young twigs not behaving exactly like the stem and the different species of trees differing in their chemistry. The difficulties associated with micro-chemical experiments are to be taken into account, *e.g.* in the case of the work of Fabricius. Finally, the replacement of starch by fat in the tree stem does not stand alone in the botanical world. It is only an example of the processes which are carried out also in other storers of reserve materials, especially seeds, and are not absent in the winter buds of woody plants.[3]

2. The Descending Sap-stream and the Circulation of Sap.[4]— The organic building materials which are formed in the leaves from the carbonic acid of the air by assimilation, have often to traverse a very long distance in the tree before they reach the places of consumption—the growing or storing organs. Even leaving out of account the 150 metre-high Australian eucalypti and the over 100 metre-high conifers of the Pacific coast and considering only our 60 metre-high spruces and silver firs, there are considerable distances from the twigs to the growing root-tips which must be traversed with considerable rapidity. When the root begins to grow the necessary building materials are already on the spot and everything suggests that they hasten thither from a considerable distance, even if it is assumed that the requirements are to a large extent met by the reserve materials of the root. The rapidity of this translocation of material in trees is considerable ; it is of the same order as the rate of the transpiration stream. Dixon [5] determined the rate at which the plastic substances must flow through the bast of the thin stem of attachment, to build up a potato, to be 50–110 centimetres per hour, for the assimilates in the leaf-stalk of *Tropaeolum*, 3.5–7 centimetres per hour. These measurements are, however, not exact, as the concentration of the elaborated sap was not sufficiently known. Measurements, as yet unpublished, by the editor, give values of several decimetres per hour for the mean velocity of the descending sap in trees. Such performances are no less astonishing than those of the ascending water current in the wood.

No less wonderful is the certainty and promptness with which the building materials arrive at the places where they are required for growth and storage, be it downwards to the roots or upwards to the growing fruits. We have seen that growth does not take place where the materials flow in but that the materials flow in where growth is taking place. The growing parts of the plant are centres of attraction for building materials and it is undoubtedly of the highest importance that a knowledge of these attracting forces should be acquired.

If the translocation of materials took place in the form of diffusion

[1] Renvall, Beihefte z. bot. Zentralbl., 1, XXVIII, 1912, p. 282.

[2] Meyer, A., Die angebliche Fettspeicherung immergrüner Laubblätter. Ber. D. Bor. Ges. 36, 1918, and Coster *loc. cit.*

[3] Czapek, Biochemie, 2. Aufl., 1913, p. 751.

[4] From a Lecture by E. Münch, on the Dynamics of Sap-currents. Abstract in Ber. D. Bot. Ges. 44, p. 68, 1926.

[5] Dixon, H. H., The Transpiration Stream, London, 1924, p. 57.

in the solvent medium, the streaming taking place in the direction from the places of production to those of consumption would be easily esplainable. A fall of concentration is set up at one end by the consumption of the dissolved materials which must result in diffusion in the direction of the place of consumption.

It has, however, long been clear that diffusion, as a driving force for the migration of substances, can only be involved to a vanishingly small extent.[1] It would work far too slowly and consequently only effect in the course of years what goes on in the plant in an hour. There must therefore be mass movements of whole solutions which travel from the leaves to the places of consumption and the driving forces of these sap currents must be other than diffusion. The term "**Descending Sap-stream**" which the old physiologists applied to this stream of dissolved assimilates is retained for convenience.

The descending sap-stream undoubtedly moves in the conducting channels of the bast—the leptome, and in fact, as we showed in Chap. V, 1, in the sieve tubes. The other cells of the bast are not concerned in the transport of assimilates to a distance, because the companion cells are absent in conifers and are not connected together continuously over long distances in the broad-leaved trees while parenchyma cells are not present in the bast of monocotyledons. Ringing of the shoot does not result in the interruption of the descent of sap if only the outer parts of the bast and cortex, rich in living parenchyma cells, are removed. Interruption only occurs if the young living sieve tubes in the innermost layers of bast are cut through.[2]

The short cut from the assimilating leaf-cells into the sieve tubes and from these into the growing or storing cells at the place of consumption, is made through the bundle sheath and other transition cells whose physiological significance is still unknown, most probably entirely or mainly through the plasmodesms which, though of small dimensions, penetrate the cell walls in the direction of flow in great numbers. Possibly the plasma membrane is more permeable for dissolved substances and consequently for the sap in this direction than in the other.

That the descending sap-stream runs in the bast and not in the wood—other kinds of tissue capable of conducting do not exist in older shoots after the formation of bark and heartwood commences—is among the oldest and most certain conclusions of plant physiology. If doubt has been thrown on this recently in many quarters (Dixon, 1924, Birch-Hirschfeld, Kastens,[3] who more or less definitely name the wood as the path of the descending sap-stream), it may only be due to the fact that no sufficient driving force could be found for the copious and rapid current of sap in the scanty conducting channels of the bast. Regular and adequate descending sap currents in the wood, such as these authors assume, are for various reasons quite impossible, at least in high trees.

The tracing of the paths of the descending sap-stream was carried

[1] Birch-Hirschfeld, L., Unters. über die Ausbreitungsgeschwindigkeit gelöster Stoffe in der Pflanze. Jahrb. f. wiss. Bot. 59, p. 171, 1920.

[2] Strasburger, Leitungsbahnen, p. 916.

[3] Kastens, E., Beit. z. Kenntnis d. Funktion d. Siebröhren. Diss. Hamburg, 1924, and Mitt. a. d. Inst. f. allg. Bot. in Hamburg, Bd. 6, p. 33, 1924.

out by the physiologists of the 18th century, especially by Heinrich Cotta, 1806,[1] then by Th. Hartig, Strasburger[2] and others, by means of ringing experiments, which have never given any other result than that, above the place of ringing, all the life phenomena, formation of shoots and growth in thickness, proceeded in the same way as before the ringing, so long as the root only worked normally, but that the shoots and roots below the place of ringing, after the exhaustion of the reserve materials stored up there, ceased to grow and sooner or later starved. Ringed trees only live a few years if they do not succeed in forming new leaves below the ring, whilst a single ringed branch may remain alive for decades and make further growth above the ringing place, if the roots are nourished by other branches.

Such experiments (*compare* Fig. 137) led Heinrich Cotta, 1806 (*loc. cit.*), to the discovery of the "**Circulation of Sap.**" The "raw sap" absorbed by the roots ascends in the wood to the leaves, then, so far as it does not evaporate there, descends from the leaves as "elaborated sap" in the rind, reaches the wood through the medullary rays and rises again there.

If the expressions raw and elaborated sap, which were originated without a knowledge of leaf assimilation or even of the law of the conservation of matter, are translated into the language of modern physiology as "solution of nutrient salts" and "solution of assimilates," Cotta's representation of the closed circulation of sap is still correct to-day. It has, however, since Sachs, been given up in plant physiology, though mistakenly, as may be easily proved.

The sieve-tube sap of trees contains, as stated in Section V, 1, about 20 parts of dissolved substances in 100 parts of water; fresh sapwood, on the other hand, contains, according to the species, about 100–150 parts by weight of wood substance to 100 parts of water.[3] To provide the necessary organic substances to form the annual ring—the trifling proportion of inorganic substances may be neglected—a quantity of sap must flow to the cambium whose water content is 5–8 times as great as the water content of the completed annual ring. The greater part of the solvent water of the descending sap-stream has thus no place in the new annual ring; it must therefore, after the dissolved substances have been laid down as wood in the growing cambium, pass over out of the cambium into the wood, to again ascend to the leaves, partly to evaporate and partly to be employed again in the solution and transport of the assimilates. The quantity of water circulated in this way requires the water content of 5–8 of the youngest annual rings, and so in many species the water content of the whole conducting sapwood, neglecting the water evaporated from the rind, the amount of which at least in bark forming species, is only very small.

It is clear that such a considerable quantity of water, supplied to the sapwood by the cambium, must be of great physiological importance. In it we see the supply of water to the sapwood which, in the description

[1] Cotta, H., Naturbeobachtungen über die Bewegung und Funktion des Saftes in den Gewächsen, mit vorzüglicher Hinsicht auf die Holzpflanzen. Weimar, 1806.

[2] Strasburger, Bau und Verrichtung der Leitungsbahnen. Jena, 1891.

[3] Hartig, R., Unters. a. d. Forstbot. Inst. in München III, Berlin, 1883.

of the cohesion theory of the ascent of sap, we require as a supplement to the transpiration stream, to fill up the emptied vessels. The circulation of sap would be capable of filling up the conducting sapwood after the complete emptying of the vessels, including the imbibition water of the cell walls.

The force by which the solvent water of the descending sap-stream is driven out of the cambium into the wood, is obviously of an osmotic nature. By the precipitation of the dissolved building materials in the form of wood, the sap loses its osmotic absorptive power and is then driven out of the cells by the pressure of the tissues—the pressure of the tense cell wall and the neighbouring cells. Ursprung and Blum [1] found that the osmotic pressure of the cambium (of *Robinia pseudacacia*) was actually much smaller when it became active. The osmotic value, which in winter (March) was 42–45 atmospheres, fell in June to one-third and the wall pressure of the cambium cells was then very small. The semipermeable plasma membrane is easily permeable to water. It resists the passage only of osmotically active substances and solutions. If the mechanical tension of the cell wall exceeds the osmotic force of the cell content, water passes out; as can be easily shown by simple experiments with pigs' bladders.[2]

The pressure in the living cells of the bast and cambium is generated in the leaf cells. The dissolved assimilates formed from the carbonic acid—mainly sugar—suck in water from the water channels of the leaf veins, the cell becomes distended and squeezes sugar solution into the sieve tubes by osmotic pressure. This pressure is propagated thence through the viable sieve tube elements down the whole shoot to the root tips—in fact, as we have shown, over a distance of several metres in a few seconds (p. 134). The plant makes use of the unique property of osmotic cells of simultaneously sucking in water and squeezing out solution and thus of acting at the same time as a suction and force pump, to actuate the circulation of sap

The tensile strain in the water of the wood, which are normally present in transpiring trees, assist the passage of water from the cambium into the wood by a sucking action and, together with the pressure in the sieve tubes, help to overcome the resistances to the descending sap stream.

In this way the consumption of assimilates by the growing cambium, *i.e.* the conversion of dissolved substances into insoluble ones, results automatically in the flowing in of formative sap through the sieve tubes to the place of consumption in proportion to that consumption, and the giving off of water from the cambium into the conducting channels of the wood. The sap-stream is, as it were, filtered by the growing cambium, in which the dissolved substances are held up. The passing of water out of the cambium provides the room and the necessary hydraulic pressure gradient for a constant stream of formative sap from the leaf to the cambium.

[1] Ursprung und Blum, Eine Methode zur Messung des Wand- und Turgordruckes, etc. Jahrb. f. wiss. Bot. 63, 1924, p. 100.

[2] *Comp.* Pfeffer, Studien z. Energetik, 1892, p. 265, and Osmotische Untersuchungen, 1877, p. 223; *comp.* also Chap. V, 1.

As was shown in the discussion of exudation pressure, the root pressure and the exudation stream depend on similar processes ; namely, the squeezing out of water from the growing cambium of the root and the subsequent pushing of solution out of the sieve tubes ; the resulting fall in turgor leading to the absorption of soil water into the sieve tubes.

Similar streamings of sap also occur in other cases of conversion, by which dissolved osmotically active substances are changed into solid or otherwise osmotically inactive ones, especially in all cases of the storing up of reserve materials. If, for example, in the storage cells of the medullary rays, starch or fat is formed from sugar, osmotic forces disappear and the superfluous solvent water is squeezed out of the storing cell into the neighbouring conducting channels of the wood, since in the latter no counter pressure opposes it but rather, for the most part, a sucking tension prevails.

Sap movements also follow on the formation of resin, ethereal oil, hydrosols, crystals and nuclear materials, or when osmotically highly active substances pass over it into less osmotically active ones. If grape sugar is converted into cane sugar, the solution loses half its osmotic value and excretes half of its water out of the cell. The formation of high molecular tannins, adsorptions and other processes by which osmotic forces are diminished, will work in a corresponding way. Pressure gradients and sap currents of the same nature also arise when certain parts of the tissue destroy osmotic substances by respiration more rapidly than other parts.

Conversely, whenever solid substances are dissolved, there follows the sucking in of water and the squeezing out of solution. A special case of this is the mobilising of reserve substances by hydrolysis in the storage organs, *e.g.* the reconversion of starch into sugar in germinating seed and fruits. They absorb water, either directly through their covering or out of the vascular bundles of the radicle, and squeeze sugar solution into the radicle.

The movements of materials are thus bound up with chemical transformations which, from solid or non-diasmosing substances, produce osmotically active bodies capable of travelling and finally precipitate them in insoluble or otherwise less osmotically active forms. Among the non-nitrogenous substances the sugars should be mentioned and among the nitrogenous ones, the crystallisable, water soluble amides, of which asparagin is widely distributed. The protein substances get an opportunity of moving as such over long distances only in the sieve tubes, since the constituents of the latter are connected together by comparatively wide pores whose plasmodesms are traversed by vacuoles.

That the growing parts of the plant do actually excrete water, as is to be expected according to these physical laws, is not always visible to the outside. As a rule the currents thus set up circulate in the inside of the plant between the living parenchyma and the dead organs of the wood. In special cases, however, they make their appearance outside in the form of bleeding pressure at wounds and as guttation. If strong shoots with the rind removed are placed in a moist chamber the exposed cambium goes on growing and exudes copious drops of water. Exudations of water are specially to be observed on fungi, *e.g.* in the growing

fructifications of the large tree fungi and on the mycelium and fructifications of the dry rot fungus and others. In such thallophytes the mycelium is not organised into conducting channels for formative sap and channels for water, as in our trees. The solvent water liberated by growth cannot, as in trees, pass into conducting channels. It is exuded to the outside.

To the function of the wood channels of absorbing and conducting away the solvent water set free by the storing up of materials, there corresponds the remarkable fact that the bast is, almost without exception in the plant world, accompanied by wood. For this reason wood channels are also formed in plenty in tubers and fruits where they have scarcely any loss by evaporation to supply. Here they have to carry off the solvent water in case of the storage, and supply it in case of the solution of the reserve materials.

The sap-stream ascending in the wood is not driven exclusively by transpiration. Transpiration does indeed move forward the greater part of the wood water, but only so much as it itself consumes. Even when transpiration is suppressed the circulation of sap goes on, as the leaf parenchyma cells absorb as much water as they utilise for the solution and carrying away of the newly-formed assimilates. The amount of this water is not inconsiderable. With a 20 per cent. concentration of the formative sap and a production of material of 5,000–10,000 kilogrammes, it amounts to 25,000–50,000 litres per hectare per annum ; or, with 500 stems to the hectare, to 50–100 litres per tree per growing season, and thus to about 1–3 per cent. of the total water of vegetation.

The water current of the wood contains in solution the nutrient substances absorbed from the soil by the roots and carries them to the leaves. The living leaf cells can absorb into themselves through the plasma membrane the inorganic foodstuffs necessary for their life and for the formation of the assimilates from the dilute solution of the wood water, just as the root cells can from the soil water. Thus sulphates and nitrates and also part of the phosphates are transformed into organic compounds in the leaf cells,[1] magnesium is taken up in the chlorophyll ; iron also plays a part in the formation of chlorophyll, though not an actual constituent of that substance. Nitrogenous compounds are also even worked up in the roots.[2] Lime salts, absorbed in excess, are in many plants exuded from the leaves in the guttation water without having first passed through the green cells.

Besides the nutritive salts, the ascending wood water generally contains organic substances in solution [3] which serve in the spring for the building up of the young shoot and are also accumulated in the fruits (p. 851).

That organic substances, exceptionally and for short distances, may also travel *upwards* in the bast, was made clear by ringing experiments

[1] Schimper, Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze. Flora, 1890, p. 260.

[2] Müller-Thurgau, Bot. Zentralbl. 80, 1899, p. 74.

[3] Fischer, A., Beitr. z. Physiologie der Holzgewächse, Jahrb. f. wiss. Bot. 22, p. 73. *Comp.* also what was said about reserve substances and exudation sap.



FIG. 138. Roots of several Spruces naturally grafted. With four occluding stumps. (Mch.)

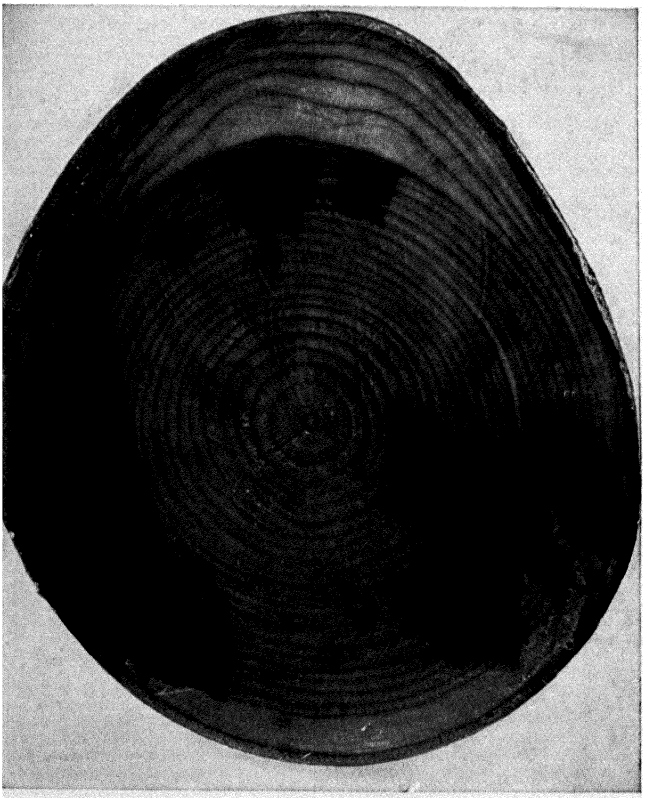


FIG. 139.—Cross section of Maple stem. The wood in the blackened part was killed 5 years previously by a fungus as far as immediately below the cambium. In spite of this, the cambium has continued to grow, in fact, seven times as rapidly. After Münch.

[*To face p.* 365.

by Leclerc.[1] It may also be inferred from the fact that the stumps of felled trees continue to live for decades and may put on increment and form callus tissues, if their roots have grown into union with the roots of neighbouring trees[4] (Fig. 138). This is to be seen quite commonly in silver firs and Douglas firs, frequently also in spruces and larches, rarely in pines. Branches which die off owing to the exclusion of light, are supplied with nutrient substances for a short distance upwards from the stem. By their anatomical structure, the sieve tubes are equally capable of conducting in either direction. If the place of consumption lies towards the tip, as in fructifications, the formative sap flows upwards in the sieve tubes supported by currents in the wood. In this case the sieve tubes are so arranged that they are in connection with the series of sieve tubes coming from the leaves. Embryonic tissues are supplied from below through the elements of the primary phloem. That the lower, basal parts of ringed branches are not supplied with plastic substances from below, is due, according to Strasburger,[3] to the absence of such a connection between their sieve tubes and the leaves.

The medullary rays serve as conducting channels in the radial direction. In most species, the conducting and storage of plastic substances in the medullary rays is kept apart from the conducting of water and entrusted to its own kind of cells. This is the case indeed, not only in conifers like pine and spruce, where the marginal cells of the medullary rays take the form of borders of tracheids, but also in broad-leaved trees, in which the marginal cells are distinguished from those in the middle, by differences in their height and pitting. The silver fir, however, has none but parenchyma cells in the medullary rays, but has instead bordered pits on the tangential walls of the late wood tracheids, which serve for the transmission of water in a radial direction.

Peripheral movements of sap are likewise possible in the bast, as the sieve plates in conifers are situated only on the radial walls, and in hardwoods, all round. Use is made of this possibility when the bast is wounded, as well as when there is a stimulus to growth on one side, such as the pressure stimuli with which we have already become acquainted, which cause a one-sided growth of the annual ring, often on the side directly opposite to the position of the branches. If there is no such stimulus operating to divert it, the sap appears to travel downwards strictly in the direction of the fibres, for, if the conducting channels are interrupted by a living, but owing to shortage of light, only feebly assimilating branch, the increment of the stem does not take place below this branch, so that a sunken furrow is formed running downwards from it.

Cambium growth is mainly bound up with the direct supply of materials through the sieve tubes, and the sieve tube contents cannot be entirely replaced by the reserve materials in the storage cells of the wood. For when a stem is girdled, there is, as a rule, no growth below

[1] Leclerc du Sablon, Compt. rend. Paris, 1905 (3–4 year old trees, *Pyrus, Cydonia, Evonymus japonicus*). *Comp.* also Strasburger, Leitungsbahnen, p. 892.

[3] Wichmann, E., Wurzelverwachsungen und Stocküberwallungen bei Abieteen, Zentralbl. f. d. ges. Forstwesen, 1925, p. 250. On the polarity at work therein, *see* Neef, Jahrb. wiss. Bot. 61, 1922.

[4] Leitungsbahnen, p. 905.

the ring, even when the starch stored there is still present in plenty. Cases have indeed been observed in which the cambium of defoliated stems continued to grow until the reserve materials were exhausted.[1] According to Strasburger, it is the albuminous substances of the sieve tube contents which are required to supplement the non-nitrogenous organic compounds in order to make cambium growth possible. According to Kastens, the cell-division hormones (Haberlandt) [2] are normally formed in the leaves and young shoots and are conducted to the cambium only through the sieve tubes. If the supply of hormones is prevented by ringing, cambium growth does not occur, even if all the other substances are present. The conclusion drawn from these observations—that the sieve tubes conduct such supplementary substances *only*, and that the building materials themselves were conducted downwards, not in the sieve tubes but in the xylem (Kastens)—is however not substantiated.

The cambium, as Münch [3] has shown, is completely independent of the wood for its nutrition. If, for instance, the wood is killed up to just under the cambium by fungi or the injection of poisons, the growth of the cambium proceeds just as well as before, and, in fact, even more vigorously, so that annual rings of up to seven times the previous breadth appear (Fig. 139). If a strip of rind is loosened from the wood so that it still remains connected with the rind of the tree above and below, and a piece of tinfoil or the like is placed underneath it, the cambium continues to grow, producing at first thin-walled parenchyma and then wood and bast. This also contradicts the view of Dixon (1924), Birch-Hirschfeld and Kastens, that the assimilates are conducted to the growing cambium, not through the bast, but through the wood.

[1] Hartig, R., Das Erkranken und Absterben der Fichte . . . . Forstliche Naturwiss. Zeitschr. 1, 1892.

[2] Haberlandt, G., Über Zellteilungshormone . . . . , Biol. Zentralbl. 42, p. 145, 1922.

[3] Münch, E., Versuche über Baumkrankheiten, Naturwiss. Zeitschr. f. Forst- u. Landwirtsch. 8, 1910, p. 409.

CHAPTER XIII

FLOWERS, FRUITS AND SEEDLINGS[1]

1. Flower.—When Linnaeus divided plants into Cryptogams and Phanerogams he showed more scientific sense than those who translated these words as Flowering Plants and Flowerless Plants. Certainly it was long after Linnaeus that it was first proved that the greater number of the cryptogams are not flowerless but, as the true meaning of the word implies, " hidden flowered." We now not only know that the algae, mosses and ferns possess sexual organs ; we also know the most important stations on the line which leads from the inconspicuous flowers of these plants to the phanerogamous flower.

The phanerogamous flower is usually defined as a shoot whose leaves have been formed in a particular fashion for the service of propagation. This character is most clearly apparent in the conifers. The female flowers, the cones, of the spruce are shoots with scaly leaves and the male catkins likewise represent shoots, but with delicate leaf structures on which the pollen sacs develop. The likeness of these structures externally to the conelike spore-sac carriers of the horsetails and club mosses (*see* Fig. 140) is obvious, and actually closer investigation shows that the spore containers of the latter on the one hand, and the pollen sacs of the former on the other, are fundamentally the same thing. The differences between the apparatus devoted to sexual reproduction in the higher cryptogams and that of the phanerogams may be conceived as adaptations to life in drier soil and in drier air than were present on our globe during the period in which luxuriously developed ferns, horsetails and club mosses formed the dominant figures in the vegetable kingdom.

In cryptogams and phanerogams the plant begins its independent existence with a period of travel, which affords it an opportunity of reaching more favorable conditions for its development away from the locality occupied by its parents. The travelling condition of the cryptogams is the **spore.** It is a small, light, cell and carries only little nutriment with it on its way, so that the mother plant can produce thousands of spores and hand them over to the wind for dispersal. In the higher cryptogams therefore, it is only on the germination of the spore

[1] v. Tubeuf, Samen, Früchte und Keimlinge der forstlichen Kulturpflanzen. Berlin, 1891 ; Hempel u. Wilhelm, Bäume und Sträucher des Waldes. Wien, Hölzel ; Lebensgeschichte der Blütenpflanzen, etc. Stuttgart, Ulmer.

after its wanderings are over, that the sexual organs with the ovum and the male fertilising elements are produced. Under the simplest imaginable conditions, in a drop of water on wet soil, fertilisation of the ovum takes place, which then grows on into the new fern, horsetail or club moss.



FIG. 140.—(1) Entire plant of the common Club Moss (*Lycopodium clavatum*) with conelike sporangiophores. Every leaf of these sporangiophores carries a sporangium (2) at its base, which on ripening springs open by a transverse slit and releases the spores (3). B.L.

In the phanerogams the ovum is formed in the ovary, and so in the interior of the protecting mother plant, and is still kept there after fertilisation until, already developed into the young plant with seed leaves—as yet not unfolded, it is true—and the first rudiments of the root and packed tight in the seed coat, it betakes itself to its travels. For this travelling condition of the phanerogams, heavy and for that reason endowed with many kinds of distributing apparatus, has been reserved in science the name "**Seed.**" On this account the phanerogams and cryptogams are also contrasted as "seed plants" and "spore plants" respectively, and these expressions in fact point to the differences between the two groups of plants better than the older terms. Many remnants of former cryptogamic arrangements are found in the phanerogams, especially the conifers. As these, however, are only disclosed by closer study and are not of great importance for understanding the life of our trees, I shall not go into them here. A detailed account of these relationships is to be found in every textbook of botany.

2. Flowering and Fruiting Conditions.—In order to carry out seed harvesting and natural regeneration systematically, the forester must be able to estimate with some degree of certainty how often and under what conditions seed is to be expected from the various species of trees. For this a knowledge of the physiological conditions of flower

and seed formation will stand him in good stead. These conditions, it is true, have been sufficiently investigated almost only for the beech, whilst with regard to the other species our knowledge of the matter is only in its initial stages.

The power of bearing flowers and fruit, or fertility, is attained by all our trees only at a certain age ; by trees with light fruits in general earlier than by those with heavy ones. That fertility is a function of age and not of the size attained with age, is shown by the much earlier flowering of the stool shoots of old trees and cuttings (hazel) than of seedlings of the same size. The appearance of fertility, however, depends also on development in so far that trees in the open come into flower earlier than those grown in close stand, and in a warm climate earlier than in a cold one. The following are in general the minimum ages for fertility in years :

Birch	10–12	Norway maple, some years earlier	
Alder	12–20	Ash	30–40
Pine	15	Elm	about 40
Larch	20	Spruce	30–40
Hornbeam	20–30	Oak (pedunculate earlier)	40
Lime	25	Beech	40–50
Field maple	25	Silver fir	60–70
Sycamore	30–40		

Great deviations occur in individual cases. In many specimens of all species of trees flowers and fruit are seen before the age given. The larch, for example, often bears flowers even at 10 years, but not fertile seed. Exceptionally, under unfavorable growth-conditions, even 7-year-old pines bear ripe seed.[1] In its youth the pine regularly bears at first only female flowers, the male ones first appearing some years later. In many seed years the spruce bears plenty of fertile seed even on 15–20-year-old trees, and this not in any way in consequence of a condition of distress, but often actually on the strongest individuals. I have found pedunculate oaks bearing fruit repeatedly when barely man-high, and so on.

Even at the age of fertility most species of trees do not flower and fruit every year, but at intervals of several years. As was proved by Hartig for the beech, the formation of fruit exhausts the reserve materials (Chap. XII, 1), and only when the storage cells in stem and root have been replenished is the full formation of fruit again possible. This requires different lengths of time, according to the abundance of seed production, the locality and the species, and in general takes longer with large-fruited than with small-fruited species. If flowers appear before this, they often produce only empty fruits, as occasionally seen in beeches.

Flower formation appears to be to some extent independent of this readiness to form fruit. It depends very much on the weather, and in fact on the weather at the time when the buds are being formed, as the flowers are already prepared in the bud towards the end of the

[1] Münch, E., Verhalten der Nachkommen fremder Kiefernrassen, Forstwiss. Zentralbl. 1924, p. 126.

summer (Chap. II, 3). Flower buds are thicker and fuller than vegetative buds and are clearly recognisable as such in the beech even in September. Abundant flower buds are only formed on the beech in hot, dry summers.[1] **Mast years,** therefore, according to Ney,[2] generally occur in years in which there is much, though also sour, wine, because the vine behaves just like the beech as regards the production of flowers. It is possible to trace back for over a hundred years, that the great beech-mast years, among which may be mentioned especially 1811, 22, 34, 77, 88, and, in the current century, also the smaller mast years 1909, 12, 16, 18 and 22, without exception followed on years with great summer drought. In other species also, though not in all, markedly however in fruit trees, dry, warm weather in the previous year favours flower formation. With the pine, it should be noted that the cones take two years to ripen, so that the third summer before the shedding of the seed is the one which determines its amount. The flowering of the spruce also undoubtedly depends on some kind of special weather condition, because it occurs in many years simultaneously over large stretches of country, also often in definite altitudes or otherwise climatically defined areas. Lakari[3] states that in Finland a seed year for spruce and pine follows two years after a hot, dry summer. For Saxony, Zimmermann[4] has traced out the seed years of the spruce and the weather of the two years previous to each, but can find no kind of relation between weather and seed production.

The promotion of flower production by summer drought is explained, according to Klebs,[5] by flower formation being favoured by everything which leads to the production of an excess of carbohydrates in the tree as compared with the quantities of nutrient salts absorbed. An increase in the proportion C : N, *i.e.* carbon : nutrient salts, increases the probability of flower formation. In hot summers the absorption of nutrient salts is reduced by the dryness of the soil, and the production of carbohydrates increased by sunny weather. For this reason, well-lighted, isolated trees and parts of trees flower and fruit abundantly. Copious flowering may be induced in fruit trees, according to gardening experience, by paring off a narrow ring of rind or by binding the stem rind with a " fruit girdle " (Molisch).[6] Above this disturbance of the descending sap stream the assimilates are dammed up and fall to the benefit of the flowers and fruits, whilst the nutrition of the roots, and with it the absorption of nutrient salts, is diminished.

In order that the flower may become fruit, further conditions must be fulfilled. Fertilisation must be abundantly effected unchecked by rainy weather, and during the formation of the fruit, moisture and warmth must not be lacking. The beech, at least, requires ample rainfall in the summer of the seed-year and the acorn frequently does not ripen

[1] Seeger, Samenproduktion der Waldbäume in Baden. Naturw. Zeitschr. f. Forst- u. Landwirtsch. 11, 1913.

[2] Ney, C. E., Die Lehre vom Waldbau, Berlin, 1885, p. 387.

[3] Lakari, Meddel. f. Forstvetenskapliga Försögsanstalten. Helsinski, 1921.

[4] Not yet published.

[5] Klebs, Probleme der Entwicklung, I–III. Biol. Zentralbl., Bd. 24, 1904, and later works; Fischer, H., Flora, XCIV, 1905, p. 478. Ber. Dtsch. Bot. Ges. 19, p. 280.

[6] Molisch, Pflanzenphysiologie.

in too cold weather; not to mention the sweet chestnut, whose fruits, in the cooler districts of Germany, ripen only in the warmest summers. In the pine, many cones drop off during the course of the two years' development, though the causes of this are still unknown. That frosts, insect attack and other dangers also contribute to the result that not every flower year is also a seed year, can only be mentioned in passing.

All these causes working together bring it about that many of our forest trees fruit abundantly only at intervals of several years.[1] According to experience, better seed years follow each other, with alder, birch, sycamore and Norway maple, annually, with the field maple more seldom; with larch, lime, almost every year; with the hornbeam annually, a quarter, and every third year a full yield; elm, every second year; pine, a little every year, an abundant yield every 3–4 years; silver fir, every 2–3 years; spruce, every 3–5 years or more seldom; beech and sessile oak, every 5 years, the pedunculate oak more frequently. These figures are valid only for the species in question as a whole. As, however, all trees of the same species are not generally in bearing simultaneously, longer intervals apply to the recurrence of seed bearing in one and the same tree, as Bühler points out. However, all assertions of this sort, often differing greatly from each other, can only be regarded as the first stage. According to climate, weather and soil, great variations occur, especially in the chief species of trees; *e.g.* during the last 20 years, which were distinguished by many summer droughts, beech and oak fruited much more often than the average. Sessile oaks in places remain without any yield for ten years and then fruit for several years in succession. The spruce, for example, fruits much more frequently in the Black Forest, on richer soil, than in the Erzgebirge, and in moist, fertile valleys more frequently than on poor sites. The striking phenomenon that in seed years generally only some of the trees fruit has been more closely investigated by Münch [3] in the spruce. He was able to prove that in certain seed years only late-sprouting trees bear cones; the early-sprouting ones probably have their turn in other years. The consequence of this silviculturally important phenomenon is that, according to the year, the seed produces plants of different dispositions as to leaf opening, and therefore different suitability for certain localities. The various individuals, even of the same species, thus react quite differently to the same weather factors, by reason of their individual predispositions, and the fact that all species of trees do not bear seed in the same years leads to the conclusion that for every species other internal and external causes must act simultaneously in order to lead to the production of fruit.

3. The Female Flowers and their Parts.—In the phanerogams, the origin of the new plant, the **Egg Cell (Ovum)**, which is to be fertilised, is enclosed in the **Ovule**, everywhere a fairly uniformly constructed body of tissue from which later the seed develops. These

[1] Schwappach, Die Samenproduktion der wichtigsten Waldholzarten in Preussen Zeitschr. f. Forst.- u. Jagdwesen, 1895; working up the 20 years' official publications.

[3] Not yet published.

ovules at the time of fertilisation commonly possess a roundish structure, not reaching the size of a pin's head, in which the following parts may be distinguished with the microscope: a central kernel and one or two integuments arching up over it, leaving a gap right above its apex, which has received the name of "**Micropyle**" or little opening. In the interior of the central kernel a large hollow space—a giant cell—is visible; the **Embryo sac,** at the end of which, directed towards the micropyle, is the egg cell. If the place where the ovule is attached to the flower lies at the end directly opposite to the micropyle, the ovule is called **orthotropous** or straight, if the latter bends itself so that the micropyle comes to lie near this place of attachment, it is termed **anatropous** or reversed.

The female flower of *Taxus* consists of a quite inconspicuous little shoot with scale leaves, on whose apex stands a single ovule which protrudes half way out of the leaves. In our other conifers the ovules are found at the base of scale leaves which, in the abietineae (spruces, pines, silver firs, larches) are arranged spirally, in the cupressineae (Juniper, Arbor vitae) generally in two membered whorls, round the floral axis. The female flower of the juniper shows three such scales, each with an orthotropous ovule in its axil, and these scales later become fleshy and coalesce to form a "**Berry-cone**"—the juniper berry. In the arbor vitae and cypresses the number of ovules concealed behind the scales is greater and the flowers take the form of small, true cones as their scales become leathery or woody.

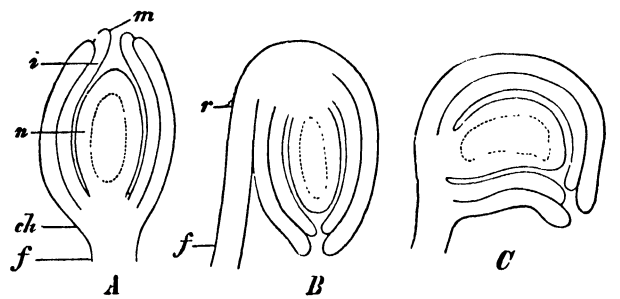


FIG. 141.—Ovules. (*f*) Stalk by which the ovule is attached to the ovary (Funiculus); (*ch*) base of the ovule (Chalaza); (*m*) apex of the ovule with the gap (Micropyle) left by its coverings; (*n*) central kernel of the ovule (Nucellus) with the embryo sac (the boundary of this is dotted). (*A*) Orthotropous, (*B*) Anatropous, (*C*) Campylotropous ovule. B.L.

The spirally arranged scales of the cones of the abietineae consist of two superposed parts, of which the upper one bears two anatropous ovules, with their micropyles therefore turned downwards towards the place of attachment of the cone (*see* Fig. 143). These two anatropous ovules are characteristic for all the abietineae, even where, as in the pines, the scales appear single. The seed-bearing part of the scale of the above-mentioned genera is called the ovuliferous scale or seed scale, the other, the bract scale. The latter protrudes beyond the ovuliferous scale in silver firs and larches and also in the Douglas fir, whilst in the pine (Fig. 143) and spruce it remains short and inconspicuous.

In the flowers of the broad-leaved trees the shoot-nature is concealed by a great shortening and widening of the floral axis. In addition, the carpels, *i.e.* the leaves on which or in whose vicinity the ovules lie, are united into a closed seed-container, the **Ovary,** with style and stigma; indeed the floral axis itself also often takes part in

the formation of the ovary. This is the case in inferior ovaries which, among forest trees, are met with in the *Sorbus* species, the beeches, oaks, hornbeams, birches, alders and hazels. The conifers are called naked-seeded plants, **Gymnosperms**; the broad-leaved trees belong to the covered-seeded plants, the **Angiosperms.** The ovule of *Taxus* alone, however, is actually uncovered throughout life. At its base there develops a juicy covering, red at the time of ripening, a seed mantle (aril) which does not close round it up to the top. The cones of the other conifers, like the berry of the juniper, are closed at least for a time, so that the seeds are completely covered as in the angiospermous plants, but style and stigma are never present. It would therefore be better to avoid the term "naked seeded" and to replace it perhaps by "cone plants" or conifers. From a comparison with the flowers of angiosperms and with the male flowers, the cones must actually be characterised as inflorescences which are composed of many individual flowers. As we are here considering life phenomena and not morphology, it seemed to me permissble, for simplicity's sake, not to abandon the term flower.

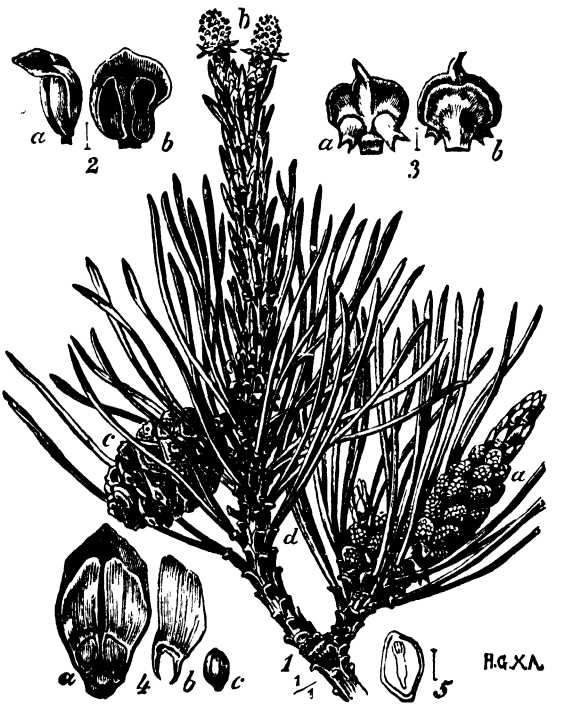


FIG. 143.—*Pinus sylvestris.* (1) Three-year-old twig. The terminal long shoot of the current year bears, below the terminal bud, two female flowers (*b*) with scaly stalks. On a corresponding position on last year's shoot, a cone (*c*) which was pollinated in the previous year and ripens in the October of the current year. Only in the spring of next year would it open to let most of its seeds escape. (*d*) Terminal shoot of the present year, with male flowers in the axils of its lower scale-leaves. (2) Stamens (*a*) from the side, (*b*) from below. Two pollen sacs are present, which spring open by splitting longitudinally. (3) Ovuliferous scale, (*b*) from below, (*a*) from above. In the middle, the keel (*camp.* Fig. 157). (4) Ovuliferous scale with ripe, winged seeds (*a*), (*b*) the wing clasping the seed in a clawlike manner. (5) Section of the seed with the four-cotyledoned embryo in the middle of the albumen. B.L.

The six genera of broad-leaved trees last mentioned belong to three families which, under the name Querciflorae or oak flowering, occupy one of the lowest ranks in the system of the dicotyledons. Their female flowers each consist of a single ovary which in some (*e.g.* hornbeam, beech, *see* Figs. **146, 153**) bears at its upper end a wreath of inconspicuous scales as evidence of a floral envelope. Correctly speaking, only the stigmas are in fact present at the time of flowering as the chamber of the ovary and the ovules, except in the beech and sweet

chestnut, are wont to develop only after pollination. In the oak the stigmas are three of four broad flaps, in the others (beech) two to three, in the sweet chestnut, four to six, long fibres which seem very well adapted to intercept the pollen blown by the wind, and, in the early flowering species (hazel, birch, alder), by reason of their bright red colour, are greatly warmed up by the rays of the first spring sunshine. This may benefit the growth of the pollen tube. According to Nawaschin's

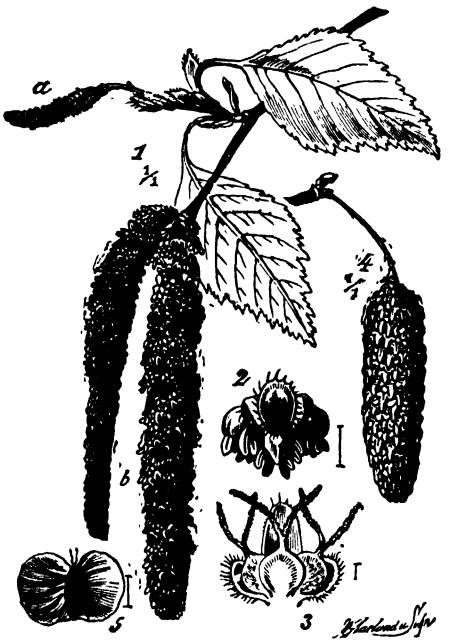


FIG. 144.

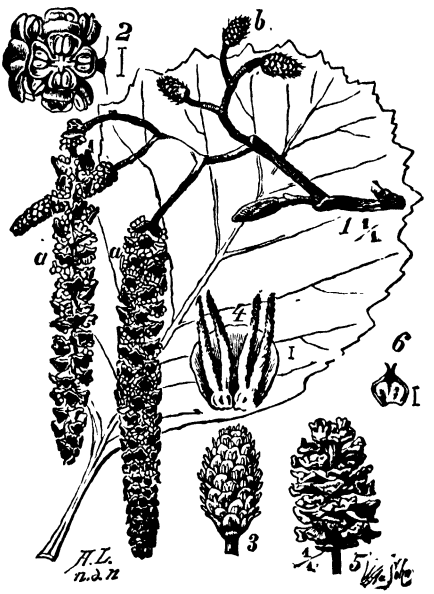


FIG. 145.

FIG. 144.—Birch. The male catkins (*b*) pass the winter at the end of the previous year's shoot, the female ones (*a*) form the upper part of leafy shoot of the present year. (2) Scale of the male catkin with flowers. (3) Three-lobed scale of the female catkin with three flowers. (4) Ripe fruit catkin. The three-loped scales do not persist, as in the alder, but fall off. (5) The winged fruit. B.L.

FIG. 145.—Alder. The male (*a*) and female (*b*) inflorescences winter together in a sort of corymb at the end of last year's twig. (2) Group of three male flowers, each with a four-leaved perianth, such as is found above each catkin scale. (3) Female catkin. It consists of an axis with scales, each of which bears two flowers in its axil (4). (5) Female catkin after the seed has fallen. The scales have become five-lobed, woody structures. (6) Ripe fruit ("seed"). B.L.

investigations on the beech and alder, these stigmas are the only things that develop from the actual carpel rudiments. The remainder of the ovary owes its origin to a subsequent growth of the floral axis lying below it. In the birches (Fig. 144), alders (Fig. 145), hornbeams and hazels it is two-chambered and contains in each chamber one to two ovules; in beeches and oaks, where it arises through the union of three carpels,[1] it is, as a rule, three-chambered, with six ovules; in the sweet chestnut, four- to six-chambered with eight to twelve ovules. In all cases, however, only a single one of these ovules in each flower

[1] V. Klebelsberg, Samenanlage von *Quercus robur* und intraseminale Gefässe. Öster. bot. Zeitschr., 60, 1910. See Büsgen, Cupuliferen, p. 114

develops further. This finally fills up the whole of the ovary so that the fruits of all the trees mentioned are one-seeded nuts.

More striking than the flowers themselves are the coverings or enveloping organs which enclose them and serve to protect the young fruit, and in the hornbeam (Fig. 145, 5) also as a means of its distribution when ripe. In the catkin-shaped inflorescences of the alder and birch, they are more or less woody scales, in the alder five-lobed and per-



Fig. 146.

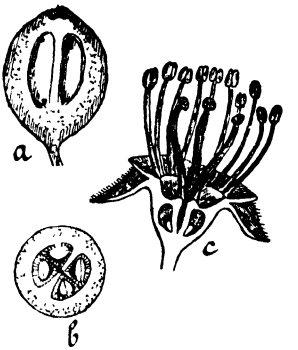


Fig. 147.—(*a*) and (*b*) Fruit of the Wild Service Tree in longitudinal and transverse section (*c*) Flower of the Pear Tree. showing the structure of the fruit.



Fig. 148.—Bisexual and male flowers of the Ash. Mag. After Engler and Prantl.

Fig. 146.—Hornbeam. Both the male and the female inflorescences emerge from buds on the twig of the previous year. Both are catkins. The female catkin forms the end of a terminal shoot of the current year, which also bears foliage leaves below it. The male catkin (1) springs from a lateral bud. (2) Shows a male flower magnified. It consists of a scale into union with which the bifid, tufted anthers (3) have grown. (4) Two female flowers each consisting of a single ovary with two long stigmas and surrounded by a special envelope, in the axil of a catkin scale. (5) Ripe fruit with its envelope, which has grown into a three-lobed bract, and the apical perianth teeth. B.L.

sistent, in the birch, three-lobed and falling at the time of ripening of the fruit. They give the catkins of these trees the appearance of small cones, except that in the latter each scale bears ovules, whilst in the alder two and in the birch three complete ovaries are found in the axil of each scale.

The flowers of the hazel and hornbeam stand in pairs in the axils of inconspicuous leaflets. The protection of the young fruit is here undertaken by special involucres which develop from the base of each ovary and become, in the hazel the well known lacerated husks (Fig. 154)

and in the hornbeam, three-lobed wings. In the oak, beech and sweet chestnut, the enveloping organs arise through proliferation of a part of the floral axis, covered with small scaly or hairlike outgrowths, which finally encloses each acorn as a basin, each pair of beech nuts as a four-lobed cup and generally each three chestnuts as an, also four-lobed, prickly capsule.

The *Sorbus* species, among which the wild service tree, the mountain ash and the white beam may be regarded as trees of our woods, together with the apple and pear trees, belong to the systematically high order of the Pomaceae. In the formation of their inferior ovaries a cup-shaped cavity in the floral axis takes part and is only more or less incompletely differentiated into carpels. Two to five of them are found in the wild service tree and its near relatives, and can be recognised as separate structures only in the middle of the ovary. In many, however, the presence of several styles, often also not completely separated, is the only indication of carpel-like structures. The ripe fruit encloses in its interior a number of hard-walled chambers in which the seeds are situated (*see* Fig. 147).

The ovaries of the elms, ashes, limes and maples are superior. They at least permit it to be recognised at the time of ripening that they are built up of carpels, of which two are present in the elms (Fig. 152), ashes (Fig. 148) and maples and five in the lime. The fruits of the elms and ashes are one-seeded, winged nuts, though in the former two and in the latter even four ovules are formed in each flower. In the maple fruit four ovules are present of which only two are found as seeds in the double winged, fissile fruit; in the lime even nine of the ten ovules originally formed are doomed to destruction for the benefit of a single one. The ripe fruit develops into a one-seeded nut.

4. The Male Flowers and their Parts. Sex Distribution.— The leaf structures entrusted with the production of the pollen do not occur in the same flower as the ovules in any of the conifers. All our conifers have unisexual flowers, those of the two sexes being borne on separate trees in *Taxus* and the juniper, but occurring on the same individual in the others. In monoecious trees the female flowers stand as a rule in the upper parts of the crown and the male ones further towards the points of the twigs. Trees are found which form male flowers alone at first and only later female ones also. Hermaphrodite cones occur in the spruce [1] and bisexual cones are also observed in the larch and common juniper, which besides barren scales, bear anthers below and ovules above.[2] The pine [3] is female during its first years of fertility. The sub-variety *Lapponica*, however, in deep shade, produces as a rule only male flowers in its first years of fruitfulness and also in open situations purely male trees occur here and there, which seem rare in the common form. Female flowers apparently first appear on the suppressed plants when the top comes more into the light. The female stage of the Swedish pine begins between the 7th and the 25th

[1] Keissler, Beihefte zu Bot. Zentralbl., 1900, 353; Rytz, Naturf. Ges. Bern, XIII, 1913.
[2] Ann. Bot., XXVII, 1913 (*Larix*); Renner, Flora, XCIII, 1904, and XCVII, 1907 (*Juniperus*).
[3] Sylvén, Medd. f. Statens Skogsförsöksanstalt, 1908.

years and later, the transition to monoecism lies between the 25th and 35th years. Specimens female throughout life occur, especially in *Lapponica*. Among the broad-leaved trees the flowers of birches, alders, hazels, hornbeams, beeches and oaks are as a rule unisexual. According to A. Schulz, every alder, however, possesses a few female catkins in which bisexual flowers or transition forms between such and

FIG. 149.



FIG. 149.—Aspen. (1) Male, (2) female flowering twig. Both male (3) and female (4) flowers stand in the axils of fringed scales. Each of the former consists of a disc on to which the stamens have grown, the latter of a bi-carpellary ovary surrounded at the base by a cup. (5) Longitudinal section of female flower. (6) The closed and (7) the dehisced capsular fruit. (8) The haired fruit. (9) Ground plan of male flower. (10) Leaf. B.L.

FIG. 150.

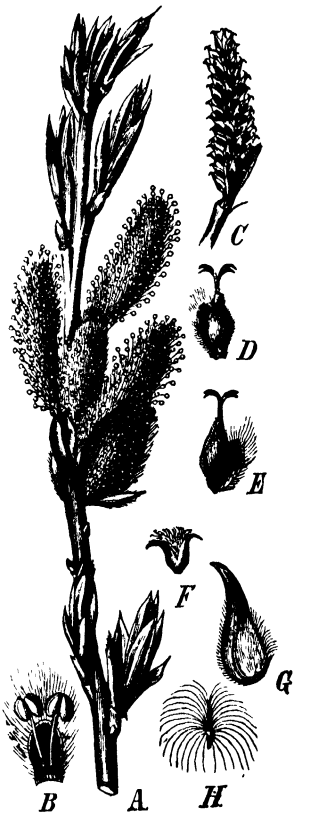


FIG. 150.—The Common Osier (*Salix viminalis*). (*A*) Male twig, (*B*) male flower, consisting of two anthers in the axil of a bract. (*C*) Female catkin. (*D*) and (*E*) Female flowers, each consisting of an ovary in the axil of a bract. (*F*) and (*G*) Fruit, (*G*) enlarged. (*H*) The hairy seed. The nectaries unfortunately not distinguishable in the illustration. B.L.

purely female ones are found. Schulz [1] found bisexual flowers also in birches, though more rarely, and in the hazel only twice. In oaks, imperfect stamens at least occur in the female flowers, and bisexual flowers are also observed in the beech. Poplars and willows bear unisexual flowers distributed on different individuals (dioecious) (Figs. 149 and 150) and limes and robinias have bisexual flowers throughout. Among the elms, besides trees which bear bisexual flowers almost exclusively, others are also found, the greater number of whose flowers

[1] Beitr. zur. Morphologie u. Biol. der Blüten. I, II, Ber. Dtsch. bot. Ges., 1892.

are male. Ashes and maples behave peculiarly. In ashes (Fig. 148) male, female and bisexual flowers occur in varying distribution as well as hermaphrodite structures between carpels and stamens. Schulz found in the neighbourhood of Halle on the Saale, the following modifications: (1) Fairly numerous trees with male flowers exclusively; (2) a smaller number of trees with only female or only hermaphrodite flowers; (3) trees which in many years had only male flowers but in other years had in addition bisexual and female flowers on one or more branches (trees behaving in this way were also fairly numerous); (4) trees which, otherwise male, always bore female or hermaphrodite flowers on a few particular branches. One tree, as an example of the converse, bore male flowers only on one branch and fruit-producing flowers elsewhere, so that while fruit was everywhere else produced in plenty the one branch always appeared empty. In all, Schulz counted nine different cases of sex-distribution in the ash. The character of a tree very often changed with the years, probably as the result of external influences. In general, in Schulz's opinion the ash is on the road to becoming dioecious. It may be mentioned that great variability prevails in the form of the flower parts of the ash. In the willows, according to Schulz, change of sex occurs, especially in cuttings. These often become monoecious; more rarely of the opposite sex to their parent plant. Monoecism or sex alteration also often occurs after the pollarding of poplars. In the Norway maple, Wittrock [1] observed two kinds of flowers; female ones which appear hermaphrodite but possess only rudimentary stamens which do not open their anthers, and male ones with rudimentary ovaries. In the inflorescences of 40 per cent. of the specimens examined, the flowers first developed were female and the later ones male. In other cases the apical flowers prove to be male and the rest, some male and some female, mostly male; or the flowers first developed are male, the later ones female; or finally the whole of the flowers are either male or female In most trees Wittock found only one of these types of inflorescence formed. The Norway maple would accordingly in all cases be either monoecious or dioecious. Similar conditions were also shown in the sycamore and field maple. In St. Gallen (600 metres above sea level) a male period of 10–20 days was observed on Norway maples, 1–5 days after which the unfolding of female flowers took place for 4–6 days. A second male period occurred at the end in most cases.[2] In the ash-leaved maple (*Acer negundo* L.) dioecism is the rule.

The dioecism of the poplar is of particular interest because of the behaviour of our Lombardy poplars. Of these trees, introduced during the last century, only a small number of female specimens are known as: [3] in the garden of the Forest Academy at Hann.-Münden, in Frankfurt on the Oder, Berlin, Braunschweig, Schwetzingen and Karlsruhe, other specimens on the Vinaric-Neudorf Road in Bohemia, in Warsaw and in Styria. The trees are therefore multiplied by layers and when,

[1] Bot. Zentralbl., 25, 1886. *Comp.* also Darwin, The various flower forms in plants of a given species.

[2] Jahrbuch d. St. Gallischen naturwiss. Ges., 1903. St. Gallen, 1906.

[3] Hampl, Österr. Forstztg., 11, 1893. Ref. Bot. Zentralbl., 1894, 4, 155. Further: Bot Jahresber., 15, 1887, II, 124, and 22, 1893, II, 44.

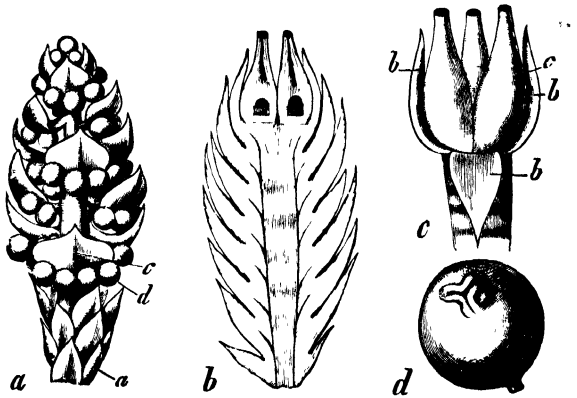


FIG. 142.—(a) Male flower of the Juniper. Each stamen (*c*) bears several pollen sacs (*d*) on the under side. (b) Twig ending in a female flower. (c) Female flower still further enlarged, (*b*) the three scales, (*c*) the three ovules. (d) Juniper berry, showing the free ends of the fruit scales. B L.

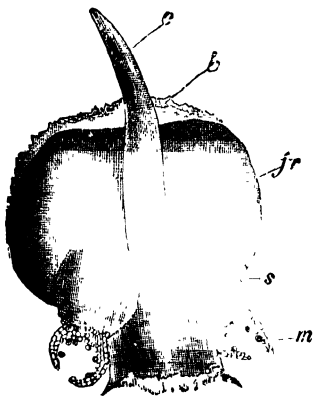


FIG. 157.—Ovuliferous scale of the Pine with the two anatropous ovules (*s*). (*m*) Their micropyles surrounded by long outgrowths of the integument. (*c*) A keel-shaped projection of the scale (*see* p. 386). (*b*) The bract, which later becomes insignificant. B.L.

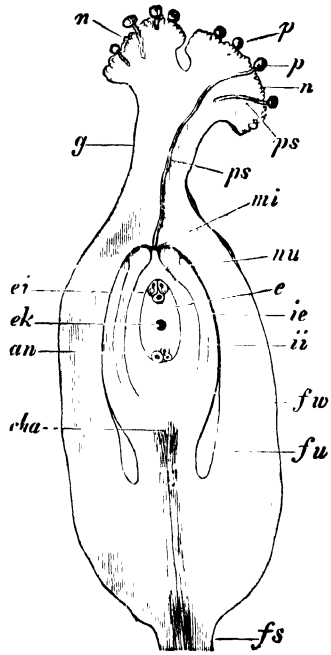


FIG. 158.—Ovary with an ovule. On the stigma (*n*) are pollen grains (*p*), some of which have sent out pollen tubes of various lengths, one of which (*ps*) has reached the micropyle (*mi*). (*ie*) and (*ii*) The two integuments, (*nu*) the nucellus of the ovule, (*cha*) the base, (*fu*) the funicle of the ovule. (*e*) The embryo sac with its nucleus (*ek*). In (*e*) have been formed by a peculiar form of cell division, at its upper end, the ovum with its two sister cells, the so-called synergids (*ei*), and, at its lower end, the cell group (*an*). (*fs*) The stalklike base of the ovary. (*g*) Stigma. B.L.

[To face p. 379.

some decades ago, a widespread dying off of Lombardy poplars [1] became noticeable, this was associated with the long-continued asexual propagation. The problem has not, however, been satisfactorily cleared up. According to Hampl the female trees fruit in June and differ in form from the male ones by their branches not being so strongly directed upwards and therefore spreading out further from the stem. A. Schulz conjectures that the said female specimens may have arisen by change of sex in cuttings.

On the determination of sex through the processes of fertilisation much work has been done in the science of genetics.[2] We cannot go into these complicated questions here, especially as forest trees have not been dealt with in this connection. Reference must be made to the textbooks of Genetics by Baur, Goldschmidt, Häcker and Johannsen.

The conifers differ widely from the broad-leaved trees in the structure of the stamens. In the dicotyledons, is found as a rule, at the top of the filament, an anther with four pollen sacs, a pair on each side of a middle portion which is called the connective, whilst in the conifers the number of pollen sacs varies. In pine, spruce, silver fir and larch there are 2 of them, in the juniper, arbor vitae and *Taxus* 3 to 5 and 8. The stamens of *Taxus* exactly resemble the individual parts of the fructification of the horsetail (Fig. 151). In the latter, the sporangiophores and in the former, the filaments have the form of small plates which are connected at the middle to a stalk and bear on their under sides, anthers laden with powder, only, in the case of *Taxus* the powder is actually pollen grains, while in the horsetail it consists of spores in which it is impossible to detect whether on germination they will bring forth male or female sexual elements.

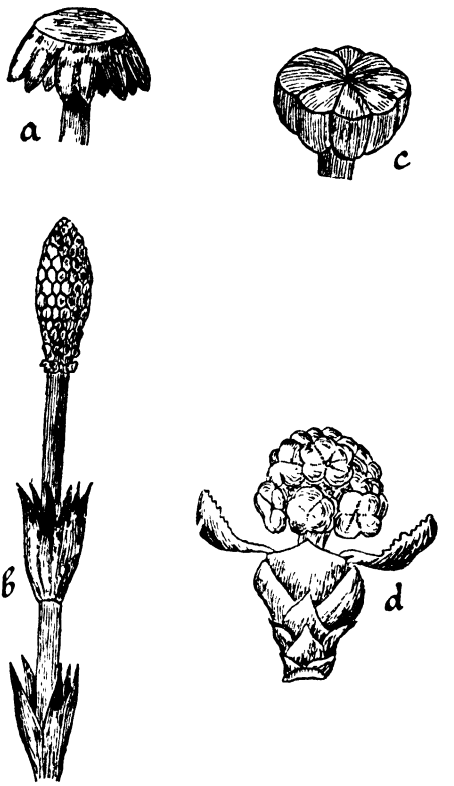


FIG. 151.—Comparison of the sporangiophore of a Horsetail and the male flower of *Taxus*. (*a*) Plate-shaped sporangiophore from a fructification of the horsetail (*b*). (*c*) Plate-shaped anther from the male flower of *Taxus* (*d*). (*a*), (*b*), and (*c*) after Kerner von Marilaun, (*d*) after Warming.

The male flowers of our conifers are shaped like cones; these cones are however smaller than the female ones and are deciduous, as when the

[1] Other reasons have been given for the dying off, lowering of the water table, frosts, etc. (Geisenheyner, Mitt. d. Dtsch. Dendrol. Ges., 1908, p. 202.)

[2] *Comp.*, for example, Correns, Ein Fall erperimenteller Verschiebung des Geschlechtsverhaltnisses. Sitzungsber. k. Preuss. Ak. Wiss. LI, 1917.

pollen is shed they have fulfilled their function. The red colour of the male flowers of the spruces and firs, which recalls the strawberry, may again have its reason in the favouring of heat absorption by this colour, which here benefits the development of the pollen grains. The reddish or violet tints of the female flowers of the spruce, larch, etc., may be explained in the same way.

The male flowers of birches, alders, hazels, hornbeams, willows and poplars are just as simply constructed as the female ones and like them are arranged in catkins. Willow catkins are short and little capable of movement; the male flowers, in addition to the anthers, contain nectaries and attract pollen-distributing insects by honey scent as well as by a conspicuous yellow or red coloration of the anthers. On the other hand, the catkins of the other plants mentioned, betray their dependence on the wind as a means of transport of the pollen, by their mobility in the wind which greatly favours the blowing away of the pollen. The rapid elongation of the catkins into long oscillating tassels at the time of flowering is especially conspicuous in alders, birches and hazels. The male catkins of the oak, and the male inflorescences of the beech which form long-stalked heads, oscillate at the smallest impulse. The form of the male flower is evident from the illustrations given. In the alder, beech, oak and sweet chestnut they possess an inconspicuous floral envelope, whilst in the other cases mentioned, they consist only of stamens which are attached in the axils or on the upper sides of scale-like leaf structures which stand on the axis of the catkin.

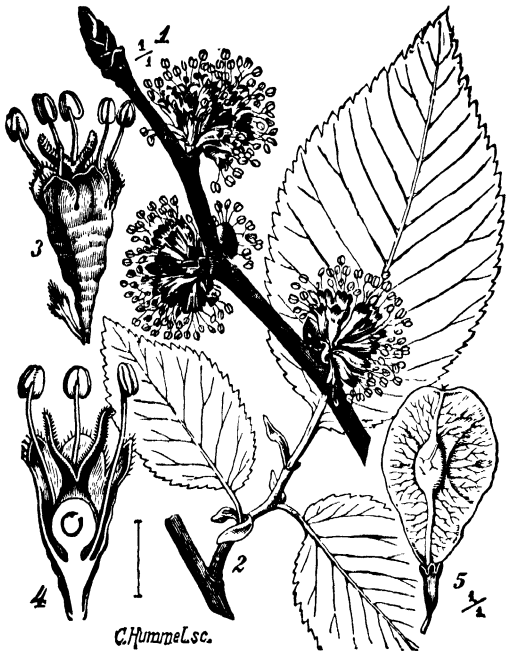


FIG. 152.—Common or Field Elm. (1) Twig bearing tufts of flowers. (2) Leafy twig. (3) Flower with bracts, five-tipped perianth, five stamens and one ovary with two stigmas. (4) Longitudinal section of flower. (5) Fruit, grown out beyond the floral envelope. B.L.

Among the trees with hermaphrodite flowers, the elms (Fig. 152) have 4 to 8, the maples 8, the lime, many stamens which are, however, produced by branching from 5 rudiments. The robinia, as a papillionaceous flower, possesses 10 stamens, 9 of which, as in most of the family, are united together for some distance into a tube open at the upper end. The *Sorbus* species and their allies, have many stamens, generally 20, which, like the petals, stand on the upper margin of the flower cup.

5. Pollination and Fertilisation.

Time of Blossoming.

Abies pectinata	May, June.
Picea excelsa	April, June.
Pinus sylvestris	May, June.
„ *Austriaca*	About 14 days later.
„ *strobus*	End of May, beginning of June.
„ *montana*	End of May, June.
„ *cembra*	June, July.
Juniperus communis	Pollination towards mid-June, fertilisation beginning or mid-July.[1]
Salix caprea	March, May.
„ *alba*	March, April.
Populus tremula, nigra	March, April.
Betula pubescens, verrucosa	April, May.
Alnus incana	March, April (♂ originated on June 4, ♀ on June 14 of previous year).[2]
„ *glutinosa*	March, April.
Carpinus betulus	June.
Corylus avellana	February, April.
Fagus sylvatica	April, May (♂ originated at beginning of June of previous year).[3]
Quercus pedunculata	April, May, June.
„ *sessiliflora*	About 14 days later.
„ *pubescens*	April, May.
„ *cerris*	April.
Castanea vesca	June.
Ulmus campestris, montana	March, April.
„ *effusa*	March, April.
Tilia parvifolia	End of June, beginning of July.
„ *grandifolia*	10–14 days earlier.
Acer pseudoplatanus	April, May.
„ *platanoides*	Before leafing.
„ *campestre*	At same time as, more rarely after, leafing.
Fraxinus excelsior	April, May.

The fertilisation of trees, like all living beings, consists in the union of the living substance of two cells, especially their nuclei. Every single particle of that part of the nuclear substance which is important for the fertilisation, fuses with a particle of the nuclear substance of the other cell, whilst, at the same time, the cytoplasmic bodies—of which that of the male cell, which consists almost entirely of nucleus, is almost

[1] Norén, Upsala Universit. arsskrift, 1907.
[2] Lohwag, Österr. bot. Zeitschr., 60, 1910.
[3] Büsgen, Blütenentwicklung und Zweigwachstum der Rotbuche. Zeitschr. f. Forst- u. Jagdwesen, XLVIII, 1916. Springer, Berlin.

vanishingly small—also enter into union with each other. In these processes there takes place the union of the characters of both parents in the egg which will set its stamp in the first place on the new plant. The fertilised cell, or zygote, contains the transmissible factors—the **gene**—of both parents, which according to circumstances may unfold themselves during the development of the zygote into the mature plant and produce visible characters or may lie dormant and concealed for generations. Invisible dispositions may often be brought to light by crossing experiments.[1]

In the conifers,[2] a relationship may be detected between the position and form of the anthers and their mode of opening. When the floral axis is vertical (*Pinus*, *Picea*) dediscence occurs by means of a longitudinal split, in *Abies*, whose male flowers are below the twig, by a transverse slit. In the larch the obliquely directed fissure forms a gutter down through which the pollen of the upright anther can easily slide.

The pollen grain [3] is not the actual fertilising cell.[4] The latter develops first in its interior and is conducted through the pollen tube, which grows out of the pollen grain on the stigma, down through the style to the ovum. The pollen grain is enclosed in a firm coat, the outermost layer (Exine) of which is provided with contrivances of many kinds for favouring its dispersal. The pollen grains of the pines, spruces and silver firs possess flight-bladders filled with air, which are absent in the Douglas fir, hemlock spruce (*Tsuga*) and larch, as well as in the juniper and its allies. In these and other anemophilous plants the rounded, non-sticky and generally not easily adhering surface of the grains must suffice to make them the sport of the wind.

Pollen grains bear keeping in dry air well. Even in the moisture-free air above sulphuric acid, they remain alive for some time. They perish more rapidly in moist air; though alder pollen lived equally long in moist and in dry air.[5]

That the transport of the pollen grains further than from the stamen to the stigma of the same flower or even from one flower to another flower on the same individual may be advantageous or even necessary for the plant, has been demonstrated by Darwin in his work on the effects of cross- and self-fertilisation in the plant kingdom. He found in many cases that plants from seed of crossed flowers of different specimens were stronger and more fruitful than those which originated from flowers whose pollen was used to pollinate their own stigmas. Indeed many flowers in general produced no seed when self-fertilised. Moreover, plants resulting from the crossing of different flowers of the

[1] An excellent account of Genetics and Breeding is given in Fruwirth's Handbuch der landwirtschaftl. Pflanzenzüchtung, Berlin, Parey; also Baur, E., Einführung in die experimentelle Vererbungslehre, Berlin, Borntraeger.

[2] Goebel, Flora 91, Erganzungsband zu 1902.

[3] Details *see*: Lebensgeschichte der mitteleuropäischen Blütenpflanzen. Stuttgart, Ulmer; 1–3 prothallium cells, 2 gametophytes in 2.4% of the grains in spruces. Pollak, Am. Naturalist, XL, 1906, 253. On the dehiscence of the anthers of *Carpinus*, *Fagus*, *Quercus* and *Corylus*, *see* Pauchet, Compt. rend. CXLIV, 1226; Thibaut, Staubfäden der Gymnospermen. Thesis. Lille, 1896. Bot. Zentralbl., 1898, 129; Steinbrink, Kohäsionsmechanismus der Antheren. Ber. d. Dtsch. Bot. Ges., XIX, 1901.

[4] Juel, Flora, Bd. 93, 1904.

[5] Pfundt, Jahrb. f. wiss. Bot., XLVII, 1910, p. 1.

same individual did not generally show the superior growth of the progeny of crossed individuals. Christian Conrad Sprengel, the actual discoverer of the relationships between flowers and insects,[1] had already, through his observation of the structure of flowers, deduced the principle: "Nature wishes crossing to occur," and he succeeded in showing that almost all the peculiarities, even of bisexual flowers, may be understood from this point of view. Every detail of the form and development of such flowers acts so as to hinder prolonged self-pollination and, on the other hand, to favour cross-fertilisation. An absolute avoidance of self-pollination, it is true, is not to the benefit of the plant. When, owing to infrequent visits by insects or for other reasons, crossing does not take place, except for a few cases, self-pollination is better than no pollination at all. Research into the importance of pollination of female flowers with pollen from the same branch (self-fertilisation) or crossing in our forest trees, has hitherto been carried out only by Sylvén [2] on pine and spruce. In the pine the result is not yet quite clear, though self-pollination seems to be successful. In the spruce, self-pollination produced seed of small weight and small percentage germination; though in the case of one variety (Kammfichte) it was just the opposite. Of the seedlings produced by self-fertilisation 33½ per cent. died during the summer, but only 9.9 per cent. of the control plants obtained by cross-fertilisation. The plants which did survive were equally strong.

Burck [3] is of opinion that crossing may be superior to self-pollination with respect to the progeny only in hybrid plants.

The surest means of preventing self-fertilisation is **dioecism**, which we have already met with, as the rule in willows, poplars, *Taxus* and the ash-leaved maple and as occurring, and apparently on the increase, in the ash. According to Darwin, a form of dioecism also occurs in the common hazel. In many specimens of this plant the male, in others the female flowers, are ready earlier than the flowers of the opposite sex on the same individual. So long as this condition persists, crossing is naturally the only possible mode of fertilisation, and in fact the one which actually occurs.

In non-dioecious trees generally, mutual pollination between flowers of one and the same individual unavoidably occurs in many cases, by reason of the enormous number of flowers; though, according to Darwin, the danger of the production of degenerate progeny which lies in this is lessened by two circumstances: first, the flowers on different sides, or even only on different shoots, of a tree are not so nearly related to one another as those on the inflorescences of a short-lived plant which produces only a few shoot-generations; and secondly, in accordance with experience in other plants, the self-fertilised flowers of an inflorescence possibly fall off if flowers cross pollinated from other individuals are also present in the same inflorescence.

[1] Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen. Berlin, 1793. Facsmile reprint by Mayer & Müller, Berlin, 1893.

[2] Mitteilungen d. forstl. Versuchsanstalt Schwedens. VII, Stockholm, 1910. Ref. Bot. Zentralbl. Bd. 116, 1911, p. 486.

[3] Rec. d. trav. botan. Néerland, Vol. IV, 1907, p. 117. Bot. Zentralbl., Bd. 108, 1908, p. 599.

In the monoecious trees crossing is often favoured by the position of the inflorescences, The female flowers of the abietineae are generally found higher up the tree than the male ones, so that the pollen cannot shower down on them directly, but they have the chance of taking up the mixed pollen of their own and other trees drifting about in the air. When male and female flowers are situated closer together, as in alders, birches, beeches (Fig. 153), hornbeams, oaks, etc., the female flowers likewise stand in all cases above the male ones, at least at the time when the pollen ripens, which is at any rate an advantage for crossing, while, if this does not take place, self-pollination is not made impossible as the pollen is borne upwards by the wind.



FIG. 153.—Beech. The female and male inflorescences develop on a shoot of the current year. The female is a two-flowered capitulum enclosed in a four-sectioned involucre (cupule); the male is a long-stalked, many-flowered capitulum without a cupule, springing from the axil of a leaf. (2) Male flower with cup-shaped perianth. (3) Female capitulum. (4) Cross section of the pair of fruits of a female capitulum. (5) Fruits in the cupule. (6) Fruit (beech nut). (2) and (3) Magnified. B.L.

Those of our trees which have bisexual flowers, like many other plants of similar type, possess a means against the self-fertilisation of individual flowers in the ripening of the stamens and stigmas at different times (**Dichogamy**). In the limes, many species of maples and the relatives of the robinia—in the last mentioned of which, however, a cleistogamous form occurs [1]—the pollen is scattered from the flowers before their stigmas are capable of receiving it (**Protandry**). The latter are, therefore, dependent on cross-fertilisation, especially when, at the same time, the structure of the flower makes it almost impossible for the pollen of a stamen to reach the stigma of the same flower. This is the case, for instance, with the large-leaved lime, where the filaments are, up to the end, bent away from the style towards the outer margin of the flower. In the mountain ash and its allies the stigma ripens before the pollen of the same flower is scattered (**Proterogyny**), and by this means foreign pollen has the chance of forestalling that originating in the same flower. The other floral arrangements are, however, such that, if the worst comes to the worst, self-fertilisation can occur. The elm and ash, like

[1] Tuzson, Jahrb. f. Systematik, etc., XL, 1907, p. 1.

the mountain ash, have pre-ripening of the stigma and, according to Kerner, the same characteristic is also widespread among our monoecious plants. In the green alder (*Alnus viridis*), for instance, the stigmas are ripe 4–5 days earlier than the male flowers. It is remarkable that, according to Kerner, the dioecious willows have pre-ripening of the stigmas. As it easily happens in consequence, that the male flowers of one species flower simultaneously with the female ones of another species which is as yet producing no ripe pollen, this condition favours the production of hybrids, so that, besides the 26 species of willows in the German flora, more than twice as many hybrids have been observed.

The striking fact that among our trees—and not only our native trees—so many species have unisexual flowers, is associated by Darwin with their being so often adapted for pollination by the wind. The adaptations of plants which favour this method of pollination, *i.e.* large stigmas protruding far out of the flowers and easily transported pollen, favour self-pollination at the same time. Darwin, therefore, sees in unisexuality of the flowers, common also in wind-pollinated herbaceous plants, a device for making self-fertilisation difficult and so tending to prevent the degeneration of the seed thereby threatened. The disadvantage of less certainty in pollination in unisexual flowers is not of moment for trees, since their longevity prevents the occasional failure of fertilisation being critical for the preservation of the species. Among the forest trees with unisexual flowers the following are pollinated by the wind: all conifers, also birch, alder, hazel, beech (Fig. 153), oak (Fig. 159), hornbeam and poplar; by insects: the willows and, though apparently not everywhere, the edible chestnut, whose male flowers bear nectar.[1] Among our hermaphrodite flowering trees the transfer of pollen in the elm (and the not purely hermaphrodite ash) is effected by the wind. Only the robinias, limes, maples and *Sorbus* species require the help of insects and are consequently equipped with nectaries, scent and striking colour, the



FIG. 154.—Hazel. The male and female catkins are present through the winter. The female ones are in the form of buds out of which the red stigmas protrude in spring. (2) Male flower. (3) Anther. (4) Older female flower in longitudinal section, surrounded by the cupule. (5) Fruit with, (6) without, cupule. (7) Leaf. B.L.

[1] Büsgen, Cupuliferen in Lebensgeschichte der Blütenpflanzen Mitteleuropas, hrsg. v. Kirchner, Loew u. Schröter, Bd. II, p. 143.

latter being possessed by the perianth (in the willows, by the anthers) and in many cases helped in its effect by flowering taking place before the opening of the leaves.

As pollination in anemophilous plants is left entirely to chance, pollen is produced in enormous quantities, so that at flowering time it forms whole clouds and on falling gives rise to a " sulphur rain." The smallness of the pollen grains and in conifers, the flight bladders, make possible the transporting of pollen by the wind to incredible distances; according to Hesselman,[1] even to 700 to 900 kilometres in not small quantities. In the spruce, whose female flowers are sexually ripe somewhat before the male ones, this flight of pollen may play a part in fertilisation; less so in the pine, which is generally protandrous. As Hesselman shows, such conditions may be important for the isolation or the smoothing out of the differences in climatic races.

In the conifers, the place in the female flower which the pollen must reach if it is to fulfil its function, is the top of the ovule. In *Taxus*, owing to the position of the ovule at the end of a small shoot, this is immediately attainable. At the time when the pollen ripens, in March or later according to the locality, a small drop of slightly acid liquid appears on the tip [2] of the ovule which remains for several days and is capable of renewal. It contains [3] glucose and calcium, also apparently a kind of mucilage and perhaps malic acid, and is ready to catch the pollen grains. The latter do not always reach the open immediately after the dehiscence of the pollen sacs but remain lying between the plate shaped caps of the stamens until a light, dry, current of air causes these to shrivel somewhat and carries the pollen with it. The grains caught by the drop of liquid are drawn, as it shrinks, into the pollen chamber on the summit of the ovule. From there the fertilising cell is conducted to its appointed place through a tube growing out of the pollen grain through the tissue surrounding the ovum. The juniper (Fig. 142) and the other cupressineae [4] behave like *Taxus*.

The ovules of the abietineae, with their openings turned downwards, intercept the pollen with two prolongations of their envelope (the integument), which at first spread apart and then bend in towards the summit of the ovule and so carry the pollen there, where it develops the pollen tube (Fig. 157). In the larch a sticky substance has been detected at the tip of the integument which holds fast the pollen grains. By the growth of the outer side of the integument these are then pressed into the interior of the ovule on to the summit of the nucellus, whilst the cutinised integument forms a protective covering for the young seed.[5] The pollen slides down to the ovules between the cone scales, which are smooth and gape apart at the time of flowering, guided in many pines by a keel running down the middle line of the scale (*see* Fig. 157). Here

[1] Hesselman, H., Beobachtungen über die Verbreitungsfähigkeit des Waldbaumpollens Mitteil. d. forstl. Versuchsanstalt Schwedens, H. 16, 1919, p. 54; *see* also Malmström, C., *ibid.* H. 20, 1923.

[2] Fujii, Ber. Dtsch. Bot. Ges., XXI, 1903, p. 211.

[3] Tison, Mém. soc. linnéenne de Normandie, XXIV, 1910, p. 51.

[4] Norén, Zur Entwickungsgeschichte des *Juniperus communis*. Upsala Univ. Arsskr., 1907. Good abstract in Bot. Zentralbl., Bd. 105, 1907, p. 49.

[5] Himmelbauer, Mikropylenverschlüsse der Gymnospermen. Sitsungsber. d. k. Akad. Wien, math. naturw. Kl. CXVII, 1908, p. 1.

also the pollen, emptied out of the anther sacs, awaits a suitable air current for transport by accumulating in the small collecting basket formed by the two groove-like depressions and the upright connective of the next lower stamen. After pollination the cone scales come together again at the margins and bar the entrance of unwelcome intruders to the ripening seed.[1]

In the pine, short hairs grow to meet each other from the parts of the cone-scale surfaces that are pressed together, which unite so strongly that it is easier to split the scales themselves than to loosen the connection. The connecting layer only ruptures under the tension of the contracting tissues on the lignification and drying of the cone. The force with which the cones spring open in the seed kiln has been proved to be at least $\frac{1}{20}$th metre kilogramme.[2] In the larch, spruce, silver fir



FIG. 155.—Female inflorescence of the Beech before the opening of the flowers (left) and at the time of pollination (right). The flowers project above the cupule and the stigmas have unfolded. After Büsgen in Cupuliferen.

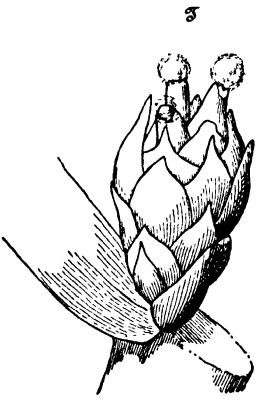


FIG. 156.—Flower of the Juniper with drops of liquid on the openings of the three ovules. H.W.

and Douglas fir there is no coalescence, but there is a thick felting together of hairs which spring from the surface of the scales (spruce) or some other form of protection of the ovule by hairs.

The road which the pollen tube has to traverse from the surface of the nucellus to the ovum is only a short one, but it nevertheless requires a fairly long time to do it. In *Taxus*, according to Strasburger, the actual fertilisation only takes place about mid-June, in the spruce 1–6 weeks after pollination. In the juniper, the growth of the pollen tube last no longer than 2–6 weeks.[3] The pine is pollinated in May. The pollen tube, however, does not reach the ovum during the same summer, but fertilisation only takes place more than twelve months later, so that a summer and a winter intervene between pollination [4] and fertilisation: according to Sludsky (*loc. cit.*), however, only 2–3 weeks.

[1] On the method of closing up *see* v. Tubeuf, Forstl.-naturw. Zeitschrift, 1893, p. 446, and 1896, p. 132.

[2] Busse, Arbeitsleistung des Kiefernzapfens. Naturw. Ztschr. f. Forst- u. Landwirtsch. hrsg. v. Tubeuf, Bd. IX, 1911.

[3] Sludsky, Ber. Dtsch. Bot. Ges., XXIII, 1905, p. 212. Miyake, Ann. of Bot. XVII, p. 351 (Spruce); Norén, Upsala Univers. Arsskr., 1907. Development of flower of *Juniperus communis*.

[4] The ovules in *Pinus* are formed about 3 weeks before fertilisation (? pollination). Ferguson, Science XVII, 1903, p. 458; *P. laricio*: Chamberlain, 1900.

The pollen of the broad-leaved trees does not reach the ovule directly but only the stigma (Fig. 158). The pollen tube must, therefore, grow through this and through the style, where one is present, in order even to reach the neighbourhood of the ovule. Only then can it seek it in the interior of the ovary and penetrate to the ovum within. In doing so it follows the path of least resistance or is guided, like the hyphae of parasitic fungi in the tissue of their host plant, by chemical stimuli. Protein substances and sugars act attractively on pollen tubes, albumenoses and peptones, poisonously. Tyrosin and leucin are without effect. Diastase acts even in 0.1 per cent. solution.[1] That the freely motile male fertilising cells of mosses and ferns are led to the egg-cells by such stimuli has been proved with certainty. In forest trees their co-operation must be assumed, at least for the last part of the journey, in the vicinity of the egg-cell. If, as in the beech, besides the single ovule to be fertilised, there are others present which regularly die off early, these contribute by their position in the ovary to the correct guidance of the

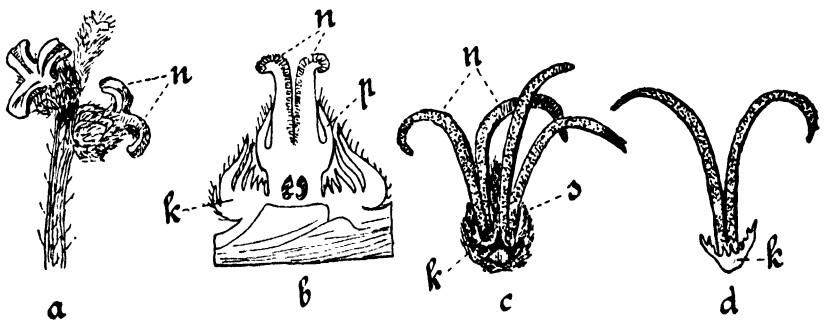


FIG. 159.—(*a*) Two female flowers of the pedunculate Oak. (*b*) Longitudinal section of such a flower. (*k*) Cupule. (*p*) Perianth. (*c*) Two female Hazel flowers with their bracts. (*d*) One of these flowers. The still not completely developed ovary is entirely surrounded by the cupule (*k*), which later becomes the slit husk of the hazel nut. (*n*) In all cases the large stigmas. After Hempel u. Wilhelm.

pollen tube. In the beech [2] the tissue of the outer integument conducts the pollen tube from the micropyle to the nucellus of the ovule. In this case a fortnight to three weeks elapses between pollination and fertilisation.

Having reached the ovule, the pollen tubes usually make their way through the gap which the integuments leave open above its summit (micropyle). Just in a number of our trees, however, is this apparently easy way avoided and the pollen tube penetrates into the tissue of the ovary from the opposite side, *i.e.* from the place of attachment of the ovule. Thus, according to Nawaschin's investigations,[3] the pollen of the birch normally germinates on the stigmas of the as yet much undeveloped ovaries. After having grown down as far as the

[1] Lidforss, Zeitschr. f. Bot., I, 1909, p. 443.

[2] Büsgen, Zeitschr. f. Forst- u. Jagdwesen, XLVIII, June, 1916.

[3] Über die gemeine Birke und die morphologische Deutung der Chalazogamie. Mém. de l'acad. d. sc. St. Péterbsbourg, sér. VII, T. XLII, 1894; Ber. Dtsch. Bot. Ges. XII; Benson, Trans. Linn. Soc. London, 2 Ser. Bot. Vol. III, 1894. Only betulaceae and corylaceae, not however fagaceae, chalazogamous. Embryology of the Hazel: Bot. Zentralbl., 1895, III, p. 104. A new example of chalazogamy (*Juglans*): Bot. Zentralbl., 1895, III, p. 353. On *Juglans*, also Benson and Welsford, 1909; *Carya*: Billing, 1903; Ulmus: Nawaschin, Bull. d. l'Acad. d. St. Petersbourg, sér. 5, T. VIII, 1898.

base of the stigma, the pollen tube enters into a period of rest of four weeks, during which the ovules first come to perfection. After the elapse of this time it grows on into the base of the ovule (the chalaza), and from there towards the place where the egg cell is situated. Having reached its vicinity, it branches, and one of its branches enters into union with the egg cell. Nawaschin found the same behaviour in the alder, hazel and walnut. In the elm the pollen tubes grow to the summit of the nucellus from the chalaza or across through the envelope (integument) of the ovule. In *Acer negundo*[1] the pollen tube pushes forward intercellularly through the integument to the nucellus without utilising the well-developed micropyle. The latter has then only the function of an intercellular space which allows access of the air consumed in the respiration which is necessary for the formative process in the ovule.

6. Distribution of Fruit and Seed.—The first result of fertilisation is the development of the ovum into the multicellular embryo. Hand in hand with this go alterations in the other parts of the ovule, and also in the carpels, whose final result appears in the formation of the fruit and ripe seed. This is synonymous with the suitable equipment of the embryo for travelling and for the period of germination during which, in the absence of adequate assimilating mechanism, it must supply the organic substances it requires from the store carried with it.

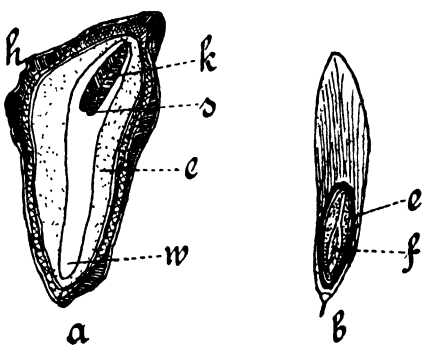


FIG. 160.—(*a*) Section of the seed of the Silver Fir. (*h*) Seed coat with swellings filled with resin. (*e*) Endosperm. (*k*) Cotyledons. (*s*) Plumule. (*w*) radicle. After Hempel und Wilhelm. (*b*) Section of the Ash Fruit. (*e*) Endosperm. (*f*) Seedling. After Engler und Prantl.

The seed itself is formed from the ovule of which the outer parts develop into a single or double seed coat and the interior is either completely occupied by the growing embryo (beech, oak, sweet chestnut, alder, birch, hazel, hornbeam, willow, poplar, elm, robinia, sycamore, service tree) or besides the embryo gives rise to a special nutrient tissue (**Endosperm**) (ash, lime, conifers, Fig. 160). In addition to nitrogenous bodies this endosperm contains a large supply of fatty oil which together with the former is consumed on germination. Spruce seed[2] contains 25–30 per cent. and pine and silver fir seed 26 per cent. Lime seed is said to contain 58 per cent. oil.[3] Ash fruits gave at most 20 per cent., and in the press residues 9–10 per cent. Where a special nutrient tissue is absent the food of the

[1] Rössler, Ber. Dtsch. Bot. Ges. XXIX, 1911, p. 370. Recent literature on Chalazogamy *see* Wolpert, Flora, Bd. 100, 1909 (*Alnus alnobetula*) and v. Klebelsberg, Österr. Bot. Ztschr., LX, 1910, p. 392, *Pterocarya*: Karsten, Flora, XC, 1902; Nawaschin, 1913.

[2] Wehmer, Pflanzenstoffe. Jena, 1911, G. Fischer.

[3] Müller, Carl, Über ein fettes Öl aus Lindensamen. Ber. Dtsch. Bot. Ges., 1890, p. 372. The seed of the Rape, cultivated as an oil plant, contains 42.23%; oil radish, 38.12%; oil palm, 48.75%; walnut, 57.43% of oil. Further data as to the oil content of fruits and its recovery *see* Rusnov, Zeitschr. f. d. ges. Forstwesen, 1917, p. 309.

seedling is stored in its own organs, especially in the cotyledons: In the hazel nut and beech nut they are rich in oil (the former contains 50–60 per cent., the latter 42.90 per cent. of oil in the seed), and in the oak and sweet chestnut, besides the never-failing nitrogenous substances, contain chiefly starch. In these cases also these materials are consumed in germination.

Thus beech seeds with 38.19 per cent. fat, only contained 5.43 per cent. after eight days, during which they had germinated. The materials required to form the endosperm and to nourish the embryo are partly derived from the nucellus, whose cells are dissolved. They are also partly supplied to the growing fruit from the twig that bears it and partly pass over into the seed from the wall of the fruit. Thus the wall of the fruit of the beech nut [1] possesses a very juicy internal tissue which at first almost entirely fills the interior of the fruit but, in proportion as the embryo grows, shrinks up and is finally only represented by a dark brown lining. In the elm and ash also, the fruit wall supplies part of the nourishment of the seed.[2]

Only in a few cases (firs, spruces, pines, larches, robinias, poplars and willows) among our forest trees does the seed, apart from the carpels, set out on its travels by itself. In all others it is the whole fruit which travels but, as it almost always contains only one seed, is often falsely termed a seed. Among the conifers, in the juniper alone does the seed not travel naked but enclosed in the well-known berry formed of the ovuliferous scales. The juicy red coat of the ripe yew seed is an aril which from its origin belongs to the seed itself and has nothing in common with the carpels of other plants.

The seeds of the pines, spruces, silver firs and larches, as well as the hemlock spruce (*Tsuga canadensis*) and the Douglas fir, possess a thin wing to assist in their dispersal, which separates with the seed itself from the inner side of the seed scale. They are adapted for distribution by the wind. The seeds of the junipers, incapable of flight, are distributed by birds (fieldfares), which devour and digest the fleshy covering but pass the seed itself uninjured through the digestive canal. *Taxus* seed is also adapted for distribution by animals and apparently attracts many different birds by its sweet aril. The seeds of poplars and willows are provided with flight hairs. Alder fruits, which are floated along by water, possess a kind of swimming cushion in the pericarp (Fig. 161).

The flight organs of the wind-disseminated broad-leaved trees are attached to the fruit. In the birches, elms, ashes and *Acer* species, they consist of wings which are formed by parts of the fruit wall (pericarp); in the hornbeam, the large three-lobed bract which partly envelops each fruit, and in the lime, a pale yellowish green leaf on the common stem of the whole corymbose inflorescence, acts as a flight apparatus. The mountain ash, with its sweet variety found about 80 years ago at Peterswalde (Bez. Mährisch-Schönhagen),[3] attracts birds for its distribution.

[1] Büsgen, Zweigentwicklung und Fruchtbildung der Buche. Zeitschr. f. Forst- u. Jagdwesen, 1916.

[2] Jönsson, Vikariate im Pflanzenreich usw. Lund, 1910. Bot. Zentralbl., 1911, Bd. 116, p. 356.

[3] Kraetzel, at Hölzel, Wien and Olmütz, 1890.

The distribution of the large and heavy fruits of the oak, beech and sweet chestnut is effected only by animals who seek their rich store of starch and oil. Among birds, the jay especially, provides for the distribution of these species by sticking the fruit in the soil for its winter store, generally at a considerable distance from the tree, and often failing to find it again when the ground is covered with snow in winter. If one observes the untiring and continuous activity for weeks in the autumn of the jays which congregate near the mast-bearing trees, it is easy to understand how, from a single oak, beech or sweet chestnut, a plentiful undercrop arises in this way, often over large areas, in the pine forest. Mice drag the fruit into their holes, out of which whole bunches of beech seedlings often sprout in spring. Squirrels also contribute to the distribution. They devour many fruits, it is true, and, in conjunction with mice and finches, may destroy whole masts ; they carry the fruits to some extent to places of concealment where they cannot germinate, but they often lose much seed on the way. The results of this distribution by animals are at any rate sufficient for the maintenance and spread of the species.

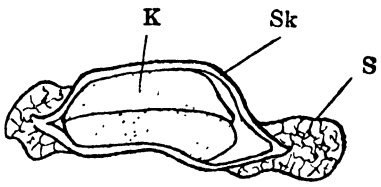


FIG. 161.—Section of Alder fruit. Enlarged. (*K*) Embryo. (*Sk*) Fruit wall. (*S*) Swimming cushion.

It might be thought that too great a sacrifice of nutrients and seed is constantly being made by the trees to the animals in dissemination of this kind, as if the nutrient content were considered as merely a useful adaptation for transport. It should be considered, however, that, with the longevity of our forest trees, an extraordinarily small percentage of the total progeny of an individual is sufficient to ensure the continuance of the species. Focke is of opinion that if 1 per cent. of the acorns of a tree are hidden, of these only 1 per cent. germinate, and of these again only 1 per cent. grow into large, old trees, sufficient is effected for this requirement, the only one with which nature is concerned in making her arrangements.

The distribution of the wild service tree is presumably effected, like that of *Taxus* and the juniper, by birds which seek its fruits. The seeds are not destroyed too often by the birds' beaks because they are enclosed in a hard stony shell which originates from the innermost layer of the pericarp. A stay in the crop of the bird does not injure the germinating power of the seeds ; indeed, according to Darwin, they remain alive in the bird's stomach for days. Juniper seed is thrown out by the fieldfare with the undigested parts of the food through the mouth.[1]

The wind appears to play the main part in the distribution of the seed of the robinia, like other tree leguminosae, by tearing it loose from the husks, which remain on the tree, and, as only strong winds can do this, carrying it far away.

The time at which the seeds or fruits betake them to their travels varies.[2] In many species the seed leaves the mother plant soon after

[1] Danckelmann, Zeitschr. f. Forst- u. Jagdwesen, 1898.

[2] v. Tubeuf, Samen, Fruchte und Keimlinge der forstlichen usw. Kulturpflanzen. Berlin, 1891.

ripening. Thus the seeds of the aspen and goat willow and the fruits of the elms and birches, which ripen in the spring and early summer, fall immediately. The fall of the seed proceeds pretty rapidly in the elm, whilst in the birch it lasts into November. The birch seed that is last to fall is mostly empty. In the silver fir, Weymouth pine, Douglas fir, oak, beech, hazel, wild service tree and the maples, whose seeds ripen in September and October, the bulk of the seeds or fruits also fall soon after ripening. The fruits of the black alder ripen in October and November and are shed in the first months of the following year. Fruits remaining long on the tree even after they are ripe are above all those of the ash, which ripen from August to October, but only fall in February and March of the following year. Spruces, larches, Scots and Austrian pines and mountain pines behave in the same way. To them is added the robinia. It is important for seed-collecting practice to know that the silver fir, Weymouth pine, Douglas fir, hemlock spruce, elm, birch and sycamore shed at least the bulk of their seed or fruit pretty much at one time, whilst with the larch, most pines, alders, ashes, hornbeams, junipers, etc., the fall lasts for some weeks; also that the spruce cones often open on warm, dry days even in December and allow a large part of the seed to escape. Pine cones, in order to provide fully germinable and lasting seed, must remain hanging on the tree up to the middle of December.

7. Germination.[1]—A number of tree seeds retain their germinating capacity only for a short time. These include especially those which ripen in the spring and fall soon after ripening, such as the seed of the poplars, willows, and in part also of the elms and birches. Willow seed, sown just after the ripening of the capsules, germinates even in 12 hours. If it is allowed to lie even for a few days it requires longer to germinate. With the poplars 2–3 days are required for germination, with the elms some days longer.[2] The germinability (viability) of such seed is retained only for days or weeks—in the elms and birches at most until the spring of the following year. Viability is retained by the autumn-ripening seeds of hazel nuts, acorns, beech nuts and silver fir seed up to the spring after ripening. Germinability lasts 1–2 and even 3 years in the hornbeam, lime, alder, sycamore and mountain ash; 2–3 years in the larch and Weymouth pine; 3–4 years in robinia, ash and Scots pine; 4–5 years in the spruce. These data are subject to great limitations; how quickly the seed is spoilt depends above all on the method of storage. If shut up air-tight and dry in bottles, conifer seed can be kept for several years without injury to its germinating power. It remains longer capable of germination if the wings are not removed than it does after treatment in the wing-removing machines. But viability lasting much longer even than this has been observed in resting seeds. Peter took soil samples from depths down to 24 centimetres in 20–46-year-old woods on what had previously been arable land.

[1] Very copious data on germination and seedlings, and also observations of an ecological nature on the importance of the form of the cotyledons, etc., with over 600 illustrations and an ample bibliography, are found in: J. Lubbock: A Contribution to our Knowledge of Seedlings. 2 vols., London, 1892.

[2] Wichura, Flora, 1857.

He obtained from these, under favorable germinating conditions, a number of arable-land weeds such as ground ivy, whose seed appeared to have rested in the ground 40 years, and field mustard for 25 years. These long resting periods were only to be explained by the absence of oxygen and light having prevented the germination of the seed which had accidentally reached a certain depth. The rapid appearance also of the most varied plants on clearings is, in many cases, to be explained by the seeds from the previous felling period resting in the soil during the whole life of the wood grown on the land since that time, and obtaining better conditions by the clearing of the crop. It is true that neither the causes that prevent germination during the life of the wood nor those which promote it after clearing are known. Of the fact itself, however, there is no doubt, because species of plants often appear in great numbers on a cleared area whose seeds could not have reached the area in any other way. Thus it was repeatedly observed that after the clearing of close pine woods, lupins appeared which had been cultivated on the ground 50–60 years before it was afforested. Bier [1] has closely investigated such cases of suspended germination. Often, after the clearing of dense beech woods whose deep shade precluded the presence of any kind of vegetation for a hundred years, common broom and other wildlings appear as if sown, although the blowing in from neighbouring clearings of this difficultly transported seed is excluded.

In other cases, however, the rapid stocking of clearings is to be explained by seed blowing in from the neighbourhood (*Senecio. Epilobium*, grasses) or being carried by birds (raspberry, strawberry, etc.) or by the survival of isolated though feeble plants in the light shade of the forest.

Such sources of error in the judging of the resting period of seed are absent if preserved material is worked with. Thus Becquerel found that the seeds of leguminosae of the year 1819, labiatae of 1829, and malvaceae of 1842, were still capable of germination in 1906.[2] Seeds of *Nelumbium luteum* from Texas preserved their power of germination in Paris for 55 years.[3] Spruce seeds, after drying well at 30–40 degrees till they have lost 1–2 per cent. of their weight, remain germinable longer when they are preserved in air-tight vessels than when preserved with access of air,[4] whilst pine seeds, which otherwise behave like spruce, occasionally showed a diminution of germinating power in a cool air-tight chamber.[5] With all forest tree seed the germinating capacity falls off with age. In commercial tree seeds there is usually a certain proportion of empty fruit or seed, especially in poplars, willows, birches and elms. That not seldom only 10–25 per cent. of birch fruits germinate is indeed to be traced to the wide distribution of the gall midge *Hormomyia Betulae* Wtz. which lives in these fruits. The seeds of most forest trees are germinable immediately after ripening. The seed of poplar, willow, elm and birch, scattered early in the summer, germinates at once, and the sessile oak acorn does so a few days after falling

[1] Bier, A., Keimverzug. Mitt. D. Dendrol. Ges., 1925, p. 187.
[2] Compt. rend. Paris, 1906.
[3] Poisson, Bull. soc. botan. de France, Tome L, 1903, p. 337.
[4] Haak, Zeitschr. f. Forst- u. Jagdwesen, 1909.
[5] Clemens, Naturw. Zeitschr. f. Forst- u. Landwirtsch. Jahrg. 9, 1911.

in the autumn and sends forth a finger-long tap-root in mild weather until the winter. The pedunculate acorn is not so quick to germinate, and is consequently much more easily kept over winter. Spruce and pine seed is germinable immediately after extraction and equally so at any time of the year.

Other kinds of seed pass through a voluntary germination rest. Silver fir seed is capable of germination only after some months, the beech nut only by the end of December. Maple seed also germinates first in spring, but then at very low temperatures, even in snow.

With *Taxus* if sowing does not take place immediately, germination is delayed for 2 or even 3–4 years. These phenomena of the course of germination are due to internal properties of the seed which have been further investigated in the ash.[1] Its seeds, though the seed coat is easily permeable to water, when sown in one spring, only germinate in the next. During this waiting period, from about 10 days after sowing, the embryo fills itself with starch. At first only half as long as the seed, it grows at the same time to the full length of the latter, which it attains after half a year's lying in moist earth. Then only is the seed capable of germination. The radicle can now be easily squeezed out, whereupon more rapid growth sets in.

Ash seed only lies over when once it has been dried after ripening. If, on the other hand, it is taken still green from the tree at the end of August or beginning of September and placed at once in moist earth and kept there over winter, it germinates straight away in the following spring.[2] With the Weymouth pine, change of temperature greatly promotes germination. To bring about satisfactory germination, the seed, after being moistened, must first be kept cool for some time (cellar method) and then placed in the germinating chamber.[3] In the seed bed it germinates in the next spring only when it is sown in the autumn or at least very early in the spring. Late spring sowings for the most part lie over the whole summer. Beech nuts may also lie over if they have been dried too much in storage. If very dry weather follows the sowing of pine seed in spring, germination does not take place, and strange to say often does not even do so in the summer of the same year after the soil has become moist, but not till the following spring. The germinating enzymes seem to become inactive through the drying. It then requires a long time to restore their activity.

The delay in germination of the seed of the Cembran pine lasts from one to several months. In this case also it depends on internal processes and cannot be brought to an end by abrasion or soaking of the seed coat. De Vries was able to eliminate the delay in germination of the evening primrose (*Oenothora*), whose seed does not respond to abrasion and soaking of the testa, by squeezing in water. Seed whose testa offers great resistance to the entrance of water is termed " hard

[1] Lakon, Naturw. Zeitschr. f. Forst- u. Landw. Bd. IX, 1911, and Bd. X, 1912. Findeis, Sitzungsber. d. K. Akad. Wien math.-naturw. Kl. I, 1917, p. 126. (The growth of the ash embryo before germination lasts four months. It is started by absorption of water.)

[2] Cieslar, A., Über die Erntezeit der Früchte der gemeinen Esche. Zentralbl. f. d. ges. Forstwesen, 1920, p. 90.

[3] Grisch und Lakon, Die Keimprüfung der Weymouthskiefernsamen. Landwirtschaftl Jahrb. d. Schweiz, 1923.

shelled." This condition is found especially in leguminosae (*compare* Bier). The hard shelled character may be removed by eating away the outer layer of the testa with concentrated sulphuric acid, as well as by the means mentioned above, whereupon the seed soaks in water easily and germinates.

Taxus seed, like Cembran pine seed, soaks very slowly because the outer layer of the testa is strongly cutinised, but it does not germinate any more quickly when this layer is removed. Easily soaked conifer seeds have on the outside a lignified layer of cells with pit canals which absorbs water readily. According to Tubeuf,[1] delayed germination to the following spring of seed artificially wintered and sown in the spring, occurs partially with the hemlock spruce (*Tsuga*), Douglas fir (*Pseudotsuga*) and robinia, completely with the juniper, *Taxus*, maple, hornbeam, lime, ash and mountain ash (*Sorbus*). Germination tests must take account of delayed germination. For pine and spruce, 14 days is enough,[2] for Weymouth pine even 24 days is insufficient. Corrosion of pine seed by sulphuric acid promotes germination, smearing with vaseline hinders it in the pine and spruce. Removal of the pericarp promotes germination in the ash and lime.[3] Covering the seed too deeply checks germination and injures the seedling.[4]

The value of delayed germination to the seed may, in certain instances, consist in enabling it, even in an environment which for the moment is favorable for germination itself, to await ungerminated the best season for the further development of the seedling.

Physiological exchanges in dry seeds are extraordinarily small, if not entirely absent. Air-dry barley grains with 10–15 per cent. water, evolved in Kolkwitz's experiments, ½–1½ milligrammes carbon dioxide per kilogramme.[5] Respiration increased rapidly on moistening, especially when the temperature and the oxygen content of the respired air were raised. Husked cereal grains, preserved in nitrogen by Becquerel [6] for more than a year, evolved no trace of carbonic acid but, nevertheless, germinated later. In an ordinary natural dry condition, the grains finally gave off a little carbonic acid and absorbed some oxygen. In consonance with these results, Maquenne [7] found that nearly dry grains in a vacuum chamber, had within 2 weeks developed a gas pressure of over 1 millimetre which, apart from variations with the temperature, was then maintained. Seed made absolutely dry, remained in part capable of germination for over 2 years in the vacuum chamber.

The condition of dry seed has been compared with that of a machine [8] which has stopped but can, however, be set in motion again, though with the greater difficulty the longer it stands motionless. Still better

[1] Samen, Früchte und Keimlinge der forstlichen unsw. Kulturpflanzen, Berlin, 1891.
[2] Hiltner u. Kinzel, Naturw. Zeitschr. f. Forst- u. Landwirts., 1906.
[3] Puchner, H., Die verzögerte Keimung der Baumsämereien. Forstwiss. Zentralbl., 1922, p. 445.
[4] Dengler, Über die Wirkung der Bedeckungstiefe auf das Auflaufen und die erste Entwicklung des Kiefernsamens. Zeitschr. f. Forst- u. Jagdwesen, 1925, p. 385.
[5] Ber. Dtsch. Bot. Ges., XIX, 1901, p. 285.
[6] Compt. rend. Paris, 1906.
[7] Compt. rend. Paris, 1902.
[8] Kochs, Biol. Zentralbl., X, 1890; Schulz u. Singol, *ibid.*, 1914, p. 546.

is the comparison of its behaviour with that of colloids, whose condition undergoes irreversible changes with time without special external cause. As these colloids " age " without chemical changes taking place in them, so seeds slowly lose their germinating power, also without showing this chemically. The cessation of respiration does not necessarily coincide with death.

The rate of germination of the seeds of one tree may differ. Thus it was found [1] that in a pine the seed originating from larger cones germinated sooner and produced larger 1-year-old seedlings. The weight of the seed diminished with the weight of the cones and the plants raised from the heavier seeds were the better. Better and quicker germination of the larger seeds has also been proved for the silver fir and Austrian pine. Germinating power also differs according to the colour of the seed. Dark coloured seeds of spruces and Scots pines (*Pinus sylvestris*) are more viable than lighter ones, and the latter also produce worse plants.[2] Empty and unripe seeds are always lighter coloured, though good yellow or white grains also occur. Haack [3] ascribes as an advantage to dark seeds for sunny situations that they are better protected from exess of light. Unfortunately data as to their internal temperature in sunshine are lacking.

Among the external conditions for germinations, in addition to oxygen for respiration and suitable temperature, the presence of water must be mentioned. It is absorbed by the swelling seeds, at first rapidly and then more slowly. Beech nuts,[4] for instance, lying in water at 16–18 degrees C., absorbed in 7 hours 11 per cent., in 22 hours 19.1 per cent. and in 31 hours 27 per cent. of their original weight of water; 5–8 per cent. more through the basal spot on the fruit where the epidermis is absent than through the corners. The embryo itself lying in water had absorbed after 7 days 36 per cent. and after 22 days 42 per cent. of water, and thereafter only 1 per cent. more. In 100 parts by weight of dried beech seed [5] 21.46 per cent. water was found. Ten-days-old beech seedlings, raised in the dark, contained 83.23 per cent. water.

Towards light,[6] seeds do not all behave similarly.[7] There are " light resistant " seeds whose germination is retarded or prevented by light. Among these are the seeds of *Nigella sativa*, those of many species of *Allium* and many garden plants and of *Phacelia tanacetifolia*. Others—the " light seeds "—germinate only in the light. Thus Kinzel [6] obtained 95 per cent. germination with the seeds of *Poa pratensis* in 10 days in

[1] Friedrich, J., Österr. Zentralbl. f. d. ges. Forstwesen., XXIX, 1903; Busse, Zeitschr. f. Forst- u. Jagdwesen, XLV, 1913, p. 300.

[2] Eisenmenger, Österr. Forst- u. Jagdzeitg., 1906, Bd. XXIV.

[3] Keimung und Bewertung von Kiefernsamen. Zeitschr. f. Forst- u. Jagdwesen, 1906; Pittauer, Hell- u. dunkelfarbige Samen der Schwarzkiefer. Zentralbl. f. d. ges. Forstwesen. XL, Wien, 1914.

[4] Oelkers in Büsgen, Cupuliferen, p. 24.

[5] Sanio, Bot. Zentralbl., Bd. 102, 1906, p. 301.

[6] Gassner, Beiträge zur Frage der Lichtkeimung. Zeitschr. fur Bot., VII, 1915. Jena, G. Fischer. The same, Jahrb. f. wiss. Bot., LV, 1915: Kinzel, Frost und Licht als beeinflussende Kräfte bei der Samenkeimung, mit besonderer Berücksichtigung der Entwicklung (Nachreife, Keimdauer usw.) und anderer biologischer Eigentümlichkeiten der Samen aus den verschiedenen Pflanzenfamilien. Stuttgart, 1913, E. Ulmer.

[7] Lehmann, Summary report in Jahresber. d. Vereinigung f. angewandte Botanik, VIII, 1910. Berlin, Borntträger. The same, Zeitschr. f. Bot., IV, 1912, p. 465. (Light and temperature.)

the light at 20 degrees C., but none at all in the dark. According to Gassner, light promotes the germination of *Chloris* (grass) at temperatures over 20 degrees, but hinders it at lower temperatures. Rhododendrons germinate only in light; the germination of *Nicotiana macrophylla* is promoted by light. *Veronica peregrina* germinates 3–10 days earlier in the light than in the dark. The wood grasses *Poa nemoralis* and *Agrostis stolonifera* also have light-sensitive seeds, *i.e.* whose germination is promoted by light. Light seems to exert no influence on dry seeds, though its effect is dependent in a high degree on the age of the seed and the temperature of the seed bed. According to Gassner's experiments (*Ranunculus, Oenothera, Chloris*), germination in the dark of light-sensitive seeds is started by nitrogenous compounds even in low concentration. Ottenwälder [1] found potassium nitrate to be ineffective in inducing germination in the case of *Epilobium*, but acids, to a great extent, effective. Seven-hour treatment of pine seeds with carbonic acid promotes germination.[2]

The manner in which light may act in germination has been more closely investigated in the case of *Phacelia tanacetifolia*.[3] Here the testa contains a water-soluble substance which hinders germination in the light but not in the dark. The substance lies at the chalaza end. The same substance is also contained in the leaves and the extract from the leaves acts in the light as germination-preventing. Alcoholic extract from the testa is ineffective. Boiling does not destroy the substance. From this work also, mention may be made of "false germination," in which the embryos, in consequence of swelling up with moisture, emerge from the testa but do not go on growing.

On the influence of nitrates and other agencies there exist still other researches on agricultural and wild plants, into which, however, we cannot enter.

Among the seeds of the conifers, which form chlorophyll even in the dark,[4] the germination of the pine, spruce, larch and Weymouth pine, also of *Thuya occidentalis* (Kinzel [5]), is favorably influenced by light. The rays of all colours affect the germination of pine seeds, those of long wave-length the most, the short-waved blue rays much less. The germination of spruce seed, which is on the whole much less influenced by light, is only promoted by red and yellow light, whilst blue light, which in *Veronica peregrina* checks starch formation, injures it. Pine seed responds to even small amounts of light; "for the full effect, the light must have the strength which we need in order to read comfortably" (Haack [6]). Petroleum lamp and incandescent electric light, which are both comparatively rich in the less refrangible half of

[1] Zeitschr. f. Bot., VI, 1914, p. 785.

[2] Schmidt, W., Zeitschr. f. Pflanzennahrung und Düngung, B., 4, Jahrg., H. 4.

[3] Magnus, W., Hemmungsstoffe und falsche Keimung. Ber. Dtsch. Bot. Ges., 38, p. (19), 1920 (Generalversammlungsheft); Peters, Th., Die Wirkung des Lichts bei der Keimung der Samen. Ber. Dtsch. Bot. Ges., 42, p. 381, 1924. (The inhibiting substance is so altered by light as to stop germination, even when the solution which has been in the light is applied to seeds kept in the dark.)

[4] Burgerstein, Ber. Dtsch. Bot. Ges., XVIII, 1900, p. 168.

[5] See note 6, p. 396.

[6] Die Prüfung des Kiefernsamens. Keimungsphysiol. Untersuch. a. d. mykol. Laborat. d. Forstakademie Eberswalde. Zeitschr. f. Forst- u. Jagdwesen, 44, 1912. Berlin, Springer.

the spectrum, are recommended by Haack as the best sources of illumination for germination tests. In Haack's experiments the germination of pine seeds resulted just as quickly and completely with a daily illumination of 8 hours as with constant illumination, and the influence of light was found to be equal at all the temperatures tried. In many cases it has been possible to replace the influence of light by the use of chemical substances; though the method of action of light is not yet clear. It is worthy of note that, as Gassner found with the grass *Chloris ciliata*, light may act as a check also at higher temperatures in the presence of germination inducing substances, whilst it promotes germination of seed in dilute solutions.

Haack suggests for seed testing stations 25 degrees C. as the germinating temperature for pine and spruce. Temperatures under 5 degrees are ineffective. Above this, the higher the temperature the quicker does germination result. A change of high temperatures exerts a stimulus to germination in the pine but not in the spruce.

Germination itself begins with the bursting open of the hard shell of the seed or fruit along particular lines of cleavage, pre-determined by the anatomical structure, in which accumulation of water so far diminishes the strength of the shell that the pressure of the growing contents is able to overcome it.[1]

In *Corylus avellana* this pressure is exercised by the growing cotyledons and reaches a magnitude of 3.305 atmospheres. Against a mean resistance of the moist shell of 4.17 kilogrammes is opposed a mean bursting pressure of 4.75 kilogrammes. In the stone pine and, indeed, in other pines, the pressure, which rises to 3.678 atmospheres, is produced by the growth of the endosperm. In the beech the active pressure of the radicle is supported by the somewhat swollen teeth on the leaf base of the cotyledons which surround it and transmitted to the pericarp. These teeth are still visible in the fully grown cotyledons. Their importance could not be understood until it was recognised that they are embryonic organs whose function is exhausted with the bursting of the seed coat (Büsgen, Cupuliferen).

8. The Seedling.—Immediately on emerging, the radicle of the seedling turns towards the soil under the influence of its sensitiveness to gravity. The distance which this structure, sensitive to dryness, has to travel to reach it is not great, because tree seeds when they have fallen, generally lie so that the rootlet emerges, if not directly downwards, at least horizontally. Having reached the earth, the rootlet begins at once to establish itself there by forcing its way between the particles of the soil and then anchors itself firmly by means of root hairs and lateral roots. As regards the further stages in germination, two types may be distinguished. In the hazel, the oak (Fig. 165), the yew and the edible chestnut, the cotyledons remain stuck in the seed coat; only the short stalks by which they are attached to the plumule elongate so that the young shoot-tip may be pushed out of the shell and raised upright (*see* Fig. 165). The cotyledons remain below ground (Hypogeal

[1] Müller, G., Beiträge zur Keimungsphysiologie. Untersuchungen über Sprengung der Samen- und Früchthüllen bei der Keimung. Jahrb. f. Wiss. Bot., LIV, 1914.

Germination) and nourish the seedling with their reserve materials without themselves taking part in assimilation. The seedlings of other forest trees, after fixing the radicle in the soil, have the difficult task of withdrawing the cotyledons from the seed coat so that they may become green in the light and take part in the work of nutrition. The withdrawal of the cotyledons [1] begins at the moment when the at first positively geotropic plumule (spruce, pine) becomes negatively geotropic at the base. A spontaneous bending movement of the tip may assist. It tries to erect itself and thereby lifts with the cotyledons the whole seed coat as a cap, if it is sufficiently strong to overcome the load of the

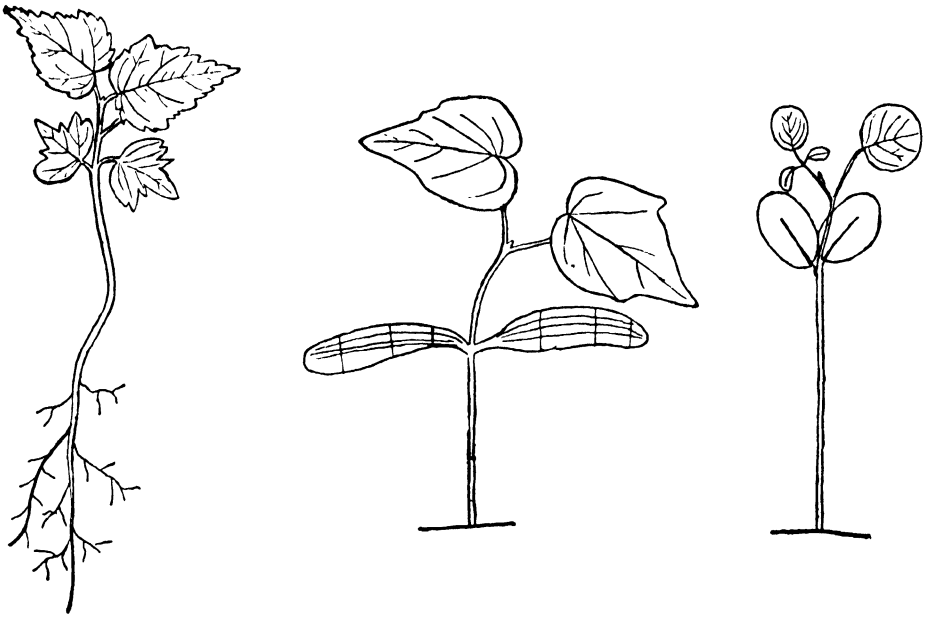


FIG. 162.—Seedlings of the Lime (left), Norway Maple and Robinia (right). After v. Tubeuf.

soil that covers it. In these cases (Epigeal Germination) the cotyledons reach the light and nourish the seedling by their own assimilation.

There are also many kinds of contrivances for fixing the seed coat in the earth. Thus in *Ulmus effusa* the radicle breaks through the broad wing of the fruit as it lies flat on the soil, making a hole in which the somewhat thickened base of the small stem jams itself firmly.[2] The seed coat is now, as it were, nailed to the soil and the cotyledons alone follow the pull of the upward growing plumule. The latter bends itself like a knee whilst it exerts this pull and thereby gains the advantage of breaking through the earth weighing upon it with the neck instead of the more tender tip of the shoot.

The divergences in form presented by the cotyledons from the later leaf structures (*see* Figs. 162–166) are in part explained by the differences in their functions. Their thickness and the smallness of their surface

[1] Sperlich, Jahrb. f. wiss. Bot. 50, 1912.

[2] Klebs, Beiträge zur Morphologie und Biologie der Keimung. Untersuchungen a.d. Tübinger botan. Institut. hrsg. von Pfeffer, Bd. I, XI, 1884.

development show that, even when they emerge from the seed coat into the light and become green, they are in the first place store houses of reserve materials and only in the second place organs of assimilation and transpiration. The leaf structures, which follow the cotyledons or seed-lobes, the **primary leaves,** have not yet the form and never the arrangement of the leaves of the mature plant. Rather are these only gradually attained. How far this leaf metamorphosis may be regarded as a shortened recapitulation of the ancestral history of the species in question (biogenetic law) is to be carefully tested in each individual case. It is more probable that in the form of the cotyledons there are presented adaptations to the life conditions.

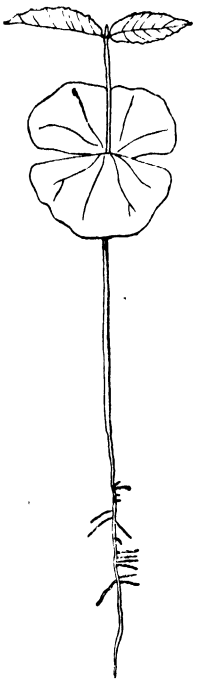


FIG. 163.—Seedling of the Beech. Reduced. The teeth on the leaf-base are concealed. After Büsgen, Cupuliferen.

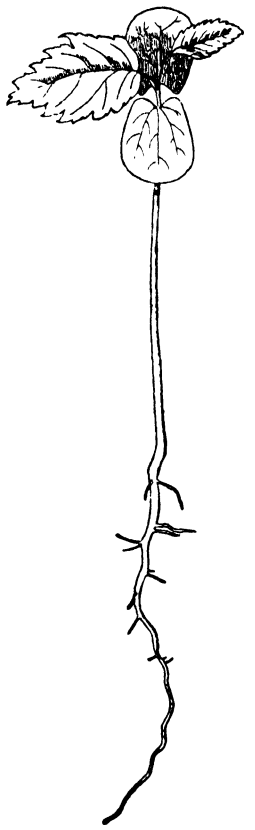


FIG. 164.—Seedling of the Hornbeam. Somewhat enlarged. After Büsgen, Cupuliferen.

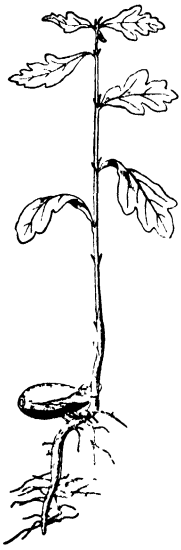


FIG. 165.—Seedling of the Pedunculate Oak. After Büsgen, Cupuliferen.

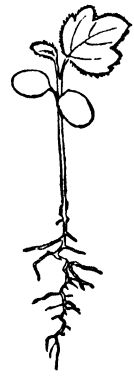


FIG. 166.—Birch seedling. Enlarged. After Büsgen, Cupuliferen.

The seedling of the larch, which is green in summer and sheds its needles in the autumn, besides ordinary one-year needles, also produces, according to Schenk,[1] up to about the fifth year, some which last over two summers, and Schenk is inclined to see also in this ecological peculiarity an indication of ancestors of our larch which, like the cedars, possessed evergreen needles.

As a rule the number of cotyledons in our broad-leaved trees is 2, in the conifers about 6 to 8. In both cases they are arranged in whorls (or opposite), even when the later leaves are arranged spirally.

[1] Sitzungsber. d. Niederrhein. Ges. f. Natur- u. Heilkunde zu Bonn, 1893.

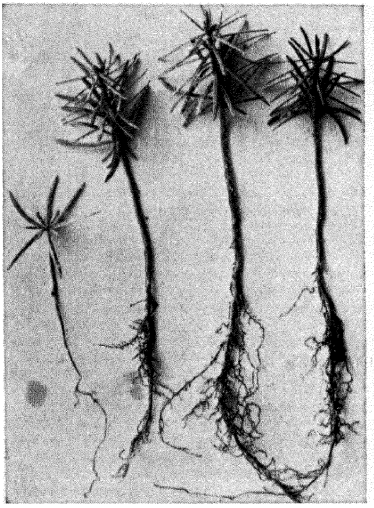


FIG. 169.—One 1-year and three 3-year Silver Fir seedlings. Somewhat reduced.

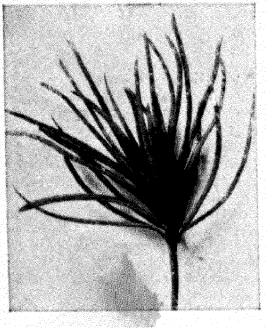


FIG. 167.—Part of a Pine seedling. The toothed primary needles above the smooth cotyledons.

[*To face p.* 401.

The cotyledons of the conifers (*see* Figs. 167–169) are generally needle shaped, though differing in many ways from the later needles. Thus, for example, in the silver fir they bear the white, longitudinal, stomatiferous bands on the upper side, whilst on the later needles these appear on the under side. On the seedlings of the pine, above the cotyledons and also on the leading shoot of the second year are found spirally arranged single needles, whilst the later long shoots of this tree have only inconspicuous scales, the needles first appearing in their axils on the well-known dwarf shoots. Only in the third year does the branching of the plant begin, with the development of a few long shoots from buds, collected like a whorl in the neighbourhood of the end of the shoot, in the axils of the needle-like primary leaves. The first annual shoot of the seedling shows many irregularities and differs from the later shoots in the order of its branching.[1]

The form of seedlings is influenced by light.[2] It is striking that in the spruce seedling, adapted for poor illumination, the shoot below the cotyledons elongates in dim light, the cotyledons, however, differing from other leaves, rather become larger in the dark than in the light. In the pine with diminishing brightness, the plumule increases in length, whilst the cotyledons become shorter.

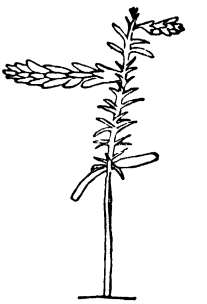


FIG. 168.—Seedling of *Thuyopsis dolobrata*. After v. Tubeuf.

The seedlings of the *Thuyas* and their relatives (Fig. 168) deserve special consideration. These plants possess, as is well known, scale-like leaves which lie close to the twig almost throughout their length. It is quite otherwise with the seedlings. Until into their second year their stems, above the cotyledons, bear spreading needles, and even among the first lateral shoots, some occur which have needles instead of scale leaves. If such needle-bearing twigs are cut off and treated as cuttings, they grow up into fine bushes which likewise possess, not scale leaves like their mother plant, but needles. They can be multiplied by cuttings. From some of these remarkable growths indeed fruit with germinable seed has been obtained from which, however, the scale-leaved mother plant is again produced. The bushes and trees with the seedling characters have come into commerce as a special genus under the name *Retinospora*. In the following table the most widespread *Retinosporas* are correlated with their mother plants, according to Beissner,[3] to whom we mainly owe the clearing up of these relationships.

Mother plant.	Transition form.	Juvenile form. (*Retinospora*).
Thuya occidentalis.	*Th. occ. Ellwangeriana.*	*Th. occ. ericoides.*
Biota orientalis.	*B. or. meldensis.*	*B. or. decussata.*
Chamaecyparis pissifera.	*Ch. p. plumosa.*	*Ch. p. squarosa.*
Chamaecyparis sphaeroidea.	*Ch. sph. Andelyensis.*	*Ch. sph. ericoides.*

[1] Berthold, Untersuchungen zur Physiologie der pflanzlichen Organisation, II, p. 29. Leipzig, 1904, Engelmann; Anatomical *see* Hill and Fraine, Ann. of Bot., XX, 1906, p. 471; Chauveaud, Bull. d. Mus. d'hist. nat., 1904, p. 502 (*Taxus*).

[2] Wiesner, Photometrische Untersuchungen, I. Wiener Akad., 1893, Bd. 102, Abt. I, p. 344.

[3] Beyerinck, L., Beissner's Untersuchungen bezüglich der Retinosporafrage. Bot. Ztg., 1890, p. 517; Beissner's Handb. der Nadelholzkunde, 2. Aufl., p. 498. Berlin, 1909, Parey.

In pines (*Pinus canariensis* and *pinea*), by taking cuttings, bushes have been obtained which, like the seedlings, bear spirally arranged single needles.

An external condition which prolongs the retention of seedlings in the juvenile condition of foliage is unfavorable nutrition, and Beyerinck thinks that *Retinospera* forms might perhaps even be obtained by cultivation in pots without any taking of cuttings. At any rate pot cultivation may form an excellent means of obtaining specimens from which cuttings with the juvenile character may be taken.





FIG. 170.—Above: South-west German lowland Pine, flat-crowned, strongly branched, inclined. Below: Highland Pines, with pointed crowns and slender branches, upright. After Münch.

[*To face p.* 403.

CHAPTER XIV

LOCAL RACES[1]

It is universally agreed that the individuals which in classification are comprised in a species or still smaller systematic unit, need not resemble each other absolutely in all their parts.[2] Just as among the 1,500 million human beings on the earth no two are absolutely alike, so do the individuals of the plant world differ from one another, often in important properties, and indeed it is not only external influences such as varied nutrition, warmth, moisture, etc., which lead to these differences (modifications *q.v.*), but individual (genotypic) differences also exist in the hereditary factors transmitted from the parents. True, there are in the plant world also individuals with completely equivalent hereditary factors. Among these are the plants which have originated through cuttings, layers, root suckers, brood buds or by vegetative means generally; they resemble in all their hereditary factors the mother stock and their likewise vegetatively produced sisters. The produce of self-fertilisation of one plant may also contain the same genotype; in this case one speaks of "**Pure Lines.**" Vegetatively produced individuals of the same hereditary factors together form a "**Clone.**"

With our forest trees, the great majority of which are multiplied by cross-fertilisation, these cases have nothing to do. By cross-pollination new combinations of hereditary factors are brought together in infinite variety which guarantees a practically unlimited variation of the individuals. The smaller individual differences in the plant world easily escape observation because we have not such an acute sense for them as we have for differences in men. Often, however, the expert eye of the plant breeder is able to discover them, and he employs them to breed out new varieties with, for him, more suitable characteristics. If a certain deviation from the "**Normal type,**" *i.e.* the commonest form in respect of certain properties, occurs only sporadically, it is called a "**Sub-variety,**" such as the broom-like (fastigiate), unbranched "snake" or "monstrous," thickly branched (globuse, etc.) forms.

[1] Summaries: Fabricius, Naturwissenschaftl. Zeitschr. f. Forst- u. Landwirtschaft, 1908. Engler, A., *ibid.*, 1913. König im Merkheft zur forstlichen Saatgutanerkennung. Neudamm, 1925. Rubner, Pflanzengeographische Grundlagen des Waldbaues, 2. Aufl. Neudamm, 1925. There further literature.

[2] Cajander, Einige Reflexionen über die Entstehung der Arten, insbes, innerhalb der Gruppe der Holzgewächse. Acta Forestalia Fennica, 21, 1921.

If such types occur in whole populations widely distributed, they are spoken of as "**Varieties.**" Within these small units, however, agreement is also confined to certain characteristics, and great differences may exist in others which are apparently unimportant for classification. Groups of this kind can be made up into true species just as well as into sub-species, varieties, forms, etc., according as their differences from others appear in the subjective estimation of the systematist, important or subsidiary.

Besides the externally visible, morphological differences with which the systematic botanist has almost exclusively concerned himself, there also occur, as research has recently proved and as agriculturists with their numerous sorts and strains have long known, considerable differences which only emerge in certain life manifestations. Heat requirement, resistance to certain diseases and injuries and much else may differ in different individuals. Morphological and physiological peculiarities may be associated accidentally or, as we shall see, from inherent causes.

If such peculiarities in the hereditary factors are not vital, such as certain forms and colours of seed and fruit, small variations in leaf-form, etc., various types may occur side by side in the same habitat. Individuals with different physiological factors may also occur together in this way. If, however, the locality, especially the climate, is so conditioned that the form or the particular physiological character of certain individuals is favoured or injured in a considerable degree, the members of the crop best adapted to the effects of the locality sooner or later attain an advantage and surpass and dispossess the less suitable. A **Natural Selection** takes place which ultimately in extreme cases leads [1] to pure crops of a definite **Local Race** (soil or climatic race, physiological variety [Cieslar]).

Perhaps the clearest instance of this kind is given by the behaviour of early- and late-sprouting spruces investigated by Münch (*see* Chap. II, 5). In frost-damaged spruce plantations, it can be seen how, step by step, the early spruces are thrown back by repeated frosts and overgrown by the late spruces, until finally only a population of frost-hardy late spruces is left (Fig. 172) which transmit to their offspring their disposition to break their buds late, so that a frost-hardy climatic race is produced.

The earlier idea that the transmission of "acquired characteristics" was involved, *i.e.* that the climate of the locality may affect the trees in such a way that the latter little by little alter their characteristics in the sense if a direct adaptation and transmit to their progeny this reaction to external conditions, cannot be any longer maintained in the face of the present day position of genetics,[2] which, on the ground of a crushing accumulation of facts, has arrived at the conclusion that modifications are not transmitted. Whence originate those genotypic variations which lead through natural selection to climatic or local races

[1] Kienitz, Über Formen und Abarten heimischer Waldbäume. Berlin, 1879. Oppermann, Die Weisskiefer in Jütland. Das forstl. Versuchswesen in Dänemark, 1922, 2. Münch, Beiträge zur Kenntnis der Kiefernrassen Deutschlands. Allgem. Forst- u. Jagdztg. 100, 1924, 101, 1925.

[2] Baur, E., Einführung in d. experimentelle Vererbungslehre.

may remain doubtful. They may be produced by mutations of a homogeneous original form, but they may also have existed as long as the species themselves.

In agricultural plants, natural selection has led to the "native strains" which correspond to the local races of our forest trees. There is a difference, however, in the much more complete elimination of the unfit with trees than with agricultural plants, because in the forest out of the thousands of young plants in a crop only a few individuals obtain the advantage, crowd out the unfit and reach the stage of production, whilst the agricultural plants are mostly so cultivated that if possible every plant is preserved until the ripening of the seed. In them separation by natural pressure of competition is absent, and it is to be concluded that the local races of forest trees are more sharply bred out in the course of thousands of years and represent purer strains than the native strains of agricultural plants.

In agriculture, natural breeding is accelerated by artificial selection inside a pure line [1] and, assisted by artificial fertilisation, guided into the paths most desired for man's use. The cultivated varieties thus originated may differ in many characteristics from the wild plants of the same species and surpass them many times in their rate of growth. In forestry artificial breeding [2] has not gone beyond insignificant beginnings and, on account of the extraordinary difficulties presented by the slow development of forest trees and for other reasons, is less promising.

It is of great importance that the same effect of the locality on the selection of biotypes which has been proved in so many directions from the forest botany side has nowadays been found also in small herbaceous plants.[3]

The following factors of the locality have, up to the present, become recognised as environmental influences which lead to the formation of **morphological local races.**

Snow, which injures the evergreen species of trees by breaking and crushing them in consequence of the winter loading of the crowns, acts the more destructively the weaker and more brittle the branches and stems and the greater the quantity of snow the crown intercepts by reason of its breadth and shape. Lowland pines from regions with little snow, such as the south-west German lowland pine from the plain of the Rhine, are regularly damaged or completely crushed [4] by snow if they are transplanted into the mountains, even at elevations of 400 metres. On the other hand, the upland pine, indigenous to the German

[1] Baur, E., Die wissenschaftlichen Grundlagen der Pflanzenzüchtung, 1921. Fruwirth, Handb. d. landwirtschaftl. Pflanzenzüchtung. Berlin, 1922–23.

[2] Fabricius, Holzartenzüchtung. Forstwissensch. Zentralbl., 1922. Löffler, Grundlagen Aufgaben und Ziele einer forstlichen Pflanzenzüchtung. Tharandter forstlich. Jahrb. 74. Fischbach, C., Über die Benutzung der bei den Waldbäumen vorkommenden Unterarten zu forstwirtschaftlichen Zwecken. Allgem. Forst- u. Jagdzeitg., 1848, p. 325 (contains the oldest proposals for breeding on agricultural lines.)

[3] Turesson, G., The plant species in relation to habitat and climate. Hereditas, VI, 1925.

[4] Kienitz, Formen und Abarten der gemeine Kiefer (*Pinus silvestris*), Zeitschr. f. Forst- u. Jagdwesen, 1911, p. 4. Engler, A., Einfluss der Provenienz des Samens auf die Eigenschaften der forstlichen Holzgewächse. Mitteil. d. Schweiz. Zentralanstalt f. d. forstl. Versuchswesen, X, 1913, p. 191. Comprehensive experimental work, especially with the pine. Münch, E., *loc. cit.*, 1924–25. Vanselow, Die Keifernfrage in Hessen, Allgem. Forst- u. Jagdzeitung, 102, Bd., 1926, p. 273.

secondary mountain chains and still more the pine from the higher elevations of the Alps and from the far north, can cope even with the heaviest loading of snow by reason of its slender, often almost columnar crown and its fine pliant branches (Figs. 8 and 170). The spruce protects itself against overloading by snow either by a narrow crown with short pliable branches which, when loaded with snow, lie close to the stem and then present a small intercepting surface or by the pendant posture of the twigs of higher order (comb type) which is said to preponderate in the standing crop on snowy mountain sites (Sylvén, 1915) (Fig. 170). All the conifers of the higher mountain sites in North America also possess a pointed or columnar form, whilst among lowland races of the same species broad-crowned forms predominate. This difference is especially striking in the Douglas fir, whose continental mountain races (*glauca*-varieties) are distinguished by the slender form of their crowns from the widely branched coast forms.[1]

The columnar form of crown is also interpreted by Wiesner as an "adaptation" to over strong **light** rich in the injurious rays of short wave-lengths, especially the ultra-violet, such as prevails in southerly or elevated continental regions with low atmospheric humidity. The crown so formed is protected against the intense zenith light, especially rich in such rays, which only strikes the crown tangentially. The conifers from such regions are regularly provided with a bluish wax deposit (*glauca-*, *argentea-*, *violacea*-varieties of Douglas fir,[2] of *Picea pungens*, *Abies concolor*, the pines of the Auvergne,[3] the spruces and Cembran pines of high mountain sites, etc.) or, if this is absent, with a thick hypodermal layer. The needles of spruces from seed from high elevations resemble light-needles in structure more than do those of lowland spruces (Engler, 1905). By such means they protect themselves both against strong cuticular evaporation and against excessive light[4]; two climatic influences which regularly go together, since in dry air and in the rarefied air of high mountains the ultra-violet rays are less absorbed by water vapour.

The root-form also differs in different climatic races, as was proved by Cieslar and Engler[5] for the spruce. Spruces from high-mountain seed are more strongly rooted than the progeny of lowland races. This corresponds to the difference in water demands due to the difference in the force of evaporation in the respective localities.

The **wind** has also a strongly selective and therefore race-forming action. In windy, insular or coastal localities the tall growing forms cannot maintain themselves. They are destroyed and give place to the spreading or even creeping ones, so that a crop of no forestry value arises, consisting of bushy and scrubby "rank-forms," which even transmits its forms to its progeny, cultivated in more favorable

[1] Münch, E., Anbauversuche mit Douglasfichten verschiedener Herkunft und anderen Nadelholzarten. Mitteil. d. Dtsch. Dendrol. Ges. 33, 1923, p. 61.

[2] v. Tubeuf, Naturwissenschaftl. Zeitschr. f. Land- und Forstwirtschaft, 1919, p. 10; Münch, 1923.

[3] Schott, *Pinus silvestris* L., Die gemeine Kiefer. Forstwissenschaftl. Zentralbl., 1904. The same, Rassen der gemeinen Kiefer, *ibid.*, 1907. Large historical and experimental work.

[4] Engler, A., 1913. Schott, 1904 and 1907.

[5] Engler, A., Einfluss der Samenprovenienz auf die Eigenschaften der forstlichen Holzgewächse. Mitteil. der Schweiz. Zentralanstalt f. d. Forstl. Versuchswesen, VIII, 1905.

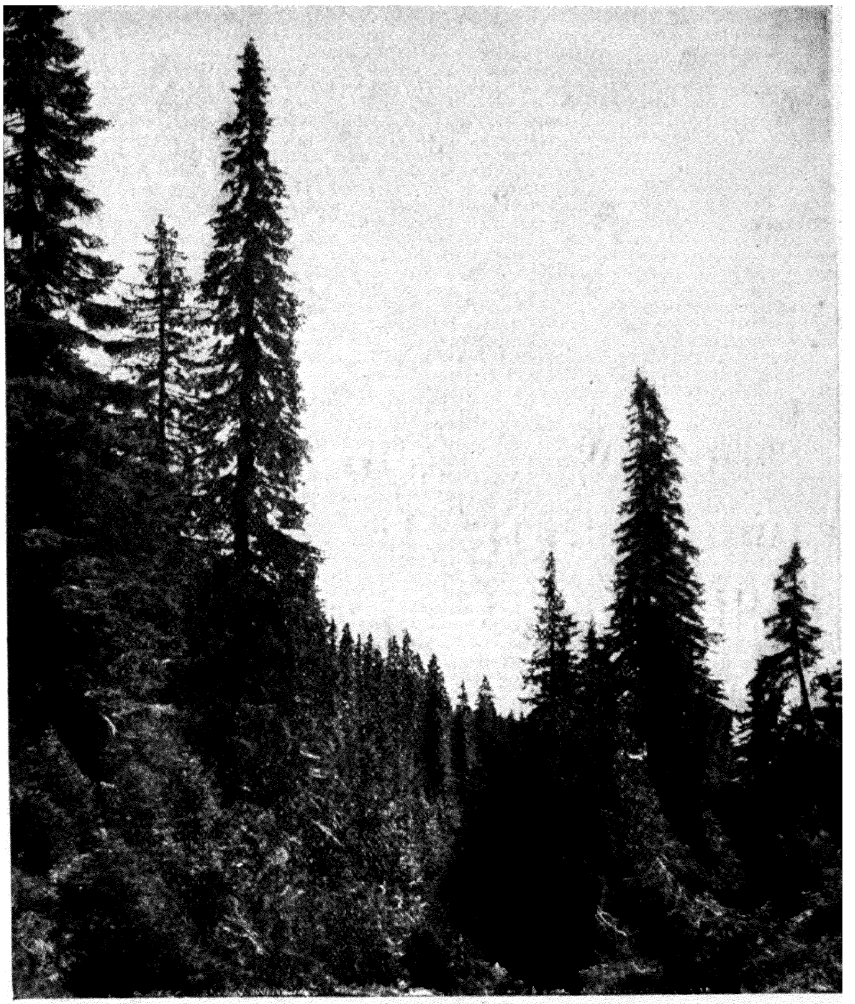


FIG. 171.—Spruce-forms in snowy, elevated site in the Riesengebirge. Phot. Zückert. (Mch.)

[*To face p.* 406.

localities. This is most striking, according to the many years' researches of Oppermann[1] and Hauch[2] in the beech and oak in Denmark. Moreover, in the highest, stormy, situations in the mountains, the trees are often shorter and broader branched than lower down. The effect of the wind may often overcome the effect of snow which leads to the other extreme in crown-form. In these forms it is not a case only of the direct modifying effect of the wind; much rather has the transmissibility of such forms been proved by numerous experiments. The more wide-spreading rank forms of the beech, in consequence of their shape can utilise overhead light under the shade of higher trees better than upright-growing stems. Yearlong raising of beech undergrowth under heavy shade, therefore, favours the rank forms rather than the tall-growing ones, and leads to misshapen beech crops.[3]

Crooked-growing and wide-branched rank forms are, according to Oppermann (1912), to a great extent, unintentionally bred by man. In forests which have been long subject to man's attacks, the finest and tallest trees have always been cut out and the badly formed stems disposed to crooked growth left. Oppermann quite rightly ascribes to this an extraordinarily powerful influence on the tree-forms in old civilised countries. **Pasturage** also has, according to him, a similar effect. The browsing of cattle injures the slender forms more than the bushy, thickly-branched ones, which can heal the damage more easily. The bent form of the Süntel beech and the pine of Bonaduz[4] have been traced to such influences.[5] In cultural experiments with the pedunculate oak extending over many years, the stem-form of the mother trees is transmitted in a most striking way.[6]

Theoretically it is to be expected, though it has not yet been experimentally proved, that the **closeness of the canopy** and the **quality of the locality** also have a selective action on the hereditary tree-form. The denser the canopy and the more vigorous the sorting out of the crop the more completely are the creeping and bush forms destroyed, for in a close crop only the forms most decidedly upward-aspiring can continue to live. This may, however, not apply generally, as, according to Oppermann, the rank beeches are distinguished by stronger growth and vigorously destroy the forms that strive to broaden out. If the locality is so unfavorable that a close canopy does not come into existence and upright growth is impossible, the forms disposed to broad, low growth have the advantage, as they achieve reproduction earlier and more abundantly than the others. This appears to have led to

[1] Oppermann, Renkbuchen in Dänemark. Zentralbl. f. d. ges. Forstwesen 35, 1909, p. 108. The same, *loc. cit.*, 1922.

[2] Hauch, Erblichkeit der Buche und Eiche. Zentralbl. f. d. ges. Forstwesen, 1909. The same, Provenienzversuche mit Eiche. Forstl. vorsogsvaesen i Danmark, IV, 1914, p. 295. (Lammas shoots and leafing.)

[3] Engler, A., Untersuchungen über den Blattausbruch. . . . Mitteil. d. Schweiz. Zentralanstalt f. d. forstl. Versuchswesen, X, 1913.

[4] Engler, 1905 and 1913. Oppermann, 1922. Münch, 1925.

[5] On the transmissibility of growth-forms, etc., *comp.* also: Boden, Wirtschaftlicher Wert der Süntelbuche. Zeitschr. f. Forst- u. Jagdwesen, 38, 1906; Lebensgeschichte der mitteleurop. Blütenpflanzen, II, 1, Cupuliferen by Büsgen. E. Ulmer, Stuttgart; v. Klitzing, Erblicher Krüppelwuchs bei Kiefern. Zeitschr. f. Forst- u. Jagdwesen, 1914, p. 442; Bud-variation of the beech *see* Hesselman, Svensk bot. tidskr., V, 1911. Ref. Bot. Zentralbl., 1911, Bd. 117, p. 483.

[6] Cieslar, Zentralbl. f. d. ges. Forstwesen, 1923, p. 97.

races with unfavorable forms, especially on bad high moor soils with old original stocks (Münch, 1925).

The single-stemed, upward-aspiring form of growth usually exhibited by our trees, is thus only a special case of the various growth-forms possible for trees. It has only become predominant because forest trees as a rule grew up in close canopy, in which lower forms of the same species cannot maintain themselves.

There are therefore undoubtedly cases in which the stem and crown-forms, just like any other morphopogical property such as leaf-form, are transmitted with great constancy to the progeny. Among them is, for instance, the hereditary quality of the bush and globose forms in the spruce found by Engler and V. Tubeuf. We have already stated in Chap. I, 11, however, that this does not exhaust the problem of the transmission of stem-form. In many, indeed in most cases, it is not the stem-form itself which is directly transmitted, but certain inner properties which lead to particular stem-forms only under certain circumstances. In the pine, according to Münch (1925), it is often only the greater or less resistance of the stem to mechanical bending which is transmitted. If mechanical influences such as wind pressure and snow-break remain small, as in a mild climate or in close canopy and a sheltered situation, races remain straight-stemmed which under other external conditions would be forced into bad stem-forms. The geotropic energy with which a stem strives to adjust a bending or injury it has suffered, is also hereditary, though it also may be modified by the locality. This property can also indirectly influence the stem-form very strongly. It is very important for forestry to recognise this connection and to have regard to it in the choice of seed and the tending of woods.

Naturally all these formative influences may work with or against each other, so that the cause and biological significance of the stem-form are not always recognisable in an individual case.

Among the factors of locality which lead to the forming of **physiological** local races, **heat** and the **length of the growing season** must be mentioned in the first place. Races of trees from regions with a short growing season and bad forest growth (high mountains and far north), when transplanted to mild situations, retain the short duration of their vegetation, fail to utilise the longer growing season, and so remain behind the indigenous local races. In general they come into leaf earlier, it is true (except the pedunculate oak, which behaves in the opposite way), because less heat suffices for their vegetation (*see* Chap. II, 5), but they cease their growth early in the summer.[1] When the transfer is in the opposite direction the trees seek to retain their inherited long vegetative period, grow on into the autumn and perish with frost. This has been proved especially for the spruce, pine and Douglas fir.

[1] Cieslar, Über den Einfluss des Fichtensamens auf die Entwicklung der Pflanzen nebst einigen Bemerkungen über schwedische Fichten- und Wiessföhrensamen. Zentralbl. f. d. ges. Forstwesen, 1887, p. 189. The same, Über die Erblichkeit des Zuwachsvermögens bei den Waldbäumen. *Ibid.*, 1895, p. 7. The same, Neues aus dem Gebiete der forstlichen Zuchtwahl. *Ibid.*, 1899, p. 49. The same, *ibid.*, 1907, p. 1 and 49; Maass, A, Mitt. d. forstl. Versuchsanst. Schwedens, 1911, H. 8, p. 132 (Darmstadt pines in Sweden); Engler, 1905 and 1913; On the behaviour of oaks from different climatic localities in Europe in comparative cultural experiments over many years, *see* Cieslar, Zentralbl. f. d. ges. Forstwesen, 1923, p. 97. On races of the larch *see* Cieslar, Waldbauliche Studien über die Lärche, Zentralbl. f. d. ges. Forstwesen, 1904, p. 1.

The dependence of the inborn vigour of growth on the length of the growing season of the place of origin, is shown by the result, among others, of a comparative cultural experiment with seeds of *Pseudotsuga Douglasii* var. *glauca* from nine climatically-different sources, which were grown in South-west Germany at an elevation [1] of 350 metres.

Months with a mean temperature of over 10 degrees at the place of origin	2	4	5	6
Mean height of 12-year-old plants in centimetres	91–122	135–159	180–192	263

The **summer warmth** of the place of origin acts in the same sense, for **heat requirement** is also hereditary. However, this influence seems to be less than that of the length of the growing season, for a high total heat cannot entirely replace a long growing season. The trees and tree races of the Pacific coast of North America are among the most vigorous growths of the plant world, though the summer heat is less there than in the interior of the continent, whilst the growing season, on account of the equable climate, is very long.

Experiments by Cieslar [2] with spruces from various sources which were cultivated side by side in Vienna gave the following results, among others :

Origin. Region.	Elevation in m.	Mean height of plants in cm.
Sweden . . .	—	34
Sudeten . . .	1140	50
,, . . .	860	73
,, . . .	510	88

According to Eneroth,[3] the yield, compared with that of the indigenous race of pines, diminishes by 27-35 per cent. when the mean temperature of the place of cultivation in July to September is higher by 1 degree than that of the place of origin. Numerous further experiments by Cieslar, Engler, Schwappach,[4] Kienitz,[5] Gross,[6] with pines, spruces, larches and maples always gave the same results. Only for the silver fir and beech could Engler detect no climatic races differing in vigour of growth, and also with the ash the progeny of trees from 1,400 metres elevation showed the same rate of growth as plants from lowland seed. Cieslar (1923) found great differences, according to source, in the vigour and duration of growth in the pedunculate oak (in which the most vigorous sorts had also the largest leaves).

Vigour of growth, so important in forestry, thus depends not only on the quality of the locality at the place of cultivation, but also, in a high degree, on the inherited disposition of the plants. This also comes

[1] Münch, 1923.

[2] Cieslar, Zentralbl. f. d. ges. Forstwesen, 1905, p 195.

[3] Eneroth, O., Meddelanden f. Statens Skogsförsöksanstalt, H. 23, Nr. 1.

[4] Schwappach, Die Bedeutung und Sicherung der Herkunft des Kiefernsamens. Flugblatt und Mitteil. Dtsch. Dendrol. Ges., 1914, p. 24.

[5] Kienitz, Zeitschr. f. Forst- u. Jagdwesen, 1922, p. 65, 1926, p. 397.

[6] Gross, Anbauversuch mit Kiefern verschiedener Herkunft im Tharandter Reviere. Mitteil. a. d. Sächs. forstl. Versuchsanstalt zu Tharandt, Bd. II, H. 5, 1925.

to light with special clearness in a place of cultivation climatically alien to the native habitat, if the plants are transferred to a warmer climate. If they enter a severer climate the inborn vigour of growth does not achieve its full value. Injuries through frost, crushing by snow and diseases occur and throw the plants back, so that they ultimately remain behind the indigenous plants.

Warmth and length of growing season do not seem to be the only breeding influence affecting vigour of growth, for, in cultural experiments, races are also found whose native climate cannot, as regards growing season and warmth, simply be placed in parallel with their vigour of growth. Thus in most parts of Germany and Switzerland, the Belgian and the East Prussian Baltic pines flourish excellently, both about equally well, though the warmth and the growing season in the two native places are quite different. Both races grow better in many parts of Germany than the indigenous ones. It appears from this and from other facts, that vigour can be bred also by means of other environmental influences, climatic and indeed also soil properties. The more favorable the sum of all the conditions for growth the more completely are all the slow-growing biotypes rejected, whilst in a poor locality great power of growth cannot be fully utilised, and therefore also cannot be bred in by natural selection.

By the destruction of sensitive types, **frost** may also lead to physiological races. Maritime pines which survived the severe winter 1879–80, as well as their descendants, proved themselves frost hardy and suitable for cultivation in Germany, whilst plants from any casual seed of this species are too frost-tender.[1] We have already ascribed the culling out of early spruces in frost localities to late frosts (Fig. 172). But autumn and winter frosts as well as the frost drought of winter are also important. Pines from mild South-west Germany freeze to death in Sweden,[2] and Livland pines [3] from the south of Sweden in northern Sweden.[4] A difference of more than 1–2 degrees of latitude has already a marked effect. Douglas firs from the southerly latitudes of the Pacific coast die of frost in Germany, whilst those of more northerly or more elevated origin flourish without injury. It is most probable that the failure by forest districts of the alder plantations [5] in North Germany is to be traced to such causes.

The assumption of a striking yellow-brown or violet winter colour by pines from a source where the winter climate is severe, whilst pines from a mild maritime climate remain dark green in winter, is associated with winter frost-hardiness. (Engler, Kienitz (1922), etc.)

[1] Schmidt, A., Die Seekiefer. Forstwissenschaftl. Zentralbl., 1922.

[2] Wibeck, E., Über das Verhalten der Kiefern und Fichten von ausländischem, besonders deutschem Saatgut. Mitt. a. d. forstl. Versuchsanstalt Schwedens, 1912, H. 9.

[3] v. Sivers, Über die Vererbung von Wuchsfehlern bei *Pinus silvestris L.* Mitteil. Dtsch. Dendrol. Ges., 1895, p. 138. The same, *ibid.*, 1911, p. 150. The same, Allgem. Forst- u. Jagdzeitg., 1900, p. 308; 1909, p. 195. Zeitschr. f. Forst- u. Jagdwesen, 1914, p. 244.

[4] Wibeck, Über naturliche und künstliche Verjüngung in den Wäldern Nordschwedens. Mitteil. a. d. forstl. Versuchsanstalt Schwedens, 1913, H. 10. Schotte, G., Tallfröets Proveniens. *Ibid.*, H. 20, Nr. 5.

[5] Bansi, Provenienz der Roterle. Zeitschr. f. Forst- u. Jagdwesen, 1924, p. 166. A not yet completed investigation by the editor (Münch) proves that the progeny of the alders that are failing behave differently in growth from the indigenous ones, and makes the idea, that damage by frost of plants derived from a milder climate may be the cause of the failure of the artificially established plantations, a very likely one.



FIG. 172.—A frosty-hardy local race of the Spruce arising in a frost locality. The early spruces are being killed or crippled by repeated late frosts, whilst the late spruces remain uninjured and alone form the crop of the future. After Münch and Liske.

[*To face p.* 410.

Whilst the knowledge of climatic races has already been much advanced by forest-botanical research, the investigation of **physiological soil races** is still very backward. These have up to the present been proved only for the ash.[1] The occurrence of this tree in the most varied habitats—on moist fertile marsh soils and on the margins of streams on the one hand and on dry calcareous slopes on the other—depends on the dispositions of different races. The " lime-ashes " and their descendants are satisfied with less moisture and flourish on dry soil much better than the " water-ashes." In one experiment on dry soil the lime-ashes were almost three times as heavy as the water-ashes.

Recent, not yet published, experiments of Oberförster Gärtner and the editor confirm their idea that the soil requirements of different spruces also vary to a wide extent. In spruce plantations which experience a check in growth as the result of drought and deterioration of the soil, the early spruces especially are left behind in growth, whilst some of the late spruces go ahead undamaged, so that the early spruces on such soils remain on the average considerably behind in height-growth.

The behaviour of trees towards parasitic **diseases** and animal **pests** has not yet been systematically investigated, though individual and racial differences in this respect have been proved incidentally many times. Individual stems of the pine and their descendants are especially prone to the pine blister (Resin top) [1] caused by *Peridermium pini ;* many are completely immune from the needle-shedding fungus [2] (*Lophodermium pinastri*). Especially susceptible to the latter disease in Germany are the pines from western Hungary, southern France [3] and the High Alps, very immune are the northern (Engler) and Belgian (Schott) pines. Many beeches are very susceptible to the canker fungus.[4] In a general defoliation by nun moth caterpillars (*Liparis monacha*) individual spruces remain strikingly immune, and in fact, according to several accounts,[5] especially the late spruces, whose buds break so late that the larvae, which require fresh young foliage, cannot feed themselves on emerging in the spring. This power of resistance appears to have led to race formation, as the lowlands specially menaced by this insect are occupied predominately by late-sprouting, green-coned spruces.

The physiological and morphological racial characteristics are retained with great tenacity on transfer to alien localities and are transmitted there also to succeeding generations. Lowland spruces, removed to elevated sites, retained up to an advanced age their sensitiveness to frost, which depends on their too lengthy growing period, and again produced descendants with the characters of lowland races.[6] Northern pines grown in the Saxon Erzgebirge produced, at 60 years

[1] Münch u. Dieterich, Kalkeschen und Wassereschen. Forstl. Wochenschrift Silva, 1925, p. 129.

[1] Klebahn, Flora, 1918 ; Stahl, Festschrift

[2] Zederbauer, Zentralbl. f. d. ges. Forstwesen, 1912 and 1913.

[3] Mayr, H., Schüttekrankheit und Provenienz der Föhre. Forstwissenschaftl. Zentralbl., 1911, p. 1 ; Herrmann, E., Naturwissenschaftl. Zeitschr. f. Forst- u. Landwirtschaft, 1910, p. 205.

[4] Hartig, R., Lehrbuch der Pflanzenkrankheiten.

[5] Wachtl, Neue Gesichtspunkte über die Entstehung von Nonnenkalamitäten. Zentralbl. f. d. ges. Forstwesen, 36, 1910, p. 145.

[6] Engler, 1913.

of age, progeny of the slow growth which is characteristic of the northern pine.[1] The descendants of pines of alien race grown in Germany resembled their mothers completely in rate of growth, and also in part in susceptibility and in stem and branch-form, although fertilisation by native pollen was to be assumed.[1] According to the general experience of genetics, therefore, nothing is to be expected from " acclimatisation " by " direct adaptation " for the improvement of imported alien races of trees. It is to be noted, however, that unsuitable races can be improved in a comparatively short time by natural selection, if natural selection is offered a sufficient choice. As the physiological races are never bred out pure, races alien to the locality also generally contain a few trees better suited to the new habitat, which work themselves gradually up out of the main body of unsuitable trees and finally alone form the crop. Such crops thereby become better by degrees, as observation shows in the pine and spruce, though at the same time they cannot reach, at least in one rotation, the results of breeding such as the native stock has undergone.

The scientific discovery of local races is not only important for genetics but has proved extraordinarily valuable for forestry. Ignorance of racial differences, based on the earlier rigid conception of species, for a long time led to the haphazard employment of trade seed when required, which produced the most evil results and left behind on thousands of hectares, unsatisfactory crops which now detract sensibly from the yield of the forest.

Besides these vitally important racial differences in form of growth, vigour, heat-requirement, etc., there are also to be found individual and racial differences in characters which are indifferent for the continuance of the species. Thus the fruits are very often different in size and shape from tree to tree. According to Cieslar (1923) the oaks (*Q. pedunculata*) from a warm climate have in general larger fruits (*e.g.* Slavonia 7.67 grammes, South Sweden 1.32 grammes per acorn). In the same crop and without any perceptible difference in nutrition, individual oaks bear strikingly small, other unusually large, some globular and others longish fruit. The extent of variation of the fruit of the same species due also to nutrition is thereby considerably increased. Differences in the fruit of the hornbeam are shown in Fig. 173. Büsgen easily detected 18 forms of the beech within a small area, which differed in the size and form of the fruit and cupule. Considerable variations are also found in the leaf-form in the oak and beech. Especially great are the differences in trees which hybridise between closely allied species, like the pedunculate and sessile oaks (Kienitz, 1879, Oelkers [2]) and the pubescent and common birches, whose variations, and hybrid forms have been closely investigated by Morgentaler.[3] The seeds and seed-wings of the Scots pine are also of manifold form and

[1] Münch, Verhalten der Nachkommen fremder Kiefernrassen in zweiter Generation. Forstwissenschaftl. Zentralbl., 1924, p. 45.

[2] Oelkers, Stiel- und Traubeneiche. Eine Variationsstatistische Untersuchung. Zeitschr. f. Forst- u. Jagdwesen, 1913, p. 18.

[3] Morgentaler, Beitrag zur Kenntniss des Formenkreises der Sammelart *Betula alba L.* mit variationsstastischer Analyse der Phänotypen. Promotionsarbeit. Zurich, 1915. Reprint in: Vierteljahrsschrift d. naturforsch. Ges. in Zurich, 1915, 60. Jahrg.

colour. Neighbouring trees in the same crop may produce quite differently coloured seed, though the same tree always brings forth year by year only seed of the same colour (Schott, Münch, 1924). The grains are always either all black, or all light yellow or all speckled. It is the same also with the form and colour of the seed-wings; different from tree to tree but always the same, within a certain limit of variation, in the same tree.[1] There are also dark- and light-seeded varieties in the Austrian pine.[2]

The many attempts to make use of these external differences as distinguishing characteristics for physiological races have only been successful to a small extent. Thus the seeds of North Swedish pines are light brown, those of South Swedish, dark brown to black, more rarely speckled.[3] The form-variations of pine cones are also very striking. In this connection so much is established, that the cones of pines from high and northerly situations, taken through and through, have larger and more clear cut and recurved apophyses than those from the usual

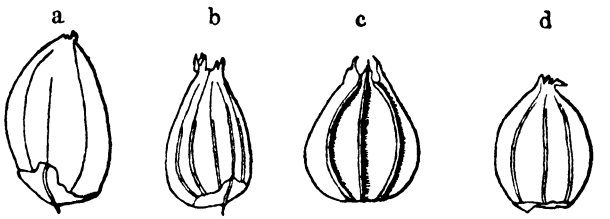


FIG. 173.—Fruit-forms of the Hornbeam from various trees. Enlarged three times. After Büsgen, Cupuliferen. (*a*) *magna*, (*b*) *minor*, (*c*) *costata*, (*d*) *Mariae*.

German localities. Engler considers these differences to be the direct effect of light; in strong light, not only the foliage leaves but also the cone scales, which indeed also must be regarded as leaf structures, are more strongly developed. Later, however, it appeared (Münch, 1924) that the cone-form of pines of different origin is hereditary, though the modifying action of light is not thereby placed in question. Cone-form is, however, not a certain means of differentiation for local races, because differences occur among the individual trees of the same physiological race, and races of different origin may bear the same form of cone. In the mountain pine (*Pinus montana* [4]) also, the very varied forms of the cones do not allow of any conclusion as to the physiological differences or to the very diverse stem forms. On the other hand, according to a preliminary communication by Schmidt [5] the serodiagnostic method seems to be a suitable one for indicating physiological race-characteristics even in the seed grain.

How very greatly the whole shape of the tree can vary from stem to stem even under external conditions that are as alike as possible and,

[1] Sylvén Nordschwedische Kiefer. Skogsvardför. Tidskrift, 1916; 1914 (Spruce). Kurdiani, Zur Frage über die Rassen der *Pinus silvestris*. Zentralbl. f. d. ges. Forstwesen, 1908. p. 229 (Colour of pine seed). Schotte, Variation des Kiefernsamens. Naturwissenschaftl. Zeitschr. f. Land- u. Forstwirtschaft, 1906, p. 22.

[2] Pittauer, Zentralbl. f. d. ges. Forstwesen, 1914.

[3] Schotte, G., Mitteil. d. forstl. Versuchsanstalt Schwedens, H. 2, 1905.

[4] v. Tubeuf, Mitt. Deutsch. Dendrol. Gesellsch., 1912.

[5] Schmidt, W., Herkunftsermittlung bei Kiefernsaatgut. Silva. 1926, Nr. 30.

therefore, on account of hereditary disposition, is shown not only in the morphological local races previously discussed, but also in crops of the same origin. Very striking is the multiformity of the spruce—"Every spruce has a different look"—in which a series of types with different forms of branching may be found in every crop (comb type, plate type, ribbon type, brush type).[1] By careful search the same thing is found in all species of trees. According to Baur, from a pine wood of a few acres a long series of sorts differing very greatly in size, rate of development, quality of timber, needle-form, etc., may be bred out. The thickness and constitution of the rind also varies from tree to tree and also according to local race. The lowland pine from South-west Germany is characterised by a thick bark (Münch, 1924–1925) and, according to Seitz, "plate pines" and "scale pines" may be distinguished in old pine woods according to the form of the bark-scales. If and how far such rind patterns, and the corresponding rind-forms which also occur in beech and other species of trees, admit of inferences as to physiological race characteristics, has not yet been sufficiently investigated. According to Engler (1905), the spruce of the High Alps has a thicker rind than the lowland spruce and also transmits this characteristic to its offspring in lower situations.

The size of the plants in the first years corresponds in general to the size of the fruit, though in the oak, according to Cieslar, the difference had quite disappeared after 12 to 18 years. Old pines provide smaller seeds than younger ones and the seedlings are of correspondingly different sizes. This difference in the size of plant due to the age of the mother trees is, however, according to Schotte,[2] soon smoothed out, whilst Busse [3] found more lasting and perhaps permanent differences in the size of the progeny. Pines and spruces from the far north and from the High Alps have, according to Cieslar, Schotte, Engler and others, seeds of smaller weight than those from milder situations.

[1] Sylvén, N., Studien über den Formenreichtum der Fichte. Mitteil. a. d. forstl. Versuchsanstalt Schwedens, 6. H., 1909; 11, H. 1915. (The comb-spruces surpass all other branching-forms in diameter and height. They are found especially in snowy situations.) Schröter Über die Vielgestaltigkeit der Fichte. Zurich, 1898. Heikenheimo. Über Fichtenformen und ihren forstwirtschaftlichen Wert. Meddelanden f. Forstvetenskapliga Försögsanstalt Helsinski, 1919. (Distinguishes ten cone-forms and the branching-types according to Sylvén, in Finland.)

[2] Schotte, G., Mitt. a. d. forstl. Versuchsanstalt Schwedens. H. 11, 1914, p. IX.

[3] Busse, Zeitschr. f. Forst- u. Jagdwesen, 1926, p. 72.

INDEX

A

Abnormality, 40
Absciss-layer, 4, 31, 259
Abscissed branches, 30, 31, 265
Absorbing rootlets, 273, 274, 282, 283
Absorptive power, 83, 284, 315, 321, 322, 362
Accessory shoots, 11, 23, 71, 99
Acclimatisation, 412
Acidity, degree of, 338
Acropetalous, 53
Adhesion, 317
Adventitious bud, 46, 73f.
—— root, 279
Aeration of soil, 271
—— of the tree, 155f.
Aesculin, 148
After-light, 27
After rest, 62
Age, 38
—— determination, 130, 160
—— greatest, 38
Aging of epicormic branches, 78
—— of trees, 29, 51
Agony shoots, 75
Air, access of, 317f.
Air-bubbles in vessels, 317f., 320
Air content, 314, 319
Air-dry, 192
Air-passage, 156
Anatomy of leaves, 208f.
Anemophilous plants, 382f.
Angiosperms, 373
Angle of attachment, 26
—— of divergence, 25–26, 29
—— —— of roots, 279
—— geotropic, 26
—— of inclination, 26
Animals, biting by, 147, 148–149, 155, 407
Anisophylly, 226, 249
Anisotropic, 194
Annual ring, 157f.
—— —— boundary, 178–179
—— —— breadth, 160f.
—— —— false, 99, 158
—— —— formation, causes, 178–185
Annual rings of roots, 160
—— shoot, 2–5
—— shoots, boundaries, 5
—— —— length, 13f.
Anthocyanin, 224, 240, 262
Aphotometric, 249
Apical cells, 90
—— growth, 3
Area increment, 160
Ascent, rate of, 311
Ash-analysis, 326, 330f.
Ash-content, 230, 330f.
—— —— of cambium, 184
—— —— of exudation sap, 289
Assimilation, 233f., 256f.
—— energy of, 257
Assimilation-co-efficient, 234
Assimilation-number, 239
Asymmetry of leaves, 203
Atmospheric humidity, relative, 305, 321
Autumn wood, 101, 178f.
Axillary buds, displacement, 6
—— —— formation, 53
—— shoot, 5

B

Bacteria, 233, 239, 282, 297, 343f.
Balsam, 149
Bark, 141f., 414
Bark-fissures, 153
Bark-folds, 5, 70
Bark-scorching, 25, 145
Bast, 96, 133f.
Bast-fibres, 131, 137–138
Bast-parenchyma cells, 133, 137
Beam of uniform resistance, 167f.
Beech wood, round staves, 194
Bending movements, 40f., 48
—— —— at the opening of buds, 44, 69
—— —— of roots, 279–280
—— —— of seedlings, 399
Bending, resistance to, 167f,
Bending-stimulus, 168, 176
—— —— nature of, 176
Berry cones, 372
Betulin, 142
Biogenetic law, 400
Biotypes, 405
Bisexual flowers, 377
Bleeding, 287f.
—— mechanics of, 290f.
Blue coloration of pine timber, 122
Board roots, 166, 171

Bordered pits, 119f.
Borings, 160
Branch arrangement, physiological, 36–37
—— bending, by cold, 27
—— —— by light, 40–49
—— formation, 25, 34–37, 173
—— generations, 36–37
—— litter, cutting of, 72
—— system, 28, 34–37
Branching, types of, spruce, 414
Breakage, security against, 167f.
Browning of wood, 122
Browsing by game, 34, 72, 147
Brush shoot, 17, 202, 353
Bud, 53f.
—— open, 58
Bud-arrangement, 5f., 35, 44
Bud-characters, 79
Bud-cotyledons, 59
Bud-material, 7
Bud-mutation, 46
Bud-rudiment, 59–61
Bud scales, 53, 55–59, 68
—— —— lamellae, 70
—— —— number of, 58
—— ——, scars of, 5
Bud-stem, 71, 94
Bud-trace, 5, 53
Buds, distance apart, 8–9
—— growth of, 68
—— number of, 9–10
—— protection of, 68
—— resting of, 61f., 104
—— unfolding of, 65f.
Bundle-sheath, 94
Burrs, 73
Bush forms, 408
Buttress roots, 166, 171

C

Calcium oxalate, 54, 56, 148–149, 333, 338–339
Callus, 136
—— plugs, 136
Cambiform cells, 133, 137
Cambium, 93, 94–95, 97, 102
—— growth of, 365–366
—— inter-fascicular, 93
Cambium-sap, 109
Cane sugar, 135, 238
Canker fungus, 77, 411
Capillarity, 319, 322
Carbohydrates, 65, 184, 224, 236f.
Carbonic acid, 233–234, 244f.
—— ——, sources of, 246–247
Carotin, 233
Casparian strips, 286
Caterpillars, defoliation by, 71
Cattle, 34, 72, 407
Cell, 80f.
Cell-division, 88f., 266
Cell-division hormones, 104
Cell-elongation, 20
Cell-ridges, 221–222
Cell-wall, 87–88
Cellar method, 394
Cells, absorptive power of, 210, 315f.
—— size, 90
Cellulose, 106f.
Central cylinder, 286
Centrifugal force, 39
Change of disposition, internal, 50f.
Changing trees, 2
Characteristics of timber, 131–132
Chemical conversions, 363
Chemotaxis, 232
Chemotropism, 280
Chloroplast, 231f.
Chlorophyll, 86, 220, 281f., 364
—— formation of, 220, 233, 364
Chlorophyll content, 223–224, 233, 239
Choice, power of, 284
Chorism, 265
Chromosomes, 87
Cladoptosis, 30–31, 265
Cleaning of root-system, 273
Clearings, flora of, 393
Climate, 161–164, 185, 203, 408–410
Climatic races, 16, 41–42, 67, 161–162, 261, 404f.
Clone, 403
Close stand, 76
Closing membrane of pits, 119–120
Coagulation, 1, 127, 135
Co-efficient of shading, 253
Cohesion, 313f.
Cohesion-tension, 27, 313f.
Cold, 1, 2
—— protection against, 56, 68, 146
Cold plants, 257
Collenchyma, 141
Colloids, 81, 88, 109–110, 127, 135, 178, 233, 289
Colophonium, 149
Coloration, autumn, 240, 261–262
—— by oxidation, 235
—— winter, 262
Colour change, 240
Colouring matters, 262
—— —— injection of, 310, 313
Comb type, 406
Companion cells, 137
Compensation-point, 228, 250
Complementary cells, 125
Compression, resistance to, 167f., 177, 186f.
Concentration gradient, 209–210
Conducting channels, 177, 208–209, 317, 323, 360
Conducting power, 177, 310
Cone-breeding of pine, 23
Cone forms, 413
Cone plants, 373
Cones, 7, 372–373, 386, 413
—— proliferating, 4

Coniferin, 109
Coppice forest, 73
—— shoots, 11, 21, 73f., 202
Coppicing, power of, 73–74
Cork, 141f., 155–156, 266
—— formation of, 73, 141f., 294
Cork-cambium, 141, 156, 266
Correlations, 12, 29, 36, 39, 42, 44, 75–76, 203, 272
Cotyledons, 399–401
Crop cleaning, 250
Cross fertilisation, 282f.
Cross-section of stem, form of, 165f.
—— —— roots, form of, 166, 171
Crown, centre of gravity of, 170
—— rounding off of, 18, 406
Crushing, resistance to, 177
Crystals, 141, 148–149
Cryptogamic flowers, 367, 372
Cultural experiments, 271, 297, 326
Cuticle, 91, 141, 211
Cutin, 91
Cuttings, 38, 51, 72, 401–402
Cyclophysis, 51–52
Cylindrical form of stems, 165, 168, 171
Cytoplasm, 87

D

Decomposition of litter, 165, 247
Defoliation, 71, 158, 164, 181, 352–353
—— by caterpillars, 164, 411
Degeneration, 383
Density of crop, 254–255, 274–275, 407
Denitrification, 344
Depth of soil, 271
Diameter growth, 70–71, 93, 98f., 144, 156f.
—— —— of branches, 25
—— —— of roots, 102, 293–294
Diameter-increment, 156f., 165
Diameter-variations, 103, 318
Diastase, 237
Dichogamy, 384–385
Diffusion gradient, 285, 360
Dioecism, 376f., 383
Dispersal of seeds, 389f.
Divergence, angle of, 25–26, 29
—— —— (of roots), 279
Division of labour, 80
Domatia, 207, 211
Dormant buds, 10, 46, 70f.
Dorsiventral leaves, 248
—— twigs, 6, 44, 203–204
Double ring, 158
Drip-points, 207
Driving forces of sap currents, 320f., 360f.
Drought-years, 163–164, 202
Dry peat, 199, 344
—— period, 2
Dry-trees, 2
Dry-weight, specific, 191, 192f.
Drying up, 217
Dryness, 1–2, 163, 263
Ductility, 107
Durablity of timber, 129
Dwarf shoots, 5, 10, 21f., 71–72, 159
Dye-woods, 122

E

Eagle's eyrie of silver fir, 18
Early frosts, 267, 410
—— sprouting trees, 65
—— spruces, 67, 404, 410, 411
—— wood, 99, 178f., 184
Eccentricity, 165f., 172–173
—— of roots, 171
Edaphon, 281, 345
Egg cell, 371
Elaborated sap, 109–110, 176
Elastic limit, 194
Elasticity, 41
Embryo, 389f.
Embryo-sac, 372
Empty spaces, 54, 70
Endodermis, 94, 209, 286
Endosperm, 389
Enveloping organs, 375, 376
Enzymes, 235, 239, 394
Epicormic branches, 46, 50, 70, 230
—— —— causes, 75f.
Epicormic shoots, 70–71, 78
Epidermis, 91, 97, 139f., 211
Epinasty, 172
Epiphyll, 55
Epithelial cells, 149–150
Epithem, 206
Epitrophic, 172–173
Equilibrium, condition of, 76
—— dynamic, 316
Equilibrium-position, 45
Ether-injection, 216-217
Etiolation, 240
Euphotometric, 225, 249
Evaporation, 68, 211, 215f., 241, 302f., 406
Evergreen plants, 116-117, 208, 218, 260–261, 356
Exchange relations bet. crown and roots, 272–273, 282–283
Exodermis, 286
Exposure, 256
External conditions, 39–42, 51–52, 295
—— —— for germination, 396
Exudation-pressure, 288, 312, 363
Exudation-sap, 288–289

F

False axis, 36
—— leader, 45
—— ring, 158
Fanlike arrangement, 35, 44
Fastigiate trees, 25

Fat, 154, 357f.
Fat-trees, 357–358
Ferments, 262, 266, 293
Fertilisation, 381f.
Fertility, 369
Fibre, neutral, 173–174
Fibres, course of, 39
—— torsion of, 97
Filtration-resistance, 318
Fine faggot-wood, 259
Fire protection, 146
Fissibility, 195
Flank shoots, 34–35
Flat-root, 269
Flattening (of cells), 178–179
Flight-organs, 390f.
Flora of clearings, 393
Flora, nitrophilous, 346–347
Flower buds, 23, 61
Flower-formation, 61, 368f.
—— —— on dwarf shoots, 23
Flowers, 367f.
—— male, 376f., female, 371f.
Flowering season, 381
Fluorescence of chlorophyll, 243
Fluting of stems, 159–160
Foliage, load of, 25
Forces, mechanical, 167f.
Forcing methods, 63–64
Fore-light, 27
Fore-rest, 62
Forest-fires, 146, 199
—— limit, 74
—— litter, 198–199
—— types, 347–348
Form, change of, 49–52
Formaldehyde, 238
Formative sap, 109–110, 176
Formic acid, 238
Fraxin, 148
Freezing, 264
Freezing-point, lowering of, 356
Frictional resistance, 322–323
Frost hardiness, 1, 67, 356, 410
Frost-localities, 67
Frost-ring, 146, 158
Fruit cultivation, 78
Fruit-formation, 354, 368f.
Fruit-girdle, 370
Fruit-shedding, 267
Fruit tree, 24, 272, 370
Fruits, 368f., 412
Fungal infection, 46, 78, 126, 129, 147, 155, 366, 411
Fungi, mycorrhiza, 295f., 298
—— wood-destroying, 129, 191

G

Gas bubbles, 317–318
Gas-exchange, 215f.
Gene, 382
Genotype, 40, 52, 403f.
Geotropic, angle, 26
Geotropism, 33f., 40f., 210, 408
—— negative, 44
—— of seedlings, 398f.
—— of young pine shoots, 45
Germinability, 392–394
Germination, 392f.
—— delay in, 392–393, 395
—— epigeal, 399
—— hypogeal, 398
—— conditions for, 396–397
Germination-enzymes, 394
Germination-pressure, 398
Germination-rest, 392f.
Germination-testing, 395, 397–398
Girth, greatest, 38
Glandular hairs, 150
Globose spruces, 72, 408
Globular shoot, 71
Glucosides, 148, 355
Gnat larvae, 117
Grafting, 50, 161
Gravity, 40–46, 69, 172f., 249, 279
Great period, 8, 14–15, 18–19, 234
Green-manuring, 297
Greening, 65–66, 231, 252
—— of lime wood, 122
Greying of spruce wood, 122
Growing point, 7, 53–54, 60, 88f.
—— season, length of, 162, 408–409
Growth, apical, 71
—— of buds, 68, 90
—— checking, 163
—— intercalary, 71
—— by layers, 180–181
—— in length of needles, 222
—— —— roots, 292f.
—— —— stool shoots, 75
—— in thickness of needles, 204
—— sliding, 92, 95, 98
Growth-curves, 14–15, 245, 256, 341
Growth-enzymes, 104–105, 176
Growth-factors, 244, 256, 340–341
—— —— law of operation of, 341
Growth-forms, 406–407, 414
Growth-hormones, 104, 176
Growth-stimulus, 165f., 171f.
Growth-zones, 19–20, 90
Guard cells, 213, 219–220, 237
Guttation, 206, 290, 363
Gymnosperms, 373

H

Hadrome, 96
Hail, 213
Hair-tufts, 207
Hairs, 56, 91, 211, 387
Hard bast, 133, 137–139
Hard cells, 137f., 211–212
Hard-shelled seeds, 394–395

Hardness, 175, 195f.
Harp-trees, 44
Hartig net, 296
Hausteria, 129
Healing tissue, 73, 152, 165, 365
Heart-root, 262, 278
Heartwood, 121f., 151, 154
—— coloration, 122
—— false, 126
—— formation, 121f.
—— mineral content, 334
Heartwood-substance, 125f.
Heartwood-trees, 122
Heat, 256–257, 409
—— evolution of, 235–236
—— protection against, 145–146
Heat-curves, 256–257
Heat-damage, 145
Heat-rays, 255
Heat-requirement, 65, 409
Heath soil, 271
Hedge plants, 72, 155
Height, greatest, 14, 37
Height-growth, 13f., 168
Height-increment, 15–16
Heliotropism, 47f.
Hemi-cellulose, 88, 106, 120, 355
Hereditory factors, 41, 42–43, 52, 67, 403f.
Hormones, 64, 104, 128, 176, 366
Horny knots, 30, 129
Humus, 198, 247, 344f.
Humus acid, 271
Hybrid, 385
Hydrolysis, 120
Hygrophilous, Hygrophytes, 2, 207, 302
Hygroscopicity, 194f.
Hypoderm, 141, 211
Hyponasty, 172
Hypotrophy, 172, 173

I

Ice formation, 1, 70, 266
Illumination, electrical, 60, 63, 185
Imbibition, 315, 318
Impregnation, 108, 120, 128, 188
Increment, measurement, 102, 165
Incrustation, 107–110
Inheritance, 41, 403
Inhibiting substance, 176
Inner rind, 96, 133f.
Inosite, 236
Insect-pollinated plants, 385
Integuments, 386
Intercellular spaces, 88, 149, 286
Interior light of tree, 251
Internal temperature of trees, 144–145
Internodes, 5f., 8–9, 114
Interruptions of the increment, 163–164
Iron pan, 271
Isolation (of trees), 75–77, 145, 164
Isotonic, 84

J

Jamin chains, 320
Juvenile form, 47, 50–51, 78, 229–230
—— leaves, 78, 229–230

K

Knot-holes, 30
Knots, 30, 129

L

Lammas shoot, 10f., 99
—— —— concealed, 11
Large shrub, 28
Late frost, 66f., 70, 72, 146
Late-sprouters, 65
Late-spruces, 67, 404, 411
Late-wood, 100, 178f.
Later forms, 230
Lateral bud, 3
—— roots, arrangement, 279
Latex, 56, 148
Law of minimum, 340–341
—— of operation of growth-factors, 341
—— of optimum, 244
Layers, 74, 270
Leader, false, 45
—— growth of, 41
Leading shoot, direction of, 43–44
—— —— replacement of, 4
—— —— sprouting of, 66, 72
Leaf, emptying of, 264
—— size of, 200f., 225
Leaf-arrangement, 5f., 46, 247
—— —— of seedlings, 6–8
Leaf-base, 55, 57
Leaf-blade, 55, 57–58, 206–207
—— —— unfolding, 69
Leaf-cushion, 223
Leaf-dimorphism and age, 50–51
—— —— of epicormic branches, 77
—— —— of lammas shoots, 12
—— —— of seedlings, 399f.
Leaf-fall, 262
Leaf-form, 200f., 412
Leaf-litter, 198–199
Leaf-margin, 205
Leaf-mass, 200–201, 302
Leaf-parenchyma, 220f.
Leaf-primordium, 7, 53f
Leaf-red, 240
Leaf-scar, 5
Leaf-stalk, 55, 57, 205
Leaf-surface, total, 200
Leaf-teeth, 55, 206
Leaf-veins, 208–210
Leafing, 65f.

Leaves, 198f.
—— number of, 201
—— quantity, 199
Leguminosae, root-nodules, 297, 343
Lenticels, 155–156
Leptome, 96
Leucoplasts, 86, 135
Leverage of the wind, 77
Libriform fibres, 137, 295
Life, duration of, 38
—— —— (of leaves), 260f.
Light, bendings due to, 40, 41, 47–48, 212, 247
—— disposition for, 47–48
—— effect on position of branches, 27–28, 406
—— fixed position as regards, 251
—— increased assess of, 76–77, 164
—— measurement, 250f.
—— passage of, through leaves, 242–243, 252
—— strength of, 36, 239–240, 250f.
—— utilisation of, 17, 243, 250f.
—— in woods, 250f.
Light-beeches, 66
Light-demand, 17, 242, 252, 396, 397
Light-demanding trees, 14, 17, 254
Light-increment, 75, 164
Light-leaves, 77, 202, 224f., 252
Light-sense-organs, 212
Light-stimulus, 40–41, 47f., 69, 218, 247f., 396, 397 (germination)
Light-supply, specific, 253
Lighting, 36, 204, 231
Lightning, 146
Lignification, 106f.
Lignin, 106–109
Lime-content, 264, 326–328, 337–338, 341
Lime-manuring, 341
Limiting layer, 107
—— value, osmotic, 322
Lipoids, 82–83
Litter, harvesting of, 265
Local races, 18, 41–43, 371, 403f.
Locality, 16, 38, 41–42, 161, 191, 247f., 301f., 347, 405f.
Lombardy poplar, 378–379
Long shoot, 10, 21f.
Loss of weight on sprouting of buds, 353
Luminous bacteria, 242
Luxury consumption, 285, 304, 326
Lying-over of seed, 394

M

Maceration, 107
Main axis, 28, 32, 45–46
—— root, 44–47, 272
Malformations, 272
Manuring, 337, 339, 345
—— with carbonic acid, 245
—— excessive, 337
Maple secretion, 148
Mast years, 31, 61, 164, 355, 369f.
Mature form, 47, 49–51
Mechanics of bleeding, 290f.
Medullary rays, 110f., 113–116, 365
—— —— of rind, 139
Medullary sheath, 93
Membrane, resinogenous, 150
Membrane-mucilage, 212
Membrane-thickening, 118, 120
Meristem, 55
Metatracheal parenchyma, 114
Micropyle, 372
Middle-lamella, 88, 106, 266
Middle-rest, 62
Mineral-content of exudation sap, 288–289
—— —— of leaves, 263–265, 330f.
Mineral substances, 325f.
Minimum, law of, 340–341
Modification, 40, 403f.
—— scope of, 43
Modifying power of, 42
Monoecism, 367f. 384
Mountain pine, 33, 41, 270
Movement, nastic, 69
Mucilage cells, 148, 212
Mutation, 405
Mycorrhiza, 295f., 338, 345

N

Native strains, 405
Natural selection, 67, 404
Nature, laws of, 40
Narrow rings, 129
Narrow-wood, 185
Nastic movements, 69
Needle-sheath, 22
Needle-shedding disease, 265, 353, 411
Needle-structure, 2
Needles, dimorphism, 50
—— fall of, 267
Neiloid, 171
Nitrate plants, 346–347
Nitrification, 165, 343–346
Nitrogen, sources of, 343–344
Nitrogen-absorption, 299, 342f.
Nitrogen-content, 237, 263–264, 299, 331, 342–343
Nitrophilous soil-flora, 346–347
Nodes, 8
Nodule-bacteria, 297–298, 343
Normal curves of bud-opening, 66
Normal form, 40, 403
Nourishment, withdrawal of, 76
Nucleolus, 87
Nucleus, 87
Nutrient solution, 183, 329
Nutrients, absorption of, 281f., 327f.
—— mineral, 325f.
—— shortage of, 337
Nutrition of roots, 270

O

Occlusion-tissue, 73, 152, 165, 365
Oil, 148
—— of turpentine, 149, 153–154
Ombrophilous, ombrophobous, 213, 239
Optimum curves, 244, 256
Origin, plate of, 409–410
Orthotropism, 44
Osmosis, 82–85, 134, 291, 315
Ovary, 372–373
Overhead light, 251
Overheating, 145
Ovule, 371f.
Ovule-tip, liquid at, 386
Ovuliferous scale, 372
Oxalate nest, 53–54
Oxidation, 233f., 263
—— of heartwood, 127
Oxygen-supply to roots, 271

P

Palisade parenchyma, 220f.
Panphotometric, 249
Paraboloid, cubical, 170f.
Parasites, 300
Paratracheal parenchyma, 114
Parenchyma, 90, 110f.
—— metatracheal, 114
—— paratracheal, 114
Parenchymatous sheath, 209, 221
Peat soil, 271
Pectin, 88, 107
Peeling, damage by, 147
Pendant branches, 25, 28, 43, 50, 159
Periderm, 141
Pericycle, 94
Period, great, 8, 14–15, 19, 234
Periodicity, 12, 62, 65, 292
Periphysis, 51
Permeability of the plasma, 64, 82–84, 177, 284, 351
—— of lenticels, 156
—— of stomata, 216–217
Phanerogamous flower, 367
Phelloderm, 141
Phellogen, 141
Phenology, 65–66
Phenotype, 40, 52
Phloem, 96
Phosphoric-acid-content, 264, 338
Photometry, 36, 248f.
Phototaxis, 232
Phototrophy, 48
Phyllotaxy, 5f.
—— of seedlings, 5–8
Physiological exchanges in buds, 54
—— —— in the cambium, 184
Physiological exchanges in seed, 395
Pigments, 233
Pine-blister disease, 411
Pine-cones, 413
Pine needle-shedding disease, 265, 353, 411
Pines, races of, 41–42, 171, 405–406
Pinnate leaf, 210
Pioneer roots, 273–274
Pit, 119f., 311, 323
Pith, 53–54, 71, 96, 129–130
Pith-connections, 93
Pith-dome, 53
Pith-flecks, 117
Pith-hollow, 54, 70
Place of origin of seeds, 408–410
Plagiotropic, 44
Plane of branching, 35–36
Plant breeding, 403f.
Plants, size of, 414
Plasma-membrane, 82, 85
Plasma-streaming, 86
Plasma-utricle, 134
Plasmodesms, 85, 319
Plasmolysis, 84, 321
Plasticity of wood, 194
Plastids, 86
Plate-pines, 414
Plate-roots, 271
Poisoning, 234, 245
Poisonous substances, 148, 336, 339
Polarity, 38–39, 75
Pollarding, 74
Pollen grain, 382
—— tube, 387f.
Pollination, 381f.
Pot experiments, 326
Preserving of seeds, 392–393
Pressure, measurement of, 180–181, 290
—— osmotic, 153, 219, 315, 362
Pressure-filtration, 136, 362
Pressure-wood, 174–175, 197
Preventitious buds, 71, 75
Prickles, 24
Primary leaves, 400–401
—— needles, 72, 400–401
—— wood, 92, 106
Primeval-forest, 199, 346
Procambium, 92
Probability curves, 9
Production of material, annual, 258–260, 304, 331
Profile position of chloroplasts, 231–232
—— —— of leaves, 248
Proleptic shoots, 12, 99
Properties, internal, 39, 51–52
—— technical, 186f.
Prosenchyma, 90
Protection against animals, 24, 56–57, 147, 148, 155, 212, 333
Protective heartwood, 126
—— sheath, 286
Protein, 135, 237–238 (in the leaf)
Protophloem elements, 92, 96–97
Protoplasm, 80
Protoplasmic threads, 80

Protoxylem elements, 92
Pulsation theory, 291
Pure culture, 298
Pure lines, 403

Q

Quality-coefficient, 187
Quality of timber, 186f.

R

Race-formation, 403f.
Radicle, 43, 398
Radiometer, 255
Rainfall, amount of, 27, 303
Rank-beeches, 33, 406–407
Rank-forms, 33, 406–407
Raphides, 56
Rapidity of descending sap-stream, 359
—— water streaming, 311, 322
Raw-fibre, 238
Raw-humus, 199, 299, 345f.
Raw-resin, 149
Raw-sap, 361f.
Reaction-norm, 39
Reaction-velocity, 65
Red coloration, 263
Red-leaved trees, 224, 240
Red-wood, 174f., 197
Regeneration shoot, 21, 78
Regular branches, 75
Release, 49
Reproduction, vegetative, 74, 403
Reserve material containers, 350f.
—— materials, 16, 68, 332, 350f.
Resin, 149f.
Resin-blisters, 152
Resin-cracks, 152
Resin-ducts, 149f.
—— —— of needles, 223
—— —— pathological, 152
Resin-galls, 150
Resin-groove, 154
Resin-tapping, 153–155
Respiration, 64, 211f., 233f.
Respiration-ferments, 262
—— of seeds, 395
Respiratory-cavity, 215
Resting-condition, 1–2, 53, 61f., 95–96, 104, 392f.
Resting-period, 10–12, 61f., 86, 102–103, 355
—— —— of tropical trees, 64–65
Retinospora of the *Arbor vitae*, 401
Retromigration of mineral substances, 264, 329–332
Rhizogenous layer, 293
Rind, 96, 133f., 414
—— green, 139–141
—— mineral content, 333–335
Rind-parenchyma, 133, 137
Rind-pressure, 180–181
Rind-substances, 147–149
Rind-tannin, 147–148
Ring-bark, 143
Ring-breadth, 159, 161f., 191
Ring-formation, half-year's, 13
Ringed spurs, 5
Ringing, 39, 76, 105, 165, 178, 310, 351, 360, 366
Ripe-wood, 122f.
—— —— trees, 122
Root, anatomy, 94, 269f., 293f.
—— annual rings, 160
Root-buds, dormant, 72
Root-cap, 282, 293
Root-coalescence, 39, 365
Root-col'ar, 74
Root-cortex, primary, 285
Root-crippling, 272
Root-excretions, 282, 293, 299
Root-hairs, 281–282, 283–284
Root-knot, 270
Root-nodules, 297, 343
—— —— of leguminosae, 297, 343
Root plate, 271, 277
Root-pressure, 290, 315
Root-spread, extent of, 274f.
Root-suckers, 21, 50, 73–74, 78
Root-swelling, 168, 171
Root-system, 269f.
—— —— form, 269f.
—— —— functions, 281f.
Root-tip, 281f.
Root-wounding, 77
Roots, lateral, 46, 73, 271
Rosette shoots, 72

S

Salicin, 148, 355
Salt hunger, 340
Sap, ascent of (theories) 312f.
—— circulation of, 285, 359f.
—— outflow, 134
Sap-streaming, 86, 134, 136–137, 210, 290–291, 359f.
—— —— peripheral, 365
Sap, transmission of, 136–137, 209–210
Sapwood, 122f., 319
—— mineral content, 334
—— width of, 123–124
—— trees, 122
Saturation deficit, 315
Scale-bark, 143
Scale-pine, 414
Scales, 372
—— arrangement of, 7
Scimitar growth, 46
Scar-formation, 266
Sclerenchyma, 133, 137–138
Sclerophelloid, 156
Secondary bud, 33, 72
Secretion-pressure, 149

Seed, 368, 372, 389–390
—— colour of, 396, 13
—— dispersal of, 389f.
—— fall of, 392
—— ripening of, 392
Seed-scale, 372
Seed-year, 31, 61, 355, 370
Seedlings, 6–8, 398f.
—— of cupressineae, 51
—— geotropism of, 43
—— heliotropism, 47
Selenium cell, 255
Self-cleaning, 30, 250
Self-fertilisation, 383–385
Self-pruning, 29–30, 250
Semipermeability, 82–83
Sense-organs, 212–213
Sensitiveness to stimuli, 39–40, 44f., 49, 66
Separation-layer, 4, 30, 265–266
Sex, determination of, 379
Sex-distribution, 376f.
Shade-bearing species, 14, 17, 254
Shade-beeches, 66, 202
Shade-buds, 66, 231
Shade-leaves, 200–201, 224f., 252, 331
Shade-tolerance, 254
Shading, coefficient of, 253
Sheet-bark, 143
Shoot-apex, 53
Shoot-arrangement, physiological, 36
Shoot-elongation, 18f.
Shoot-growth, 3–4, 8, 12, 20, 23
Shoot-production, power of, 18
Shoot-tip, loss of, 3–4
Shoots, arrangement of, 34–37
—— proleptic, 12, 99
Short roots, 273
Shrinkage, 194, 319
Shrub, 28, 32f.
Sieve-plates, 85, 133
Sieve-tube sap, 135–136, 176, 361
Sieve-tubes, 133f., 176, 360f.
Silica, 340.
Silver fir aphis, 46, 72.
Sloping position, 48, 169, 173
Snake trees, 10, 158
Snow, pressure of, 25, 42, 46, 405–406
Soaking of seeds, 394–395
Soft bast, 133f.
Soil, condition of, 270
Soil-flora, 347
Soil-flora, nitrophilous, 346-347
Soil-innoculation, 297
Soil-nutrients, 325f.
Soil-races, 404, 411
Soil-respiration, 246–247, 271
Soil-water, 281
Solar energy, 241, 316
Sowing by birds, 391
Specific gravity, 126–127, 192f.
Spectro-photometer, 255
Spectrum, 242-243
Spheroblast, 71
Spiral arrangement, 6–8, 250
—— structure, 112
—— tracheae, 118
Spongy cork, 143–144
—— parenchyma, 220
Spores, 367
Spreading, power of, 30
Spring, date of, 65
Spring, early, 65
Spring-frosts, 66, 67, 70, 72, 146
Spring-shoots, 72
Spring-wood, 178, 184
Sprouting of buds, 63f., 231, 352–353
Sprouting of buds and age, 67
—— of the spruce, 51
Stag-headedness, 76–77
Stamens, 379–380
Starch, 236f.
—— consumption of, 68, 353–354
—— conversion, 2, 20, 54, 62, 219, 237, 263, 356–357
Starch-leaves, 236, 238
Starch-sheath, 209
Starch-trees, 357–358
Statoliths, 210
Static laws, 77
Stem-forms, 41, 165f., 405f.
Stereome, 96
Stimulability, 49
—— of root-tips, 279–280
Stimulating substances, 64, 104–105, 175
Stimulus-action, 43f., 49, 69–77, 166, 168–169, 176–177, 265, 270, 292
Stipules, 55, 57, 68
Stomata, 56, 213, 227
Stomatal slits, width of, 213, 217–218
Stone-bark, 144
Stone-beech, 143
Stone cells, 137–138
Stool-shoots, 11, 21, 73f, 202
Storage organs, 116, 292, 295, 350
Strasburger cells, 137
Stratified crowns, 37
Street trees, 24
Strength, 107, 186f.
Strengthening, mechanical, 167f., 294
Suberin, 91
Substances, incrusting, 108–109
—— transformation of, 20, 54, 350f., 362
—— translocation of, 350f.
Substitute fibres, 114
—— leader, 44, 72
—— shoot, 3, 4, 44, 70, 77, 352–353
Sub-variety, 40, 224, 240, 401
Sugar-content of exudation sap, 288–289
—— of sieve-tube sap, 135
Sugar-formation, 236
—— through frost, 1, 64, 356–357
—— through shaking, 176
—— during shoot growth, 20
Sugar-leaf, 236
Summer drought, 2, 17, 41, 60–61, 162–163, 346, 370

Summer-felling, 191
Summer-warmth, 409
Sun-buds, 230
Sun-leaves, 224f., 252, 331
Süntel beech, 33
Supplementary buds, 9, 74
Surface-arrangement, 232, 248
Surface-development, 225
Swelling, energy of, 84
—— power of, 106
Symbiosis, 299–300
Symplast, 80, 291
Sympodium, 36

T

Tangential strain, 180–181
Tannin, 137, 147
Tannin content, 125, 147–148, 262
Taproot, : 69, 276
Tapering of stems, 165, 168, 170
Taxin, 149
Temperature of interior of tree, 145–146, 198, 357
Tensile strain, 315f., 362
Tension, resistance to, 194
Tension-wood, 295
Terminal bud, 3, 10
Terminal-parenchyma, 115
Thermotaxis, 232
Thickening of roots, 171
Thickening ridges of vessels, 92, 118–119, 157, 179–180
Thorns, 4, 24
Threshold plasmolysis, 322
Timber-quality, 186f.
Timber-value, 70
Timbers, characters of, 131–132
Top-drying, 76–77
Topophysis, 51
Torsion of fibres, 97
Torus, 119
Tracheæ, 117f.
Tracheids, 112, 117f., 179, 187–188
Transfusion tissue, 221
Transpiration, 215f., 226, 303f., 315
Transpiration and ash-content, 306–307
Transpiration-safeguards, 211, 217, 226
Transverse tracheids, 112
Tree, 28f., 34
Tree-architecture, 2
Tree-bush, 28
Tree-colouring process, 313
Tree-construction, artificial, 34
Tree-crown, shape, 17, 32, 37, 272, 405f.
Tree-form, 2f., 38f., 42, 50f.
Tree-height, 13f., 37
—— and depth of root, 275
Tree-limit, 162
Trembling leaves, 205
Tropical trees, 1–2, 12, 64, 145, 159, 203, 207
Tropophilous, tropophyte, 2, 302
Truffle culture, 295
Tubular bundle, 93
Turgor, 90, 210–211
Turgor-pressure, 20, 84, 136, 176
Twigs, fall of, 31
—— casting of, 30–31
Tyloses, 125, 127–128, 151, 265

V

Vacuoles, 82
Vanillin, 109
Variation, extent of, 412
Variegation, 219, 220
Variety, 403
Vascular bundle, 92f.
Vegetative cone, 7, 54f., 60, 88f.
Vegetation, water of, 364
Venation of leaves, 208–209
Vernation, 54–55
Vessels, 117f.
—— length of, 121
—— number of, 188–190
Viscosity of plasma, 81
Volume-weight, 184, 192f.

W

Wall-pressure, 83, 315
Wall-thickening, 118–119, 157, 179
Warm-plants, 257
Washing-out of soil, 344
Water, loss of, 1, 215
Water-conduction, 177, 208–209, 309f., 314
Water-consumption, 301f.
Water-content, 187, 193, 307f., 361
Water-current in the tree, 309f., 359f.
Water-economy, 1, 274, 301f.
Water-excretion, 363–364
Water-shedding from tree crowns, 26, 207–208
Water-shoot, 50, 71f., 78
Water-storers, 212, 311
Water-streaming, theories, 312
Water-supply, 77, 182–183, 270–271
Water-threads, 314
Wax covering, 211–212, 214, 226
Weeping trees, 32–33, 39, 43
White-wood, 175
Whorls of branches in conifers, 10
Wide-wood, 185
Wilting, 217, 260, 306
—— rate of, 306
Wind, action of, 17, 34, 77, 98 (torsion of fibres), 165, 167f., 406–407
—— direction, 169
—— leverage, 77
—— shelter from, 247
Wind-pollinated plants, 382f.
Wind-pressure, 77, 167–168
Wind-protection of stomata, 215–216

Winter-coloration, 410
Winter-colour of evergreens, 262
Winter-condition, 1–2, 62, 356
Winter-felling, 191
Winter-form, 53
Winter-frost, 63, 410
Winter-hardiness, 1–2
Winter-rest, 63, 234
—— —— involuntary, 63
Witch's Brooms, 46
Wood, analyses of, 335–336
—— specific gravity of, 126–127, 192–193
—— structure of, 174, 186–191
Wood-ash, 336
Wood-elements, functions of, 120
—— —— proportional sizes, 120–121
Wood-fibres, 112, 117f.
Wood-impregnation, 128, 188
Wood-parenchyma, 114f.
Wood-rings, 157f.
Wood-rot, 129, 155
Wood-water, 316f., 364
Wound-cork, 104
Wound-heartwood, 126
Wound-hormones, 64, 128
Wound-stimulus, 104, 292
Wound-structures, 73, 126, 152
Wound-tissue, 73, 266

X

Xanthophyll, 233
Xerophilous, xerophyte, 2, 182, 208, 301
Xylan, 109
Xylem, 96
Xylem-bands, 287

Y

Yellowing of leaves, 263f., 329
Youth, growth in, 14

Z

Zygote, 382

LIST OF AUTHORS CITED

A

Aaltonen, V. T., 271, 276
Aberson, 281
Acqua, 87
Adler, 120–121
Ahrends, 237
Ahrns, 237
Albert, 59
Albrecht, 212
v. Alten, 125, 273, 294
Andersson, G., 162
André, H., 184
Antevs, 103, 157, 357
Arends, J., 220
Areschoug, 21, 228
Arnoldi, 55
Arrhenius, Sv., 246
Askenasy, 61, 68–69, 243, 313, 318
Aso, 336
Atkins, 62, 351, 356.
Austerweil, 155.

B

Baba, 340
Baccarini, 325
Bachmann, 309, 314, 315
Baertel, 110, 127
v. Baeyer, 238
Bailey, 108, 115, 119, 149
Baker, 312
Ball, 172, 175
Bancroft, 329
Bansi, 410
Baranetzki, 45, 174
de Bary, 117, 121, 139, 144, 158–159, 180, 214
Bauer, E., 236, 240, 327, 332, 342, 353
Baule, B., 341
Baumann, 282
Baumert, P., 98, 206
Baur, E., 40, 379, 382, 404, 405, 414
Bauschinger, 107, 186, 194
Becquerel, 257, 393, 395
Beissner, 401
Benecke, 344
Bennecke, 85, 216
Benson, 388
Berger, 228
Bernard, 221
Bernardini e Corso, 336
Bernbeck, O., 17, 271, 305
Berthold, 4, 5, 11, 20, 23, 39–40, 53, 60, 64, 69, 90–91, 198, 357, 401
Bertog, H., 116, 123, 187, 259
Beyerinck, L., 104, 401–402
Biedermann, 233
Bier, 393, 395
Bierberg, 86
Billing, 388
Birch-Hirschfeld, 310, 360, 366
Blanck, 282
Blum, 20, 84, 90, 219, 321–323, 362
Bode, H., 313, 318, 320
Boden, 407
Boehm, 312
Böhm, J., 145, 198, 312, 317
Böning, K., 175
Bokorny, 339
Bonnier, Gaston, 185, 282
Bordage, 268
Bordner, 172
Borggreve, 74
Bornebusch, 347
Bornemann, F., 244
Bos, 63
Bose, 291, 312
Boshart, 206
Boudier, 216
Bougault, 216
Boysen Jensen, 17, 253
Braun, Alex., 97–98
Braun, 108
Braunscheidt, 54
Breitenlohner, 145, 198
Brenner, 208
Brieger, 128
Briggs, 260, 304
Brown, 102, 241, 259, 260
Bücher, 172
Bühler, 199, 254, 371
Büsgen, 9, 18, 32, 45, 53, 61, 155, 159, 196, 198, 200, 214, 220, 273, 277, 294, 309, 338, 374, 381, 385, 387, 388, 390, 396, 397, 407, 412
Burck, 206, 383
Burgeff, 295
Burger, H., 11, 16, 20, 66, 199, 201, 303
Burgerstein, 63, 112, 114, 301, 337, 397
von Burkom, 19
Burns, 305
Burtt, 10, 26, 36
Busse, 54, 60, 387, 396, 414

C

Cajander, 347, 403
Caldwell, 260
Carter, 221
Caspari, 27
Caspary, 286
Cavers, 88
Celakovsky, 223
Chamberlain, 288, 387
Chauveaud, 221, 294, 401
Cholodny, 281
Chouchak, 282
Christison, D., 164, 182
Church, 7
Cieslar, 17, 46, 66, 108, 155, 173, 174, 252–253, 394, 404, 406–409, 412, 414.
Clark, 288
Clausen, P., 267, 340
Clemens, 393
Colville, F. V., 356
Conwentz, 32
Copeland, 204, 316, 318
Correns, 379
Coster, Ch., 123, 127, 358
Cotta, H., 166, 361
Councler, 335
Coville, T., 64
Cranner, Hansteen, 88, 282, 285, 336–337, 339
Cuboni, 240
Curtius, 238
Czapek, 82, 83, 87, 88, 91, 107, 120, 121, 142, 209, 232, 235, 240, 241, 263, 359

D

Danckelmann, 65, 74, 162, 391
Daniel, 159
Darwin, 7, 34, 280, 378, 382, 383, 385, 391
Dassonville, 183
Daube, 334
Deinega, 55
Delbrouck, 25
Deleano, 235, 329
Dengler, 216, 217, 395
v. Derschau, 88
Devaux, 144
Dieterich, 411
Dietrich, 226
Dingler, 90, 260, 267
Dixon, H., 62, 115, 291, 309, 313, 314, 317, 351, 356, 359, 360, 366
Döbner, 12, 260
Döll, 57
Dostal, 5
Douliot, 90, 293
Dufour, 214, 227

E

Eames, 92, 114
Ebermayer, F., 109, 198, 199, 246, 258, 259, 306, 309, 327, 336, 342–343
Ehrenberg, 149, 338, 345
Ehrlich, 107
Eichhorn, 116, 188, 190
Eisenmenger, 396
Elfving, 312
Eneroth, O., 409
Engler, 389
Engler, Arnold, 17, 35, 40, 48, 63, 66, 68, 174, 229, 230, 261, 262, 273, 292, 405–411, 414
Ernest, 281
Escombe, 241
Espe, 214
Esser, 113
Essner, 115
Estabrook, 218
Ewart, A. J., 86, 175, 311, 323
Exner, 186, 192, 193

F

Faack, 336
Faber, 37, 108
Fabricius, 186, 198, 358, 403, 405
Fahrenholtz, 230
Falck, R., 299
Falkenstein, Vogel v., 345
Fallada, 340
Fehér, 267
Feist, 57
Ferguson, 387
Feucht, 143, 347
Figdor, 204, 206, 288
Findeis, 394
Fischbach, C., 405
Fischer, 147
Fischer, A., 62–63, 134, 350, 357, 358, 364
Fischer, H., 245, 370
Fitting, 83, 265
Flammarion, 185
Flander, 343
Flaskämper, 294
Flury, 13, 168
Focke, 391
Fouard, 338
Fraine, 401
Franck, A., 150
Frank, 295–297, 343
Franzen, 238
Fricke, 254
Friedrich, J., 89, 103, 165, 181, 318, 319, 396
Fritzsche, 124
Fruwirth, 382, 405
Fuchs, 265, 267
Fünfstück, 61
Fujii, 386
Fujioka, Mitsunaga, 128
Furlani, 260

G

Gabnay, 176
Gärtner, 411

Ganong, 27
Gardiner, 80
Garthe, 277
Gassner, 396, 397, 398
Gast, 238
Gaunersdorfer, 126
Gayer, 186, 198, 254
Geisenheyner, 379
Geleznoff, 309
Geleznow, 27
Gerber, 143
Gerloff, 80
Gerneck, 337
Gerresheim, 210
Gerry, 114, 125, 128
Giesenhagen, 89
Giltay, 259
Glatfelder, 209, 225
Glatzel, 69
Godlewski, 312
Goebel, 5, 6, 44, 53, 55, 59, 206, 382
Gohren, 259
Goldschmidt, 379
Gossner, 332
Gradmann, 215, 305
Grafe, 109
Graser, 274, 278
Graves, 250
Greisenegger, 340
Griffon, 224, 252
Grisch, 394
Groom, P., 114, 182, 200, 311, 318
Grosglick, 230
Gross, 409
Grüss, 67, 70, 109, 110
Gulbe, 103
Gully, 282
Gurnik, 123
Guttenberg, 170

H

Haack, 396–398
Haak, 393
Habenicht, 205, 208
Haberlandt, G., 64, 96, 104–105, 107, 120, 128, 129, 144, 149, 178, 182, 210, 211, 213, 223, 239, 280, 355, 366
Haböck, 213, 239
Häcker, 379
Hagen, 219
Ham, S. P., 28
Hamm, J., 71, 73–74
Hampl, 378–379
Hannig, 150
Hansen, 312
Hansteen-Cranner, 88, 282, 285, 336, 337, 339
Harder, R., 51, 228, 244, 250, 257
Harsch, 124
Harter, 263
Hartig, R., 29, 77, 97–98, 99–100, 101, 105, 115–116, 123, 126, 145, 146, 158, 164, 169, 171–173, 174, 177, 179, 182, 187, 188f, 192, 194, 198, 259, 307–308, 312, 314, 319, 323, 334, 335, 354, 361, 366, 411
Hartig, Th., 61, 71, 74, 93, 99, 102, 109, 190, 269–270, 289, 322, 351, 357, 361
Hartmann, H., 46, 347
Hauch, 30, 407
Hausrath, 342
Havelik, K., 126
Hayoz, 321
Heck, 104, 185
Heikertinger, 147, 148, 339
Heikinheimo, 414
Heilbronn, A., 81
Heinsius, 262
Helbig, 340, 345
Heller, 149
Hellriegel, 304
Helms, 340
Hempel, 30, 367, 388
Henry, A., 57, 163, 344
Henze, A., 192
d'Herelle, 298
Hergt, 202
Hering, 39, 43
Herrmann, A., 23, 125
Herrmann, E., 411
Hertel, 205
Hesse, 284
Hesselman, H., 16, 162, 163, 165, 199, 227 228, 275, 345–346, 349, 386, 407
Heyer, 204
Hibbard, 295
Hill, A., 220, 401
Hiltner, 297, 343, 395
Himmelbauer, 386
Hinze, 69
Höber, R., 83
Höfler, K., 84
Höhlke, 149
v. Höhnel, 30, 144, 200, 201, 303, 304, 318
Van t'Hoff, 235, 257
Hoffmann, 260
Hofmann, E., 78
Hofmeister, 172
Hohenadl, W., 177
Holle, H., 313, 317, 318, 322
Hollendonner, 187
Honda, Seiroku, 168, 336, 340
Hooke, Robert, 80
Hoppe, 27, 335
Hornberger, 344
Hotter, 297, 343
Hryniewiecki, 280
Huber, B., 217, 305, 316, 318, 323
Hunger, 293

I

Ihne, 65
Iljin, 218, 219, 220, 237

Iterson, Van, 7
Iwanoff, L., 219, 306
Iwanowska, 338
Iwanowski, 243

J

Jaccard, 33, 100, 111–112, 116, 163, 172, 174, 175, 177, 178, 295, 323
Jamin, 320
Janka, 186, 195-197
Janse, J. M., 39, 291, 312, 323
Jencic, 255
Jensen, P. B., 228
Jönsson, 240, 390
Johannsen, W., 40, 62, 379
Joly, 313, 317
Jonescu, 357
Jost, L., 19, 37, 71, 76, 85, 95, 99, 113, 114, 158, 159, 177, 220, 257, 280, 315, 340
Juel, 382
Jungner, 205

K

Kakehi, 340
Kamerling, 107, 267, 301
Kannegiesser, 37
Karsten, 89, 90, 389
Karzel, 38, 173
Kastens, 105, 360, 366
Keissler, 376
Kerner, 73, 385
Kienitz, M., 42, 117, 123, 155, 404, 405, 409, 410, 412
Kienitz-Gerloff, 80, 85, 219
Kihlmann, 34
Kinzel, 395, 396, 397
Kirchhoff, 237
Kirchner, 23, 37, 214, 225, 273, 385
Kirschew, N., 220
Kjellmann, F. R., 6
Klebahn, 156, 411
v. Klebelsberg, 374, 389
Klebs, 11, 12, 38, 60, 62, 63, 64, 76, 104, 184, 229, 267, 370, 399
Klein, G., 128, 238
Klein, L., 72
Kleinstück, 109
Klinken, 95
v. Klitzing, 407
Kniep, 45, 178, 243, 267, 268
Knuchel, 201, 252, 255
Knudson, 95, 102
Kny, L., 6, 90, 112, 115, 140, 158, 180, 249
Koch, A., 297, 344
Kochs, 395
Köhne, 212, 214
Kölbl, 248
König, 403
Körnicke, 118
Koernicke, M., 119
Kohl, 183, 219
Kokkonen, 271
Kolkwitz, 243, 261, 395
Koning, 262
Kooper, 237, 263
Korstian, C., 322, 356
Kosaroff, 308
Kostytschew, 92, 94
Krabbe, 180–181
Kräss, 127
Kraetzel, 390
Krantz, H., 344
Kraus, G., 136, 161, 176, 177, 333, 339
Krauss, G., 223, 278, 327, 333
Kretzschmar, 86
Kreussler, 218, 241, 252
Kroemer, 286
Krüger, 96
Kruticky, 209
Kübler, 327–328
Kügler, 141
Kühn, 62, 63, 158
Kümmler, A., 219
Künkele, 130
Küster, 39, 60, 61, 165, 178, 220
Küstner, 178
Kuhla, 80
Kuntze, G., 282
Kunze, M., 170
Kupka, 156
Kurdiani, 413
Kylie, 238

L

Lämmermayr, 174
Lagerberg, 347
Laitakari, E., 16
Lakari, 369
Lakon, G., 117, 220, 266, 267, 394
Lamarlière, Génau de, 228
Lang, G., 98, 186
Lange, 117
Langer, 271
Larkum, 54, 60
Leclerc du Sablon, 353, 355, 365
Lee, 266
Lehmann, 396
Leick, 145, 357
Leiningen, Graf zu, 229, 331, 348–349
Leisering, 7
Lemoigne, 337
Lenz, 289
Leon, 171
Lepeschkin, 82, 83
Lewin, 149
Lewitzky, G., 88
Lidforss, B., 356–357, 388
v. Liebig, 257
Liese, 71, 275, 287, 293, 294, 295

Lindner, 318
Lindroth, 126
Linnaeus, 367
Linsbauer, K., 89, 217, 218
Liske, 67
Livingston, 218, 305
Löffler, 405
Lönroth, 347
Loew, 23, 214, 225, 273, 336, 339, 340, 385
Löwi, 219
Lohse, 128
Lohwag, 381
Lorenz, 195
Lorge, 143
Losch, 294
Lothelier, 183
Lubbock, J., 392
Lubimenko, 239–241
Lundergardh, H., 38, 45, 80, 244, 245, 246, 247, 250, 257
Lundström, 207
Lutz, 181, 182, 184, 353
Lyon, 288

M

Maass, A., 170, 408
MacDougal, 104, 318
Märker, 124
Mäule, 108, 165
Magnus, Werner, 12, 266, 397
Malmström, 386
Mamelli, 337
Mangin, 235, 296
Maquenne, 395
Marilaun, Kerner v., 203, 208, 214, 379
Markfeldt, O., 94
Marshall, 115, 291
Mason-Jones, 175
Massopüst, 130
Matthäi, 256
Matthes, 271
Maximow, 1, 235
May, 260
Mayer, A. G., 243, 340
Mayr, H., 116, 149, 151, 152, 194, 254, 411
Mazé, 282, 337
Meillère, 236
Meinecke, 247
Meissner, 204, 222, 288
Melin, E., 298–300, 343, 345
Mer, E., 100–103, 173, 174, 263, 356
v. Merklin, 144
Merwin, 288, 290
Metz, 356
Metzger, C., 77, 166–168, 277
Mevius, 338
Meyer, A., 80, 286, 359
Meyer, F. J., 92, 94, 117, 130
Middendorf, 162
Minder, 243
Mitscherlisch, E. A., 16, 341
Miyake, 387
Miyoshi, 288
Möller, A., 16, 60, 337, 345
Mogk, 29, 66
Mohl, 80, 160
v. Mohl, 100, 103, 266
Molisch, 1, 51, 63, 78, 125, 216, 236, 237, 243, 265, 266, 267, 288, 292, 310, 311, 334, 370
Montemartini, 228
Monteverde, 241
Montfort, 302
Morgentaler, 412
Mottier, 87
Müller, Arno, 236
Müller, C., 95, 389
Müller, G., 398
Müller, N. J. C., 55, 56
Müller, P. E., 199, 340
Müller-Pouillet, 197
Müller-Thurgau, 64, 271, 364
Münch, E., 17, 40, 42, 67, 85, 104, 123, 125–129, 134, 143, 146, 149, 152–155, 169, 171, 176, 177, 188, 247, 286, 320, 324, 359, 366, 369, 371, 404, 405–408, 410, 411, 413, 414
Muenscher, 307
Muntz, 242
Mylius, 286

N

Nachtigall, 9, 19
Naegeli, 80
Nagaoka, 340
Nathansohn, 108, 119
Nawaschin, 374, 388, 389
Neef, F., 39, 95, 365
Neese, 55
Neger, F. W., 1, 98, 122, 127, 156, 216, 221, 265, 267
Ney, C. E., 199, 254, 369
Nicolas, 219
Nicolic, 220
Nielsen, 117
Niklewski, 357
Nobbe, 12, 260, 282, 283, 297, 343
Noelle, 273, 284, 286, 287
Nördlinger, 31, 102, 114, 158, 160, 163, 169, 194, 195, 262
Noll, 281, 338
Nordhausen, 206, 229, 281, 321
Norén, 381, 386
Nothmann, 86
Nottberg, 149

O

Oelkers. 163, 246, 247, 255, 309, 396, 412
Olschowy, 329
Oltmanns, 247

Omeis, 188, 192, 294
Oppermann, 33, 404, 407
Osterhout, 351
Ottenwälder, 397
Otto, 237, 263

P

Pässler, 147, 330, 331, 343
Palladin, 235
Pantanelli, 83
Pauchet, 382
Payen, 109
Peklo, 296, 297
Pennington, 172
Pergola, 222
Peter, 392
Peters, Th. 397
Petersen, 174
Petraschek, 155
Pfeffer, W., 82, 83, 85, 149, 288, 290, 362
Pfeiffer, H., 265, 282
Pfund, 255
Pfundt, 382
Philipps, Pr. 176, 356, 357
Pilaski, 304
Pilz, 123
Pittauer, 396, 413
Plant, 287
Plaut, 286
Plester, 240
Pohl, F., 295
Poisson, 393
Pojarkova, A., 1
Pollak, 382
Popesco, 137
Porodko, 280, 281
Porsch, O., 317
v. Portheim, 38, 339
Pouget, 282
Praël, 126
Prantl, 55, 389
Prianischnikow, 282
Puchner, H., 395
Puriewitsch, 241

R

Raatz, 94, 95, 129
Raciborski, 282
Räuber, 147, 148, 339
Ramann, 198, 199, 201, 202, 236, 246, 255, 264, 325, 327, 330, 332, 333, 335, 339, 340, 342, 244, 353
Rand, 250
Rasdorsky, 171
Raunkiär, 67
Reed, 282, 339
Rees, 295, 311
Reiche, H., 128
Reinau, E., 244, 259
Reinders, 290
Reinhardt, 222
Reinke, 206, 242
Renner, O., 216, 288, 302, 305, 309, 313, 315, 316, 317, 319, 321, 324, 376
Renvall, A., 205, 359
Reuss, H., 100
Rhumbler, 81
Richter, 264, 289, 290
Rieckert, 255
Riegler, 27
Rigg, G. B., 356
Rippel, A., 16, 88, 210
Rissmüller, 331
Rivers, 272
Robertson, Th. Br., 16
Römer, 329
Röse, 31
Rössler, 389
Rogers, 27
v. Romberg, 149
Romell, 99, 246
Rosenthal, 162
Rosenvinge, 44
Rossmässler, 2, 28
Roth, F., 107, 155
Rothert, 19, 107, 281, 326
Rubner, 159, 199, 348, 403
Rudau, B., 127
Rumpf, G., 286
Ruot, 337
Rusnov, 389
Russel, 355
Russow, 99
Rytz, 376
Rywosch, 209, 221, 223, 224, 230

S

v. Sachs, J., 14, 20, 180, 192, 222, 281, 311, 312, 361
Sajfert, 340
Salomone, 340
Samek, 255
Sanio, 149, 159, 187, 188, 396
Saposchnikoff, 237
Sarauw, 295
de Saussure, 235
Savart, 255
Schaffnit, 2, 262, 264
Schander, 2, 262, 264
Schechner, 67, 219
Scheit, 221, 312
Schellenberg, 105, 119, 120, 141, 351, 355
Schenck, H., 26, 146, 199
Schenk, 400
Schermbeck, 315
Scherrer, 88
Schierlinger, 153
Schild, H., 193
Schiller, 204
Schilling, E., 107, 128

Schimper, 236, 338, 339, 364
Schleiden, 80
Schley, E., 176
Schmetz, L., 220
Schmid, 297, 343
Schmid, J., 46
Schmidt, A., 410
Schmidt, W., 263, 343, 397, 413
Schmidts, 358
Schneider, 188
Schneider-Orelli, 64
Schott, 16, 406, 411, 413
Schotte, G., 16, 410, 413, 414
Schoute, J. C., 7, 94, 95, 130
Schramm, 122, 227, 229
Schreiber, 261
Schreinemacher, 329
Schreiner, 282, 329
Schroeder, 10, 288, 289, 331
v. Schröter, J., 23, 37, 214, 225, 273, 335
Schröter, 395, 414
Schubert, J,. 16
Schüepp, O., 16, 89
Schütz, 237, 238, 263
Schütze, 294
Schulow, 282
Schultze, 237, 238, 263
Schulz, A., 377–379, 395
Schulze, F., 108, 121
Schumann, 58
Schwabach, 149, 216
Schwackhöfer, 147
Schwalbe, 154
Schwappach, 127, 163, 175, 186, 188, 191, 259, 342, 347, 371, 409
Schwarz, F., 163, 164, 167, 170, 174, 183, 270
Schwendener, 7, 8, 166, 320
v. Schwerin, 224
v. Seckendorff, 27
Seeger, 370
Seelhorst, 271
Seeliger, 51, 67
Seitz, 414
Seliger, 219
Senn, 232
Shantz, 260, 304
Sieber, 184
Sierp, 90
Sigmond, 329
Simon, 12, 64, 116, 234
Singol, 395
Sinott, E. W., 356
v. Sivers, 410
Skinner, 329
Sludsky, 387
Smith, 243
Snow, 284
Soar, J., 221
Solereder, 130
Sonntag, 107, 175
Späth, 11, 12, 99
Sperlich, 43, 399
Sprengel, 383
Stahl, 25, 56, 70, 146, 148, 149, 202, 205, 207, 211, 217, 218, 224, 225, 230, 232, 240, 242, 264, 325, 339
Stalfelt, 201, 202, 212, 218, 228, 229, 242, 244, 259
Stauffer, 125, 188, 189
Stein, 216
Steinbrink, 317, 382
Sterner, 162
Stiles, 83
Stocker, O., 302
Stoklasa, 281, 282, 339
Stoll, 232, 238, 239
Stone, 121
Stopes, 310
Strasburger, 80, 85, 95, 99, 103, 112, 119–121, 123–125, 134, 151, 157, 158, 178, 182, 221, 222, 223, 286, 288, 290, 310, 311, 312, 314, 318, 320, 323, 351, 360, 365, 366, 387
Strugger, 219, 237
Süchting, 345
Suroz, 357
Suzuki, 237
Swart, 263, 331
Sylvén, N., 6, 376, 383, 406, 413, 414

T

Takahashi, Kenzo, 128
Tammes, 5
Taubert, 225, 228–230
Teodoresco, 137
Tetzner, 154
Thibaut, 382
Thielmann, 219
Thomas, 143, 202
Thompson, 114
Thomson, 112
Thonet, 194
Van Tiegham, 293
Timpe, 240
Tischendorf, 15, 160
Tischler, 241
Tison, C. R., 4, 266, 267, 386
Tolsky, 276
Tonkel, 308
Traklionow, 64
Tröndle, A., 64, 83
Troschel, E., 120, 194
Tschermak, 249
Tschirch, 149, 152, 288
v. Tubeuf, 117, 126, 145, 155, 284, 355, 367, 387, 391, 395, 406, 408, 413
Tunker, 271
Turesson, G., 405
Tuttle, G. M., 356
Tuzson, 112, 126, 384

U

Ulbricht, 289
Ullrich, H., 237

Ursprung, 20, 84, 90, 172, 174, 175, 210, 219, 291, 317, 318, 321–323, 362

V

Vageler, 246
Vandekvelde, 356
Vanselow, 405
Varga, 265, 267
Vater, 274–278, 303, 331, 340, 341, 345, 349
Vesque, 320
Vischer, 229
Vöchting, 24, 32, 38, 72, 75, 183, 220, 272
Volkens, 267
Vonhausen, 145
de Vries, 165, 180, 394
Vuillemin, 6

W

Wachtl, 411
Wächter, 250
Wagner, M., 255
Wakker, 271
Walter, H., 84, 99, 205, 302, 309
Warming, 379
Warnebold, 337
Warnke, 215
Warsow, 214, 221
Weber, F., 62–64, 81, 156, 217, 219, 237, 257, 358
Weber, R., 15, 16, 37, 100, 126, 160, 164, 177, 188, 258, 273, 323, 326, 327, 332–334, 354
Weevers, Th., 351, 355
Wehmer, C., 82, 232, 331, 389
Weis, 348
Weiss, 214
Weisse, 8, 204
Welsford, 388
Werner, O., 238
Wessely, 144
Westermaier, 312
Wibeck, E., 272, 410
Wichmann, E., 365
Wichura, 392
Wiedemann, E., 17, 60, 163, 272, 273, 345–346
Wiedersheim, 172
Wiegand, 211
Wieler, 99, 100, 101, 182–184, 282, 288, 293, 295, 310
Wiesner, 4, 12, 24, 27, 36, 45, 48, 144, 172, 173, 204, 208, 213, 219, 239, 240, 248–252, 260, 266, 305, 401, 406
Wigand, 2
Wildt, 294
Wilhelm, 30, 158, 339, 367, 388
Will, A., 122, 340
Willfarth, 329, 337
Willstätter, 234, 238, 239
Wimmenauer, 65, 162
Wimmer, 329, 337
Winkler, 1, 7
Wislicenus, H., 109, 127, 155, 238
Van Wisselingh, 87, 91, 106, 108
Wittich, 344
Wittrock, 378
Wohlleb, 282
Wolpert, 389
Woltereck, 39

Y

Yapp, 214, 227

Z

Zaleski, 237
Zdarek, 185
Zederbauer, E., 241, 255, 261, 273, 411
Zeijlstra, 114, 210
Ziegenspeck, H., 286
Zielsakowsky, 277
Zimmermann, A., 311, 314, 334
Zimmermann, 370
Zollykofer, 210
Zon, 250
Zuckerkandl, 86

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COMMON NAMES OF PLANTS USED IN THE TEXT

with corresponding Scientific Names

A

Acacia, False, *Robinia pseudacacia.* L.
African Blackwood, *Dalbergia melanoxylon.* L.
Alder, *Alnus glutinosa.* Gärtn.
Alder Buckthorn. *Rhamnus frangula.* L.
Ambatsch, *Aeschynomene elaphroxylon.* Taub.
Apple, *Pyrus malus.* L.
Arbor vitae, *Thuya.* L., *Biota.* Endl.
Ash, *Fraxinus excelsior.* L.
Ash, Mountain, *Sorbus aucuparia.* L.
Aspen, *Populus tremula.* L.
Austrian Pine, *Pinus Laricio austriaca.* Poir.

B

Balsam Fir, *Abies balsamea.* Mill.
Balsam Poplar, *Populus balsamifera.* L.
Bamboo, *Bambusa arundinacea.* Retz.
Banana, *Musa.* L.
Barberry, *Berberis vulgaris.* L.
Barley, *Hordeum vulgare.* L.
Beetroot, *Beta rubra.* L.
Beech, *Fagus sylvatica.* L.
Begonia, *Begonia.* L.
Bilberry, *Vaccinium myrtillus.* L.
Birch, *Betula.* Tourn.
Bird Cherry, *Prunus padus.* L.
Birthwort, *Aristolochia sipho.* L'Hér.
Black Alder, *Alnus glutinosa.* Gärtn.
Black Elder, *Sambucus nigra.* L.
Black Poplar, *Populus nigra.* L.
Blackthorn, *Prunus spinosa.* L.
Bramble, *Rubus.* L.
Broom, *Spartium scoparium.* L.
Bladder-nut, *Staphylea pinnata.* L.
Box, *Buxus sempervirens.* L.
Buckthorn, *Rhamnus.* L.
Butcher's Broom, *Ruscus aculeatus.* L.

C

Cabbage, *Brassica.* L.
Canker Fungus, *Nectria galligena.* Bres. and *ditissima.* Tul.
Carrot, *Daucus carota.* L.
Casuarina, *Casuarina equisetifolia.* Forst.
Cedar of Lebanon, *Cedrus Libani.* Lk.
Cembran Pine, *Pinus cembra.* L.
Chestnut, Edible, *Castanea sativa.* Mill.
Chestnut, Horse, *Aesculus hippocastanum.* L.
Chestnut, Sweet, *Castanea sativa.* Mill.
Club Moss, *Lycopodium.* L.
Common Birch, *Betula verrucosa.* Ehrh.
Cork Elm, *Ulmus campestris*, var. *suberosa.* Ehrh.
Cork Oak, *Quercus suber.* L.
Cowberry, *Vaccinium vitis idaea.* L.
Crack Willow, *Salix fragilis.* L.
Cress, *Lepidium sativum.* L.

D

Dogwood, *Cornus sanguinea.* L.
Douglas Fir, *Pseudotsuga Douglasii.* Carr.
Dry Rot Fungus, *Merulius lacrymans.*

E

Ebony, *Diospyros ebenum.* Retz.
Elm, *Ulmus.* Tourn.
English Elm, *Ulmus campestris.* Spach.
Evening Primrose, *Oenothera biennis.* L.
Eucalyptus (Australian), *Eucalyptus globulus.* Lab.

F

Feather Moss, *Musci pleurocarpi.*
Ferns, *Filicinae.*
Field Elm, *Ulmus campestris.* Spach.
Field Maple, *Acer campestre.* L.
Field Mustard, *Brassica arvensis.* Scheele.
Flax, *Linum usilatissimum.* L.
Fly Honeysuckle. *Lonicera xylosteum.* L.
French Bean, *Phaseolus vulgaris.* L.

G

Ginkgo, *Ginkgo biloba.* L.
Goat Willow, *Salix caprea.* L.

Gooseberry, *Ribes grossularia*. L.
Grasses, *Gramineae*.
Green Alder, *Alnus viridis*. De C.
Grey Poplar, *Populus canescens*. W.
Ground Ivy, *Raphanus Raphanistrum*. L.
Guelder Rose, *Vuburnum opulus*. L.

H

Hawthorn, *Crataegus oxyacantha*. L.
Hazel, *Corylus avellana*. L.
Heather, Common, *Calluna vulgaris*. Salisb.
Hemlock Spruce, *Tsuga canadensis*. Carr.
Hemp, *Cannabis sativa*. L.
Hickory, *Carya, Hicoria*. Nutt.
Hip, fruit of *Rosa*. Tourn.
Holly, *Ilex aquifolium*. L.
Honeysuckle, *Lonicera periclymenum*. L.
Hop Hornbeam, *Ostrya vulgaris*. Will.
Hornbeam, *Carpinus betulus*. L.
Horse Bean. *Vicia faba*. L.
Horse Chestnut, *Aesculus hippocastanum*. L.
Horsetail, *Equisetum*.

I

Indiarubber Tree, *Ficus elastica*. L.
Ivy, *Hedera helix*. L.

J

Juniper, Common, *Juniperus communis*. L.
Juniper, Virginian, *J. virginiana*. L.

K

Kohlrabi, *Brassica oleracea* v. *gongylodes*. L.

L

Laburnum, *Cytisus laburnum*. L.
Larch, *Larix europaea*. DC.
Larch, American, *Larix americana*. Mich.
Lawson's Cypress. *Chamaecyparis Lawsoniana*. Parl.
Lignum vitae, *Guajacum officinale*. L.
Lichens, *Lichenes*.
Lilac, *Syringa vulgaris*. L.
Lime, Large-leaved, *Tilia grandifolia*. Ehrh.
Lime, Small-leaved, *Tilia parvifolia*. Ehrh.
Ling, *Calluna vulgaris*. Salisb.
Lombardy Poplar, *Populus pyramidalis*. Rosier.
Lupin, *Lupinus*.

M

Magnolia, *Magnolia*. L.
Mahogany, American, *Swietenia Mahagoni*. L.
Mahonia, *Mahonia aquifolium*. Nutt.
Maize, *Zea mais*. L.
Male Dogwood, *Cornus mas*. L.
Mangrove, *Bruguiera gymnorhiza*. Lam.
Maple, *Acer*. L.
Maple, Ash-leaved, *Acer negundo*. L.
Maritime Pine, *Pinus maritima*. Poir.
Mezereon, *Daphne mezereum*. L.
Mildew, *Microsphaera alni*. Wallr. var. *quercina*.
Mosses, *Musci*.
Mountain Ash, *Sorbus aucuparia*. L.
Mountain Pine, *Pinus montana*. Mill.
Mulberry, *Morus*. Tour.
Mustard, *Sinapis*. L.
Mustard, Field, *Brassica arvensis*. Scheele.

N.

Needle-shedding Fungus, *Lophodermium pinastri* (Schrad.). Chev.
Norway Maple, *Acer platanoides*. L.

O

Oak, *Quercus*. L.
Oats, *Avena sativa*. L.
Oil Palm, *Elaeis guineensis*. Jacqu.
Oleander, *Nerium oleander*. L.
Olive, *Olea europaea*. L.
Osier, Common, *Salix viminalis*. L.

P

Pea, *Pisum sativum*. L.
Peach, *Prunus persica*. Stokes.
Pear Tree, *Pyrus communis*. L.
Pine, *Pinus sylvestris*. L.
Pine-blister Fungus, *Peridermium pini*.
Plane, *Platanus*. Tourn.
Plum, *Prunus domestica*. L.
Pomegranate, *Punica granatum*. L.
Poplar, *Populus*. L.
Poplar, Canadian, *Populus canadensis*. Moench.
Potato, *Solanum tuberosum*. L.
Privet, *Ligustrum vulgare*. L.
Pubescent Birch, *Betula pubescens*. Ehrh.
Pumpkin, *Cucurbita pepo*. L.
Purging Buckthorn, *Rhamnus cathartica*. L.

Q

Quebacho, West Indian, *Thouinia striata*. Radlk.
Quince, Japanese, *Cydonia japonica*. Pers

R

Radish, *Raphanus sativus*. L.
Radish, Wild, *Raphanus raphanistrum*. L.
Rape, *Brassica napus*. L.
Raspberry, *Rubus idaeus*. L.
Red-berried Elder, *Sambucus racemosa*. L.
Red Clover, *Trifolium pratense*. L.
Red Currant, *Ribes rubrum*. L.
Rice, *Oryza sativa*. L.
Robinia, *Robinia pseudacacia*. L.
Rose, *Rosa*. Tourn.
Rowan, *Sorbus aucuparia*. L.

S

Savin Tree, *Juniperus sabina*. L.
Scots Pine, *Pinus sylvestris*. L.
Sea Buckthorn, *Hippophae rhamnoides*. L.
Service Tree, *Sorbus aria*. Cranz.
Sessile Oak, *Quercus sessiliflora*. Smith.
Silver Fir, *Abies pectinata*. DC.
Sloe, *Prunus spinosa*. L.
Spinach, *Spinacea oleracea*. L.
Spindle Tree, *Evonymus europaeus*. L.
Spruce, *Picea excelsa*. Lk.
Stone Pine, *Pinus pinea*. L.
Strawberry, *Fragaria vesca*. L.
Summer Wheat, *Triticum vulgare* (*aestivum*). Vill.
Sunflower, *Helianthus annuus*. L.
Sweet Chestnut, *Castanea sativa*. Mill.
Sycamore, *Acer pseudoplatanus*. L.

T

Tanning Sumach, *Rhus typhina*. L.
Teak, *Tectonia grandis*. L.
Tobacco, *Nicotiana tabacum*. L.
Tomato, *Solanum lycopersicum*. L.
Tree of Heaven, *Ailanthus glandulosa* Desf.
Tulip Tree, *Liriodendron tulipifera*. L.

V

Virginia Creeper, *Ampelopsis quinquefolia* R. & Sch.

W

Walnut, *Juglans regia*. L.
Wavy aira, *Aira flexuosa*.
Wayfaring Tree, *Viburnum lantana*. L.
Wellingtonia, *Sequoia gigantea*. DC.
Whin, *Genista*. L.
White Alder, *Alnus incana*. Willd.
Whitebeam, *Sorbus aria*. L.
White Poplar, *Populus alba*. L.
Wild Cherry, *Prunus avium*. L.
Wild Clematis, *Clematis vitalba*. L.
Wild Service Tree, *Sorbus torminalis*. Cranz.
Willow, *Salix*. Tourn.
Winter Rape, *Brassica oleifera*. DC.
Wych Elm, *Ulmus montana With*.

Y

Yew, *Taxus baccata*. L.

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