THE BOOK WAS DRENCHED

UNIVERSAL
LIBRARY

OU_162943

UNIVERSAL
LIBRARY

OUP—552—7-7-66—10,000

OSMANIA UNIVERSITY LIBRARY

Call No. 581/M46P Accession No. 14930

Author Maximov

Title Plant in Relation to water

This book should be returned on or before the date last marked below

THE PLANT IN RELATION TO WATER

A Study of the Physiological Basis of Drought Resistance

By

N. A. MAXIMOV

Professor in the Institute of Applied Botany Leningrad

AUTHORIZED ENGLISH TRANSLATION

Edited, with Notes, by

R. H. YAPP

Mason Professor of Botany in the University of Birmingham

LONDON
GEORGE ALLEN & UNWIN LTD
MUSEUM STREET

FIRST PUBLISHED IN 1929

All rights reserved

PRINTED IN GREAT BRITAIN BY
UNWIN BROTHERS LTD., WOKING

BIOGRAPHICAL NOTE

PROFESSOR R. H. YAPP, who undertook to edit the English version of *The Plant in Relation to Water*, was himself one of the foremost workers in the field of botanical inquiry which it covers. Unfortunately, soon after he had accepted the invitation to revise the English text of Professor Maximov's book, he was stricken with a serious illness, and after a year's suffering, borne with the greatest heroism and patience, he died in January of this year. Confined to a bed of sickness, he worked with the utmost diligence and interest at the task he had undertaken, ably assisted by Miss Carman. He had only just finished the revision of the final proofs when the end came. It had been his ardent wish that he should be spared to complete this last piece of work, in which he was so greatly interested, since it was so closely connected with his own researches. It seems, therefore, fitting to give readers of this English version a short account of the late Professor Yapp.

He was born in 1871 in the village of Orleton in Herefordshire. After attending the Secondary School in Hereford, he entered a business firm in Leominster. In the face of considerable obstacles, by attending evening classes and lectures at Nottingham, he ultimately achieved his ambition to go to the University, and he entered St. John's College, Cambridge, in 1895, gaining a scholarship there. After graduating with first-class honours in Botany, he was awarded the Frank Smart studentship, and accompanied the University expedition to the Malay States, under the leadership of Mr. W. W. Skeat. Studying a natural type of vegetation under these propitious conditions, he became interested on his return to Cambridge in the vegetation of the fens, and spent many vacations, even after he had left Cambridge, in the fens studying, particularly the relation of the plants to their habitat and to the water content of the soil. His account of Wicken Fen, published in the *New Phytologist* in 1908, will indicate his special interest in the physiological and morphological problems of plant ecology.

This is still more strongly brought out in a paper published in 1912 in the *Annals of Botany* on "Spiraea Ulmaria and its Bearing on the Problem of Xeromorphy in Marsh Plants". In this article Yapp gave a critical account of the structure of this typical marsh plant as influenced by the varying amounts of water lost by transpiration from its leaves. Yapp was appointed Professor in University College, Aberystwyth, in 1903, and was soon attracted to the problems offered by the vegetation of the Dovey Estuary. This he studied with the same enthusiasm and energy that he had devoted to the fens, and two excellent articles on the "Saltmarshes of the Dovey Estuary" appeared in the *Journal of Ecology* in 1917 and 1921 respectively. More general considerations of ecological problems were discussed in later papers dealing with the "Concept of Habitat" and the "Concept of Association", the former paper being his presidential address to the Ecological Society in 1922.

Professor Yapp left Aberystwyth in 1914 to take up the Professorship of Botany in Queen's College, Belfast, and in 1919 he went to Birmingham as Mason Professor of Botany. For the last few years he had been busy planning and supervising the erection of new botanical laboratories in which, alas, he was never to work himself. Nor was it given to him to complete many investigations which were in progress. A tragic fate called him away.

Professor Yapp was a clear and inspiring teacher, finding many interesting ecological and physiological problems for his research students to investigate. He was a keen and trained observer and had a critical mind with a wide philosophical outlook. Had he lived he would have established for himself the reputation of a profound thinker. Though cut off in his prime, British botanists are indebted to him for many valuable contributions to science; they will cherish in their hearts a warm memory of his noble and genial manner.

F. E. WEISS

AUTHOR'S PREFACE TO THE ORIGINAL RUSSIAN EDITION

THE agricultural character and continental climate of Russia, with its periodical droughts—to which even the most productive districts are subject—necessitate the selection or creation of varieties of crop plants capable of resisting the injurious effects of drought. In this task, however, our plant breeding institutions have encountered so many difficulties that up to the present we are unable to boast of as great a measure of success in breeding drought resistant varieties, as has been undoubtedly attained by the Russian experiment stations in controlling the effect of drought by rational methods of soil cultivation. This lack of success must be in great part attributed to our inadequate knowledge of the real nature of drought resistance itself, and of its physiological basis.

My original intention was to confine myself to an account of the present state of our knowledge of drought resistance in plants and other related problems. But none of the Russian textbooks of plant physiology contained a sufficiently modern and detailed treatment of the subject of the water relations of plants to provide the foundation necessary for such an account. I was therefore compelled to extend the scope of my work. Hence in this book the exposition of the problem of drought resistance itself is preceded by a discussion of the chief laws which govern the absorption and transpiration of water, and which therefore determine the relations between plants on the one hand and soil and atmospheric moisture on the other. The result has been that the book is really a monograph dealing with the general relations between the plant and water.

The main purpose of the book, then, is to give those engaged in experimental research, as well as students of botany and agriculture, an account of what has been and still is being done in the elucidation of problems connected with the drought resistance of plants. In addition to this, I have given detailed and critical descriptions of the more important methods

employed in studying the various aspects of the water balance of plants. I have thought it necessary to deal with methods in considerable detail, as my book is intended to serve not only as a manual for investigators, but also as a work of reference on questions regarding water relations for plant physiologists and ecologists, as well as for workers at agricultural experiment stations.

Although the results of many investigations, by both Russian and foreign scientists, on the water relations and drought resistance of plants are summarized in my book, it is no mere compilation. Having myself worked in this field, in addition to directing the work of others, for over ten years, I consider that I have the right not only to hold but also strongly to advocate my own views in regard to many of the questions discussed. But what the book may thus lose in objectivity, it will, I hope, gain in unity of treatment. In all cases, however, in which my own opinions are markedly at variance with generally accepted views, I have endeavoured to prove them by argument. This will enable the reader to arrive at his own conclusions respecting these debatable matters.

My book does not claim to be exhaustive. The essential questions concerning the relation of the plant to water, and the more important investigations on this subject, have been discussed more or less in detail. But the literature is so extensive, and includes so much that is no longer even of historical importance (especially where obsolete or inexact methods were used), that I have not thought it necessary to give a complete bibliography. As regards transpiration and cognate questions, a very full bibliography is to be found in **Burgerstein's** well-known monograph *Die Transpiration der Pflanzen* (1904, 1920, 1925). Unfortunately there is no similar monograph on the absorption of water by plants, but reference may be made to **Benecke-Jost's** *Pflanzenphysiologie* (4th edit., 1924), and to **H. Walter** (1925). **Stiles's** *Permeability* (1924[a]) also contains a valuable list of literature. No bibliography has previously been compiled on the subject of drought resistance

in plants. This is the first attempt to present in due perspective a picture of the many-sided relations of plants to water, and to give a critical survey of the factors probably concerned in determining drought resistance. This being so, it is hardly to be expected that the book should be free from defects, perhaps even serious ones. I should therefore welcome comments and criticisms, which shall be taken into account in my future writings.

The idea of the present book was conceived as early as 1918–20, when I was a Professor in the Faculty of Agriculture in the Polytechnic Institute, first in Tiflis and afterwards in Kuban. At that time I was in close touch with the special problems of agriculture in arid districts, and found that the data published in the principal textbooks were insufficient to elucidate these problems. The realization of my idea, however, became possible only on my return to Leningrad, when I was able to avail myself of the excellent libraries of the Botanic Garden and of the Institute of Applied Botany.

The greater part of the manuscript was ready for the press at the beginning of 1925. Literature received subsequently, such as the detailed investigations of **Huber** (1924) and **H. Walter's** interesting book (1925), could not therefore be fully discussed. Owing to the kindness of the Director of the Institute of Applied Botany, Professor N. I. Vavilov (to whom I tender my best thanks), my book finally appeared (in 1926) as a supplement to the *Bulletin of Applied Botany and Plant Breeding*.

I gratefully acknowledge the assistance received from many, especially foreign authors, who kindly sent me copies of their papers, many of which had appeared in somewhat inaccessible journals. I wish to mention in particular—Professor B. Livingston (Baltimore), who not only sent copies of his own valuable works, but also encouraged his numerous pupils to do the same; Dr. H. Shantz (Washington), who forwarded copies of all his important papers; Privatdozent H. Walter (Heidelberg), who furnished me with the principal results of his

interesting investigations prior to publication; and Professor A. Burgerstein (Vienna), the veteran specialist, who most kindly sent me on two occasions lists of works on transpiration additional to those mentioned in his monograph. Thanks are also due to Professor S. Savinov for kindly revising the chapter dealing with the physics of transpiration, to Mme. T. Krasnoselsky-Maximov for reading the proofs, and to M. I. Tumanov for compiling the indices. To all these I express my profound gratitude.

N. A. MAXIMOV

LENINGRAD
December 1, 1925

AUTHOR'S PREFACE TO THE ENGLISH EDITION

THE present English edition of my book differs in certain respects from the original Russian edition. I have considered it an advantage to abridge considerably Parts I and II of the book, in which the absorption and loss of water by the plant are discussed. The first two chapters of the Russian edition have been condensed into one, and two other chapters, namely those on Guttation and the Transpiration Stream respectively, entirely omitted. The excellent treatment of the latter subject by H. H. Dixon has made it possible to do without a detailed account of this important question. I have also omitted the consideration of certain less important investigations mentioned in the Russian text.

These abbreviations of Parts I and II have been made in the hope that the book might be more readable, and thus appeal to a wider circle of readers. At the same time the comparatively detailed treatment of questions connected with the water balance and drought resistance of plants (Part III) has been retained, as these questions have not previously been systematically elucidated.

Owing to the fact that the Russian edition was published more than two years ago, it has been necessary to make certain alterations in order to bring the new edition more or less up to date. Unfortunately, for various reasons, I have been unable in the present edition to deal fully with the new work which has appeared since the original edition was published. This would have required too great an alteration of the text and would have delayed still further the publication of an English edition. I have therefore limited myself to adding brief notices of the more important researches published since the first appearance of my book. These recent investigations, however, have necessitated no modifications of—but have rather confirmed—the fundamental views put forward in the first edition.

I must acknowledge with the deepest gratitude the excep-

tional care which has been taken by Professor R. H. Yapp, the editor of the English edition. He has not only taken considerable trouble in connexion with the arrangements for publishing the book, but has entirely revised the English text forwarded to him. There is scarcely a sentence which has not been altered and rendered more idiomatic. Indeed, so far as I am able to judge, Professor Yapp has succeeded in freeing the book from any appearance of being a translation from a foreign language. It may be said without exaggeration that the whole of the text has been rewritten, notwithstanding the fact that the translators of the book—Mme. Irene Krassovsky and Mlle. Alma Trost—had conscientiously and successfully performed the task of accurately interpreting the Russian text, a task requiring a great deal of skill and labour on their part.

In addition to revising the text of the translation, Professor Yapp has added many valuable and interesting footnotes, either containing new or original data or else making good certain omissions on my part. In general, Professor Yapp has devoted as much care and labour to my book as if it had been his own, and I am happy to know that it has met with so much sympathy on the part of its first English reader. This leads me to hope that its subsequent readers also will receive it with kindly consideration.

N. A. MAXIMOV

LENINGRAD
April 1928

EDITOR'S PREFACE TO THE ENGLISH EDITION

SEVERAL years ago, when Professor Maximov had nearly completed his book on *The Physiological Basis of Drought Resistance in Plants*, I suggested to him that a fairly full summary in either English, French, or German would be welcomed by botanists in Western Europe and America. In reply, Professor Maximov raised the question of the desirability of publishing a complete English translation, adding that if this were possible, he hoped I would consent to edit the translation. The present English edition is the outcome of this and further correspondence.

This is not the place in which to discuss the merits of Professor Maximov's book as a whole, but attention may perhaps be drawn to one or two of its distinctive features. The major part of the book consists of a critical historical account of the development of our knowledge of the relations of the plant to water. The inclusion in this account of summaries of the more important results of recent Russian investigations, which are thus made available to many Western botanists unfamiliar with the Russian language, is particularly welcome. Again, the author's critical discussions of research methods and results illustrate the extreme difficulty of devising physical apparatus or experiments which can satisfactorily imitate or even measure physical processes as carried on in such a complex organism as a living plant. Cases in point are Livingston's well-known porous cup atmometer, Brown and Escombe's multiperforate septa, and the current quantitative methods—most of them unsatisfactory—of determining transpiration. On the other hand, of course, provided that the limitations of the methods employed are clearly recognized, and that due caution is observed in arguing from artificial to natural conditions, the value of the results obtained is in many cases undeniable. But perhaps the most distinctive, certainly the most original, portions of the book are those in which the author expounds his

own views, particularly on such subjects as the concepts of xerophytism and drought resistance.

Professor Maximov kindly gave me a free hand as regards the text of the English edition. While endeavouring throughout to render faithfully the author's meaning, and to maintain the essential character of the book, I have examined the subject-matter somewhat critically, and have not hesitated to make such minor alterations as seemed to me desirable. In some cases the text has been condensed, in others a slightly fuller account has been given of the work of particular authors than is contained in the original. A number of small corrections and additions have also been made. For convenience of reference, the various chapters have been divided into sections, with appropriate subject headings. The text, as thus revised, has been submitted to and approved by the author. In order to secure consistency in the spelling of the names of Russian authors, I have adopted, on the advice of Professor Julius Tillyard, the system of transliteration recommended by the *Slavonic Review*. To avoid confusion, however, in cases where the spelling of names in the text differs from that employed in the original publications cited, the alternative spellings also are given (in brackets) in the bibliography. At Professor Maximov's request, I have in a number of cases supplemented the text by editorial footnotes. These are signed "Ed." and enclosed in square brackets.

In the bibliography of the original book, the works of Russian and foreign authors respectively were contained in separate lists. In the present edition these lists have been combined, and the bibliography somewhat enlarged. Similarly, the originally separate author index has been included in the general index, heavier type being used for authors' surnames. The index is considerably fuller than in the Russian edition.

My task as editor has been a pleasant one, and the more so on account of Professor Maximov's unfailing courtesy during the progress of the work and his readiness to accept my suggestions. I tender my grateful thanks both to him and his trans-

lators and to the following, who have generously assisted in various ways. Professor D. Thoday kindly criticized Chapter I and made a number of useful suggestions; he has also contributed a paragraph to the footnote on p. 53. Dr. G. A. Shakespear has given much valuable help by reading and criticizing the revised typescript of the many physical portions of the book. Professor J. Percival has verified, and where necessary corrected, the names of the varieties of cereals mentioned in the book. Professor H. J. W. Tillyard, Dr. S. R. Carter, Mr. M. F. Liddell, and other colleagues have supplied information on special points. Finally, Miss A. M. Carman has devoted much time to compiling the index, reading the proofs, and checking bibliographical and other references. Her assistance in these and in many other directions has been invaluable.

R. H. YAPP

THE UNIVERSITY
BIRMINGHAM
June 1928

CONTENTS

PAGE

BIOGRAPHICAL NOTE 5

AUTHOR'S PREFACE TO THE ORIGINAL RUSSIAN EDITION 7

AUTHOR'S PREFACE TO THE ENGLISH EDITION 11

EDITOR'S PREFACE TO THE ENGLISH EDITION 13

ILLUSTRATIONS 21

INTRODUCTION 25

PART I

THE ABSORPTION OF WATER BY THE PLANT

CHAPTER I

THE ABSORPTION OF WATER AND THE WATER RELATIONS OF THE PLANT CELL 35

The Absorption of Water by the Cell 36

Suction Pressure of the Plant Cell 38

Methods of Determining Suction Pressure 40

The Water Relations of the Living Plant Cell 43

The Dependence of Growth on the Saturation of the Cell 45

The Absorption of Water by the Root 47

Exudation Pressure and Suction Pressure of the Root 48

Active and Passive Root Suction 55

Amount of Water Absorbed by the Root System 55

CHAPTER II

THE ABSORPTION OF WATER FROM THE SOIL 60

The Absorption of Water under Natural Conditions 60

The Water Relations of Different Soils 62

The Demands of Different Plants on Soil Moisture 63

The Wilting Coefficient of the Soil 65

The Resistance of the Soil to Root Suction 71

Transpiration and the Translocation of Water in the Soil 78

THE PLANT IN RELATION TO WATER

CHAPTER III

PAGE

THE INFLUENCE OF ENVIRONMENTAL CONDITIONS ON ABSORPTION 83

INFLUENCE OF ENVIRONMENTAL CONDITIONS ON THE ABSORPTION OF WATER BY THE ROOT SYSTEM 83

(*a*) The Temperature of the Soil 83

(*b*) Reaction of the Soil Solution 87

(*c*) The Absorption of Water from Bog Soils—Soil Toxins 88

(*d*) The Oxygen Content of the Soil 91

(*e*) The Concentration of the Soil Solution—Halophytes 92

ABSORPTION OF WATER BY THE AERIAL ORGANS OF PLANTS 95

PART II

THE LOSS OF WATER BY THE PLANT

CHAPTER IV

THE METHODS OF INVESTIGATING TRANSPIRATION 101

THE PHYSIOLOGICAL RESULTS OF TRANSPIRATION 101

QUANTITATIVE METHODS OF INVESTIGATING TRANSPIRATION 106

(1) Methods of Determining the Water Vapour Transpired 107

(2) Gravimetric Methods of Determining the Amount of Water Lost 114

(3) Volumetric Methods of Determining the Amount of Water Absorbed by Cut Shoots 123

METHODS OF CALCULATING RESULTS: CONCEPTS AND TERMINOLOGY 126

CHAPTER V

THE INFLUENCE OF ENVIRONMENTAL CONDITIONS ON TRANSPIRATION 133

TRANSPIRATION AND EVAPORATION 133

THE PHYSICAL LAWS OF EVAPORATION 135

EVAPORIMETERS AND ATMOMETERS 139

THE DAILY MARCH OF TRANSPIRATION AND OF METEOROLOGICAL FACTORS 148

THE EFFECT OF INDIVIDUAL ENVIRONMENTAL FACTORS ON TRANSPIRATION 156

(*a*) Atmospheric Humidity or Saturation Deficit 157

(*b*) Air Movements 161

(*c*) Light 164

CHAPTER VI

THE STOMATAL APPARATUS OF THE PLANT 171

THE STOMATAL APPARATUS OF THE PLANT 171

THE STATIC DIFFUSION OF GASES THROUGH SMALL APERTURES 172

THE MECHANICS OF STOMATAL MOVEMENTS 176

METHODS OF INVESTIGATING THE MOVEMENTS OF STOMATA 178
THE DIURNAL MARCH OF STOMATAL MOVEMENTS 186
EFFECT OF LIGHT AND OTHER FACTORS ON STOMATAL MOVEMENTS 189

CHAPTER VII

PAGE
THE REGULATION OF TRANSPIRATION BY THE PLANT 194
THE REGULATION OF TRANSPIRATION BY THE PLANT 194
ATTACKS ON THE THEORY OF STOMATAL REGULATION 195
RELATIVE TRANSPIRATION AND INCIPIENT DRYING 199
THE MECHANISM OF REGULATION—STOMATAL AND NON-STOMATAL 209

PART III

THE WATER BALANCE AND DROUGHT RESISTANCE OF PLANTS

CHAPTER VIII

THE WATER BALANCE OF PLANTS 219
THE WATER BALANCE OF THE PLANT 219
THE DIURNAL WATER DEFICIT IN PLANTS 222
TRANSIENT AND PERMANENT WILTING 228
THE BEHAVIOUR OF PLANT CELLS DURING WILTING 234
MOVEMENTS OF WATER IN THE PLANT 238
EFFECT OF WILTING ON CARBON NUTRITION 240
DEATH OF PLANT CELLS AND TISSUES FROM DESICCATION 243

CHAPTER IX

XEROPHYTES 249
ECOLOGICAL CLASSIFICATION OF PLANTS ACCORDING TO THEIR WATER RELATIONS 249
THE GROUP OF XEROPHYTES 249
THE SUCCULENT TYPE 251
DESERT EPHEMERALS 254
THE TRUE XEROPHYTES 255
STRUCTURAL PECULIARITIES OF XEROPHYTES 259
HIGH OSMOTIC PRESSURES AND THEIR SIGNIFICANCE 271
ARE XEROPHYTES TRULY XEROPHILOUS? 276
RECENT AMERICAN WORK ON THE PHYSICO-CHEMICAL PROPERTIES OF PLANT SAPS 278

CHAPTER X

THE "EFFICIENCY OF TRANSPIRATION" 284
TRANSPIRATION AS A TEST OF XEROPHYTISM 284
THE QUANTITATIVE ESTIMATION OF XEROPHYTISM 287
THE "EFFICIENCY OF TRANSPIRATION" ("WATER REQUIREMENT OF PLANTS") AND DROUGHT RESISTANCE 295

THE PLANT IN RELATION TO WATER

The Efficiency of Transpiration and Environmental Conditions 310
(*a*) Atmospheric Humidity 313
(*b*) Temperature 315
(*c*) Soil Moisture 317
(*d*) Soil Fertilizers 320
(*e*) Light 321

CHAPTER XI

PAGE

THE RELATIONS BETWEEN WATER AND LEAF STRUCTURE 325
Drought Resistance and Xeromorphic Structure 325
The Concept of Xerophytism 325
Anatomical Differences in Leaves Inserted at Different Levels on the Stem 328
Physiological Differences in Leaves at Different Levels on the Stem 336
Influence of Water Supply on Leaf Structure 342
Influence of Light on Leaf Structure 346
Transpiration of "Sun" and "Shade" Leaves 348
Influence of Environmental Moisture on the Structure and Water Relations of Plants 359
(*a*) Atmospheric Moisture 360
(*b*) Soil Moisture 364

CHAPTER XII

DROUGHT RESISTANCE IN PLANTS 374
The Essentials of a Xerophytic Organization 374
The Selection of Drought Resistant Varieties of Crop Plants 375
Cell Size and Drought Resistance 376
Different Kinds of Drought and Drought Resistance 385
(*a*) Atmospheric Drought 386
(*b*) Soil Drought 391
The Basis of Drought Resistance 393
Susceptibility to Drought at Various Stages of Development 396
Analysis of the Problem of Drought Resistance 399

BIBLIOGRAPHY 403

INDEX 435

ILLUSTRATIONS

FIG.		PAGE
1.	Oats (*A*) and wheat (*B*) during the flowering period, with root systems carefully dissected from the soil. Depths of root systems shown in feet (from Weaver)	29
2.	Vesque's first potometer	48
3.	Vesque's second potometer	56
4.	A root hair in the soil (after Sachs)	61
5.	Livingston and Hawkins's auto-irrigator	81
6.	Condensation method of determining transpiration (after Guettard)	108
7.	Freeman's method of determining transpiration by passing air through a vessel containing the shoot of a plant (from Burgerstein)	109
8.	Cannon's hygrometer method of determining transpiration (from Burgerstein)	110
9.	Livingston's clip for the quantitative cobalt method (from Rübel)	113
10.	Sensitive balance for transpiration experiments (after von Hoehnel)	116
11.	Briggs and Shantz's large containers and spring balance for transpiration experiments	*Facing* 116
12.	Diagrammatic section of container with convex cover and porous pot (from Maximov)	118
13.	Briggs and Shantz's automatic recording balances for great weights	*Facing* 123
14.	Kohl's apparatus for studying water absorption by the plant under varying environmental conditions (from Burgerstein)	124
15.	The Piche atmometer (from Livingston)	141
16.	Porous porcelain cup of Livingston's atmometer (from Rübel)	141
17.	Atmometer for recording evaporation by weight (from Rübel)	142
18.	Atmometer for recording evaporation by volume (from Livingston)	142
19.	Livingston's spherical atmometer (from Rübel)	143
20.	Livingston's flat atmometer (from Rubel)	143
21.	Livingston and Thone's non-rain-absorbing atmometer	145

FIG. PAGE

22. Determination of the daily march of transpiration and evaporation by means of automatic recording balances and atmometers (from Briggs and Shantz). *Facing* 149

23. Comparison of the daily march of solar radiation and of transpiration from various plants (from Briggs and Shantz) 152

24. Diagrammatic representation of the diffusion of water vapour through small openings (from Jørgensen and Stiles) 173

25. Darwin's porometer (after Darwin and Pertz) 180

26. The use of burettes as potometers (from Lloyd) 198

27. Comparison of the march of transpiration (*T*), evaporation of water from an atmometer (*E*), and the condition of the stomata (*S*) (from Knight) 208

28. Fluctuations in the water content of leaves of *Zygophyllum Fabago* (continuous line) and the march of moisture deficit (dotted line) during three days (from Krasnoselsky-Maximov) 225

29. Abstraction of water by wilting leaves from lemon fruits (photo. by Bartholomew) *Facing* 239

30. Semi-desert plants with root systems considerably larger than the aerial organs (from Weaver) 256

31. Deeply sunken stoma of *Dasylirion filifolium* (from Haberlandt) 260

32. Stoma of *Xanthorrhoea hastilis* with ventilating cavity surrounded by thick-walled cells (from Tschirch) 261

33. Cross-sections through the leaf of *Stipa capillata* (from Kerner) 261

34. *Selaginella lepidophylla: A*, in a turgescent, and *B*, in a wilted state (from Hieronymus) 263

35. Epidermal cells of leaf of *Passerina*: *a*, in a wilted state, and *b*, saturated with water (from Thoday) 265

36. A general view of Briggs and Shantz's experiments for determining the water requirement of plants *Facing* 298

37. Plant container used by Montgomery and Kiesselbach, with an arrangement for the uniform moistening of the soil 318

38. Venation of a lower leaf of *Nicotiana rustica* (after Zalenski) 329

39. Venation of an upper leaf of *Nicotiana rustica* (after Zalenski) 329

40. Three leaves from one flowering shoot of *Spiraea Ulmaria* (from Yapp) 335

FIG. PAGE

41. Apparatus used by Géneau de Lamarlière for the determination of the relative transpiration of "sun" and "shade" leaves 350

42. Structure of the leaves of two specimens of bean, grown under electric light 356

43. Influence of air moisture on the structure of bean leaves (after Lebedintsev) 361

44. Influence of soil moisture on the structure of bean leaves (after Kokin) 368

45. Influence of periodic wilting on the structure of sunflower leaves (after Tumanov) 371

46. Desiccation of portions of the leaf lamina by drying winds (from Yapp) 388

INTRODUCTION

ORGANIC life in all probability originated in water, and all living cells and tissues of animal as well as plant organisms must be saturated with water in order to carry on their normal life activities. The migration from water to dry land represented a great step forward in the development of the organic world. But the change of conditions threatened the organism with the danger of desiccation and the consequent loss of its vital properties. The migration, therefore, was necessarily accompanied by the development of numerous adaptations, which allowed the cell to be saturated with water under the new conditions, as it was during its life in an aquatic medium.

For the plant this problem of keeping its cells saturated with water was to a high degree complicated by the circumstance that its fundamental process of nutrition involved the intake of gaseous carbon dioxide and solar energy. Intimate contact with the atmosphere containing the carbon dioxide, and a wide expansion of the leaf surface absorbing the radiant energy were necessitated. The marine algae, acknowledged as the probable aquatic ancestors of land plants,[1] have already a basic lamellar form, the one most adapted to the requirements of carbon nutrition. The plant migrant from water to dry land had a twofold problem to solve—how to spread its assimilating surface in the aerial medium in such a way as on the one hand to keep it constantly moist, and on the other to permit the free access of more or less dry air to every assimilating cell.

This problem was solved in two ways. Some plants, e.g. many mosses and lichens, having remained on a low level of development, tend to confine their vital activity to the moister seasons, in dry periods sinking into a state of anabiosis or latent life. Such plants have evolved the capacity to endure more or less complete desiccation of their tissues.[2] Others—

[1 Cf. **Church** (1919).—ED.]

[2 **Miss Bristol** (1916) found living, resting moss protonemata in air-dried soils (from Rothamsted) which had been stored in sealed bottles for nearly half a century. In many mosses and lichens the entire plant can

the vascular cryptogams and flowering plants—achieving a higher level of development, have evolved a series of structural peculiarities which allow them to remain sufficiently moist even during relatively dry periods. These peculiarities are such as in the first place to ensure the passage of a continual current of water through the plant, from the moist soil to the drier atmosphere. This is achieved by the provision of an extremely branched absorbing and translocating system. In the second place, undue loss of water from the cells of the chlorenchyma is prevented by a special covering tissue, provided with a relatively impermeable cuticle.

The normal functioning of a higher plant depends primarily on the constancy and abundance of the water streaming through it, the critical period being the hours when the loss of water to the air is greatest. The necessity for the plant of not only obtaining water in sufficient quantities for its chemical processes, but also of allowing it to pass through its organs as through a refrigerator, makes water one of the most important of ecological factors. "No other influence impresses its mark to such a degree upon the internal and external structures of the plant as does the amount of water present in the air and soil", writes **Warming** in his *Œcology of Plants* (p. 29). The importance of water is emphasized just as strongly by **Schimper,** the other founder of contemporary plant ecology, in his classical *Plant-Geography upon a Physiological Basis* (p. 1): "No factor affecting plant-life is so thoroughly clear as the influence of water. . . . In demonstrating . . . the share taken by climate and soil in causing the characteristics of the vegetation of any region, water claims a foremost place in our consideration."

The physiological significance of water in the life of the plant is exceedingly great. Water constitutes the greater part of the plant: thus leaves usually contain 80–95 per cent of water, and

endure desiccation, but in higher plants this is true as a rule only of reproductive bodies such as seeds: cf., however, p. 243. **F. F. Blackman** (1904, p. 36) says: "Considering the matter from an evolutionary standpoint it would appear to be normal for a cell to be uninjured by drying up. When the effect is death we may attribute this to some secondary cause."—ED.]

roots 70–90 per cent, mature seeds alone attaining an air-dry condition with 10–15 per cent of water.[1] Water permeates the cellulose walls of the cells, rendering them penetrable by gases; it fills the vacuoles, giving rise to the condition of turgor by which leaves and younger growing parts of stems maintain their necessary rigidity; it represents the disperse phase of the colloids of the protoplasm—the physico-chemical processes characterizing life only taking place normally in the protoplasm when it is sufficiently saturated with water. Moreover, water together with the carbon dioxide of the atmosphere represent the indispensable raw materials for the formation of carbohydrates in the process of photosynthesis. One must note, however, that this process, though most important, only claims insignificant, and indeed negligible, amounts of water in comparison with the requirements mentioned above. Experiments have shown that in a dry Continental climate the plant does not assimilate more than 1 gr. of water for every 1,000 gr. extracted from the soil; the remaining 999 gr. merely pass through the plant unchanged, to be dispersed in the atmosphere. In a moist climate rather more is assimilated, but the amount does not exceed 2–3 gr. per kilogram of absorbed water.

The great quantity of water streaming through the plant, and the difficulty of continually making good the loss by transpiration, is seen in **Kiesselbach's** experiments (1916) with corn (*Zea Mays*) carried out at the agricultural experiment station in Nebraska. Corn was grown in cylindrical galvanized iron containers of such a size that the plants were as large as those grown under field conditions. The containers were placed in special trenches in the cornfield so that the aerial parts of

[1 According to various published results, the leaves of trees often contain less water (e.g. 54–80 per cent) than those of herbs; freshly felled timber 38–65 per cent, while algae may contain up to 98 per cent of the fresh weight of the part concerned. **Thoday** (1921) records exceedingly low amounts of water in still living vegetative shoots of certain S. African plants during the dry season, e.g. 25·7–45·3 per cent in *Passerina* sp., and about 7 per cent in *Myrothamnus flabellifolia*. The water content of plants, indeed, varies greatly according to species, size, age, the plant organ selected and its position on the plant, ecological conditions, and so on.—ED.]

the plants developed under natural conditions. The total amount of water lost from, or rather passed through, one corn plant during the entire vegetative period amounted to 100–180 kg., according to weather conditions. At the time of most rapid leaf development the loss reached 1 to 3 or even 4 kg. a day. In my own experiments in Tiflis, using containers of considerably smaller size, which slightly retarded the growth of the plants, corn transpired during the summer about 75 kg. per plant, and sunflower plants about 55 kg. Even in the moist, cool climate of Leningrad the sunflower lost up to 20 kg. per plant.

Such copious loss necessitates a correspondingly energetic absorption of water, and indeed we find that the actual extent of the root system of these plants far surpasses the meagre relics obtained when a plant is carelessly removed from the soil. Exact determinations by **Rotmistrov** (1910) and **Modestov** (1915) in Russia and by **Weaver** (1919, 1920) in America have shown that even common crop plants, such as wheat or oats, have a root system reaching far below the ploughed surface of the soil to a depth of 1 or 2 metres, and spreading almost to the same extent (Fig. 1). The total length of the root system, including all its branches, may be hundreds of metres even in small plants, while in larger plants, e.g. corn (*Zea Mays*) or pumpkin (*Cucurbita Pepo*), it may measure thousands of metres. The actual absorbing surface is enormously increased by the development of root hairs.

Thus the destiny of water in the plant differs considerably from that of other absorbed substances: it is not only absorbed but also spent. We may therefore compare the water balance of a plant to the balance-sheet of a commercial firm. To regulate income and expenditure so as never to incur too great a water deficit—this is, figuratively speaking, one of the chief problems of a dry-land plant. The whole structure of the shoot may be regarded as a compromise between two opposing necessities—to increase the surface in contact with the atmosphere so as to extract the greatest possible amount of carbon dioxide, and at

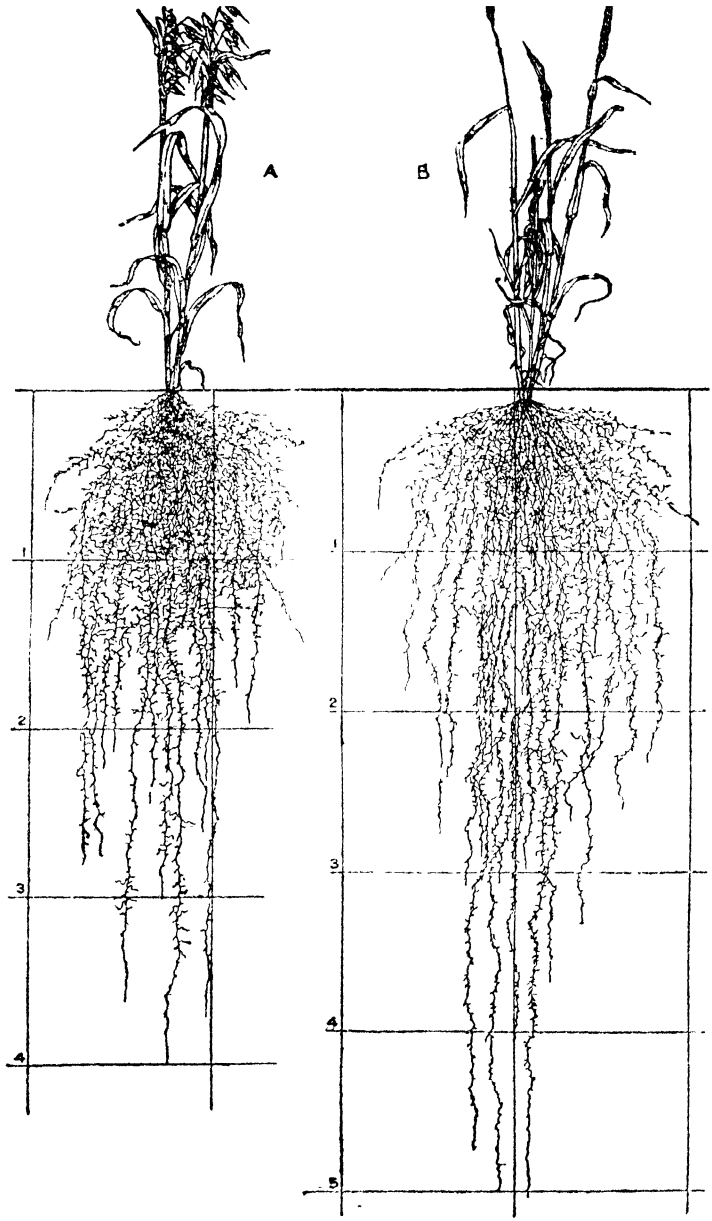

FIG. 1.—Oats (*A*) and wheat (*B*) during the flowering period, with root systems carefully dissected from the soil. Depths of root systems shown in feet (from Weaver).

the same time to limit this surface for the sake of decreasing the loss of water. Different plants solve this problem in different ways, and we shall see later how varied are the methods by which the same end is achieved.

This compromise, however, by no means always attains its object. Sometimes, especially during periods of drought, external conditions are so unfavourable that the loss of water considerably exceeds the intake. Then the water reserve decreases and the plant wilts. External wilting manifests itself by loss of turgor, but it is accompanied by more deeply seated internal changes. Prolonged wilting leads to a considerable disturbance in the vital processes of the plant, and to the destruction of its more tender parts, in particular of the root hairs. It checks the development of flower buds (which sometimes may even be shed) and leads (in cereals) to a poor yield of grain. Very severe and prolonged wilting may result in the complete death of the plant.

Different plants vary in their capacity for enduring drought. Plants from moist, shady habitats, which have rarely or never suffered from shortage of water, readily succumb to even a slight deficiency of water. On the other hand, plants of dry, open prairies, not to mention those of deserts and semi-deserts, have evolved various methods of resisting drought, and are able permanently to endure its effects. The study of the means by which the plant can resist the destructive influence of drought is of special importance to agronomy in dry localities. Drought resistance is one of the essential problems of general and applied plant ecology. It determines to a great extent the distribution of the native plants in the drier regions of the world, as well as the suitability of this or that crop plant for cultivation in so-called "dry farming" districts. But the question of drought resistance can only be dealt with after a more or less detailed study of the normal water balance of plants.

The first two parts of the present work are devoted to a study of the processes involved in this normal water balance. The first part deals with the absorption of water by plants;

the mechanism and laws of absorption, and its dependence on external conditions. The second part treats of the loss of water by the process of transpiration. Finally, in the third part are discussed the balance between income and expenditure; the conditions under which the equilibrium between absorption and transpiration is disturbed; and the means whereby plants can restore the equilibrium so necessary for their growth and development. This discussion will enable us to establish the concept of xeromorphic structure, and to ascertain the morphological, anatomical, and physiological peculiarities which help to determine the degree of drought resistance of plants.

PART I

THE ABSORPTION OF WATER BY THE PLANT

CHAPTER I

THE ABSORPTION OF WATER AND THE WATER RELATIONS OF THE PLANT CELL

The absorption of water by the cell. Suction pressure of the plant cell. Methods of determining suction pressure. The water relations of the living plant cell. The dependence of growth on the saturation of the cell. The absorption of water by the root. Exudation pressure and suction pressure of the root. Active and passive root suction. Amount of water absorbed by the root system.

THE absorbing surface through which water penetrates into the higher plant organism is the surface of the root system. Very young roots absorb water over their whole surface, but in older roots only the younger terminal portions function in this way; the older parts, being covered with a corky layer, no longer take part in absorption. The absorbing surface of the root consists of a layer of thin-walled cells, the piliferous layer, which in most cases possesses special outgrowths, the so-called root hairs. These root hairs adhere closely to the smallest particles of soil, thus producing intimate contact between the absorbing zone of the root and the surrounding medium.

According to a theory once widely accepted **(Cesalpino)**, but long since discarded, water enters the tip of the root by capillarity, through fine canals passing from the exterior to the vessels.[1] This theory is readily refuted by the facts of anatomy, for the piliferous layer of the root, which replaces the epidermis of the shoot, consists of closely fitting cells devoid of intercellular spaces. Further, the water stream, during its passage from the absorbing surface to the vessels, crosses the endodermis, which, like the piliferous layer, has no intercellular spaces. The radial walls of the endodermis are corky and therefore impervious to water,[2] so that water can only

[1 Cf. **De Candolle's** "Spongiole theory", an account of which is given in **Sachs's** *History of Botany*, p. 517, and **Reynolds-Green's** *History of Botany*, p. 249, Oxford, 1890 and 1909.—ED.]

[2 For a discussion of the composition and function of the "corky" Casparian strip on the radial and transverse walls of the endodermis, see **Priestley and North** (1922).—ED.]

cross the endodermis by passing through the actual cell cavities.

Thus the water entering the plant must needs pass through living cells, and this is true also of water escaping from the plant. The tips of the vascular bundles in the leaves are surrounded by continuous sheaths of parenchymatous cells, and the water, before being transformed into vapour, prior to the process of transpiration, must be absorbed from the vessels by living cells.[1]

The Absorption of Water by the Cell

The absorption of water by the living cell is one of the chief processes determining the water supply of the plant. As the laws governing this absorption are sometimes stated incorrectly, even in university textbooks, it is necessary to deal first with the entry of water into the living cell.

The process of absorption is usually explained as follows: the plant cell represents an osmometer filled with more or less concentrated cell sap. The walls of this osmometer, which consist of protoplasm supported by a cover of cellulose, are semi-permeable, i.e. they readily permit the passage of water, but check that of substances dissolved in it. If we immerse such an osmometer in pure water, the concentrations of the inner and outer solutions will tend to become equal, but owing to the properties of the plasmatic layer, equilibrium can be effected only by the entry of water into the cell. That is why every plant cell absorbs water, and the higher the concentration of the cell sap, the greater the absorbing power of the cell.

This explanation, however, contains a considerable error. To show that this is the case, it is only necessary to ask—how long will the absorption of water by the cell continue?

If the laws of diffusion alone are taken into account, this question must be answered as follows: the cell will absorb

[1 The radial cell walls of the bundle sheath are usually devoid of a Casparian strip: in such cases there is no actual proof that the escaping water does not travel through the cell walls.—Ed.]

water until the concentration outside and inside becomes equal. But if the cell membranes are completely semi-permeable and entirely prevent the exit of dissolved substances, it is evident that equilibrium will never be attained, and that the cell must absorb all the water from the container in which it has been immersed. If we imagine a container of unlimited dimensions, the cell walls will need to possess unlimited extensibility, which is impossible. It is necessary, therefore, to correct the explanation given above.

The cell sap is separated from the surrounding solution by two membranes, an outer one of cellulose and an inner of protoplasm. These two membranes differ in their properties. Current theories suppose that the protoplasm, having the property of semi-permeability, readily lets through water, but hinders the passage of substances dissolved in the water.[1] At the same time the protoplasm, being in essence a liquid, possesses no elasticity and does not resist the extension pressure of the cell sap. The outer cellulose layer (the cell wall), on the other hand, permits the passage of substances dissolved in the water, but possesses considerable toughness and elasticity. Its resistance to internal pressure is the greater the more it is distended, and as soon as the stress ceases the wall returns to its former dimensions, provided that the limits of elasticity have not been exceeded.

The presence of this tough, elastic wall serves to correct the usual explanation of the absorption of water by the cell. As the cell sap imbibes water it increases in volume and stretches the protoplasm, which in turn exerts a pressure on the cell wall.

[1 The semi-permeability of the protoplasm is relative, not absolute. Even in the same cell the protoplasm may be impermeable to some solutes and permeable in various degrees to others. The protoplasts of different cells also may differ in this respect. Many investigators believe that the permeability of the protoplasm is determined by the properties of the outer and inner surface layers of the protoplast (the so-called plasmatic membranes). Again, while as a rule the cell wall is relatively permeable, semi-permeable walls are not unknown. From the standpoint of permeability, the plant cell is undoubtedly a highly complex system, our knowledge of which is at present very incomplete. Various aspects of the subject are discussed by **Stiles** (1924).—ED.]

Owing to the elasticity of the wall, however, a counter-pressure on the cell contents is set up, acting in a direction opposite to that of the osmotic pressure, and tending to counterbalance it. As the volume of the cell increases, the pressure of the cell wall on the cell contents also increases, and finally the moment must come when the pressure of the wall, tending to expel water, counterpoises the osmotic pressure. The increase in volume now ceases, being replaced by a state of equilibrium that may be called the condition of complete saturation of the cell with water. If we denote the osmotic pressure of the cell sap by P, and the pressure of the cell wall on its contents (= wall pressure) by T, we obtain for the condition of complete saturation $P = T$, or $P - T = O$. In this condition water will neither enter nor escape from the cell, and no matter how high the osmotic pressure inside the cell, provided that this pressure is balanced by the counter-pressure of the distended cell wall, the cell will be in equilibrium with the surrounding pure water.[1]

This condition of complete saturation may be observed in submerged plants, such as unicellular or filamentous algæ, but is never found in dry-land plants. In the case of land plants, a portion of the osmotic pressure always remains unbalanced by the elastic counter-pressure of the cell wall. When such an unsaturated cell is immersed in water, this portion (S) is able to bring about a flow of water into the cell, and a certain increase in the dimensions of the latter. This distension continues until the increase in volume leads to such an increase of wall pressure that the osmotic pressure is counterbalanced. Under these conditions our equations will be:—

$$P > T \text{ or } P = T + S \text{ or, finally, } P - T = S.$$

Suction Pressure of the Plant Cell

The value of S has been called by **Ursprung (Ursprung and Blum,** 1916[a]) "suction force" (Saugkraft). This term is not

[1 If the cell is in equilibrium with a solution and not pure water, then $P - P_1 - T = O$, where P_1 is the osmotic pressure of the external solution.—Ed.]

quite correct, as we are dealing not with a force, but with a pressure which can be expressed in atmospheres like osmotic pressure and turgor pressure, the difference between which it represents. We may therefore use the term "suction pressure", as suggested by **Stiles** (1924).[1]

Up to the present little attention has been paid to the suction pressure of the cell, most investigators being interested only in the determination of the absolute osmotic pressure of the cell sap: indeed, until lately no methods had been devised for the direct determination of suction pressure. Only in 1916 was the first of a number of papers published, recording the results of

[1 The various pressures involved may be distinguished somewhat more fully. *Wall pressure* is the centripetally directed pressure of the distended cell wall, which compresses the protoplast and cell sap. *Turgor pressure* (in the sense in which the term is used by Lepèshkin, Thoday, Stiles, and others) is the centrifugally directed hydrostatic counter-pressure of the sap on the protoplast and cell wall. So long as the wall is distended, and whatever its degree of distension, turgor pressure is equal and opposite to wall pressure. These two pressures produce, in a saturated cell, a rigid condition known as *turgor*, *turgidity*, or *turgescence*. The *osmotic pressure* of a solution is "an equilibrium pressure, i.e. the pressure which must be applied to the solution to bring it into equilibrium with water" (**V. H. Blackman**, 1921, p. 108). *The suction pressure of a cell* is the pressure with which the cell tends to absorb or suck in water. It represents the difference between the osmotic pressure of the cell sap (which tends to cause water to enter the cell) and the wall pressure or the turgor pressure (which tend to force water out of the cell), i.e. $S = P - T$. The suction pressure of a cell is zero when the cell is completely saturated (i.e. is in equilibrium with water), but increases with the saturation deficit. Suction pressure is thus a property or condition of the cell itself, its magnitude being definitely related to, and varying with, the water deficit of the cell (cf. **Thoday**, 1918, also **Ursprung**, 1926, p. 4). **Stiles** (1924, p. 98), however, defines suction pressure as "the net pressure sending water into the cell." According to him, suction pressure is the resultant of all the pressures involved, including the osmotic pressure of the external solution. This use of the term is open to objection, for it implies that $S = O$ whenever the cell is in a state of equilibrium. This is not so if the cell is in equilibrium with a solution. In this case the suction pressure of the cell is balanced by the osmotic pressure of the external solution, but that it still exists is shown by the fact that on replacing the solution by a weaker solution or by water, the cell again absorbs water. It seems better, therefore, to limit the term "suction pressure of a cell" to the sense $S = P - T$. If, however, $T = O$, then $S = P$: hence it is admissible to speak of the suction pressure of a solution (= its osmotic pressure) or of a hydrophilous colloid (= its imbibition pressure); the pressures in both cases varying, as in the case of a cell, with the degree of saturation.—ED.]

thorough investigations by **Ursprung and Blum** (1916, 1918, 1919, 1920, 1921, 1924). These papers gave methods for determining the suction pressure of the cell and a whole series of data concerning the strength of this pressure in different organs of the plant.

Methods of Determining Suction Pressure

To find the suction pressure of the cell we must determine the osmotic pressure of the cell sap, and subtract from it the opposing pressure of the cell wall. It is not possible, however, to find both these magnitudes directly, but by patient, accurate work Ursprung and Blum succeeded in devising methods for the exact determination of the suction pressure of the cell.

1. *Indirect method by plasmolysis.*—In the first place it must be kept in view that the osmotic pressure, as determined by the plasmolytic method, always exceeds the actual pressure, for prior to visible plasmolysis a part of the water escapes from the cell and the volume of the latter decreases. Hence in exact determinations of the suction pressure of the cell this decrease in volume must be taken into consideration. Ursprung and Blum succeeded in making such exact determinations by means of consecutive minute measurements of the volume of the cell.

They first measured the unaltered volume[1] of the cell, examining it under a microscope in a drop of liquid paraffin. In this neutral substance the cell can live for a long time without increasing in volume through absorption, as would have been the case in water, or decreasing in volume through evaporation, as would have been the case in air. They then plasmolysed the cell and measured its volume in the plasmolysed state, simultaneously determining the osmotic pressure of the cell sap at the moment of plasmolysis. Taking into account the

[1 In most cases Ursprung and Blum measured areas rather than volumes, making high magnification tracings of the outlines of the cells with a camera lucida, and measuring the areas so obtained with a planimeter.—Ed.]

decrease in volume during plasmolysis, it is possible from these data to calculate the actual osmotic pressure of the sap before plasmolysis.

The wall pressure may be determined in a similar way. In plasmolysis it is at zero, while in the condition of complete saturation with water it is equal to the full osmotic pressure of the cell sap with which it is in equilibrium. The measuring of the cell volume in water, i.e. in the condition of maximum turgor, enables us to calculate the concentration of the cell sap during full saturation of the cell with water, and consequently the maximum distension of the cell wall. If we assume—though the assumption is not supported by direct experiment—that the change in wall pressure, from zero during plasmolysis to its maximum during full saturation, is directly proportional to the increase in volume of the cell as it imbibes water, we are able to calculate the second value, i.e. the degree of distension of the cell wall when the cell possessed its original volume, as in liquid paraffin at the beginning of the experiment. Having found both values—the osmotic pressure of the cell contents and the wall pressure—it is easy to calculate from the difference between the two the suction pressure of the actual cell in its unchanged condition.

This is the first, rather complex, indirect method of determining the suction pressure of the cell by plasmolysis. The second method suggested by **Ursprung and Blum** is somewhat simpler, and may be called the equilibrium method.

2. *The equilibrium method.*—The basis of this method is similar to that of the plasmolytic method of determining the concentration of cell sap. In the latter method, by a series of tests with external solutions of different concentrations, we find the concentration which will cause the protoplasm just to begin to shrink away from the cell wall. To find the suction pressure of the cell we proceed similarly to ascertain the concentration of an external solution[1] in which the volume of the cell remains

[1] The solute must be one to which the protoplast is impermeable: "solutions of sucrose are likely to be the most generally useful" (**Stiles**, 1924, p. 123).—ED.]

unchanged. The only complication in comparison with the plasmolytic method of determining isotonic coefficients, is the necessity of a preliminary measurement under a microscope of the exact volume of the cell to be investigated: this is carried out as before, in liquid paraffin. Then, after immersion in a solution of one concentration or another, the cell is measured a second time in order to see whether its volume has decreased or increased. If the volume has decreased, the suction pressure of the surrounding solution is greater than that of the cell, and the solution has drawn water from the cell; if the volume has increased, the cell has imbibed water from the solution. If the volume of the cell has remained practically or entirely unchanged, then the suction pressure of the cell is in equilibrium with that of the solution, and may be calculated either in equivalents of saccharose or in atmospheres.

The details of this method will be found in **Ursprung and Blum's** papers (especially 1916 and 1918), also in **Grafe** (1920). **Stiles and Jørgensen** (1917) employed a similar method in determining the suction pressure of massive parts of plants. Strips cut from potato tubers were placed in solutions of different concentrations, and after weighing it was found that they showed neither loss nor increase of weight[1] in a $0{\cdot}25N$ solution of saccharose; this corresponds to a suction pressure of about $6{\cdot}5$ atmospheres. For the root of carrot a considerably greater magnitude, about 17 atmospheres, was established. The suction pressure naturally depends to a great extent on the previous history of the investigated material, and especially on the degree of desiccation.

Recently (1923) **Ursprung** has considerably simplified his equilibrium method of determining suction pressure, so that it is now possible to carry out such determinations even under field conditions.

This simplified method consists in determining the linear dimensions, not of single cells, but of strips of tissue cut from

[1 **Stiles and Jørgensen** regard it as simpler, in the case of tissues, to use weight as a criterion instead of volume.—ED.]

some plant organ or another. In measuring the length of these strips a stage micrometer graduated in 1/10 mm. and a low power microscope or even a strong hand-lens (× 16) is used. The strips are cut with a sharp instrument, and the distance between the two ends is measured first in liquid paraffin, and afterwards in saccharose solutions of different concentrations. The concentration in which no change of length is observed, or where this change is least, corresponds to the average suction pressure of the whole strip. The petals of flowers are especially convenient for such determinations. In leaves, the veins may prevent the contraction of the parenchymatous tissue; it is therefore best to cut the strips across, not parallel to, the veins. This modified method was successfully used by **Ursprung** (1925) in studying the diurnal and annual periodicity of suction pressure, and in establishing the connexion between the value of suction pressure and habitat conditions. The results of these determinations will be mentioned later.

The Water Relations of the Living Plant Cell

So far we have regarded the protoplasm of the plant cell merely as an osmotic partition, without discussing the changes that take place in it under the influence of the varying concentration of the cell sap. Until very recently practically no attention had been given to these changes in spite of their essential importance, but the investigations of **H. Walter** (1923 and 1924) have done a good deal towards filling the gap. Let us now consider this highly important but so far insufficiently studied question.

The protoplasm represents a complex mixture of colloidal substances which for the most part belong to the group of hydrophilous colloids, i.e. those which are capable of swelling in water. The imbibition pressure with which they can absorb water we may call the suction pressure of the swelling colloids. Just as the osmotic pressure of a solution decreases with dilution, so the suction (or imbibition) pressure of a colloid

diminishes as it becomes saturated with water, being finally reduced to zero.

If we imagine a cell in the condition of complete equilibrium, the suction pressure of the cell sap must be equal to the suction pressure of the protoplasm. The cell wall, too, represents a swelling colloid and is also in equilibrium with the plasma and the cell sap. When the cell loses water through surface evaporation, the cell wall begins to dry first and, its suction pressure increasing, it absorbs water from the plasma, which in turn withdraws water from the vacuole.

Thus, when a cell evaporates water, the increased concentration of the cell sap is not directly due to this evaporation, but is the result of the balancing of the suction pressures of the colloids of the cell wall and the protoplasm on the one hand, and that of the cell sap on the other. Conversely, every change in the suction pressure of the cell sap, for instance in plasmolysis, involves corresponding changes in the suction pressure of the plasma. As the suction pressure of the plasma is determined by its degree of swelling, or saturation with water, it is obvious that an increased concentration of the cell sap leads to a decrease of swelling of the plasma (Entquellung), and conversely, the saturation of the cell with water increases the degree of swelling of the protoplasm.

The degree of swelling of the protoplasm has in turn a great influence on all vital processes of the cell. This is especially well seen in the germination of seeds. Dry grain, entirely unswollen, and containing only hygroscopic water, shows no signs of vital activity. As the well-known observations of **Kolkwitz** (1901) have shown, a kilogram of barley grain containing 10–12 per cent of water, exhales during 24 hours only 0·3–0·4 mg. of carbon dioxide; with 14–15 per cent it gives off 1·3–1·5 mg., while with a further increase of water content respiration increases sharply, reaching with 33 per cent, when the grain is almost completely swollen, 2,000 mg., or 2 gr., during 24 hours. As the grain ripens, the reverse process takes place: a decrease in the volume of the plasma and a corresponding decrease in

the intensity of respiration. **Iljin** (1923) has observed that the relative exhalation of carbon dioxide was: with 203 gr. of water (to 100 gr. of dry substance), 63·4; with 100 gr. of water, 21·9; with 57, 9·7; with 35, 3·1; and with 30, 1·0. With the changes in respiration corresponding changes occur also in all other vital functions of the cell.

Direct measurement of the degree of swelling of the protoplasm in the plant cell is extremely difficult, if not impossible. **Walter** substitutes for this the measuring of the suction pressure of the corresponding solutions in which he immerses the cells (for every strength of suction [= osmotic] pressure corresponds to a definite degree of swelling). For these measurements, expressed in atmospheres, he substitutes in turn the pressure of water vapour in, and the relative humidity of, the air above the surfaces of the corresponding solutions. This method depends on the fact that for every concentration and every osmotic pressure of solutions, and for every suction pressure, whether of solutions or of swelling colloids, there is a corresponding vapour pressure, which may be expressed in percentages of full saturation. Having made the corresponding calculations (cf. **Walter**, 1923), Walter found that: 100 per cent relative humidity corresponds to a suction pressure of 0 atmospheres, i.e. pure water or the condition of full saturation of the colloid; 99 per cent, 14 atm.; 98 per cent, 27 atm.; 97 per cent, 40 atm.; 96 per cent, 52 atm.; 95 per cent, 65 atm.; and so on. That is, every decrease of 1 per cent in relative humidity corresponds to an increase of suction pressure of approximately 13–14 atm.

The Dependence of Growth on the Saturation of the Cell

These calculations supplied **Walter** with a simple and convenient method of establishing the dependence of the growth of the cell, at least in lower plants (bacteria and mould fungi) on the degree of swelling of the protoplasm. His method was

to cultivate these organisms in a hanging drop of nutrient gelatin in a closed atmosphere over the surface of a solution of sulphuric acid of different concentrations. Over pure water he obtained a relative humidity of 100 per cent; over 2 per cent sulphuric acid (2 gr. of anhydrous H_2SO_4 to 100 gr. of solution), 99 per cent; over 4 per cent, 98 per cent; over 6 per cent, 97 per cent; over 10 per cent, 95 per cent; over 16·32 per cent, 90 per cent; over 22·63 per cent, 85 per cent; over 26·75 per cent, 80 per cent, etc. The degree of swelling of gelatin and the concentration of salts in it were readily proved to correspond to the concentrations of sulphuric acid used in the experiment. It could therefore be assumed with certainty that the degree of swelling of the protoplasm of the cultivated micro-organisms was also in equilibrium with the surrounding medium.

Experiments with different moulds, yeast, and bacteria have shown that for such organisms there is a limit of relative humidity, below which the organism can no longer grow. This limit is different in different organisms. The lowest value, about 85 per cent, corresponding to a suction pressure of 200 atmospheres, was found in the common moulds, *Aspergillus* and *Penicillium*. Mucors and yeast do not descend below 95–90 per cent (65–142 atmospheres), while bacteria are only able to grow with a relative humidity above 96 per cent, i.e. a suction pressure not exceeding 50 atmospheres. These observations explain why bacteria under natural conditions always grow on more or less moist substrata, while in drier habitats only moulds are met with.

Similar experiments with higher plants were more difficult, but preliminary experiments have shown that the rootlets of germinating seeds of water-cress (*Nasturtium officinale*) and peas were only able to grow in an atmosphere with a relative humidity not less than 97 per cent, or even 98 per cent; a fair development was shown at 100 per cent. These facts indicate to how great an extent the important function of growth is determined by the degree of swelling of the protoplasm, and

how quickly growth ceases as soon as water deficiency finds its expression in a suction pressure of 25–40 atmospheres. Now the atmosphere surrounding dry-land plants rarely attains a relative humidity of 97–98 per cent and may often sink to 50–30 per cent, or even as low as 10 per cent. We can understand, therefore, the necessity of such anatomical peculiarities of the plant as cuticle or cork, which covers the aerial parts, and prevents dry air from penetrating directly into the depth of the tissues, as well as the immense quantities of water that must pass through the plant in order adequately to maintain the swelling of the protoplasm of its cells. We can also understand the injurious consequences involved when, on account of drought, the plant is unable to maintain a sufficient water supply in its growing parts, and the protoplasm suffers too great a degree of water deficit. We shall return to these questions more in detail in the third part of this work, when we have studied the various aspects of the normal water balance of the plant.

The Absorption of Water by the Root

We have examined the conditions under which the plant cell develops suction pressure. These conditions are a lack of saturation with water and the presence of a solid elastic wall lined with a more or less semi-permeable layer of protoplasm. The limit of suction by the isolated cell is reached when it becomes saturated with water, and further increase in volume is prevented by the counter-pressure of the cell wall.

The conditions under which water is absorbed by the root are considerably more complex. Let us take a plant, preferably one grown in water-culture, and place its root system in a so-called potometer—an apparatus for measuring absorption. This apparatus consists of a glass container (of any shape) with a close-fitting stopper, preferably of rubber, through which passes the base of the stem of the plant, the stem being cut off just

above the stopper (Fig. 2). A graduated horizontal glass tube of narrow bore, calibrated as accurately as possible, is fixed to the side or to the bottom of the container. The whole apparatus is filled with boiled water, so as to exclude even the smallest bubble of air. The manifold types and shapes of potometers will be dealt with later; for the moment we are concerned only with the principle of the apparatus. The water absorbed by the root system is drawn from the container, which in turn draws water from the calibrated tube. From the movement of the terminal meniscus of water in the tube the amount of water absorbed by the root system may be determined with sufficient accuracy.

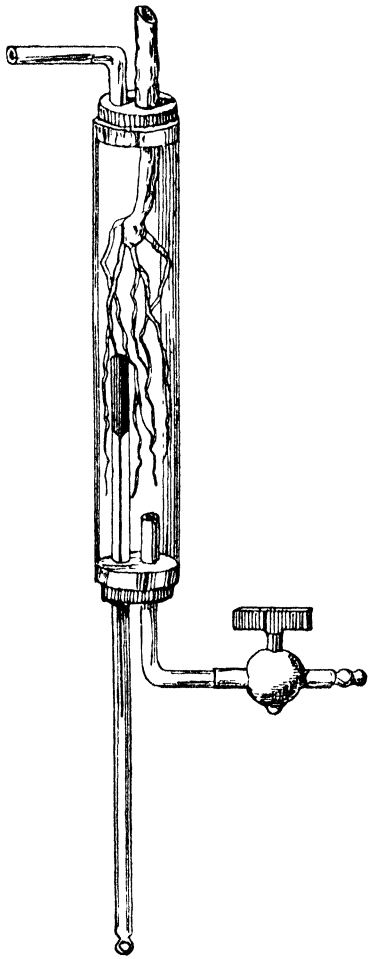

FIG. 2.—Vesque's first potometer.

EXUDATION PRESSURE AND SUCTION PRESSURE OF THE ROOT

If the rules given above for a cell immersed in water could be applied to the root system of the plant, suction should cease when this system is once saturated with water. This, however, is not the case, for after a sufficient lapse of time such a root system will have drawn all the water from the container, the absorbed water flowing from the cut end

of the stem. With an arrangement for collecting the water flowing from the cut, we could convince ourselves that the amount exuded is the same as the amount of water absorbed from the potometer.

Thus the root system of a plant not only absorbs but also expels water. It represents as it were a pump which draws water from the soil and drives it into the vessels, through which it ascends and spreads all over the plant. It is obvious that our conception of the absorption of water by an isolated plant cell must be somewhat modified when applied to the cells of the root.

Unfortunately it must be admitted that up to the present we have no generally accepted and proved explanation of the mechanism by which such a stream of water could pass in one direction through the cells of a plant. As **V. H. Blackman** (1921, pp. 114–15) remarks: "A number of mechanisms can, however, be suggested by means of which this exudation could be brought about, though how far such mechanisms are actually at work in the living cell it is at present impossible to say."[1]

As we do not know the exact mechanism by which the root absorbs water, we are unable to calculate the value of the suction pressure of the root or root hair. In order, therefore, to obtain a clearer conception of this pressure we must seek direct or indirect methods of determining it.

It would seem that the simplest method is to determine the suction pressure of the root by measuring the suction pressure of the cells of its piliferous layer. **Ursprung and Blum** (1921[b]) adopted this method, and regarded it as the most reliable. In their opinion the suction pressure of the root hairs and of the other absorbing cells of the root ought in general to be equal to the resistance to absorption shown by the surrounding medium: "If the suction pressure of the root hair were greater than necessary it would absorb more water than it transmits, and its suction pressure should therefore decrease automatically

[1 The pressure under which this exudation takes place is known as root pressure or exudation pressure.—ED.]

until it reaches the required level; conversely, a suction pressure that is too low should—if the plant is to preserve its turgidity—automatically increase until the root hair absorbs as much as it passes on" (p. 142).

Ursprung finds in his experiments, a few of which are given below, a confirmation of this view. In one experiment, the absorbing cells of the roots of *Vicia Faba*, grown in moist sawdust, displayed a suction pressure of 1·1 atmospheres; when shifted into water, their suction pressure fell after 5 hours to 0·8 atm.; after 8 hours to 0·3 atm.; after 23 hours to zero. In another experiment the original strength was 1·6 atm.; after 6 hours in water, 1·3; after 22 hours, 0·8; after 50 hours, 0·0.

This decrease in the suction pressure of the root after transference to water depends in the first instance on the increase of the cell volume, which is followed by some decrease of the general concentration of the cell sap. Thus, in an experiment in which, in addition to the suction pressure (*S*), the osmotic value of the cell sap (*O*) was determined by plasmolysis by means of saccharose solutions, the following results were obtained:—

TABLE I

	S	*O*
	Atmospheres	Gr. molecules of saccharose
In sawdust	1·4	0·33
In water—		
After 18 hours	0·3	0·33–0·32
After 4 days	0·0	0·28
After 93 days..	0·0	0·26

If **Ursprung** transferred the roots from sawdust to solutions of different concentrations instead of to water, the suction pressure of the cells gradually changed and finally (if the solu-

tions were not too strong) became equal to the osmotic pressure of the external solution. For example, roots in sawdust with a suction pressure of 1·1 atmospheres, when transferred to 0·02 mol. solution of saccharose, the osmotic pressure of which is 0·5 atm., already showed on the following day a decrease in suction pressure to 0·5 atm. This strength, which is the same as that of the external solution, was maintained in the roots for the subsequent 14 days of observation. During this period the stem lengthened by 17 cm. and three new leaves were developed.

In another experiment, a root with a suction pressure of 1·1 atm. was transferred from sawdust to 0·04 mol. solution of saccharose with an osmotic pressure also of 1·1 atm. During a fortnight's observations the suction pressure of the root remained unchanged (i.e. at 1·1 atm.), while the plant developed as in the preceding experiment.

If roots were transferred to solutions of a concentration higher than the suction pressure of the roots, the results were more complex. For instance, when roots (with a suction pressure of 1·4 atm.) were immersed in 0·20 mol. solution of saccharose (with an osmotic pressure of 5·3 atm.), all the cells of the absorbing zone died; nevertheless growth continued and in a few days a new absorbing zone developed. On the fifth day the suction pressure of the new cells was determined and proved to be 5·7 atm., i.e. somewhat higher than the concentration of the surrounding medium. The second and third determinations, made 6 and 20 days respectively after the first, revealed a strength of 5·2 atm., which was practically equivalent to the osmotic pressure of the medium.

From these experiments **Ursprung** draws the conclusion that the suction pressure of the root is equal to the suction pressure of the surrounding medium, at least under the conditions of normal water supply. He thinks that it is possible to find the resistance to absorption shown by the soil by determining the suction pressure of the root. In my opinion this is not quite correct. A root immersed in pure water, the suction

pressure of which is 0, absorbs this water vigorously, though the suction pressure of the root cells, according to Ursprung, should be in this case also equal to 0. Evidently the actual suction pressure of these cells in regard to the surrounding medium will be higher than that obtained in the experiment, but how much higher is unknown. If we accept **Priestley's** hypothesis (of the mechanism of exudation pressure), the cells of the absorbing layer are actually saturated with water and in equilibrium with the surrounding medium, root suction being induced by the more concentrated solution in the cavities of the root vessels. The value of the suction pressure of the root, then, would be independent of that of the surface cells, which might even possess no suction pressure at all.

Priestley has enunciated this hypothesis so clearly and convincingly in a series of papers (1920, 1922), that it may be called by his name, though similar suggestions had previously been made by other authors (e.g. **Atkins**, 1916),[1] and though it is

[1 **Priestley** postulates "a supply of solutes to the xylem which maintains the sap at higher concentration than the dilute solution bathing the protoplasts at the surface of the root". He suggests that this supply is ensured by (*a*) the confining of the available solutes within a relatively impermeable endodermal cylinder, and (*b*) the presence in the neighbourhood of the xylem vessels of relatively permeable protoplasts. Similarly, according to **Atkins** (1916, pp. 201–3), the osmotic pressure of the xylem sap is lower than that of the cortical cells of the root, but higher than that of the soil solution. Atkins suggests that the cortical cells act as a single, complex semi-permeable membrane, through which the xylem sap acts osmotically, causing a flow of water from the soil to the vessels, the resulting hydrostatic pressure giving rise to the phenomenon of root or exudation pressure.

Probably the suction pressures of the absorbing cells of the root undergo more or less continual adjustment to the resistance of the soil, absorption as well as translocation of water in the root cells depending on the existence of a gradient of suction pressure in the root system. Atkins and Priestley both suggest that the concentration of the xylem sap may be important in this connexion. **Ursprung and Blum** claim to have obtained direct evidence of such a gradient of suction pressure in the living cells of the root of *Vicia Faba*. They state that the suction pressure rises from 1·1 atm. in the piliferous layer to 4·1 atm. in the inner cells of the cortex. In the cells of the endodermis the mean suction pressure drops to 1·9 atm. But they can still absorb and transmit water, as the pressure at the outer surface of these cells is 4·7 atm., that at the inner surface being only 0·5 atm. According to these authors (1926, pp. 26–7), the parenchyma cells bordering on the xylem vessels show similar polar differences; on the

really an application of **Pfeffer's** original scheme. According to **Priestley's** hypothesis, the maximal value of the suction pressure of the root would depend on the osmotic concentration of the sap in the vessels of the root and its actual value on the difference of concentration between the contents of the vessels and the surrounding medium. If in this case we make use of the same considerations as in determining the suction pressure of the individual cell, then, having found the concentration of the external solution at which the suction of the root just stops, we could regard this as equal to the full suction pressure of the root and thus obtain the desired value.

It is very difficult to find directly the concentration of an external solution that would just stop root exudation. **Sabinin** (1925), therefore, during his investigation of the osmotic properties of the root system, made use of an indirect method. He determined the different rates of exudation of sap from decapitated seedlings of different plants, when their root systems were immersed, first in water, and afterwards in very dilute solutions.

Assuming the rate of filtration of water through the plasma membranes to be proportional to the pressure under which the movement of the exudation current takes place, and denoting this exudation pressure by Px, and the observed rate of exudation when the roots are in water by A, we have $A = K_1 Px$.

If the water is replaced by a solution with an osmotic pressure

outer side 4·5 atm., and on the inner a *negative* suction pressure of about − 0·35 atm. The authors conclude from this that these cells act as a combined suction and force pump, absorbing water on one side and pressing it into the vessels on the other. **Prof. Thoday** has kindly contributed the following suggestive paragraph: "The gradient of suction pressure must adjust itself from point to point to the resistance offered to filtration, until there is a steady flow through the cortex converging on the central cylinder. In this condition equal amounts of water would be crossing concentric zones of the cortex in equal times; but as the surface presented by each zone is proportional to its radius the amount of water crossing *unit area* will diminish outwards and the necessary gradient of suction pressure diminish correspondingly. As the external surface of the root is still further increased by the presence of root hairs, the difference of suction pressure between root hairs and soil should be minimal. This may explain why **Ursprung and Blum** found the suction pressure of the root hairs so closely adjusted to that of the medium in which they were immersed."—ED.]

Pe, the value of the observed rate of exudation (B) in the solution is expressed by the formula, $B = K_2(Px - Pe)$. B is negative when $Px < Pe$, and becomes zero if $Px = Pe$. If the constants K_1 and K_2 are equal, then

$$A : B = Px : (Px - Pe). \quad \text{Hence } Px = \frac{A \times Pe}{A - B}.$$

This formula enables us to calculate the value of *Px*. It is evident that *Px* is equivalent to the osmotic pressure just balancing the exudation pressure.

Sabinin has made numerous determinations of the value of *Px* in different plants. Expressed in atmospheres this value is considerable, ranging as a rule from 0·5 to 1·5 atm. even in juvenile plants.

For *Impatiens Noli-me-tangere* the exudation pressure varied between 0·44 and 1·48 atm.; for *Impatiens Balsamina* from 0·36 to 1·53 atm.; for wheat seedlings from 1·27 to 2·45 atm.; for corn seedlings from 1·46 to 2·14 atm.; and for *Xanthium Strumarium* from 0·43 to 2·18 atm.

The determinations of the values of exudation pressure were verified by measuring the osmotic pressures of the exuded sap by the cryoscopic method.

TABLE II

Plant	Exudation Pressure in Molecules of Glucose	Depression of Freezing Point of Sap	Osmotic Pressure of Sap in Atmospheres calculated from Depression	Exudation Pressure in Atmospheres calculated by Formula
Xanthium Strumarium ..	0·019	0·056	0·67	0·43
Impatiens Balsamina ..	0·016	0·031	0·36	0·35
Zea Mays	0·07	0·13	1·46	1·53

It was found that the value *Px* calculated by the formula agreed fairly well with the value of the osmotic pressure of sap found by the cryoscopic method.

Active and Passive Root Suction

It is important to note that in addition to the suction developed by the root system, due to osmotic phenomena occurring in the cells and vessels of the root itself, a prominent rôle in the life of the plant is played by another suction which develops in the transpiring leaves, and which may be transmitted to the roots through the vascular system. Many authors, for instance **Renner** (1915) in his survey in *Handwörterbuch der Naturwissenschaften*, strictly distinguish these two kinds of suction by the root, calling the first active, and the second passive suction. In practice it is not easy to decide where one ends and the other begins. Usually in daytime, owing to a sharp increase of the suction pressure of the leaves, there is a prevalence of passive suction, while during the night active suction prevails, which may manifest itself in the expulsion of superfluous water through the hydathodes. The interference due to passive suction still further complicates the determination of the active suction pressure of the root, and we must admit that up to the present we have no really exact determinations of this important quantity, and not even entirely satisfactory methods for its determination.

Amount of Water Absorbed by the Root System

Let us turn now to another question, namely, the amount of water absorbed by the root system and the methods of determining this amount.

So far as roots immersed in water are concerned, this determination presents no difficulties. For this purpose potometers are usually employed, of sizes and shapes depending on the dimensions of the root system and the special purposes of the investigation.

Vesque (1876) was the first to investigate the absorption of water by roots by the potometric method, and to discuss in detail the principal sources of error connected with this method.

14930

His apparatus, the prototype of all later potometers, was of somewhat simple construction (Fig. 2, p. 48). It consisted of a glass cylinder, 10 cm. in length and 15 mm. in diameter, the upper part of which was closed with a two-hole rubber stopper. The plant was introduced through one of the holes (for which purpose a cut was made in the stopper with a sharp razor), while

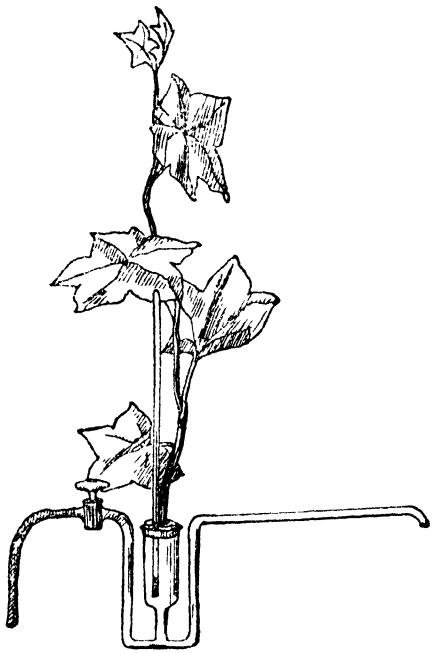

FIG. 3.—Vesque's second potometer.

in the other a graduated capillary tube, for observing the amount of absorbed water, was inserted. The lower end of the cylinder was also closed with a two-hole stopper, one hole receiving a thermometer, the other a tube provided with a tap, through which the water could be changed.

In his second memoir (1878) **Vesque** somewhat modified his apparatus (Fig. 3). The upper end of the cylinder is closed as before with a two-hole stopper, this time bearing the plant

and the thermometer. The narrowed lower end communicates directly with a T-tube. One limb of the T-tube is continued as a capillary for observing the movements of the meniscus, the other ends in a tap for changing the water. The advantages of this modified form of the apparatus are the omission of the lower rubber stopper, and a reservoir of somewhat smaller capacity. Temperature considerations make the use of a small reservoir advisable, for the cylinder together with its capillary act like a thermometer filled with water instead of mercury. The greater the reservoir and the smaller the bore of the capillary tube, the greater the disturbances of the readings of the capillary caused by fluctuations of temperature and consequent changes in volume of the water in the reservoir. As it is important for an exact determination of the absorption of water to use a very narrow capillary tube, the errors arising from fluctuations of temperature can only be reduced by diminishing the dimensions of the reservoir.

Another important fact to be taken into account is that only plants grown in water-cultures are suitable for potometer experiments with roots. If plants grown in soil are used, the results may be considerably vitiated, as roots are in general extremely susceptible to such a change of environment. Moreover, in digging up a plant it is impossible to avoid injury to the roots and the tearing off of some of the smallest branches. Roots transferred from soil to water usually suffer considerably; the young portions die off, and it is only after several days that new "water roots", adapted to the changed environmental conditions, appear on the older portions.

But the chief obstacle to an investigation of the absorption of water by roots does not lie so much in these more external complications, as in the difficulty of determining the respective limits of the active suction of the root system itself on the one hand, and on the other the passive suction transmitted to the roots from the transpiring leaves (see above). Investigators have therefore made use of isolated root systems from which the stem has been removed. The amount of water absorbed by

such a root system is readily determined, either by the potometric method or by collecting and measuring the sap flowing from the cut end. This seems to be the simplest and most reliable method of obtaining a clear conception of the amount of water absorbed by the root system itself.

Such determinations were made by **Sachs** (see **de Vries**, 1874), who compared the amount of water absorbed by the root systems of various plants with that absorbed during the same time by their aerial parts, cut off and placed in water. His experiments proved that the amount of water absorbed by active root suction is insignificant as compared with that drawn in by the suction of the leaves. For instance, in five days the roots of tobacco yielded only 16 cc. of water, while the shoot absorbed over 200 cc. during the same period.

It might be supposed that the small amount of water absorbed by the roots could be attributed to a rapid falling off of root activity owing to the separation of the root and shoot systems, and that absorption by the roots of uninjured plants might be more energetic. There are methods, however, of determining the amount of water absorbed by the roots of uninjured plants. For this purpose a plant showing marked guttation must be taken, e.g. balsam (*Impatiens Balsamina*), or a young corn plant (*Zea Mays*). If the experiment is conducted in a saturated atmosphere in order to check transpiration, and the exuded drops of water collected from the leaves, e.g. with a capillary pipette, it will be found that in this case also the supply of water from the roots is quite inconsiderable, measurable as a rule only in fractions of a cubic centimetre. Only a few plants, as for instance *Colocasia antiquorum*, famous for its abundant guttation, exude water so vigorously that drops fall in rapid succession from the tip of the leaf, so that during 24 hours up to 200 cc. may be gathered from one leaf. But such cases are rare exceptions and are met with chiefly among plants of moist and shady habitats.

The above experiments show that the amount of water obtained by the plant through active root suction is inconsider-

able in comparison with that sucked in passively by the roots, under the influence of the strong suction transmitted to the roots from the transpiring leaves.

It would not be safe, however, to draw the conclusion that the active suction of the root system plays a negligible rôle in the life of the plant. We shall see later that during the day a very considerable water deficit not infrequently arises in the plant, and that this deficit is compensated during the night. In this compensation, so important for the normal functioning of the plant, root pressure, in all probability, plays a prominent part.[1] This is shown by the fact that wilted plants recover more rapidly when their roots are watered than when their shoots are cut off and placed in water, though it might be expected that in the latter case access of water to the leaves would be easier.

[1 Root pressure is probably of importance also in bringing about the gradual filling up with water of the wood of deciduous trees during the relatively dormant period of autumn or even winter. Cf. **Farmer** (1918, pp. 245–6).—ED.]

CHAPTER II

THE ABSORPTION OF WATER FROM THE SOIL

The absorption of water under natural conditions. The water relations of different soils. The demands of different plants on soil moisture. The wilting coefficient of the soil. The resistance of the soil to root suction. Transpiration and the translocation of water in the soil.

The Absorption of Water under Natural Conditions

So far, in studying the absorption of water by the root, we have considered only the comparatively simple case, seldom realized in nature, when the root is immersed in water or in a solution, and when the sole resistance to this absorption of water is the osmotic concentration of the solution. We have seen that under these conditions, the higher the concentration of the surrounding medium, the greater must be the suction exerted by the root in order to overcome this resistance of a purely osmotic and therefore readily measurable nature.

The absorption of water from the soil, however, presents a much more complicated problem, which as yet cannot be completely analysed. The soil represents an extremely complex medium, consisting of small particles of various shapes and different properties. Water is retained by these particles, partly on their surfaces by adsorption, and partly—in the case of colloids—as water of imbibition: water may also be held between the particles of the soil by capillarity. Different soils may be distinguished by the size as well as by the chemical composition of the component particles, and it is evident that the properties of these soils in respect of water will also be different. The sum of all the forces retaining water in the soil may be called the *water retaining capacity* of the soil (**Kossovich**, 1916, p. 229). This water retaining capacity is in a high degree antagonistic to root suction. In a sense it may even be said that a struggle for water takes place between the root and the surrounding particles of soil.

This struggle for water was clearly recognized by **Sachs** as early as 1865, in his *Handbuch der Experimental-Physiologie.* Fig. 4 is a reproduction of his classical drawing. Sachs pointed out that soil consists of a multitude of microscopically small particles, which retain water at their surfaces by virtue of molecular attraction. In addition to this, water partially or completely fills the soil capillaries. A root hair readily absorbs the capillary water, as well as a portion of the water surrounding the particles. But the thinner the surrounding films become,

FIG. 4.—A root hair in the soil (after Sachs).

the more firmly are they held by the soil, until finally a state of equilibrium is reached, when the root hairs can no longer absorb water from the soil.

Sachs's explanation of the relations between root hair and soil clearly suggests that different soils must vary in regard to the readiness with which they yield up water to the roots which penetrate them. This would depend partly on the size of the soil particles, and partly on the amount of humus and other colloids capable of imbibing water, present in the soil. On the other hand, the suction pressure of the root cells is also variable, and must increase with the resistance to absorption of the soil particles. This increase of the suction pressure of the root has,

however, definite limits. We have seen above that in wilting, i.e. complete loss of turgor, the suction pressure of the cell is equal to the suction pressure of its contents, in other words, to the osmotic pressure of the cell sap. If in this condition the cell continues to lose water, its suction pressure increases still further, but very slowly, with the increasing concentration of the cell sap.

Thus the state of wilting indicates that the resistance of the soil to root suction has increased to such an extent that water is practically no longer absorbed by the root. It is true that if transpiration is excessive, wilting may set in earlier, i.e. while water is still being absorbed, but in inadequate quantities. In this case, when transpiration lessens towards evening, or if the plant is artificially protected, recovery may take place without an increase of soil moisture. But setting aside cases of wilting due merely to a preponderance of output over intake of water, we may confine our attention to the wilting conditioned by a complete interruption of the water supply absorbed through the roots. In recent literature this is known as *permanent wilting* (see **Caldwell**, 1913).

The Water Relations of Different Soils

Sachs (1859) clearly understood the importance of wilting as an indication that the water supply of the plant had ceased. By means of wilting tobacco plants he made the first attempt to compare the water relations of three kinds of soil—coarse quartz sand, loam, and humus mixed with sand. In these soils he grew tobacco, and when the plants were sufficiently developed he stopped watering them, and observed the moment of wilting in a dark, moist room. He determined how much water his soils could hold (the so-called water capacity), and how much water remained in them at the moment of wilting (the so-called unavailable water). The following are the results obtained (in percentages of the dry weight of the soil):—

Soil	Full Water Capacity	Unavailable Water
Humus and sand	46·0	12·3
Loam	52·1	8·0
Coarse quartz sand	20·8	1·5

This experiment confirmed Sachs's ideas. Coarse sand, with its large particles and low water retaining capacity, yields to the root all but 1·5 per cent of its water. Loam, consisting mainly of very small particles, retains 8 per cent of unavailable water, while the humus mixture, rich in colloidal particles, withholds from the plant 12·3 per cent.

The Demands of Different Plants on Soil Moisture

In addition to the question of the actual amount of unavailable water in the soil and the methods of determining it, there is the important question of whether this amount is constant for a given soil no matter what plant is chosen as indicator. In other words, do all plants, even those differing markedly in ecological constitution, drain the soil to the same extent by the time the permanent wilting point is reached? This question is usually answered in the negative. For instance, the experiments of **Hedgcock** (1902) appear to show that different plants do not avail themselves equally of the soil moisture. This author enumerates 132 species of plants, giving for each species the amount of unavailable water when growing in one and the same clay soil. This amount usually fluctuated between 5 and 8 per cent, sometimes falling as low as 3 per cent, or rising for marsh plants to 10–15 or even to 24·8 per cent. These empirical data might be explained by the fact that the osmotic pressure varies greatly in the roots of different plants, being considerably higher in those characteristic of dry habitats (so-called xerophytes), and considerably lower in plants of moister habitats. If the osmotic pressure is higher, the suction pressure at the

moment of wilting would also be higher, and less unavailable water would be left in the soil. Long before Hedgcock's experiments, **Gain** (1895) investigated in the following species the amount of water left in the soil at the moment of wilting: *Erigeron canadensis*, *Lupinus albus*, and *Phaseolus vulgaris*. He suggested that the drought resistance of plants might be determined by the degree to which they avail themselves of the soil water.

These apparently incontestable observations and considerations, however, were easily refuted by the careful investigations of **Briggs and Shantz** (1911, 1912, 1913[a]), of the Washington Department of Agriculture. Their researches, which mark an epoch in the history of the question, are worthy of somewhat detailed consideration.

In the first place Briggs and Shantz considerably improved the methods of determining the amount of water unavailable to the plant. **Sachs**, as well as **Hedgcock** and **Gain**, used common flower-pots in their experiments, so that water was not only absorbed by the plant, but could evaporate freely from the surface of the soil, as well as through the porous walls of the pots. This would lead to unequal drying of the soil, and so to considerable error in the results obtained. **Briggs and Shantz** (1911, 1912) removed this source of error by introducing their "wax-seal method". They used small glass containers, in which they placed 250 gr. of uniformly moistened soil, completely covering the surface with a soft mixture of paraffin wax and vaseline (*petrolatum*).[1] If the surface of the soil is sealed with a thin layer (about 1 mm.) of melted wax, it is perfectly preserved from evaporation. The mixture is so soft that when the container is sealed before germination, the plants will readily grow through the wax. At the same time, the melt-

[1 The most satisfactory wax for use at ordinary temperatures was one composed of 80 per cent paraffin (melting point 45° C.) and 20 per cent vaseline; but in warm weather, a mixture of 10–30 per cent of beef tallow with beeswax, or 8–12 per cent of vaseline with beeswax, was found to be superior. "The wax-seal method is also particularly adapted to the study of transpiration" (**Briggs and Shantz**, 1912).—ED.]

ing point of the wax being low, the mixture may be applied after germination without injury to the tender seedlings.

Another improvement introduced by Briggs and Shantz was a more satisfactory method of determining the wilting point than that depending on mere observation. They adopted as their criterion of *permanent wilting* the point at which the leaves of the plant can no longer recover in an approximately saturated atmosphere, without the addition of water to the soil. This eliminated all cases of transitory wilting conditioned by a marked excess of water loss over water intake: such cases may frequently be observed, even under optimum conditions of soil moisture, especially in tender plants exposed, for instance, to direct insolation.

Further details of Briggs and Shantz's methods may be omitted, including their highly ingenious "balancing method" of determining the wilting coefficient (see below) in such massive plants as cacti, which have no well-defined wilting point. We may now turn to the results obtained by these American investigators.

The Wilting Coefficient of the Soil

Briggs and Shantz accumulated an immense amount of experimental data, investigating over 20 different types of soils, more than 100 species or varieties of cultivated and wild plants, and making upwards of 1,300 determinations of the wilting coefficient. By the term *wilting coefficient of the soil*, Briggs and Shantz mean the moisture content of a soil, expressed as a percentage of its dry weight, at the time when the leaves of a plant growing in this soil show the first signs of permanent wilting.[1] These authors substitute this concept for the older one of *unavailable water*, for, as they point out, when permanent wilting has set in, the plant still continues to draw

[1] The term "wilting coefficient of the soil" is a convenient one, though it has been objected to by various American authors, on the ground that it is the plant and not the soil which wilts.—ED.]

water from the soil. Absorption does not entirely cease after a partial or even complete dying off of the plant; consequently the water remaining in the soil at the moment of wilting is not, strictly speaking, unavailable to the plant.

Briggs and Shantz's experiments may be divided into two principal groups: i.e. determinations of the wilting coefficients (*a*) when different plants are used as indicators, and (*b*) for different soil types.

(*a*) The experiments of the first group are of especial interest from the point of view of physiological ecology. The results obtained may be summed up in the following proposition: all investigated plants, when grown in one and the same soil, give nearly the same "wilting coefficient", independently of their ecological type, their age and the environmental conditions of light and moisture under which they were grown for the experiments.

(*b*) On the other hand, the wilting coefficients of different soils may be very different—even when the same plant is used as indicator—fluctuating from 1 per cent (or less) for dune sand to 17 per cent for clay loam.

In order to compare the relative abilities of different plants to reduce the water content of the soil before wilting occurs, it is necessary to eliminate the effects due to the use of different soils. To do this, Briggs and Shantz calculated the relative wilting coefficients for different plants. The *relative wilting coefficient* is the ratio of any single determination for a given soil to the average value of the whole series of wilting coefficients obtained from this soil. If the wilting coefficient for a particular plant is higher than the average, i.e. if it leaves more water in the soil than do other plants, the "relative wilting coefficient" is greater than unity. If, on the contrary, the plant drains the soil more than do other plants grown on that soil, the ratio is less than unity. **Briggs and Shantz** (1912) give detailed data for each kind of plant investigated by them. Their results, as regards relative wilting coefficients, are summarized in Table III.

TABLE III

Relative Wilting Coefficients for Different Plants (according to Briggs and Shantz)

Plants	Numbers of Observations	Average Value	Probable Error of Average Value	Probable Error of Single Ratio
Corn	75	1·03	± 0·003	± 0·042
Andropogon	66	0·98	± 0·008	± 0·062
Chaetochloa	48	0·97	± 0·006	± 0·035
Wheat	653	0·994	± 0·002	± 0·049
Oats	46	0·995	± 0·007	± 0·047
Barley	60	0·97	± 0·006	± 0·047
Rye	19	0·94	± 0·011	± 0·049
Rice	21	0·94	± 0·012	± 0·054
Various Gramineæ ..	77	0·97	± 0·005	± 0·040
Various Leguminosæ ..	138	1·01	± 0·005	± 0·059
Various Cucurbitaceæ..	17	0·99	± 0·016	± 0·068
Tomato	20	1·06	± 0·009	± 0·040
Colocasia	19	1·13	± 0·005	± 0·060
Hydrophytes	8	1·10	± 0·037	± 0·105
Mesophytes	35	1·02	± 0·010	± 0·058
Xerophytes	16	1·06	± 0·008	± 0·032

From an examination of this table it is evident that the wilting coefficient shows but insignificant fluctuations, exceeding but little the limits of the probable error: and further, that these fluctuations have no bearing whatever on the greater or smaller drought resistance of the plants. The one noticeable regularity in these fluctuations is that plants with coarser, scantily branched roots (Leguminosæ, *Colocasia*, and many hydrophytes and xerophytes), show a higher wilting coefficient, i.e. leave more water in the soil than plants with a more branched root system (e.g. many grasses).

Thus the value of the wilting coefficient of the soil is nearly independent of the properties of the plant, being due almost entirely to those of the soil. Briggs and Shantz therefore devoted great attention to the connexion between this wilting coefficient and other water relations of the soil, in the hope of establishing

simple arithmetical relations between some one or more easily determined physical properties of the soil and the wilting coefficient. Such an indirect method of determining the wilting coefficient, a quantity of great importance for ecology and agronomy, should render prolonged and complicated wilting experiments unnecessary.

According to Briggs and Shantz, the closest and most convenient correlation is that between the wilting coefficient and the so-called *moisture equivalent of the soil.* By this term **Briggs and McLane** (1910) denote the percentage of water which a layer of soil 1 cm. in thickness can retain when subjected to the action of a centrifugal force a thousand times greater than that of gravity. This value is regarded by them as a measure of the water retaining capacity of the soil. It is important to realize that the significance of the wilting coefficient lies in the fact that its value is directly dependent on the water retaining capacity of the soil. In fact, the experimental determination of the wilting coefficient of a soil may be regarded as a physiological (rather than a purely physical) method of determining its water retaining capacity. A similar direct relation was found to exist between the wilting coefficient and another physical constant, the *hygroscopic coefficient of the soil,* i.e. the percentage of hygroscopic water found in originally dry soil after prolonged exposure to a saturated atmosphere at a temperature of 20° C.[1] Mathematically, the relations between the wilting coefficient and these indicators of the properties of the soil in regard to water may be expressed by the following equations:—

$$\textit{Wilting coefficient} = \frac{\textit{Moisture equivalent}}{1{\cdot}84 \pm 0{\cdot}013} = \frac{\textit{Hygroscopic coeff.}}{0{\cdot}68 \pm 0{\cdot}012}$$

Such are the results of Briggs and Shantz's very important and interesting investigations. These results enabled them to

[1 According to **Briggs and Shantz**, the hygroscopic coefficient is more difficult to determine than the moisture equivalent, the latter being less readily affected by fluctuations in temperature or humidity.—ED.]

establish a definite relation between the water properties of the soil, as measured by purely physical methods, and the degree to which the soil yields water to, or withholds it from, the wilting plant, as determined by the method of wilting.

Nevertheless Briggs and Shantz's results have not escaped criticism. It seemed difficult to abandon the accepted opinion that different plants are able to avail themselves of the soil moisture in different degrees. It was equally difficult to recognize that the wilting coefficient depends on the fact that the properties of the soil are practically independent of those of the plant, and that for a given soil this coefficient varies but little no matter what plant is chosen for the experiment—a cactus or a *Colocasia*, drought resistant sorghum or marsh rice. **Crump** (1913), for example, is sceptical of the results obtained by Briggs and Shantz, and considers that, as the experiments were carried out in closed, impermeable containers, and chiefly with seedlings of cultivated plants, these results cannot be applied to plants growing under natural conditions. Again, **Shive and Livingston** (1914) point out that the amount of water remaining in the soil at the moment of wilting is determined in the first place by the conditions of transpiration, and that with dry air and strong insolation the wilting coefficient is considerably higher than with moist air and shade. **Caldwell** (1913) subjected the data obtained by Briggs and Shantz to the test of further experiment. He found that if wilting took place in a shaded room with an almost saturated atmosphere, the value of the wilting coefficient of the soil, obtained directly by wilting experiments, coincided with that calculated from determinations of physical constants. If, on the other hand, the plant was allowed to wilt in the open air, or when only lightly shaded, the calculated wilting coefficient was always lower than the value obtained by experiment, the deviation being the greater, the less the water capacity of the soil used in the experiment. In general, every combination of atmospheric conditions corresponds to a certain wilting coefficient, which increases with the dryness of the air and the insolation.

Under conditions of maximal summer transpiration in the desert of Arizona (Caldwell's experiments were conducted in the Desert Laboratory of the Carnegie Institution near Tucson in Arizona), permanent wilting set in while the water content of the soil was still 30–40 per cent in excess of that observed when a plant had reached its wilting point in a moist atmosphere.

Caldwell's investigations explain the difference of opinion between **Briggs and Shantz** on the one hand and their predecessors and opponents on the other. The explanation appears to be that equilibrium between the suction pressure of the plant and the water retaining capacity of the soil is attained only under conditions of feeble transpiration. When, however, the plant is transpiring very strongly, it is unable to obtain water from the drying soil with sufficient rapidity to replace that lost by transpiration. Hence it enters upon the state of permanent wilting before the available water in the soil has been exhausted.

It is interesting to note that the Russian investigator **S. Bogdanov** (1893), more than twenty years earlier than Briggs and Shantz, and using quite different methods, came to similar conclusions regarding the absorption of soil water by different plants. In studying the relation of germinating seeds to soil water, Bogdanov found that the seeds of all plants, independently of their properties and nature, can germinate only when the water content of the soil is not less than double the hygroscopic capacity of the soil in question. Bogdanov concluded that this quantity corresponds to the amount of water unavailable to the plant. This conclusion was made use of in agronomical practice, for calculating both the amount of water that must be added to the soil when filling experimental pots, and the unavailable water in the soil. Bogdanov's results with germinating seeds agree closely with those of Briggs and Shantz's wilting experiments: in both cases the value obtained is independent of the properties of the plants selected for experiment.

The study of wilting is important as a means not only of determining the water properties of the soil, but also of investi-

gating the water balance and even the drought resistance of plants. We shall return to the subject later, after a detailed consideration of the process of transpiration.

The Resistance of the Soil to Root Suction

We may now deal with the attempts made to determine experimentally the resistance of the soil to root suction. It must be admitted that these attempts have led to somewhat contradictory results.

The simplest method is that suggested by **Ursprung and Blum** (1921[b]). These authors consider that the resistance which must be overcome by the root hairs and other absorbing cells of the root is either static, i.e. that affecting the general absorption of water by the cell; or dynamic, if it is a question of the absorption of a definite amount of water in unit time. The strength of dynamic resistance naturally varies according to the rate of water absorption. This rate is a very variable quantity, the value of which depends on the properties and water content of the soil, the intensity of transpiration, and the dimensions and properties of the water absorbing surface of the roots. Ursprung and Blum maintain that this dynamic resistance cannot be calculated on the basis of the properties of the soil, but suggest that it may be determined by ascertaining the force required to overcome it. According to them this may be done by determining the suction pressure of the surface cells of the roots, by the methods already dealt with in Chapter I.

In order to test the correctness of this view, Ursprung and Blum conducted experiments in which the roots of plants grown in moist sawdust, i.e. in a medium with an unknown power of resistance, were transferred to solutions of known concentration, i.e. possessing a definite osmotic pressure. This osmotic pressure of the external solution opposes the suction pressure of the root, and supplies the required resistance of known and definite strength. When such experiments are

conducted under conditions of reduced transpiration, the rate of absorption of water by the root need not be taken into consideration.

These experiments confirmed Ursprung and Blum's assumptions. When roots were transferred from sawdust to pure water, the resistance of which is obviously zero, the suction pressure of the root cells—originally 1 to 2 atmospheres—after a short time (not exceeding 24 hours) fell to zero. Again, when the roots were transferred to solutions of definite concentration, which opposed a known resistance to suction, a state of equilibrium was established between the suction pressure of the root cells and the resistance to absorption of the external solution (see p. 49).

Thus in all cases where the value of the resistance to suction of the solution was accurately known, it proved to be numerically equal to the suction pressure of the root cells. From this the authors conclude that in cases where the resistance cannot be calculated, it may be measured by determining the suction pressure of the root cells. This conclusion was supported by the results of certain experiments in which **Ursprung and Blum** increased by various means the resistance of the medium to root suction. In all these cases a corresponding increase of the suction pressure of the roots was observed. Thus, on placing the roots of a plant of *Vicia Faba* in a 0·20*N* solution of saccharose, and removing the greater part of the root system, the suction pressure of the remaining roots was increased from 5·3 to 6·3 atmospheres. The drying of the sawdust in which the plants were growing also led to a considerable increase of suction pressure: e.g. in a specimen of *Vicia Faba*, from 1·1 to 2·1 atm., while on the commencement of wilting it reached 3·2 atm. Again, in *Phaseolus* the suction pressure of the roots increased from 0·8 to 1·9 atm., and, with further drying of the sawdust and incipient wilting, to 2·9 atm.; at this stage the absorbing cells began to die off. Similar results were obtained when transpiration was increased by moving the plants into drier air; also when the soil temperature was lowered from 18° to 2° C.,

thus inducing a retardation of the rate of water absorption by the root.

The results obtained by Ursprung and Blum are certainly of great interest, though it is hardly possible to agree with their conclusions. The figures obtained by their method are undoubtedly too low for the actual strength of root suction, for according to their own data, water continued to be absorbed. Moreover, the plant did not wilt even though the suction pressure of the root cells was equal to the osmotic pressure of the surrounding medium. It follows that the suction pressure of the root as a whole is always greater than the suction pressure of the cells of its piliferous layer.[1]

As root suction is ultimately conditioned by phenomena of an osmotic nature, the resistance of the soil to this suction may be measured appropriately by means of artificial osmotic systems the suction of which can be readily calculated. This method was adopted by **Livingston** (1906), who employed cylindrical osmometers of unglazed porcelain, closed at one end. The porous walls of these osmometers were rendered semi-permeable by precipitation membranes of copper ferrocyanide (Pfeffer's method). The osmometer was filled with a 1·5 mol. solution of saccharose (corresponding to an osmotic pressure of 54 atmospheres) and the upper end of the cylinder closed with a rubber stopper, through which passed a glass tube of about 4 mm. bore. By the rising or falling of the liquid in this tube it was possible to decide whether the osmometer was drawing water from the soil or the soil from the osmometer. The osmometers were placed in soils (from the neighbourhood of the Desert Laboratory, Arizona) containing known amounts of water. In soils with 5, 10, or even 15 per cent (by volume) of moisture, the column of sugar solution gradually fell, indicating that the osmometer was yielding water to the soil. With 20 per cent of moisture there was a very slight rise in some experiments, and a slight fall in others, showing that the resistance of the soil was

[1 Ursprung and Blum later obtained evidence of a gradient of suction pressure in the root. Cf. footnote, p. 52.—ED.]

in equilibrium with a pressure of 54 atmospheres. Finally, with 25 per cent, the column of liquid rose, proving that water was being absorbed from the soil.[1]

That the resistance to absorption by a soil containing a quantity of water quite sufficient for the normal existence of a plant should equal so high a pressure as 54 atmospheres is regarded by Livingston as surprising, as it considerably exceeds the osmotic pressure in the majority of plant cells. He suggests that the surface of the osmometer may be in less close contact with the soil particles than are the root hairs, or, alternatively, that osmotic pressure may play a less important rôle in the absorption of water than is usually assigned to it.

Later on, Livingston (**Pulling and Livingston,** 1915) modified his osmometer method of determining the *water supplying power of the soil.*[2] Instead of a porcelain osmometer he used a glass thistle funnel, the large open end of which was closed with a film of specially prepared collodion. The funnel was filled with a solution of 5 gr. mols. of saccharose in 1,000 gr. of water. The film was closely pressed against the surface of the soil, and the rate at which water entered the osmometer (not the osmotic pressure in atmospheres) determined. Experiments with this osmometer showed that the instrument absorbed water from even moist soil much more slowly than from water. For instance, in one experiment the average rate of absorption from water was 1·39 c.c. per hour; from a soil containing 25 per cent of moisture, 0·28 c.c.; with 20 per cent of moisture, 0·23 c.c.; with 15 per cent, 0·15 c.c. per hour. In another experiment, the mean rate of absorption from water was 1·36 c.c. per hour, and from soil containing 5 per cent of moisture,

[1 As **Livingston** points out, the osmometers act like water thermometers: allowance has therefore to be made for variations in temperature. —ED.]

[2 The "water supplying power of the soil" depends on, and in a sense is the converse of, the "water retaining capacity of the soil", or its equivalent, the "resistance of the soil to root suction". But the first is a dynamic, whereas the other two are static concepts. **Livingston and Hawkins** (1915) define the water supplying power of the soil as "the time-rate of possible water delivery at unit cross-sectional area in the soil."—ED.]

0·04 c.c. Thus water is absorbed by the sugar solution used, about five times more slowly from moist soil, and about thirty-five times more slowly from rather dry soil, than from water itself.

Even this method cannot be regarded as entirely satisfactory, for insufficiently close contact with the soil is still possible. **Livingston and Kôketsu** (1925) have therefore devised a new method for determining the water supplying power of the soil. In this, osmotic suction is replaced by capillary suction, "soil points" being used for determining the rate of water supply. These soil points are hollow cylinders of porous porcelain, open above and terminating below in a pointed cone. Before being used the "point" is dried at 100° C., weighed and stored in a desiccator. To determine the rate of water supply, a point is driven into the soil and left there for from half an hour up to two hours, according to the degree of soil moisture. The point is then taken out, cleansed with a brush from adhering soil particles and weighed a second time. The increase in weight gives the amount of water absorbed during unit time, and this amount, in Livingston's opinion, affords a measure of the water supplying power of the soil.[1]

A very useful and original method of determining the absolute value of the water retaining capacity of the soil was suggested by **Shull** (1916), who availed himself of the peculiar natural osmometer represented by swelling seeds. As is well known, certain seeds possess a semi-permeable coat; hence by soaking the seeds in salt solutions of different concentrations, we can measure the strength with which the colloids attract water, and are thus enabled to calibrate our osmometer.

According to Shull, the seeds of *Xanthium pennsylvanicum* form a convenient subject. These seeds are impermeable to

[1 **Livingston and Kôketsu** waterproofed the cylindrical part and the tip of their "soil points", leaving about 10 sq. cm. of the conical portion as the absorbing surface. Their results appear to indicate that (under the conditions of their experiments) the water supplying power of the soil, at the commencement of permanent wilting, is the same for sand, loam, humus, and various mixtures of these. It is suggested that the soil point method is particularly suitable for field investigations, which the collodion film method is not.—ED.]

salts, but swell rapidly when supplied with moisture, the suction pressure of their swollen contents attaining equilibrium with the osmotic pressure of the external solution within 10–24 hours.

By immersing seeds in solutions of sodium chloride and lithium chloride of different concentrations, Shull calibrated his seed-osmometers, which, on account of their small dimensions, permit very intimate contact with the soil. By means of these osmometers he endeavoured to measure the water retaining capacity of the soil, or, as he calls it, the "surface forces of the soil". For this purpose he buried air-dry seeds in soils containing different amounts of moisture, leaving them in hermetically sealed containers until such time as complete equilibrium was established between the seeds and the soil. The seeds were then taken out, cleansed from soil particles, weighed, and their water content determined (and simultaneously that of the soil) by means of drying. The results of these determinations for Oswego silt loam are given in somewhat abbreviated form in Table IV, on opposite page.

The table shows clearly how rapidly the retentiveness of the soil decreases as its water content increases. From the very high figure of nearly 1,000 atmospheres for air-dry soil containing 5–6 per cent of water, it falls, with twice the amount of water, to 130 atm., and with three times the original water content to 15 atm. These results entirely agree with the conception of the water retaining capacity of the soil as due to surface forces, the strength of which rapidly diminishes with the distance from the soil particles, i.e. with the thickness of the surrounding films of water. Shull's experiments with pure quartz sand show a much more rapid decrease in water retaining capacity—as the water content increases—than is the case with the heavy Oswego silt. On the other hand, the presence in the soil of colloids capable of imbibing water somewhat reduces the rate of decrease.

From an ecological point of view **Shull's** method is of special interest when applied to soils containing the amounts

of moisture corresponding to their wilting coefficients. Having selected soils of different types, Shull calculated their wilting coefficients by **Briggs and Shantz's** formulæ. He then added to his samples of dry soil sufficient water to bring them to the wilting coefficient, and determined their water retaining capacity by means of *Xanthium* seeds. The results showed that,

TABLE IV

Relation of Water Content of Soil to Intake by Seeds and Water Retaining Capacity (Surface Forces) of Soil (according to Shull)

Water Content of Soil in Percentages of Absolute Dry Weight	Intake by Seeds in Percentages of Air-dry Weight	Osmotic Pressure Equivalents of Water Retaining Capacity of Soil	
		In Molecules of Chloride	In Atmospheres
5·83 (air dry)	0·00	Saturated LiCl	965
6·23	1·91	—	697
8·68	6·16	—	418
9·36	6·47	Saturated NaCl	375
11·79	11·94	4 molecules	130
13·16	21·36	2 molecules	72
14·88	28·61	1 molecule	38
17·10	37·70	0·5 molecule	19
17·12	41·98	0·4 molecule	15·2
17·93	43·25	0·3 molecule	11·4
18·07	45·15	0·2 molecule	7·6
18·87	47·26	0·1 molecule	3·8
20·04 (moist)	50·00	—	—
—	51·44	0·0 molecule	0·0

with two exceptions, in all the soils investigated (loam, clay loam, and sand) the intake of water by the seeds was nearly uniform, i.e. from 47·31 to 50·42 per cent. The exceptions were coarse sands, in which, owing probably to less intimate contact with the seed coat, the intake was somewhat less, i.e. 34–41 per cent. Calculated on the basis of water intake, the water retaining capacity at the wilting coefficient amounts only to 3–4 atmospheres.

In view of the data obtained by **Hannig** (1912), who found that the average osmotic pressure in the roots of sixty-four different species investigated by him was equivalent to 7–8 atmospheres, **Shull** thinks the above value (3–4 atm.) surprisingly low, as in his opinion there would still be, at wilting point, a gradient of pressure equal to 4 atm. in favour of the plant. But here Shull commits the usual error of regarding the suction pressure of the cell as equivalent to the whole of the osmotic pressure of the cell sap. In reality, as we have seen in Chapter I, the suction pressure of the cell is but a part of the osmotic pressure of the cell contents. **Ursprung**, in fact, regards the actual suction pressure of the absorbing cells of the root as considerably lower not only than 7–8, but even than 4 atm. (see footnote, p. 52). It is not surprising, therefore, that an increase of the water retaining capacity of the soil from practically zero (for a very moist soil) to 3–4 atm. already induces the wilting of the plant.

Ursprung and Blum's experiments have shown, however, that the plant is able considerably to increase the suction pressure of its absorbing cells, and that when transferred to more concentrated solutions it adapts itself after a time to the new conditions. Moreover, the root cells of many plants possess a very high osmotic pressure, and are able, even with a small loss of water, considerably to increase their suction pressure. Nevertheless, according to **Briggs and Shantz**, the wilting coefficient is determined not by the properties of the plant but by those of the soil.

Transpiration and the Translocation of Water in the Soil

The explanation of the above fact must probably be sought, not in the combined resistance of the soil particles as a whole to the loss of water, but in the stoppage or excessive slowing down of the translocation of water from one soil particle to another. The particles in immediate contact with the root hairs

may lose their moisture, and thus the continuity of the films of water between the root hairs and the more distant soil particles may be interrupted. The more rapid the evaporation from the leaf surface of the plant, the sooner the time comes when the rate of movement of water through the soil no longer corresponds to that at which it is absorbed by the roots. Hence the plant may begin to wilt even with a relatively high water content of the soil. But even with the slowest rate of water absorption, the moment at last arrives when the water films in the drying soil are ruptured, and the water loses its mobility; this moment corresponds to the wilting coefficient.

Thus, with a slow rate of absorption, the plant slowly brings the soil into a condition in which the movement of water in the soil ceases. With rapid transpiration and a correspondingly rapid absorption by the root, the rate of movement of water in the soil may soon fall below that at which it is absorbed. Every rootlet and even every root hair will now be surrounded by a zone of soil desiccated to the condition of minimal moisture capacity. Under these conditions further absorption of water by the root may be greatly impeded or even entirely checked: this is followed by wilting, although the average water content of the soil may still be sufficient to supply the needs of the plant. In such a case the moment of wilting is determined not merely by the properties of the soil, but also by the interrelations of the root surface and the transpiring surface, the ramifications and the extent of the root system and the root hairs pervading the soil, and so on: in a word, by a series of properties of the transpiring plant itself. Obviously, under such conditions different plants behave differently, and this readily explains why the data of Briggs and Shantz are at variance with the results of other investigators.[1]

[1] It would appear that under certain conditions, one of which is probably a restricted rate of atmospheric evaporation, **Briggs and Shantz's** wilting coefficient is really a soil constant, determined in the main by the properties of the soil alone. Under other conditions, however, it seems that atmospheric factors, and possibly also the internal constitution of the plants themselves, may affect the value of the wilting coefficient. But in the absence of exact data regarding evaporation intensities during Briggs

The actual differences between the respective rates of translocation of water in the soil and of the transpiration current are difficult to determine experimentally, because transpiration, as we shall see later, depends to a great extent on the rate of water supply. But that such differences really exist, and that, during periods of strong transpiration, the soil in close contact with the roots of a plant is temporarily more or less desiccated, have been proved by the interesting work of **Livingston and Hawkins** (1915).

These authors attempted to investigate the relation between the diurnal march of the rate of transpiration and the corresponding march of the water retaining capacity of the soil. Plants were grown in tinned-iron cylinders, in the soil of each of which was inserted a porous earthenware cup, similar in all respects to the atmometers used by Livingston to measure the "evaporating power of the atmosphere" (see Chapter V). This simple apparatus is termed by **Livingston** (1908) an "auto-irrigator". The open end of the cup is turned upwards, and closed by a rubber stopper through which passes a glass tube ending in a rubber tube (Fig. 5). The apparatus is filled with water, and the free end of the rubber tube allowed to dip into a water reservoir some decimetres below the level of the container. In a short time a flow of water is set up through this auto-irrigator in a definite direction. The transpiring plant absorbs water from the soil, the soil by its capillaries sucks water from the porous cup, while the latter in turn draws on the somewhat lower reservoir. The loss of water in the reservoir is easily determined quantitatively: this loss indicates the amount of water absorbed by the soil, as (apart from slight fluctuations due to changes of temperature) the amount of water filling the auto-irrigator and its tube remains constant.

and Shantz's experiments, and of knowledge of possible differences between the plants used in the Washington and Tucson experiments respectively, it is difficult at present fully to explain the differences between Briggs and Shantz's results on the one hand and those of **Caldwell** and **Livingston** on the other.—ED.]

By means of this auto-irrigator **Livingston and Hawkins** were able to determine the amount of water absorbed by the soil in unit time. By simultaneously weighing the whole apparatus with the plant, they could also measure the amount of water lost during the same period of time by transpiration.[1] As no perceptible wilting took place, it may be assumed that

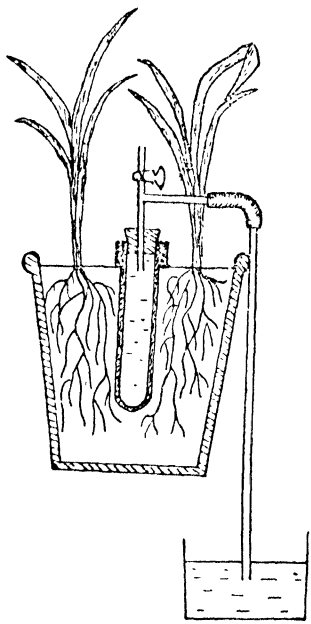

FIG. 5.—Livingston and Hawkins's auto-irrigator.

the amount of water transpired by the plant corresponded to that absorbed by the roots from the soil. The difference between the amount of water absorbed by the plant and the amount supplied to the soil by the auto-irrigator enabled Livingston and Hawkins to determine the water deficit in the soil. It is true that the total water deficit may be accounted for

[1 The surface of the soil was sealed to prevent loss of water except through the plant.—ED.]

in part by the slowness of the rate of supply from the surface of the irrigator to the soil, and unfortunately the authors give no data that would enable us to judge of the rate of this supply. But in spite of this weak point, the results obtained by Livingston and Hawkins definitely prove the existence of a temporary water deficit in the soil near the roots of a strongly transpiring plant. These authors observed that about nine o'clock in the morning the plant begins to draw more water from the soil than before, but that this increased suction by the root system is transmitted to the irrigator only after 2–3 hours. The irrigator now begins to supply water in larger quantities, but still lags behind root suction, until 5 o'clock in the evening. The water deficit in the soil thus increases from hour to hour, reaching its maximum at the time when transpiration begins to fall off as a result of the lowering of temperature and the decrease of insolation towards evening. After 5 o'clock the soil layer partially desiccated under the influence of increased transpiration begins to regain its moisture, and by the next morning the soil is once again uniformly moist.

Such is the picture at present available of the absorption of water by the plant from the soil. Much still remains to be elucidated, and we are as yet far from possessing an adequate knowledge, either of the rate of movement of water through the soil, or of the resistance opposed to the passage of water from the soil into the root. This resistance undoubtedly is of great importance in determining the whole structure of the root system. The enormous development of the absorbing surface of the root is correlated with the necessity of establishing intimate contact with as great a surface of soil as possible. This enables the root system to absorb the maximum amount of water, even when the rate of translocation of water from more distant layers of soil is insufficient to make good the inevitable water deficit which occurs during the daytime in the layers in contact with the absorbing surface of the roots. We shall return to this question of the water deficit of the soil when discussing the diurnal march of transpiration.

CHAPTER III

THE INFLUENCE OF ENVIRONMENTAL CONDITIONS ON ABSORPTION

Influence of environmental conditions on the absorption of water by the root system: (*a*) the temperature of the soil; (*b*) reaction of the soil solution; (*c*) the absorption of water from bog soils—soil toxins; (*d*) the oxygen content of the soil; (*e*) the concentration of the soil solution—halophytes. Absorption of water by the aerial organs of plants.

Influence of Environmental Conditions on the Absorption of Water by the Root System

(*a*) *The Temperature of the Soil*

One of the environmental factors which most strongly influences the water supply of the plant is undoubtedly the temperature of the soil. As the general regulator of the rate of chemical reactions as well as of vital functions, temperature must naturally exert an influence on the rate of penetration of water into the cell, and consequently on the rate of absorption of water by the root. The first experiments to prove the slowing down of the rate of root suction under the influence of a lower soil temperature were those of **Sachs** (1860). He noticed that when cold weather set in, many tender plants with large leaves, for instance tobacco or pumpkin, began to wilt, and came to the conclusion that the reason for this wilting lay in the slower rate of water supply from the soil. In order to prove this hypothesis, Sachs placed a potted tobacco plant in a warm room, and after profusely watering the soil, surrounded the pot with ice. Before long the plant showed signs of wilting, but when the ice was removed and the soil heated, the plant recovered without additional moistening of the soil.

For a more precise and detailed study of the influence of temperature on the water supply of the plant, however, potometer experiments, by which the rate of absorption of water can be directly determined, were necessary. Such experiments

were carried out by **Vesque** (1878), who showed that within the limits of 10° to 15° C. water absorption rapidly increases under the influence of a higher temperature.

Considerably later the question was reinvestigated by the Bulgarian **Kozarov** (1897), a pupil of Pfeffer. Kozarov, too, used the potometer method, and found that a fall of temperature from 20° to 0° C. retarded the rate of water supply by approximately 25 per cent, or even by 30 per cent.

If, on the other hand, we immerse an osmometer (e.g. Pfeffer's artificial cell) in water, the rate at which the liquid rises in the tube is found to depend only to a relatively slight degree on temperature. The effect of temperature on the rate of a process is usually expressed by means of the so-called *coefficient of temperature*. For the physical process of diffusion of solutes in water this coefficient (Q_{10}) is about 1·2 to 1·3, i.e. with a rise of temperature of 10° C. the rate of diffusion increases 1·2 to 1·3 times (for data on this question see **Kanitz**, 1915). The rate of absorption of water by the root, however, increases much more rapidly than this, especially with temperatures in the neighbourhood of zero.

In order to explain this difference in the effect of temperature on diffusion and root absorption respectively, we must consider the results of researches on the relations between temperature and the rate of entry of water into the plant cell.

The investigations of **Delf** (1916) and of **Stiles and Jørgensen** (1917) have yielded the results in Table V (on opposite page).

In comparing these data we notice that the rate of water absorption by the cell[1] always increases with a rise of temperature, at least up to 30° C.[2] Moreover, the temperature coefficient of absorption, though varying for different plants and

[1] Delf (using onion and dandelion) actually determined the rates of *exit* of water from, and Stiles and Jørgensen (potato and carrot) the rates of *intake* of water by the tissues employed.—ED.]

[2] "Above 30° C. a 'time factor' (**F. F. Blackman**, 1905) appears, inasmuch as with prolonged immersion in water at such higher temperatures the initial absorption is followed by excretion of water", **Stiles** (1924).—ED.]

different intervals of temperature, is always considerably higher than that of the purely physical process of diffusion. The reasons for this difference between the two processes are not altogether clear. It may be that a high temperature coefficient of a cell is connected with changes in the cohesiveness of the protoplasm, as suggested long ago and recently studied in detail by **Weber and Hohenegger** (1923). Moreover, it must not be forgotten that the cohesion of the molecules of the water itself considerably increases as the temperature falls,

TABLE V

The Temperature Coefficients of the Penetration of Water into the Cell (according to Delf and Stiles and Jørgensen)

Intervals of Temperature	Temperature Coefficients (Q_{10})			
	Leaves of Onion	Scape of Dandelion	Tuber of Potato	Root of Carrot
5°–15° C.	1·4	—	—	—
10°–20° C.	1·5	2·3	3·0	1·3
15°–25° C.	2·0	3·3	2·75	1·4
20°–30° C.	2·6	3·8	2·7	1·6
25°–35° C.	2·9	3·0	—	—
30°–40° C.	3·0	2·6	—	—

and that this increased cohesion is accompanied by slower molecular movements.

Whatever the reason for and the mechanism of this slower absorption of water under the influence of falling temperature, the retardation is of great ecological importance. A whole series of peculiarities characteristic of plants of temperate and cold climates may be correlated with the fact that refrigeration of the root system leads to a reduced water supply, and hence to a disturbance of the water balance. For instance, during cold autumn nights the soil is gradually cooled and, the sun being comparatively low, the loss of heat is not made good during the daytime. At the same time the air may still be sufficiently

warm to induce strong transpiration, which can no longer be adequately compensated by root absorption. Thus a water deficit ensues, in response to which the plant throws off its leaves.[1] Under such conditions, as pointed out by **Schimper** (1898), the prevalent plant forms tend to be such as possess in summer a typical mesophilous habit, while in winter the transpiring surface is reduced by shedding the leaves, the persistent perennial parts being more or less xerophilous. To this class of "tropophytes", as Schimper calls them, belong, for instance, our deciduous trees and shrubs.

Caution is needed, however, in generalizing from **Sachs's** data regarding the influence of a lowered temperature on the activity of the root systems of tobacco and pumpkin. Both these plants are heat-loving and a fall of temperature to 10° C. already checks their growth. In more hardy plants, such as winter cereals, low temperatures retard the water supply to a less extent, and these plants can grow and develop perfectly well in late autumn and early spring, in spite of periodical frosts. That water is actually absorbed from the refrigerated soil is shown by the fact that these cereals exude water in the form of drops. **Stahl** (1919) points out that young shoots of oat, barley and wheat continued to give off water when the pots in which they were growing were placed in snow, with a soil temperature nearly as low as 0° C., and an air temperature of − 2·2°. Similarly, the leaves of *Geranium pyrenaicum* exuded water in spite of a soil temperature of about 0°. From these observations it follows that the question of the influence exerted by temperature on the absorption of water by the

[1 The temperature of the soil is more uniform and less liable to frequent and rapid fluctuations than that of the air; and there can be little doubt that a water deficit in the plant may be brought about in the way suggested. But as yet it is by no means certain that the autumnal shedding of leaves is in all cases (especially perhaps in herbaceous tropophytes) a definite response to internal drought. Even in deciduous trees (in England), according to **Farmer** (1918, pp. 245–6), root pressure may still be sufficiently active in early autumn to replenish the water lost from the twigs and branches during the summer. On the other hand, in Central Europe, **Hartig** found the lowest percentage of water in the Birch at the end of September.—ED.]

root requires reinvestigation. In this connexion, the possibility that plants belonging to different ecological groups may respond differently to lowered temperatures must be taken into account.

Temperature is a factor which directly influences the rate of water absorption by roots. The study of other soil factors is complicated by the fact that, in addition to their direct effect, these factors may also exert an indirect influence on the water supply of the plant, by checking or stimulating the growth and development of the root system. It is, however, impossible to draw a hard and fast line between the direct and indirect influence of the soil factors. For instance, even the temperature of the soil is not without influence on the development of the root system, which develops better, though more slowly, with a lower temperature. Of the soil factors which chiefly influence the root directly may be mentioned the composition and the concentration of the soil solution, and amongst the indirect factors—the amount of oxygen in the soil and the presence of substances noxious to the roots (soil toxins).

(*b*) *Reaction of the Soil Solution*

V. Rybin (1923), in a technically irreproachable investigation, has recently studied the influence of solutions of acids and of salts on the absorption of water by roots. Previous investigators, amongst whom may be mentioned **Burgerstein** (1876), **Sampson and Allen** (1909), and **Dachnowski** (1914), had come to the conclusion that acids increase transpiration and consequently also absorption. But these workers subjected roots to the prolonged action of comparatively strong solutions, which gradually poisoned the plant (and we shall see later that the dying off of cells actually increases the loss of water). Rybin, however, by using harmless concentrations of acids (not exceeding $0{\cdot}018N$), invariably found that absorption was checked by the acid. In some cases the decrease amounted to 40 per cent of the quantity originally absorbed. That the concentrations employed were really harmless follows from

the fact that on being transferred to pure water, the rooted willow branches used in the experiments soon resumed their former rate of absorption.

Rybin's results agree with those of **M. Fischer** (1910) and **Lundegårdh** (1911), who point out that the permeability of protoplasm to water considerably decreases under the influence of weak acids. They also confirm the fact observed by **Sabinin** (1921) that in an acidified medium the root system of *Impatiens parviflora* exudes water (bleeds) more slowly, though Sabinin himself thinks this retardation is not very strongly marked.

(*c*) *The Absorption of Water from Bog Soils—Soil Toxins*

A question closely connected with that of the influence of hydrogen ions on the rate of absorption by the root system is the absorption of water from bog soils. The intricate and debatable question of "bog xerophytes", on which a very extensive literature already exists, cannot be fully dealt with here. I will therefore confine myself to one aspect of the question, i.e. the influence of bog or peat soil on the absorption of water by roots, and more particularly to the experimental work of **Montfort** (1918, 1921, 1922).

In his classical *Pflanzengeographie auf physiologischer Grundlage*, **Schimper** (1898) first advanced his hypothesis of the "physiological dryness" of bog soil, suggesting that root absorption is checked by the humic acids of bog water. The disturbed balance occasioned by impeded absorption on the one hand, and unimpeded transpiration on the other, renders many plants incapable of growing on bog soil. The plants which can thrive in this habitat are species which, owing to their "xeromorphic" structure, transpire less freely.

This concept of the "physiological dryness" of physically wet bog soil may be traced through all recent works on the ecology of bog plants. Schimper's hypothesis has been more or less accepted by most authors, though some have suggested

modifications or corrections. Thus **Dachnowski** (1908, 1910) substitutes soil toxins for humic acids, while **Schröter** (1908) regards the high water retaining capacity of peat soil as the chief factor bringing about physiological dryness. A whole series of authors beginning with **Kihlmann** (1890) and **Goebel** (1891), on whose data Schimper partly bases his opinion, consider of prime importance the low temperature of bogs, especially in spring, when the soil thaws very slowly, remaining (e.g. in the tundra of the far north) permanently frozen at a comparatively small depth. Many authors, again, lay stress on the lack of oxygen in the soil, which impedes or even completely checks the exudation pressure of the roots.

We have examined the influence of a lowered temperature on the activity of the root system, and have seen that cooling of the soil not only impedes the absorption of water, but may even induce the wilting of a plant in moist soil. So far, however, we have insufficient data regarding the response of different plants to a falling soil temperature. *A priori*, it might perhaps be expected that bog plants, characteristic of cold soils, would be relatively little susceptible to the refrigeration of their roots.

Besides the influence of temperature, an important rôle in all theories of the "physiological dryness" of bog soil is attributed to the chemical properties of the latter. A series of investigations, chiefly by American authors, has established the fact that bog soil possesses poisonous properties and produces a toxic effect on the roots of plants developing in it (**Livingston**, 1904 and 1905; **Dachnowski**, 1908, 1909, and 1910; **Rigg**, 1916). Until recently, however, there was no experimental evidence as to how far bog soil or bog water acts directly by hindering root suction, or indirectly by preventing the development of an extensive and effective root system. **Montfort** (1921) set himself to fill this gap in our knowledge.

Montfort (1920) devised a special method, the "guttation method", for studying the absorption of water by the plant under natural conditions. This method is based on the pheno-

menon of guttation, i.e. the exudation of liquid drops of water from leaves when transpiration is prevented by saturation of the atmosphere with water vapour. To induce guttation, Montfort covered his plants with glass bell-jars lined with wet blotting-paper.

In his experiments Montfort used: (i) true *Sphagnum* water, taken from a growing "primary" peat bog at a depth of 25–40 cm., i.e. from a stratum in which the roots of the bog plants develop, and (ii) an infusion of dry peat from a "secondary", already dry peat bog. The *Sphagnum* water was of a yellowish colour, giving a weakly acid reaction, varying between 0·00008 and 0·00038*N* (the acidity was determined by titration with baryta water with phenol phthalein as indicator); the peat infusion was of a dark brown colour but showed no great amount of free acid. To a certain extent the effect of these two bog waters respectively was different.

Experiments on corn with *Sphagnum* water showed that guttation—and consequently also absorption of water by the root—not only continued unhindered for many days, but frequently actually increased, at least during the early days of an experiment. Prolonged immersion in *Sphagnum* water, however, finally reduces guttation. Peat water also increases guttation at first, even in a higher degree than *Sphagnum* water, but its later retarding effect is manifested earlier and is more strongly marked.

Experiments with bog plants, chiefly *Eriophorum vaginatum*, led to similar results, though in bog plants the stimulating and toxic effects were less apparent. *Sphagnum* water had no influence whatever on guttation in *Eriophorum*, this process continuing for weeks. The stronger peat extract, however, induced even in bog plants first an increase and subsequently a decrease of guttation, which in a few days completely ceased.

Experiments in natural habitats on the whole confirmed the results of laboratory experiments. By covering selected bog plants with bell-jars or by observing them in the early morning

hours, Montfort established for practically all plants investigated by him on "primary" peat bogs a clearly perceptible and vigorous guttation. In plants devoid of hydathodes, such as *Andromeda Polifolia*, he varied his method by cutting off the stem, thus observing the exudation of water from the cut stem (bleeding) instead of guttation. But this difference of method is unimportant, as in both cases the active cause of exudation is root pressure. Only in "secondary" peat bogs, with an actual deficiency of water in the soil, was a cessation of guttation observed, due to the water retaining capacity of the dry peat. In this case the dryness is physical rather than physiological. These experiments, then, in no way support **Schimper's** hypothesis, which is completely discarded by Montfort.

(*d*) *The Oxygen Content of the Soil*

Another important question is that of the influence of oxygen, or rather of the absence of oxygen, on root activity. Long ago **de Saussure** noticed that plants wilted if their roots were supplied with carbon dioxide instead of air. This observation was subsequently repeatedly confirmed, but the first experiments of a more exact nature, but on similar lines, were those of **Kozarov** (1897). As mentioned above (p. 84), Kozarov experimented with rooted plants in a potometer. By passing a stream of carbon dioxide or hydrogen through the water in the potometer, he deprived the roots of oxygen, and was able to observe a delay in absorption. The checking influence of carbon dioxide was more marked than that of hydrogen, while prolonged exposure to carbon dioxide led to the poisoning and dying off of the roots. From this Kozarov concluded that hydrogen merely deprives the roots of oxygen, while carbon dioxide acts as a specific poison. Similar results were obtained by **Livingston and Free** (1917) with pure nitrogen instead of hydrogen. Finally, **Bergman** (1920) has observed that the poisonous influence of carbon dioxide begins

before all the oxygen is removed, thus confirming the earlier observations of **Kossovich** (1892).

Such are the data that exist regarding the influence of a deficiency of oxygen and an accumulation of carbon dioxide (in other words insufficient ventilation of the soil) on the absorption of water by the root system. Many other researches have dealt with the influence of insufficient aeration on the general development of the root system. I need not dwell in detail on the literature concerning the effect of a deficiency of oxygen on the growth of roots, especially as this has been dealt with fairly completely by **Clements** (1921). The most interesting results, from the standpoint of physiological ecology, are those of **Cannon** (1917, 1919, 1920). This author finds that different species of plants are susceptible in different degrees to low percentages of oxygen and the accumulation of carbon dioxide. In the extreme case of certain plants of moist soils, e.g. species of *Salix*, *Juncus*, and *Potentilla*, the roots continue to grow under such adverse conditions of aeration as would quickly kill the roots of most plants.

(*e*) *The Concentration of the Soil Solution—Halophytes*

In addition to its chemical composition, the concentration of the soil solution has an important influence on root suction. From purely theoretical considerations it is evident that each slight increase in the concentration of the solution surrounding a cell increases the resistance to absorption by the cell, and that when the osmotic pressure of the external solution balances the suction pressure of the cell, absorption of water ceases. From this it follows that an increase in the amount of soluble, even though neutral and harmless, salts in a soil must impede the water supply of plants growing in that soil. This explains why brining of the soil is injurious to the growth and development of the majority of both wild and cultivated plants—on this fact is based the use of salt in controlling certain weeds. Hence also the development on naturally saline soils, such as

salt marshes or on the seacoast, of a special "halophytic" vegetation, adapted to a high salt content of the soil.

These theoretical considerations were confirmed by a series of direct experiments conducted by various investigators. By adding 1 per cent of NaCl to Knop's solution, **Ricôme** (1903) observed with beans and castor-bean a marked reduction of the rate of absorption of water, which not infrequently led to the wilting of the aerial parts. A similar phenomenon was observed by **Renner** (1912) in water cultures of beans, to which 1 per cent KNO_3 had been added, the absorption being determined by means of a potometer. He noticed, however, that the delay in absorption was greatest immediately after increase in concentration of the solution, and that subsequently absorption became more rapid, the plant adapting itself, as it were, to the conditions of higher concentration. Renner suggests that the mechanism of this adaptation is the increased suction pressure of the leaves, due to their decreased water content as the result of obstructed absorption.

Montfort's experiments (1920) show that in this case we have to do not only with changes in the suction pressure of the leaves, but also with an increased suction of the root system. By means of his "guttation method", which eliminates both transpiration and leaf suction, Montfort observed that when the concentration of the solution was first increased, a delay or even a cessation of guttation took place (the already exuded drops being again absorbed). In a short time, however, guttation was renewed and proceeded more vigorously than at the beginning of the experiment. This points to an increase in the suction pressure of the root itself, which may depend on one of two causes: either the penetration of solutes from the surrounding solution into the cells and their accumulation in the cell sap, or a regulative increase of concentration of the cell sap, for instance, by the hydrolysis of poly- or disaccharides, etc.

Rybin (1923), again, observed a very marked increase in root suction when the salt solution, in which the root system had

previously been immersed for some time, was replaced by pure water. In the salt solution absorption had been retarded by 1½–2½ times, but replacement of this solution by water resulted in an absorption even greater (by 40–50 per cent) than the original rate. With a prolonged stay in water, however, this acceleration slowed down, which suggests that we have to do with an initial endosmosis of salt from the surrounding solution, and subsequently with an exosmosis into pure water. Similar phenomena were observed by **Sabinin** (1923) in his experiments on the bleeding of plants. Finally, we may mention the experiments of **Ursprung and Blum** (1921), who found that prolonged immersion in solutions of increased concentration augments the suction pressure of the cells of the absorbing zone of the root (see p. 72 above).

These experiments point to the conclusion that an increase of concentration of the soil solution is not an insurmountable obstacle to the absorption of water by roots, and that plants may overcome this difficulty by increasing the concentration of their cell sap. It is true that different plants are endowed with different capacities in this respect. The majority of our common plants can tolerate only a relatively small salt content of the soil, but halophytes and many desert plants, as **Fitting** (1911) has convincingly shown, can increase their osmotic pressure to 100 or more atmospheres. Such plants are able to develop a suction pressure sufficient to overcome the resistance to absorption of even concentrated soil solutions.

Thus the physiological dryness of saline soils, on which **Schimper** (1898) based his explanation of the "xeromorphic" structure of salt marsh plants, must be regarded as relative rather than absolute. To ordinary plants, unable sufficiently to increase their suction pressure by accumulating osmotic substances in their cell sap, these soils are actually "physiologically dry". Such plants are unable to obtain sufficient water, and either perish or at least are supplanted by better adapted halophytes. To the latter, which can develop an immense suction pressure in their cells, even strongly saline soil presents

no great obstacle to the absorption of water.[1] Provided only that the soil contains a sufficient amount of water, as in wet salt marshes and near the seashore, it is, so far as halophytic plants are concerned, both physiologically and physically moist. Halophytes not only thrive on it, but also, according to **Delf** (1911 and 1912) and **Stocker** (1924), show a somewhat energetic expenditure of water.

ABSORPTION OF WATER BY THE AERIAL ORGANS OF PLANTS

We have now examined the question of the absorption of water by the root system of the plant. In conclusion, we must consider the absorption of water by the aerial organs. The surfaces of leaves are not infrequently moistened by rain or dew, and long ago it was suggested that leaves are capable of absorbing water in spite of their cutinized epidermis and that the water so absorbed must play an important part in the water régime of the plant. **Volkens** (1887), for instance, affirms that during the dry season many plants of the Egypto-Arabian desert live exclusively on the dew deposited at night on their leaves. **Lundström** (1899), again, holds that the capacity of leaves to absorb rain and dew is widely spread, even among the plants of temperate climates. He describes a whole series of structural peculiarities, for instance, hairs, that would seem incomprehensible if not regarded as adaptations serving for the absorption of water. Finally, in many epiphytes, especially representatives of the family Bromeliaceæ, there are found special valve-like scales, which allow the entrance of water but prevent its escape. These scales were first studied by

[1] The concentrations of soil solution which salt marsh plants are called upon to endure may vary within wide limits, e.g. from about 1 per cent to 6 per cent NaCl (ordinary sea-water contains round about 3 per cent). These variations depend largely on the kind of weather which follows high spring-tides. If hot and dry, evaporation will bring about increasing concentration of the soil solution. Rains on the other hand, especially if the soil is sandy and porous, will cause leaching out of the salt, and hence reduced concentration. Halophytes appear to have the power of rapidly adjusting their cell sap to these changes, and even to the higher concentrations. See **Carey and Oliver** (1918, p. 174).—ED.]

Schimper (1889), and were more recently reinvestigated in detail by **Mez** (1904).

That plants are actually able to absorb water through the aerial parts was long since proved by the old experiment of **Hales,** who immersed the leafy tip of a cut branch in water and observed that it remained fresh considerably longer than a similar branch entirely deprived of water. From a consideration of the suction pressure of the cell it follows that every cell, no matter in which part of the plant it is situated, that is not saturated with water and is brought into contact with it, must absorb this water at its surface. The only questions are, how far is the cuticle covering the aerial organs permeable to water; how rapidly may water pass through it, and—most important of all—is the amount of water so absorbed able to play any perceptible rôle in the general water balance of the plant?

As the motive power of water absorption is due to the lack of saturation of the cell with water, the rate of absorption is in the first place determined by the nearness or otherwise of the cell to the wilting condition. Wilting leaves must absorb water more rapidly and vigorously than turgid ones, and there are many published data showing that wilting leaves, when placed with their surface in water, return in a comparatively short time to their normal turgid state. One and the same plant may therefore absorb water through its aerial parts in varying degree, depending on the extent to which it is saturated with water. The differences of opinion regarding the absorption of water by organs other than the root are to be explained by the fact that prior to the important researches of **Ursprung** (see Chapter I) many investigators did not sufficiently clearly realize the strength of the suction pressure of the cell and its significance.

Wetzel (1924) has recently reinvestigated the question of the absorption of water by the aerial parts of higher plants. He devoted his attention chiefly to plants of temperate climates, almost entirely leaving out of consideration the Bromeliaceæ and other epiphytes. In the first place he established the fact

that the phenomenon in question is widely spread. Wetzel found that nearly all the leaves investigated (over 100 species) were able to absorb water and that the cuticle, however considerable its development, was not an insuperable barrier to the passage of water. Only in cases in which the leaf possessed a waxy bloom or a thick covering of hairs, was no water at all absorbed. The rate of absorption, however, was somewhat feeble, and could not be compared with the rate of water absorption through cut vessels; thus, about one-third of the investigated leaves were unable to restore their turgor completely within 24 hours.

Of great interest are Wetzel's experiments under natural conditions. For a series of plants, including some xerophytes that grow on rocks in the environs of Heidelberg, he compared the daily loss of water with the amount the plants were able to absorb when their leaves were moistened with dew or artificially sprinkled. He found that even in wilting plants dew was unable to supply more than 5–10 per cent—and under ordinary conditions not more than 1–2 per cent—of the daily expenditure of water. From these results Wetzel concludes that so far as the representatives of the Central European flora investigated by him are concerned, absorption by the aerial organs plays no rôle in the general water supply of the plant, and can in no way replace the absorption of water through the root system. Moreover, according to earlier observations by **Haberlandt** (1877), **Wiesner** (1882), **Burgerstein** (1897), and **Iljin** (1916), the moistening of the leaf surface with water may even lead to harmful consequences, as it increases the intensity of transpiration, thus accelerating the loss of water and bringing nearer the moment of wilting. This rapid drying after surface wetting is well known to practical workers: gardeners avoid watering plants when directly insolated, and farmers know that grass mown when it is dewy dries better and more rapidly.

We may conclude, then, that only in tropical epiphytes possessing special absorbing organs may the absorption of water by the aerial parts of the plant play an important rôle in

its water régime. Other plants are obliged to content themselves with the water supplied by their roots. Dew and light rains, in so far as they only moisten the leaves on the surface of the soil, without penetrating the latter, are probably not directly utilized by our common plants. Matters are different with underground dew, which, in the opinion of many authors, may play a somewhat important rôle in the water supply of desert and even steppe plants (**Lebedev**, 1913).[1] But the question of underground dew is too little elucidated from a purely physical point of view, and is in general too debatable to be dealt with in detail, the more so that the source of the water that enters the zone of attraction of the root system is of no importance to the plant.

[1 A similar suggestion regarding the importance of "internal dew formation" has been made in the case of sand dunes and shingle beaches. See **Olsson-Seffer** (1909) and **Hill and Hanley** (1914).—ED.]

PART II

THE LOSS OF WATER BY THE PLANT

CHAPTER IV

THE METHODS OF INVESTIGATING TRANSPIRATION

The physiological results of transpiration. Quantitative methods of investigating transpiration—methods of determining the water vapour transpired; gravimetric methods of determining the amount of water lost; volumetric methods of determining the amount of water absorbed by cut shoots. Methods of calculating results: concepts and terminology.

The Physiological Results of Transpiration

We have seen that during its life the plant loses considerable amounts of water by transpiration, and not infrequently experiences difficulty in replacing this water. What is the significance to the plant of the continuous stream of water passing through its organs? Does the plant derive benefit from this "transpiration current", or does it merely submit to a purely physical necessity?

There can be no doubt that the process of transpiration is for all land plants physically unavoidable. The assimilating leaves must maintain open communication between the cells of the chlorenchyma and the external atmosphere, which contains the carbon dioxide necessary for nutrition. At the same time these cells must be sufficiently supplied with water. Now except in rainy weather and at the time of dew formation the atmosphere is rarely saturated. Hence water vapour from the intercellular spaces diffuses into the external atmosphere, the vapour pressure in the intercellular spaces falls, and this in turn causes the evaporation of water from the surfaces of the moist cell walls. The inevitable result is the process of water loss known as transpiration. It is easy to understand that the drier the climate, the greater the rate of transpiration and the greater the amount of water the plant must extract from the soil. If transpiration greatly exceeds absorption, the plant may wilt or even die.

Thus transpiration is not only a physical necessity, but may be definitely injurious to the plant. In some cases it hinders

nutrition, which is checked by wilting; in others it leads to death. This is why in years of drought plants are poorly developed or even perish, and why in arid districts such as deserts and semi-deserts we find only a sparse, stunted vegetation, strikingly different from the luxuriant vegetation of well-watered regions.

These obviously harmful consequences of excessive transpiration have led many authors to the opinion that transpiration is nothing more than an inevitable evil, which plants more or less succeed in overcoming by means of various protective adaptations, about which more detailed information will be given later. The most ardent advocates of this idea were **Reinitzer** (1881), **Volkens** (1887), **Schwendener** (1899), and his pupil **Holtermann** (1907). In Russia it was maintained with his customary ability by **Timiriazev** in his famous lecture on "The Struggle of the Plant with Drought". This lecture determined for many years the attitude towards this question of most Russian botanists and especially agriculturists.

The opposite view, supported by the majority of investigators, is that transpiration discharges a series of functions, useful and even necessary for the successful development of the plant. In the first place transpiration facilitates the absorption and upward translocation of mineral salts. Simple calculations prove that by diffusion alone, an exceedingly slow process, the plant cannot obtain sufficient quantities of salts from the soil. The accumulation of sufficient salts for the nutrition of the plant necessitates the passage of a constant stream of water from the soil into the plant. This stream, moreover, both accelerates and facilitates the passage of solutes through the plasma membranes. It is true that the plant possesses in the root pressure discussed above internal means of supporting this current. But the amount of water actually translocated by root pressure is comparatively small, and besides, the energy required for this active work of the roots is probably derived from respiration, and therefore necessitates the consumption of organic substance. On the other hand, the direct source of

the energy used in the suction of transpiring leaves is the radiant energy of the sun. This is why translocation of water by means of transpiration is incomparably more economical than the translocation due to root pressure. Further, it may be pointed out that, while root activity diminishes with decrease of soil moisture, the suction due to transpiration increases with insolation and the dryness of the atmosphere. The process of leaf suction, then, has an automatically regulated mechanism, the activity of which increases or decreases with the need of the plant for water.

Another, though less important consequence of transpiration, is the moderating of the heating effect which would otherwise be produced by the sun's rays. The work of vaporization of water in the leaf consumes, as exact quantitative determinations have proved, about 80 per cent or more of the energy of the sunlight absorbed.[1] In consequence, the temperature of intensely transpiring leaves rises but slightly above that of the surrounding air.

Strong insolation under conditions of reduced transpiration, as, for instance, in greenhouses, not infrequently leads to the overheating and severe burning of leaves, from which greenhouse plants have to be protected by shading. But we must not attach too great importance to the value of cooling by transpiration, as plants could undoubtedly adapt themselves to endure higher temperatures. Succulent plants, for instance, the fleshy stems or leaves of which transpire feebly, may be heated by sunlight to 50–60° C. without injury.

Very interesting data regarding the influence of sunlight on leaf temperatures were obtained by **Miller and Saunders** (1923). By means of an ingenious thermo-electric

[1 The actual proportion of the solar radiation absorbed by the leaf which is expended in this way must vary considerably according to conditions, see **Brown and Escombe** (1905). These authors discuss the energy relations of a green leaf exposed to sunlight, and from experimental data attempt to calculate the percentages of the energy received, which are respectively utilized in the internal work of water vaporization and photosynthesis, transmitted by the leaf, or lost by "thermal emission". —ED.]

apparatus they measured the temperatures of the leaves of various crop plants, and studied the dependence of leaf temperature on the factors of light, water supply and transpiration. Considerable attention was paid to a comparison of the temperatures of turgid, strongly transpiring leaves with those of wilted leaves with reduced transpiration. The greatest difference, 9·5° C., actually observed was in an experiment with cowpea (*Vigna sinensis*). In this instance the respective temperatures were: turgid leaf, 36·5°; wilted leaf, 46·0°; air, 37·0°. The maximum difference (for the cowpea) between the rates of transpiration of turgid and wilted leaves respectively was in the ratio 20 : 1. A large number of determinations, made between the hours of 9 a.m. and 4 p.m., showed that the average temperatures of wilted leaves were: in cowpeas, 4·65° C., soya beans (*Glycine Soja*), 2·8°; corn, 1·85°; and sorghum, 1·55° higher than those of the turgid leaves. The ratio of the average rate of transpiration of turgid leaves to that of wilted leaves was 3·5 : 1 in cowpeas and soya beans, and 2·5 : 1 in corn and sorghum. The temperature of turgid leaves, on the whole, differed but slightly from that of the surrounding air. Miller and Saunders's results show that transpiration does to some extent reduce the temperature of the leaf, but that its influence must not be overrated.

Another physiological result of transpiration has recently been pointed out by **L. Ivanov** (1923). Transpiration, according to this author, by creating a certain saturation deficit in the cells, acts as a turgor regulator, which tends to maintain in a given plant the optimal degree of turgor. Various authors, for example, **Schlösing** (1869), **Wollny** (1898), **Gain** (1895), and others, have shown that in an atmosphere saturated with water vapour plants develop abnormally. The cells are excessively turgid and the tissues poorly differentiated, the stems are elongated, and flowering and fruiting retarded or entirely inhibited. In short, the plants assume a pathological appearance in many ways resembling that of etiolated plants.

Thus transpiration facilitates the absorption and upward

translocation of water and mineral solutes, and regulates temperature and the degree of turgor. These results alone are sufficient to compel one to dismiss the view that transpiration is merely a necessary evil, and to acknowledge that it is one of the most important of physiological processes. But one must not go from one extreme to another, and suppose that transpiration is the only means of providing the plant with mineral salts. Nor is it to be assumed that the amount of salts absorbed, or of the organic substance formed with their assistance, must be directly proportional to the amount of water transpired. A series of experiments by **Haberlandt** (1892), **Hasselbring** (1914[a]), and **McLean** (1919) definitely show that the rates of absorption of mineral salts and of water are to a great degree independent of one another. In this connexion **Muenscher's** (1922) experiments are of special interest. Muenscher grew barley for a period of five weeks in water cultures, under different conditions, namely, in a dry and a humid atmosphere, in light and in shade, and finally in solutions of different concentrations. He determined the total water transpired, the total ash content, and the dry weight of the plants. These experiments proved that notwithstanding the diversity of conditions, the ash content remained practically constant, varying only from 19·3–21·1 per cent of the dry weight, and that under different conditions of growth the plants used varying amounts of water per gramme of ash content. Thus in the dry chamber the plants transpired 2,381 gr. of water per gr. of ash, but in the humid chamber only 1,259 gr. ; in the light 2,587, and in the shade 3,309 gr., and so on. Similarly, numerous experiments on the "transpiration coefficient" (see Chapter XI) have shown that the drier the climate, the more water is used per unit of dry substance produced by the plant, as well as per gramme of ash; in other words, the amount of water passing through the plant is less productive (see review of literature on *The Water Requirement of Plants*, by **Briggs and Shantz,** 1913[b]). Finally, **Huber** (1923) came to the same conclusion regarding the absence of direct relation between the water

transpired and the ash accumulated, by studying these processes in the branches of the mammoth tree (*Sequoia gigantea*), situated at different heights above the level of the soil.

Thus it would be a mistake to assert that in order to obtain the required amount of salts, the plant needs to transpire the enormous quantities of water often lost in natural habitats. This is especially true of hot, dry climates, for otherwise the most favourable conditions for growth would be found in irrigated desert regions, whereas the most luxuriant vegetation actually occurs in warm, moist climates. Undoubtedly it is very often true that the amount of water lost by the plant greatly exceeds the necessary minimum. In such cases transpiration could be reduced not only without injury, but even with advantage to the plant.

Quantitative Methods of Investigating Transpiration

The quantitative study of transpiration is both simple and complicated. It is simple if we have merely to determine the amount of water lost by a plant under artificial experimental conditions, e.g. by a detached branch with its cut end placed in water in a laboratory. It is complicated if we wish to measure the transpiration of an uninjured plant in its natural habitat, with a normally developed root system spreading unhindered in the soil. The complications are caused by the extreme variability of the atmospheric conditions influencing transpiration, and by the close correlation which exists between the intake and loss of water by the plant. Any disturbance of the conditions of water absorption, as for instance by injury to or removal of the root system, affects the rate of transpiration. This rate is also influenced by changes in the soil moisture, by soil aeration, soil temperature, and other factors which affect, as we have already seen, the absorbing capacity of the roots.

Investigators have often been led astray by failing to realize how artificial conditions affect the rate of transpiration, and in

consequence their results have lost much of their value. It is therefore necessary to preface the further study of transpiration itself by a detailed, critical survey of the principal methods used in its investigation. The very diversity of these methods indicates that there is no one method which will yield absolutely reliable results in all cases. According to the principles on which they are based, these methods can be divided into the following three groups:—

(1) The collection and determination of the water vapour transpired by the plant;
(2) the determination of changes in the weight of the plant due to the loss of water;
(3) the determination of the amount of water absorbed by the plant in exchange for that lost by transpiration.

(1) *Methods of Determining the Water Vapour Transpired*

Theoretically, one might expect the best results from the first group of methods, as in this group we merely collect the water transpired, without otherwise disturbing the plant. The historical experiments of **Guettard** in 1748 were based on this principle of collecting the water "respirated" by the plant. He introduced a branch of some shrub (Fig. 6) through a side-opening into a large glass vessel. The water vapour deposited on the inside of the glass walls ran down through an opening below into a bottle inserted in the soil. This condensation method for the determination of transpiration is extremely crude, and it may seem astonishing that as late as 1869 this method was used by such a scientist as **Dehérain.** Although the parts of the plant outside the container are under natural conditions, the air inside is saturated with water vapour, and this must undoubtedly interfere with the march of transpiration.

An improvement on this method consists in the introduction of some water-absorbing substance, e.g. calcium chloride, into the glass vessel covering the plant. By weighing this substance

before and after the experiment one may determine the quantity of water absorbed, and therefore the amount of water vapour given off by the plant. However, this method also has but an historical significance, as the plant is artificially sur-

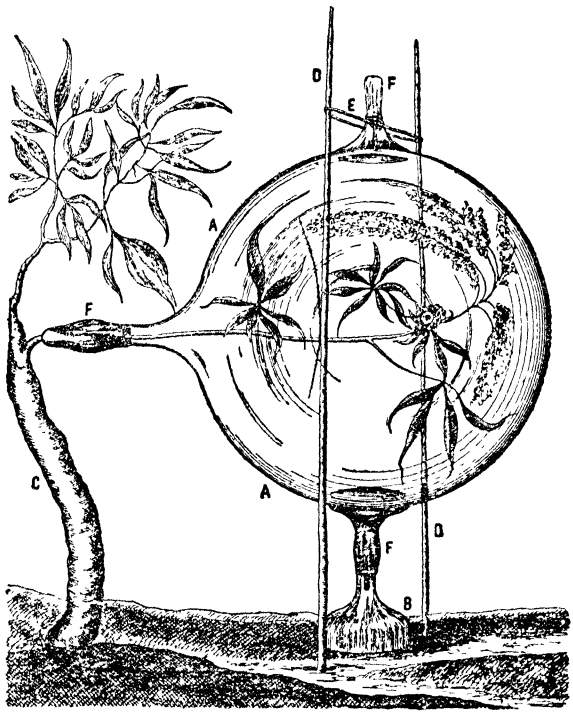

FIG. 6.—Condensation method of determining transpiration (after Guettard).

rounded by an excessively dry atmosphere, which again must modify the transpiration.

A more decided improvement is the drawing of a continuous current of air through the vessel containing the plant. The current then passes through a second vessel containing the hygroscopic substance. This method, used by **Géneau de Lamarlière** (1892) for comparing the transpiration of sun

and shade plants, was later somewhat improved by **Freeman** (1908). The following are the essential points of Freeman's method: by means of an aspirator (Fig. 7) a current of air of definite velocity is drawn through the vessel containing a branch or a leaf, which remains attached to the plant. The water vapour carried by the current of air is absorbed by phosphorus pentoxide (P_2O_5) in two U-tubes. The increase in

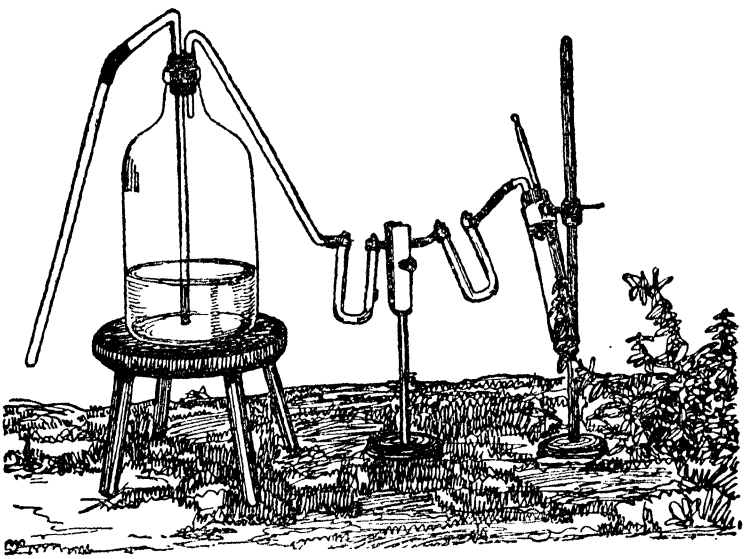

FIG. 7.—Freeman's method of determining transpiration by passing air through a vessel containing the shoot of a plant (from Burgerstein).

weight of these tubes indicates the amount of water transpired by the enclosed portion of the plant, together with that already in the air as it enters the apparatus. The initial water vapour content of the air is determined simultaneously by drawing air at the same velocity through two similar U-tubes only. The difference between the two amounts of water collected gives the actual water transpired.

Another modification of the same method has been suggested by **Cannon** (1905). This consists in observing, by

means of an hygrometer, the changes of absolute humidity occurring in a large bell-jar containing the plant (Fig. 8). A convenient form of hygrometer is Lambrecht's polymeter. Before covering the plant, the surface of the soil must, of course, be suitably protected from evaporation. This method can only be applied to plants with a low intensity of transpiration, such

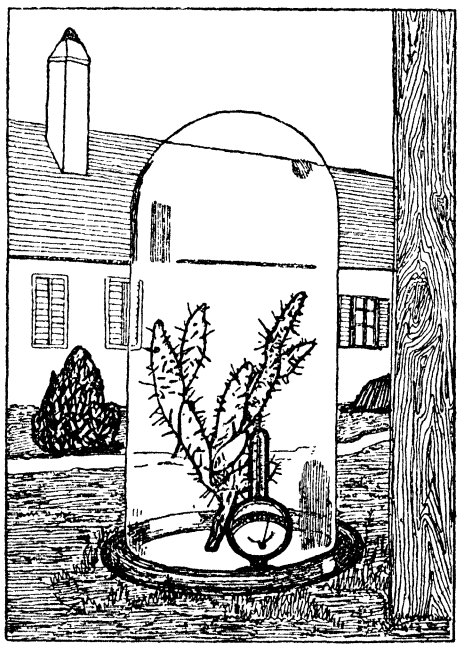

FIG. 8.—Cannon's hygrometer method of determining transpiration (from Burgerstein).

as cacti. The drawbacks of the method are that the plant is surrounded by a closed, still atmosphere, which must reduce the rate of transpiration, and that in direct sunlight the air is very soon overheated.

This latter defect is not completely removed even in **Freeman's** method, in which a continuous current of air is drawn through the vessel containing the plant (see above). In order to mix this air thoroughly, the current should be sucked through

with considerable velocity, as it is, for instance, in Assmann's psychrometer. But no hygroscopic substance would be capable of absorbing and retaining all the moisture from such a rapid current of air, so the velocity of the current must be comparatively small. This means that it is impossible to avoid overheating by the sun, as well as local immobility of the air charged with water vapour—the latter condition leading to deposition of moisture on the walls of the container. With this apparatus it is better to perform experiments only under shade conditions, as it is not really suitable for measuring transpiration from parts directly exposed to the sun. On the other hand the method has the important advantage that the organ experimented on remains connected with the plant.[1] Hence the water supply to the plant in question is not appreciably disturbed, and, as we shall see later, the conditions of water supply form one of the most important factors affecting transpiration.

Somewhat analogous to the quantitative methods described above, which depend on the increase in weight of water-absorbing substances, is the method of measuring transpiration by the colour changes exhibited by certain hygroscopic substances when saturated with water. This constitutes **Stahl's** (1894) well-known *cobalt chloride method*, which was at first only of a qualitative character, though attempts have recently been made to place it on a quantitative basis. This method is based on the fact that filter paper impregnated with a 3 per cent solution of cobalt chloride has, when thoroughly dry, an intense blue colour, but, when moist, becomes pale pink. If a slip of such paper is placed on the transpiring surface of a leaf, its colour changes, and the higher the rate of transpiration the more rapidly does this change of colour take place. By this simple method we can, for instance, readily demonstrate a considerable difference in the rate of water loss from the upper

[1 It is probably also the only reasonably satisfactory quantitative method by which the transpiration of different leaves on one and the same shoot (of an intact plant) can be simultaneously measured.—ED.]

and lower surfaces respectively, of leaves in which the stomata are wholly or mainly on one leaf surface.

During recent years Livingston and his co-workers (**Livingston and Edith Shreve** (1916), **Bakke** (1914), **Trelease** (1916), **Aleita Hopping** (1914)), by introducing a series of improvements, have given the cobalt chloride method a quantitative character. Slightly modified, it has been included by **Rübel** (1922) in his *Geobotanische Untersuchungsmethoden*, where a detailed description of the method may be found. Only the essential points of the method will be given here. It is based on the exact determination, by means of a stop-watch, of the time required for dry cobalt paper, when placed on a leaf, to assume a pink colour of a definite shade. It is essential for the accuracy of the method, that the initial and final colour tones should be precisely fixed. The filter paper must be thin, uniform, and of good quality. The cobalt chloride solution must be of a definite concentration, i.e. 3 gr. to 100 c.c. of water. The paper used in an experiment must be completely dry: to this end it may be either dried on a heated metal plate immediately before using, or, if dried previously, kept till required in a desiccator.

If the paper is allowed to assume a pink colour, it is difficult to determine exactly the end-point of the reaction. It has therefore been found more convenient in practice to stop at one of the pale blue shades. In order to determine the precise moment when the selected colour tone is reached, standard paper of the required shade is prepared by precipitating Prussian blue in filter paper, which is then dried for use. The paper so prepared serves as a permanent standard for comparison, and during an experiment it is placed side by side with the cobalt paper. This standard shade may be termed the final standard tone, and serves to indicate the end-point of the test. To fix the precise time of the beginning of the test, a second permanent standard paper is used, of a slightly paler shade than that of the absolutely dry cobalt paper. This is the so-called initial standard tone. The preparation of these per-

manent standard papers is somewhat complicated; a detailed description of the method is given by **Livingston and Shreve** (1916). The simplest plan, however, is to order the standard papers directly from The Atmometer Apparatus Co., Laboratory of Plant Physiology, Johns Hopkins University, Baltimore, Md., U.S.A. For observing the rate of water loss by leaves, which during the experiment remain attached to the plant, special clips with glass tips are used (Fig. 9). These closely but delicately press the cobalt paper to the leaf surface, and through the glass one may observe the changes in colour. Side by side under the same slip of glass are pasted two strips

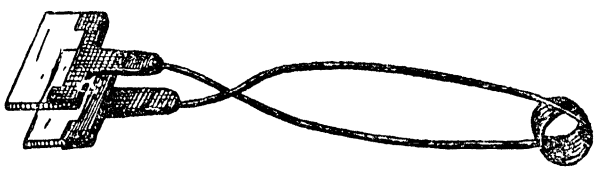

FIG. 9.—Livingston's clip for the quantitative cobalt method (from Rübel).

of the standard papers, one of the "initial", the other of the "final" tone.

The mere determination of the time required for the change in colour of the cobalt paper pressed to the leaf does not lead very far. We can indeed compare the rapidity of colour change with leaves of different plants, and note the differences in the time required, but the results will be more valuable if we relate this interval of time to some constant magnitude. As such the rate of colour change of cobalt paper placed over a free water surface, or (which is more convenient) over a moist filter paper, may be employed. Knowing both rates we can calculate the ratio of evaporation from a free water surface to that from the leaf surface. **Livingston** regards this ratio, which he terms the *index of transpiring power* of the plant, as important for the ecological classification of plants. It is allied to the concept of *relative transpiration*, also introduced by Livingston, which will be discussed later.

The cobalt chloride method is simple and convenient, and has lately been widely used. It has its drawbacks, however, in that it does not indicate the absolute amount of water lost by the plant; moreover, as it is based on a subjective estimate of the colour changes involved, it cannot be very exact.[1] It is therefore doubtful whether this method will replace more reliable objective methods of determining transpiration.

(2) *Gravimetric Methods of Determining the Amount of Water Lost*

The second group of methods of measuring transpiration is based on changes in the weight of the plant due to loss of water. At first sight it might be supposed that such methods might introduce a considerable error, for changes of weight depend not only on the loss or gain of water, but also on the gain or loss of dry substance due to assimilation and respiration. Numerous experiments, however, have shown that the weight of water lost by a plant in unit time is hundreds of times as great as the increase of dry weight. The error resulting from the neglect of assimilation and respiration is therefore only a fraction of 1 per cent. Compared with the degree of accuracy attainable, this error is insignificant, and the gravimetric method of determining the amount of water lost is undoubtedly the most reliable of all the available methods of measuring transpiration.

From the ecological point of view this method has the great advantage that it does not involve alterations of the atmosphere surrounding the plant, for during an experiment the plant is exposed, as it was during development, to the whole complex

[1 Another objection to the cobalt method—as an exact quantitative method—is that the portion of leaf actually tested is placed under wholly unnatural conditions. The part confined between two slips of glass would seldom continue to transpire at the same rate as the free portions of the lamina. Even so, the rate of transpiration might be expected to slow down as the dry paper absorbed moisture from the leaf surface, so that the result obtained would be merely the average rate for the time interval in question.—ED.]

of meteorological factors. If, however, we wish to determine the transpiration of a plant in its natural environment, we must take care that there is no unnatural interference with the supply of water to the transpiring organs.

Satisfactory results may be obtained if we weigh intact rooted plants together with the soil supplying the root system with water. But the use of considerable masses of heavy soil introduces a series of difficulties and complications. The chief difficulties to be overcome are a considerable increase of the general weight (which must inevitably affect the sensitiveness of the balance and the accuracy of weighing), and the necessity of preventing evaporation from the surface of the soil.

The average weight of soil which allows the normal development of plants of moderate size, such as buckwheat (*Fagopyrum vulgare*) or beans, varies between 5–15 kg. For well-developed plants it is usually sufficient to weigh to 1–2 gr., when an ordinary Beranger balance may be used. But more sensitive balances are often necessary, e.g. in wilting experiments, or when using plants grown in intense shade. In such cases one must weigh to a tenth of a decigram, and a balance with hanging scale pans, sensitive to 1:50,000, or, still better, 1:100,000, is required. If one scale pan has long supports (Fig. 10) there will be room for the shoot under the beam, or the form of balance figured by **Pfeffer** (1900, Fig. 29) may be employed.

In order to secure greater accuracy in weighing, the plants should be grown in the smallest possible volumes of soil. Too small containers, on the other hand, interfere with the development of the plant. Under field conditions the root systems of plants may attain considerable dimensions. The roots of our common crop plants, for instance, may extend to a depth of 2 m., with a spread of about the same width (see **Rotmistrov**, 1910; **Modestov**, 1915; **Weaver**, 1920; and others). The impossibility of weighing containers of such a size is obvious, so a standard pot, 20 × 20 cm., has been adopted for cereals, six or seven plants being grown in each.

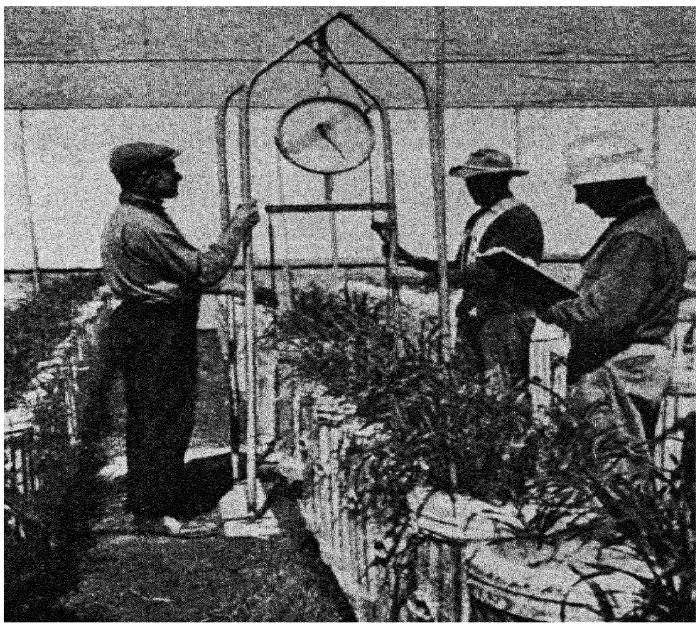

FIG. 11.—Briggs and Shantz's large containers and spring balance for transpiration experiments

experiments of this kind will be discussed later, when dealing with this question. For ordinary transpiration experiments such enormous containers are quite unnecessary.

We may now discuss the methods of preventing evaporation from the surface of the soil. Two cases may be distinguished. In the first we measure the transpiration of mature plants during short periods of time; in the second the water lost daily by the plant during its whole period of development. In the first case plants may be grown in ordinary flower-pots with porous sides and a hole in the bottom: this simplifies the care of the cultures. But at the time of the experiment the whole pot must be enclosed in some water- and vapour-proof covering. Zinc containers with a sliding roof, and an aperture for the stem, may be used: **Ganong** (1908) recommends special aluminium shells roofed with rubber.

In the second case, where it is required to determine transpiration over a considerable period, glass, glazed earthenware or metal containers, impermeable to water, must be employed. Such containers are widely used at agricultural experiment stations. In rough experiments these containers are left open at the top, sometimes covered with a layer of dry sand or cotton-wool to diminish evaporation from the soil. This, however, does not completely prevent the loss of water from the soil. For exact experiments it is necessary to provide the containers with closely fitting metal covers.

The aperture in the cover must of course be wider than the stem of the growing plant, hence the space between the stem and the cover must be closed with some waterproof substance. After numerous trials with plasticine and other cements, I finally succeeded in inventing a simple lute, which maintains its plasticity and so does not hinder the growth of the stem; at the same time it is not softened by moisture, and closely adheres to the stem and the metal cover. This lute is a mixture of powdered chalk and ordinary unrefined castor-oil.[1]

[1 **Briggs and Shantz's** (1912) "wax-seal method" (see p. 64) is another very useful method of sealing the containers, and so preventing evaporation

The question arises as to whether such hermetic sealing of the containers, by preventing access of oxygen, may not prejudicially affect the root system. My numerous experiments have answered this question in the negative. Provided only that the soil moisture does not exceed 60–70 per cent of the water holding capacity, and that the soil capillaries are not completely filled with water, the ordinary diurnal fluctuations of temperature suffice to supply the roots with sufficient oxygen. **Žemčužnikov** (1921, 1924), using the methods I have worked out and described in collaboration with **V. Alexandrov** (1917), came to the same conclusion. Nevertheless, in order to secure better aeration and more uniform distribution of the moisture supplied in watering, a useful modification of the usual method has been introduced. That this is not absolutely necessary, however, has recently been confirmed by **Žemčužnikov** (1924).

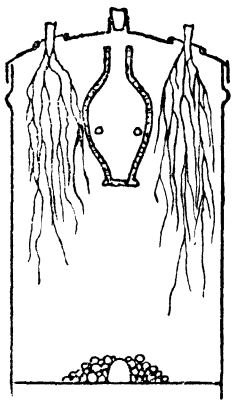

FIG. 12.—Diagrammatic section of container with convex cover and porous pot (from Maximov).

The modification consists in the insertion in the soil of a porous porcelain cup of 100–200 c.c. capacity (depending on the size of the container), with small holes in its walls (Fig. 12). A hole, fitted with a stopper, is made in the cover for watering, water being added in turn from below through the drainage outlet, and from above through the porous cup. Under these conditions plants thrive well in hermetically closed containers and, which is especially noticeable, the root system spreads uniformly throughout the evenly moistened soil. In ordinary cultures in open vessels with a dry layer of soil on the surface, the bulk of the root system is always found at the bottom of the container near

from the surface of the soil. These authors describe a method of aerating the soil in the sealed containers by sucking air through it by means of an aspirator.—ED.]

the drainage outlet, the upper layers of soil remaining unavailable. It would seem, therefore, that the method of culture of plants in covered pots can be used not only for the study of transpiration, but for other purposes as well.

It may be emphasized that only by careful previous cultivation in suitable containers such as those mentioned above, is it possible to procure plants in a fit state for transpiration experiments. The practice of transferring plants from the open soil to pots shortly before an experiment, hitherto adopted by many investigators, is absolutely inadmissible. It must be borne in mind in transpiration experiments that the conditions governing the supply of water to the transpiring organs exert a profound influence on the rate and the march of transpiration. A plant with roots injured by transplanting cannot furnish a true picture of the normal transpiration of one with an intact, normally functioning root system. Gardeners, well acquainted with this fact, transplant only at a definite season of the year (either before the buds open, or after the transpiring organs have fallen), or else in the early stages of growth (seedlings), when the injured roots are easily replaced by new ones. Unfortunately, many physiologists, when attacking the problem of transpiration, pay too little attention to these conditions. Yet **Sorauer** (1880) had already shown that plants with injured roots may only transpire half as much as plants with healthy roots.

The unwieldy nature of experiments with plants rooted in the soil, and the labour of cultivating large quantities of plants in containers, appear to be the chief reasons why most of the investigations on transpiration have been made with shoots or even separate leaves rather than with entire plants. This usual method is undoubtedly both simple and convenient. The shoots are cut from the plant (preferably under water, to avoid entry of air into the vessels) and placed with the cut end inserted through a hole in a stopper, in a vessel containing water, precautions being taken to prevent the evaporation of water otherwise than through the shoot. The plant is then

weighed at intervals on an accurate balance, the sensitiveness of which is unaffected by such an insignificant load. The various modifications of this method need not be dealt with here; they are described elsewhere in practical manuals of plant physiology. These modifications are of no special interest. It is more important to consider the changes introduced into the process of transpiration by such a method of experiment.

Close study of the many published investigations made with cut parts of plants (amongst recent works are those of **Iljin** (1914[a]), **Žemčužnikov** (1919), **Lloyd** (1908), and **Clements** and his pupils, and also of hundreds of unpublished experiments made by myself personally and by my co-workers, enables me to summarize the available data concerning the march of transpiration from cut shoots. During the hours immediately following the cutting of the shoots (the environmental conditions remaining constant), transpiration may either gradually decrease or increase, or (more rarely) it may remain constant.

A gradual decrease may be observed when there is a high tension of the environmental factors promoting transpiration. This may be due to an excess of water loss over water absorption, the increase in the water deficit often leading to obvious wilting of the leaves. Such a decrease in transpiration is found when a cut shoot is placed in direct sunlight; hence it is inadmissible to work with cut shoots in open localities and in bright weather. But a water deficit may be occasioned, not only by an increased water loss, but also by a retarded water supply. This is why we often find reduced transpiration from the cut shoots of shade plants, even when the experiments are performed in a feebly lighted room. Many shade plants have a poorly developed vascular system and a powerful root pressure, so that their shoots, when separated from the roots, are unfavourably situated in regard to their water supply. A decrease in transpiration may also be observed in such lacticiferous plants as euphorbias, poppies, etc.—the latex exuding from the cut stem gradually blocks the conducting vessels—as well as in

plants with a poorly conducting xylem, e.g. conifers and many evergreen trees. Again, if the shoots are imprudently cut in hot weather, the vessels may be blocked by air. Finally, when an experiment is continued for some time, the surface of the cut end, including the lumina of the vessels, may become infected by bacteria, or blocked by mucilage, etc. The shoots then exhibit decreased transpiration, which does not always recover its initial rate, even if the blocked surface is cut away and a new surface exposed.

The cutting of a shoot, however, does not always diminish the supply of water to the transpiring organs. It may even increase it, as when different shoots on the same plant strongly compete with one another for an inadequate supply of water from the roots. One may observe such a struggle in many herbaceous plants during the midday hours on sunny days, particularly in open localities, while in trees it is a general rule, as recently shown by **Žemčužnikov** (1919). Further, it has frequently been observed that if a portion of a plant is divided into separate pieces, the intensity of transpiration is markedly increased. **Famintsin** (1883), for instance, in his book on the metabolism of plants, cites the following experiment performed by his pupil **Krutizky**. A hawthorn shoot with eight leaves transpired 8 gr. of water a day; one with five leaves, 5·2 gr.; and a shoot with only one leaf, 4·9 gr. On the basis of the amount transpired in the third case, the first shoot should have transpired 39·2 gr. instead of 8, and the second 24·5 gr. instead of 5·2. This can only be explained by supposing that as leaves are successively removed from a shoot, the supply of water to the remaining, still attached leaves is increased.[1] Thus calculations of the transpiration of entire trees or of forests, based on figures obtained with separate shoots or leaves, are entirely misleading.

[1 **Balls** (1919) records an analogous case in the cotton plant in Egypt. He found that owing to transpiration from the leaves, the elongation of the stem is immediately checked by direct sunshine. Removal of the lower leaves, however, by reducing the loss of water, resulted in an almost instantaneous resumption of stem-growth.—ED.]

These changes in transpiration occurring after the cutting of shoots show that results obtained from experiments with cut parts of plants are unreliable. If, however, we wish to use cut parts in order to investigate the influence of external conditions on transpiration, it is best to cut the shoots (as recommended by many authors) in the evening, and to allow them to attain a state of equilibrium during the night. If, on the other hand, we desire to study the rate of transpiration in an uninjured plant under natural conditions, the most valuable information is that obtained just after the cutting of the shoot. For this reason one must shorten as much as possible the intervals between successive weighings. One can go still further and let the cut branch transpire without access to water. The resulting curve of transpiration will then be a falling one, for as the water content of the shoot decreases, the transpiration rapidly falls (the question of whether this reduction of transpiration is due directly to the lowered water content, or to the closing of the stomata, will be discussed later). If transpiration is not too rapid, the initial rate obtained immediately after cutting will approach fairly nearly to the actual rate of transpiration in the uninjured shoot before cutting.

This method of weighing without replenishing the water supply requires alertness, and a strictly critical attitude towards his own work, on the part of the investigator. With slowly transpiring subjects, such as succulents and the shoots of woody plants in winter, it gives excellent results, as has been proved by the investigations of **L. A. Ivanov** (1924) on the transpiration of conifers in winter. **Huber** (1923) has used the method for measuring the transpiration of branches of the mammoth tree (*Sequoia gigantea*) at different heights above the soil. But for rapidly transpiring plants the method is of little use, because such plants very soon wilt, and this may affect even the first weighing. Moreover, assuming negative pressure to exist in the vessels of the stem, the cutting of the shoot instantly increases the supply of water to the leaves, owing to the relaxation of tension in the water columns.

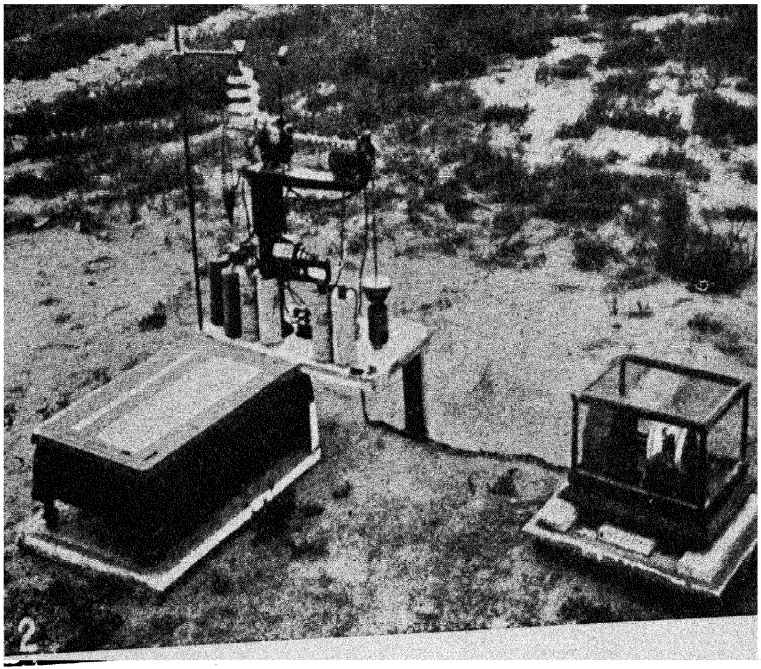

FIG. 13.—Briggs and Shantz's automatic recording balances for great weights

Such are the more important modifications of the gravimetric method of measuring transpiration. As it is very often necessary to make a series of determinations extending over a considerable period of time, attempts have been made to devise self-recording balances, in order to obtain continuous records of the march of transpiration. These devices are, in most cases, only adapted for use in the laboratory, as even slight air movements impair their efficiency. Information regarding such apparatus will be found in **Burgerstein's** monograph (1904, 1920), and in an article by **Victor Grafe** (1920). **Briggs and Shantz** (1915) have also discussed various recording balances, and described a new form of automatic transpiration scale, of 200 kg. capacity, and sensitive to 5 gr. (Fig. 13). This balance was used successfully in Colorado for four summers, even on the open prairie, in an extensive investigation of the march of transpiration in various agricultural and wild plants.

(3) *Volumetric Methods of Determining the Amount of Water Absorbed by Cut Shoots*

The third group of methods for the study of transpiration is based on the determination of the volume of water absorbed by the plant, instead of on the amount lost, during the process of transpiration. These may be termed *volumetric methods*, as opposed to the gravimetric methods described above. It is readily perceived that such methods are indirect, and presuppose that the amount of water absorbed is the exact equivalent of that transpired. That these methods are so widely used is due to their simplicity and convenience, and to the fact that they are exceptionally useful for purposes of demonstration.

The most important apparatus used in such determinations is the potometer, to which attention has already been called in Chapter I (p. 55). Extensive reference to the potometer method will be found in the physiological monographs of **Kohl** (1886) and **Eberdt** (1889), which deal with various

aspects of the process of transpiration. In these works considerable attention is paid to the influence of external conditions on transpiration. The apparatus used by both authors is usually known as Kohl's apparatus. This is really **Vesque's** potometer (see p. 56) with the addition of a bell-jar, in which the transpiring parts of the plant can be enclosed. This enables the investigator at will to surround the plant by a dry or moist, cold or warm atmosphere, etc., and so to study the influence

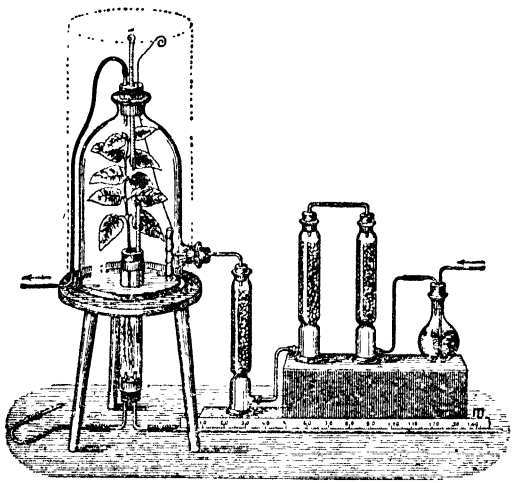

FIG. 14.—Kohl's apparatus for studying water absorption by the plant under varying environmental conditions (from Burgerstein).

of various external factors on the rate of absorption of water from the potometer. **Burgerstein,** in his well-known monograph, has justly criticized the use of the volumetric method, especially in investigations on the effect on the rate of transpiration of rapid and pronounced environmental changes. He points out that Vesque and other investigators proved long ago that there may be a considerable difference between the amounts of water respectively absorbed and transpired. Similarly, **Eberdt** himself, by weighing his apparatus simultaneously with taking the potometer readings, found a discrepancy

between the figures obtained by the gravimetric and volumetric methods respectively. In one of his experiments Eberdt obtained the following results, showing the relation between absorption and transpiration at different hours of the day:—

Time of Day	Water Absorbed	Water Transpired	Difference
8.45 a.m.–11.45 a.m.	4·95 gr.	5·53 gr.	−0·58 gr.
11.45 a.m.–3.0 p.m.	5·50 gr.	7·40 gr.	−1·90 gr.
3.0 p.m.–7.15 p.m.	6·45 gr.	5·58 gr.	+0·87 gr.

These figures clearly show that (in this experiment) during the daytime, and especially when transpiration was most intense, water loss exceeded absorption. In the evening, on the contrary, the plant was able to compensate by an excess of absorption over transpiration. A still greater divergence in the figures may be observed when there are sharp and rapid changes in such external factors as light and darkness, stillness or movement of the air, and so on. Thus **Renner** (1911) observed (by weighing his potometer) that transference from darkness to light accelerated transpiration to twice its initial value, but water absorption increased only 1·13 times. Again, a current of air from an electric fan augmented transpiration 2·5 times, while absorption increased only by 1·21 times.

Hence it is clear that figures obtained with the potometer cannot serve as an exact measure of transpiration, and that all results and conclusions obtained by this method must be regarded critically. Further, cut parts of plants are generally used in potometer experiments, rather than plants previously grown in water cultures. Hence, to the inaccuracies inherent in the potometer method, must be added those due to the cutting itself (see above). When these various sources of error are taken into account, it is no exaggeration to say that the results obtained by the potometric method have not substantially advanced our scientific knowledge of transpiration.

From the above discussion it may be concluded that, as already emphasized by **Livingston**, the only irreproachable method of investigating transpiration is the gravimetric one of weighing plants grown in containers, from which all possibility of direct evaporation from the surface of the soil is eliminated.

Methods of Calculating Results: Concepts and Terminology

Such are the principal methods employed in the determination of the rate of transpiration and absorption of water by the plant. The figures obtained by these methods indicate the absolute rate of transpiration for the plant or part of a plant used in an experiment. For purposes of comparison, however, and in order to be able to correlate the results of different experiments, it is necessary to reduce these figures to a common standard. We may therefore now discuss the units and methods of calculation to be adopted, and at the same time consider certain concepts (and their terminology) relating to the process of transpiration. Hitherto the most systematic attempt to define these concepts and the terms connected with them is that of **L. Ivanov** (1913, 1916), whose system, with some modifications, will be adopted here.

The fundamental concept of Ivanov's system is that of the *intensity of transpiration*. This term denotes the quantity of water lost by the plant in unit time, per unit of transpiring surface (usually of the leaf). As **Burgerstein** suggests (1920, p. 17), the most convenient units are: the hour as unit of time, the square decimetre as unit of surface, and the gramme as unit of weight. Unfortunately uniformity has not so far been attained in this respect, and results are variously calculated in square centimetres or even in metres, for different intervals of time, and are expressed either in milligrams or in gramme.

One must, moreover, bear in mind that determinations of the area of the transpiring surface are to a great extent con-

ventional. Usually only the surface of the leaf lamina is taken into account, the surfaces of the petiole and stem being ignored. In general this gives approximately correct results, as the loss of water from the latter parts is insignificant in comparison with that from the leaf lamina. Nevertheless, for exact determinations it is better completely to exclude even this slight source of error, and to cover the stem and petioles with tinfoil, vaseline, or other suitable material. The leaf surface is usually calculated as double the area of the lamina, no attention being paid to differences in the intensity of transpiration from the upper and lower surfaces respectively. Some plants, however, e.g. many trees with sclerophyllous leaves, have stomata only on the lower surface, and therefore only one actively transpiring surface. On the other hand the stomata of many plants, such as the sunflower, are distributed almost equally on both surfaces, the leaf therefore having two transpiring surfaces.

But we know too little of the influence exerted by the transpiration of one leaf surface on the other, to be able to introduce any corrections in the current method of calculating the transpiring surface of the leaf. A convenient method of determining the area of the lamina is to take a print of the leaf on sensitized paper:[1] the area is then measured by means of a planimeter. Failing a planimeter, the prints may be cut out and weighed. Knowing the weight of unit area of the paper (e.g. a square decimetre) and the weight of the print, it is easy to calculate the area of the latter. To obtain reliable results the paper must be of good quality and of uniform thickness. If the leaves are few and of a simple shape, and it is desired to preserve the plant for future experiments, one can trace with a pencil the outlines of the still attached leaves on a

[1] A contact print on photographic printing-out paper (P.O.P.) does very well, the print being fixed in a weak solution of sodium thiosulphate (hypo), washed, and dried. It is important that the leaf-margins should lie flat on the paper during printing: to ensure this an ordinary printing-frame may be used for detached leaves, or two pieces of glass (one above the leaf and the other below the paper) for leaves still attached to the stem.—ED.]

sheet of paper supported by glass placed under each leaf in turn.[1]

It is inadmissible to press and dry leaves before measuring their areas, as during the process of drying the leaf area shrinks considerably, losing from 20 per cent to even 40 per cent of its original size. Similar shrinkage occurs during wilting, as shown by **Thoday** (1909) and confirmed by **Alexandrov** (1923). Even without wilting, the loss of water during the midday hours may cause a reduction of the surface area of sunflower leaves by 5–10 per cent, or even 23–25 per cent, as compared with their areas when fully turgid. In exact investigations this shrinkage may be a source of serious error; one must therefore see that the leaves are not wilting at the time of measuring—in case of need the leaves can be previously placed in water for half an hour.

The intensity of transpiration is an extremely variable quantity. Under the same environmental conditions it differs considerably in different plants, and varies to a still greater extent in one and the same plant according to external conditions. Moreover, as we shall see later, even the different leaves of the same plant show different intensities of transpiration, depending on their age, position on the stem, and so on. In order to investigate the intensity of transpiration, a series of determinations may be made at different hours of the day and under various weather conditions. Or, the experiments may be conducted under standard conditions of environment, i.e. with constant temperature and air moisture, and continuous light. To ensure constant light conditions, strong electric light is required—e.g., a lamp of 2–3 thousand candles—as natural daylight is too variable.

The intensity of transpiration, expressed in absolute figures for a single plant, conveys very little. But the phrase has a new significance when we compare the intensity of transpiration

[1 It is difficult to prevent the leaf from moving during this operation, and in any case the outlines so traced tend to be somewhat too large. For attached leaves the printing method described in the previous footnote is both quicker and more accurate.—ED.]

of different plants. The calculation of transpiration in terms of unit area naturally suggests the idea of comparing transpiration with evaporation from a free water surface. This is the concept of *relative transpiration*, introduced by **Livingston** (1906). "Relative transpiration" is the ratio of the intensity of transpiration from a given plant to the intensity of evaporation from a free water surface. If T represents the intensity of transpiration, and E that of evaporation, then relative transpiration $= T/E$. The significance of this ratio, and the methods of determining E, will be discussed later, when dealing with the question of the regulation of transpiration by the plant.

Again, instead of the amount of water transpired per unit of transpiring surface, we may calculate the ratio of water lost to the total water content of the plant. This gives us the rate of water loss expressed as a percentage of the entire water reserve of the plant. I cannot admit the suitability of the phrase *economy of transpiration* suggested by **Ivanov** for this ratio, for the greater the ratio the greater the expenditure rather than the economy of water. Neither can I agree with the term *specific transpiration* suggested by **Neger and Lacon** (1914). Experiments have shown that in some cases a plant may expend 100 per cent or even more of its water reserve in a single hour. In other words, it may transpire during an hour the equivalent of all the water it contains. But the total water content of a plant is a very difficult quantity to determine exactly. To do so it is necessary to dig up the entire plant, and determine the water content of the whole root, as well as of the shoot system, a task by no means easy to accomplish. The easier method of determining the ratio of water loss to the water reserve in the shoots or even in the leaves alone is open to objection.

As water often constitutes 70–80 per cent or more of the entire weight of plants, especially of herbaceous ones, the rate of water loss has sometimes been calculated in terms of the fresh weight of the plant, instead of its total water content. This method of calculation is often met with in older works, but in

later years it has been replaced by calculations of the intensity of transpiration, i.e. the rate of water loss per unit area of surface. Quite recently, however, calculation on a weight basis was once more adopted by **H. Walter** (1925), who discards the method of calculating per unit of surface, for the reason that the absolute magnitude of the surface is in itself one of the conditions influencing water loss. Walter's arguments will be discussed later (p. 138).

Stocker (1923) attempted to compare transpiration with water absorption by calculating the amount of water transpired in terms of the surface of the root system, rather than of the surface or the weight of the leaves. As a direct determination of the absorbing root surface is impossible, he substituted the ratio of the fresh weight of the roots to the diurnal loss of water by the aerial parts. The value obtained indicates the amount of water absorbed daily per unit of the root system and, according to Stocker, the ease or otherwise with which water is obtained by the plant. Stocker carried out a comparative investigation with sclerophyllous shrubs on peat bogs on the one hand, and common mesophytes on the other. His results led him to the conclusion that the peat plants absorb more water per unit of root surface than the mesophytes, a fact which, in his opinion, constitutes a new argument against the hypothesis of the physiological dryness of bog soil.

Another method of calculation is to correlate the amount of water transpired with the cross-sectional area of the xylem (**Rübel,** 1920; **Huber,** 1924), and so to show the actual rate of the transpiration current through the wood. Few calculations on this basis are so far available, but they are interesting as affording an estimate of the actual conducting capacity of the xylem. We shall return to this question in Chapter VIII.

Especially in agronomical papers another concept is frequently met with, that of the *coefficient of transpiration*. This is the ratio of the dry substance produced by the plant during a more or less extended period of time (usually the entire growth period) to the total amount of water transpired in the same period. Formerly this ratio was expressed in the form of

a fraction with the numerator 1, the denominator of the fraction indicating the number of units of water lost during the synthesis of a unit of dry weight. Nowadays the numerator is omitted, the denominator alone being given. This concept has been employed by **Tulaikov** (1915, 1922), as well as by the American investigators **Briggs and Shantz** (1913). The latter, however, replaced the term *coefficient of transpiration* (due to Hellriegel) by the simpler expression *the water requirement of plants*.[1] But the word "requirement" may perhaps lead to misunderstanding; I prefer therefore to use the phrase *efficiency of transpiration* (Productivität der Transpiration), introduced by **L. A. Ivanov** (1913) in his course of lectures on Plant Physiology. Further, it is in my opinion better to express the "efficiency", not by the amount of water used per unit of dry weight, but by the converse, i.e. the amount (in grammes) of dry substance produced by the plant for every kilogram of water expended. This method of expression is logically more correct, for the determining process is transpiration and the determined the amount of dry substance. It is also more convenient, because an increase in the figure denoting the value of the ratio actually corresponds to an increase of the efficiency per unit of water used, while according to the usual terminology, an increase of efficiency is accompanied by a decrease in the figure representing the ratio.

The relation between two such diverse processes as those of transpiration and the accumulation of dry substance—i.e. the "efficiency of transpiration"—is somewhat complicated. The detailed consideration of this relation will therefore be postponed until the concept of drought resistance (often associated with it) is discussed. It need only be mentioned here that under more or less constant external conditions this relation is primarily determined by the nature of the plant itself, and can therefore be regarded as a physiological characteristic of the species. For instance, crops of the type of corn or millet always possess an efficiency of transpiration about twice as high as

[1 **Briggs and Shantz** (1914) employed this term to indicate "the ratio of the weight of water absorbed by a plant during its growth to the weight of the dry matter produced exclusive of the roots".—ED.]

crops of the type of wheat or barley. But general climatic conditions or even the weather conditions of a particular year markedly affect the absolute value of this ratio. For instance, under the conditions obtaining in Central Europe, the efficiency of transpiration for corn and millet is about 6–7 gr., and for wheat and barley about 3–4 gr. On the other hand, in the dry climate of South-East Russia or beyond the Caucasus, the corresponding values are only about 3–4 gr. and 1·5–2 gr. respectively.

To determine the efficiency of transpiration, prolonged experiments are necessary. The plants must be grown in containers (protected from direct loss of water) such as those described earlier in this chapter. The weight of water transpired is determined day by day, and the loss made good by means of a burette. Thus the total amount of water used can be found. Finally, the accumulated dry substance—including roots (too often neglected), fallen leaves, etc.—is ascertained. By dividing the number of grammes of dry substance by the number of kilograms of water lost, we obtain the required ratio, i.e. the "efficiency of transpiration". Alternatively, by dividing the number of grammes of water lost by the number of grammes of dry substance, we arrive at the "coefficient of transpiration" of the agriculturists, and the "water requirement of plants" of the American authors.

To sum up, we may say that in order to obtain a complete picture of the transpiration process, we must ascertain the following principal quantities: the intensity of transpiration, the relative transpiration, the rate of expenditure of the water reserve and the efficiency of transpiration. It is only through a knowledge of these quantities, or, at all events, the first and the last, that we can hope to gain a deeper insight into the phenomena of transpiration. Hitherto, of all the quantities mentioned, the intensity of transpiration (vaguely referred to by some authors as the "magnitude of transpiration"), and its derivative, the relative transpiration of plants, have been those most frequently studied.

CHAPTER V

THE INFLUENCE OF ENVIRONMENTAL CONDITIONS ON TRANSPIRATION

Transpiration and evaporation. The physical laws of evaporation. Evaporimeters and atmometers. The daily march of transpiration and of meteorological factors. The effect of individual environmental factors on transpiration—atmospheric humidity or saturation deficit, air movements, light, etc.

Transpiration and Evaporation

Transpiration is often regarded as a simple "physical" evaporation. Many authors, indeed, deem it unnecessary to employ a special term for this process, and merely refer to the "evaporation of the plant". Amongst Russian botanists such authors are in the majority, but in other countries only a minority use expressions like "evaporation" or "Verdunstung", most, especially nowadays, using exclusively the international term "transpiration". This introduction of a special term to denote the loss of water from the plant as opposed to that from an ordinary damp object or from a free water surface is due to the more complicated nature of "evaporation" from the plant. A leaf differs from a moist filter paper, for the special anatomical structure of the former complicates the process of converting liquid water into water vapour.

Since the time of **von Hoehnel** (1878) we have been accustomed to distinguish between cuticular and stomatal transpiration. Cuticular transpiration is the elimination of water vapour through the cuticle of the leaf, such as occurs in young leaves before the development of functional stomata, and in wilted leaves with closed stomata. Stomatal transpiration, on the other hand, involves the diffusion of water vapour from the saturated intercellular spaces of the leaf into the external atmosphere, which is rarely fully saturated with water vapour. The laws governing these two kinds of transpiration respectively are very different. Apart from the degree of saturation

of the atmosphere, which is important in both, the fundamental determining factor in cuticular transpiration is the permeability of the cuticle, and in stomatal transpiration the condition of the stomata. As is well known, the stomata are capable of opening and closing, thereby allowing or hindering communication between the intercellular spaces and the surrounding air. Stomatal transpiration really consists of two processes—the evaporation of water from the surfaces of the moist cell walls of the mesophyll bordering the intercellular spaces, and the outward diffusion of the vapour so formed through the stomatal openings. It is readily seen that if the second process is prevented, the air in the internal spaces will become saturated, and evaporation from the cell walls will cease. Conversely, when diffusion is facilitated by the opening of the stomata, the humidity of the air in the intercellular spaces is lowered, and evaporation from the walls of the mesophyll accelerated.

But the evaporation of water from the surface of a moist cell wall appears to be a more complicated process than evaporation from the surface of moist paper. The water impregnating the cell wall is in equilibrium with the cell contents, which possess a definite and more or less considerable suction pressure (Chapter I). According to the magnitude of this pressure, the cell wall will be more or less saturated with water, and the pressure of water vapour at its surface will be greater or less. This vapour pressure in turn will either retard or promote the vaporization of water. Further, as the power of suction is determined by the properties of the living plasma membrane, and disappears on its death, the evaporation of water from a living plant tissue differs from evaporation from a dead tissue. This is true even of a piece of parenchyma devoid of cuticle and stomata, such as a portion of a potato tuber or beetroot. **Von Mohl** (1846), for instance, showed long ago that water evaporates considerably more slowly from living than from dead cells. Again, an increase in the permeability of the protoplasm—which leads to a decrease of suction pressure, and hence to an increase in the water content of the

cell wall—must facilitate evaporation from the surface of the wall.

Transpiration, then, is a physiological process which, unlike evaporation from the surfaces of inorganic objects, does not depend on the humidity of the surrounding medium alone,[1] but also on such factors as stomatal movements, the internal condition of the leaf, and the degree of saturation of the cell walls. Thus the laws governing transpiration are of considerable complexity, and cannot be directly deduced from those governing the evaporation of water from a free water surface or from the surface of moist, lifeless objects. In order, however, to investigate the dependence of transpiration on external conditions, we must first become acquainted with the ordinary physical laws of evaporation. This is the more necessary as these laws appear to be more complex than might be supposed from an elementary study of physics.

The Physical Laws of Evaporation

The rate of evaporation (V) from a free water surface can be calculated by Dalton's equation

$$V = K(F - f)\frac{760}{P} \cdot S$$

where K is the coefficient of diffusion or evaporation; F the saturation pressure of water vapour in the air at the temperature of the evaporating liquid; f the observed vapour pressure in the surrounding space; P the observed barometric pressure (normal pressure = 760 mm. of mercury); and S the area of the evaporating surface. In a still atmosphere evaporation is almost entirely reduced to the diffusion of water vapour,[2] for

[1 Even in the case of inorganic objects, evaporation does not depend merely on the humidity (or saturation deficit) of the surrounding air. As the object loses water and the films of liquid in contact with its surface become thinner, evaporation will be more and more retarded by the forces of attraction between the molecules of water and those of the object.—Ed.]

[2 Dr. G. A. Shakespear points out to me that the process of diffusion itself may result in the setting up of convexion currents, owing to the difference between the respective densities of water vapour and air.—Ed.]

it may be supposed that a layer of saturated air is soon formed over the surface of the evaporating liquid, water vapour diffusing from this layer into the surrounding atmosphere. If free diffusion is prevented, as in a hermetically sealed vessel, evaporation very soon ceases.

Dalton's formula, however, presupposes an evaporating surface of indefinitely large area, such as the sea or a large lake, and does not hold for surfaces of small dimensions. This is because diffusion is more rapid at the edges than at the centre, for at the margins the molecules of water vapour can diffuse fanwise in all directions, instead of only perpendicularly to the surface as at the centre. It follows that, in still air, the smaller the area of the evaporating surface, the more rapid the rate of evaporation. But for areas of such small dimensions as leaves or small bowls of water, it appears (as has been mathematically calculated by **Stefan**, 1881) that evaporation is proportional not to the area of these objects but to their periphery or radius.[1]

Stefan gives the following formula obtained by means of the differential calculus:—

$$V = 4Kr\frac{F-f}{P}$$

The principal point of difference between this equation and Dalton's consists in the substitution of the quadrupled radius for the area of the evaporating surface.

For example, if we determine the respective rates of evaporation of water from two circular shallow vessels, one of which has a diameter twice that of the other, we shall find that the larger vessel, with an area four times as great as the smaller, evaporates only twice as much in a given time. Consequently, the rate of evaporation per unit area from the smaller vessel is twice that from the larger. It is unnecessary here to enter more fully into these calculations, further particulars of which will be found in the works of **Renner** (1910), **Jeffreys** (1918),

[1 Botanists have frequently assumed that evaporation from a free water surface is proportional to the area of this surface. This is only true under certain conditions. See **Thomas and Ferguson** (1917) —ED.]

and **Stiles** (1924). But it must be pointed out that all such calculations apply only to perfectly still atmospheric conditions. As soon as air currents come into play, the slow process of diffusion is relegated to a subordinate position, being largely replaced by convexion.[1] The rate of evaporation is now no longer determined by the diameter, but more nearly by the area of the evaporating surface.

Further, the depth of the surface of the liquid below the rim of the vessel affects the rate of movement of the air above the liquid, and, as **Miss Thomas and Ferguson**—a botanist and a physicist—(1917), have shown, the rate of evaporation also. These authors assume that the law of evaporation from a circular vessel is given by an equation of the type $E = Ka^n$, where E is the mass of water evaporated in unit time, a the radius of the evaporating surface, and K and n constants. Each millimetre of depth of the surface of the liquid below the brim changes the value of n. According to Stefan, if the vessel is filled to the brim, n should $= 1$. Thomas and Ferguson, however, obtained $1 \cdot 43$ (for a vessel of medium size) as the value of n when the vessel is completely filled, this value increasing with the depth of the projecting rim. Thus when the vessel was filled to within 5 mm. of the brim, the value was approximately $1 \cdot 6$, while at 30 mm. it was practically 2. At this latter depth evaporation becomes proportional to the area rather than to the radius of the vessel. The value of n also increases with increasing movement of the air.

H. Walter (1925) has recently reinvestigated, from the standpoint of transpiration, the question of the influence of the shape and size of the evaporating surface on the amount of evaporation, both in still and in moving air. In order to obtain a material approximating in physical properties as nearly as possible to the leaf, Walter employed thick cardboard (3 mm. in thickness) soaked in water until fully saturated. In

[1 Strictly speaking, evaporation still continues to be governed by the process of diffusion. But the conditions of diffusion are different in that the gradient of concentration of water vapour is much steeper, and hence, evaporation more rapid.—ED.]

one experiment four circles of cardboard, the surface areas of which were as 1:2:3:4, were found to evaporate water in the ratios 1:1·81:2·55:3·23. These ratios were the same in still and in moving air, though the absolute magnitude of evaporation was three times as great in the second case. On the whole, these results agree with the equation of **Thomas and Ferguson,** though Walter obtained a somewhat higher value for the constant *n*, i.e. 1·70 instead of 1·43. Similar results were obtained with cardboard cut in the shape of actual leaves, such as vine.

Walter explains this deviation (occurring in both still and moving air) from the area law by the fact that in moving air the air becomes partially saturated in passing over that portion of the cardboard with which it first comes into contact. On this supposition it would follow that the magnitude of evaporation from a rectangle of cardboard (placed edgewise) would vary according to whether a long side or a short side were turned towards the wind. Walter found experimentally that this was the case. Two rectangles of cardboard, each 10 cm. by 30 cm., evaporated equally in still air. In moving air, on the other hand, the piece with a long side facing the wind evaporated 20 per cent more than the piece with a short side towards the oncoming current of air.

These results led Walter to the conclusion that neither evaporation nor transpiration should be referred to any unit of surface area. He maintains that the values obtained by such a method of calculation are incomparable, as the dimensions and shapes of the leaves, and even their positions in regard to the direction of the wind, strongly influence transpiration. He proposes, therefore, to replace calculations of the intensity of transpiration by calculations based on a unit of fresh weight (see p. 130). Walter points out, however, that the figures obtained by his method afford no conception of the differences in the intensity of transpiration, which differences are conditioned by the varying structure of the transpiring organs. They only serve to indicate differences primarily determined

by the relation between the internal dimensions and the surface of the organs in question.

In my opinion **Walter's** arguments are unduly pessimistic. I can see no adequate reason for ignoring all the published determinations of the intensity of transpiration, or for discarding this method of calculating results in the future. It must, however, be borne in mind that the intensity of transpiration is not an absolute quantity, but one which is influenced by a series of conditions, amongst others being the degree of protection of the transpiring surface, and the shape and size of each individual leaf. We shall return to this question when considering the transpiration of plants of different ecological types, and shall now examine, in the light of the latest investigations, the different kinds of apparatus used in climatology and ecology for measuring evaporation.

Evaporimeters and Atmometers

The instrument in most general use at meteorological stations is the *Wild evaporimeter*, which consists of a flat brass cup (250 sq. cm. in surface area), fixed to a letter balance. Water is daily added to the cup, and the amount evaporated determined by the changes in the weight of the cup. This apparatus is not very sensitive and is of little use in ecology, where one must measure evaporation in close proximity to the plants investigated. For this reason simple flat metal or glass cups are often substituted: these are periodically weighed on a sensitive balance, or they are filled with a measured quantity of water, and the loss of water estimated by pouring back the water into a graduated cylinder. The size of these cups is generally smaller than in the Wild evaporimeter, namely about 10 cm. diameter.

Under laboratory conditions (or in the meteorological screens in which the Wild evaporimeter is generally used) the use of an open water surface does not present any serious difficulty. But it is another matter if we wish to determine evaporation

in the open, under natural conditions. Dust settles on the water, insects drown in it, wind may splash water out, birds often drink from the water, while during rainy weather the level of the water rises instead of falls. Moreover, the strictly horizontal position of the evaporating water surface by no means corresponds to the positions assumed by leaves, and the projecting edges of the cup prevent free movement of the air above this surface. These defects of evaporimeters of the open type have induced some investigators to substitute for the free water surface, the surface of some moistened object. Evaporimeters of this type are termed *atmometers*.

The simplest and oldest atmometer is the *Piche evaporimeter* (1872). The evaporating surface is a disc of filter paper attached by means of a supporting metal disc (to one side of which the paper is closely pressed) to the bottom of a graduated glass tube filled with distilled water. Both metal and paper discs have a hole in the centre, just below the glass tube. As the water evaporates from the moist filter paper, the supply is renewed from above, bubbles of air entering the tube through the hole to replace the water lost. The amount of water evaporated is measured directly by the fall of the water-level in the graduated tube.

The *Piche atmometer* (Fig. 15) is used especially in France. It is a very simple and portable apparatus, convenient in many respects, but possessing several defects. Air does not enter readily, and the moistening of the paper disc does not always keep pace with evaporation.[1] The wind, though it does not splash water out of the apparatus, as from an open cup, may nevertheless fray and tear the edges of the paper disc. Finally, the quality of the filter paper, i.e. its thickness and texture, affects the amount of water evaporated. On account of these defects the Piche atmometer has not been used extensively outside France.

On the other hand, *Livingston's porous porcelain cup atmometer* (1906) has been very widely used, particularly in America.

[1 Under conditions of rapid evaporation the margin of the paper tends to become dry; this reduces the area of the evaporating surface.—Ed.]

This instrument has undergone many modifications and improvements since it was first devised by **Livingston** in 1904.

The principle of this apparatus is based on the fact that water will evaporate from the surface of an unglazed, porous

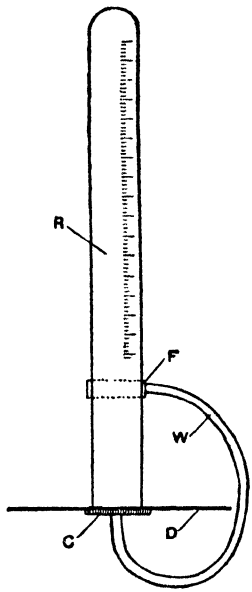

FIG. 15.—The Piche atmometer. R, graduated glass water reservoir; D, filter paper disc, supported by metal disc C, which is held in position by spring W, attached by clip F to reservoir (from Livingston).

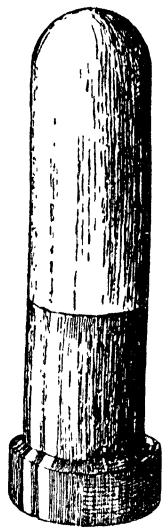

FIG. 16.—Porous porcelain cup of Livingston's atmometer (from Rübel).

porcelain vessel filled with water, in the same way as from a free water surface. At the same time, the porous cup atmometer is free from the disadvantages mentioned above of open water evaporimeters.

The porcelain cup must be completely and continually full of water, and must therefore communicate with a water

reservoir. The water evaporated from the surface is replaced by capillary suction from the cavity of the cylinder, the force of cohesion in turn drawing water from the reservoir: thus a constant amount of water in the cup is maintained. The

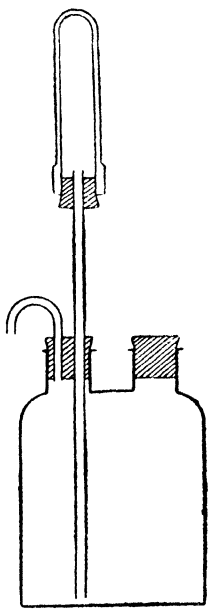

FIG. 17.—Atmometer for recording evaporation by weight (from Rübel).

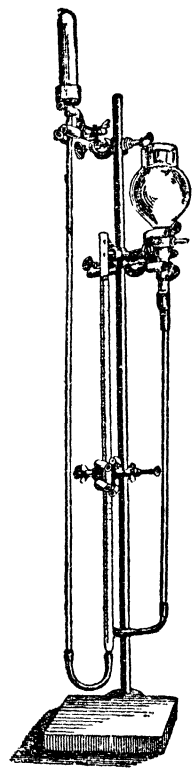

FIG. 18.—Atmometer for recording evaporation by volume (from Livingston).

reservoir must always be slightly below the level of the evaporating surface, as a head of water would cause drops to exude on the outside of the cup.

The usual type of Livingston's atmometer is a cylinder, rounded at the top (Fig. 16), about 13 cm. × 2·5 cm. The

lower open end of the cylinder is coated with shellac for about 5 cm., so that the height of the evaporating surface is about 8 cm. The opening is closed by a rubber stopper provided with a glass tube leading from the cup to the reservoir. In the simplest form this glass tube passes through a second rubber stopper into a bottle of water (a Woulff's flask is convenient, see Fig. 17). Evaporation is measured either by determining the loss in weight of the whole apparatus or by adding water to the bottle up to a mark on the neck. Instead of a bottle, the atmometer may be attached to a burette

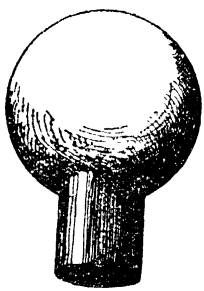

FIG. 19.—Livingston's spherical atmometer (from Rübel).

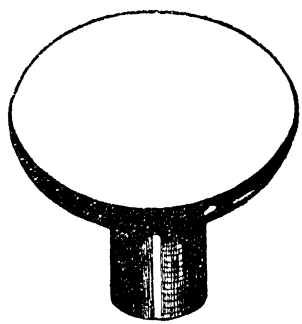

FIG. 20.—Livingston's flat atmometer (from Rübel).

(Fig. 18), in which case the volume of water lost may be observed directly. This combination is convenient for experiments of short duration.

In addition to the usual cylindrical type, Livingston uses spherical (Fig. 19) and also flat atmometers similar to those devised by **Bellani** as early as 1820 (Fig. 20). Another type employed by Livingston is the *radio-atmometer*, which is black or brown in colour, and absorbs radiant heat to a greater extent than the ordinary white atmometer. Other modifications of the initial type of atmometer need not be discussed in detail, as they have been described by **Livingston** (1915) and **Rübel** (1922).

While free from many of the defects of open water evaporimeters, the porous porcelain atmometer is not without draw-

backs, and in practice certain precautions are necessary. Thus in order to avoid blocking of the pores, distilled water only must be used. To prevent the development of algæ on the evaporating surface, the atmometer should be washed before use with a 1 per cent solution of mercuric chloride. To keep the surface clean, it must not be touched with the hands, and from time to time (e.g. every two weeks) it is advisable to cleanse it with distilled water. Further, before filling the atmometer with water, the air must first be removed by immersing the cylinder in alcohol, afterwards transferring it to distilled water. The apparatus should also be fitted up under water, in order to prevent the entrance of even the smallest bubble of air.

The ordinary form of the porous cup atmometer, with its reservoir below the evaporating surface, will readily absorb rain falling on the cylinder. This affects the results, the apparent evaporation being less than the actual evaporation. Livingston and his co-workers have overcome this difficulty and have produced an atmometer which will not absorb rain, and can therefore be used in experiments of long duration under natural conditions. The principle of this "non-absorbing" adjustment is the insertion of a mercury valve in the glass tube leading from the reservoir to the porous cup. The valve allows water to pass upwards, but prevents any backward flow in the event of rain falling on the surface of the cylinder. As first devised, this modification was complicated and delicate. Finally, however, after a series of attempts—some of which are described by **Rübel** (1922)—Livingston succeeded in simplifying it considerably. One of the latest of these rain-proof atmometers (**Livingston and Thone,** 1920) consists of a porcelain cylinder or sphere (Fig. 21) connected with the reservoir by a rather wide glass tube (6–7 mm. diam.). In this tube is inserted a simple but efficient valve consisting of two layers of glass wool, sandwiched between which is a layer (5–8 mm. deep) of mercury.

Originally Livingston assumed that he could calibrate his

instruments by directly comparing the respective rates of evaporation per unit area of surface from an atmometer and an open water surface. This assumption, however, has proved to be unjustified, for as we have already seen, the rate of evaporation depends not on the area alone, but amongst other things, on the shape and linear dimensions of the evaporating surface. To get over this difficulty, Livingston selected a particular instrument as a standard, and calibrated all others of the same type by comparing them with this "normal" atmometer. The calibration is carried out under definite conditions, accepted as normal, on a rotating table making three complete turns per minute.[1] All atmometers of the Livingston type sold by the Atmometer Apparatus Co., the sole makers (address—Laboratory of Plant Physiology, Johns Hopkins University, Baltimore, Md., U.S.A.), are calibrated in this way, each atmometer being furnished with a correction factor, by means of which its readings can be correlated with those of the original standard instrument.

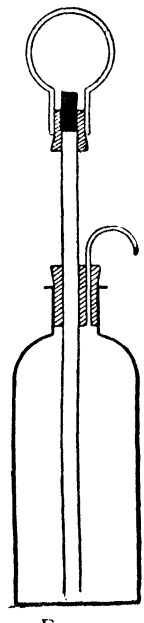

FIG. 21. Livingston and Thone's non-rain-absorbing atmometer.

Livingston's atmometer is very widely used in America, but European ecologists have shown greater reserve in adopting this method of determining evaporation. Like every evaporimeter, Livingston's atmometer gives readings which it is difficult to compare with those of other types of instrument, for the effect on evaporation of changes in external conditions varies according to the shape, size, and other properties of the evaporating surface. Hence the data obtained by means of evaporimeters can only

[1 **Thomas and Ferguson** (1917) discuss in detail methods of calibrating porous porcelain atmometers. They conclude that on the whole, provided suitable precautions are taken, calibration by means of a free water surface is preferable to the use of "standard" instruments for this purpose. They point out that there is no certainty that the porous properties of the porcelain of the standard atmometers do not change with time.—ED.]

be conditional and approximate: readings from one type of instrument will differ from those of another type, and still more widely from determinations of transpiration from the surface of the plant.

In view of these differences in the results obtained from evaporimeters of different types, repeated attempts have been made to use more exact meteorological apparatus in place of evaporimeters. As early as 1896, the Austrian meteorologist **Trabert** pointed out the close relation between the rate of transpiration and the difference between the readings of wet- and dry-bulb thermometers (the so-called psychrometric difference or wet-bulb depression). According to the investigations of **Krebs** (1894) on evaporation from the Mansfeld Lakes, each degree of difference between the average diurnal readings of wet- and dry-bulb thermometers corresponds more or less accurately to a daily linear evaporation of 2 mm. from the surface of the lake. On the basis of such results many meteorologists, e.g. **Ule** (1891) regard the psychrometer as a far more reliable instrument than any form of evaporimeter.

Amongst botanists **Huber** (1924) is in favour of this method of determining evaporation. He compared the wet-bulb depression with the readings of a *Piche atmometer*, and found that one degree of difference corresponded to an evaporation of 0·05 mm. per hour, that is 1·2 mm. in 24 hours, a magnitude slightly smaller than that obtained by Krebs.

Psychrometrical determinations must be made by means of some standard instrument, the best for the purpose being the *Assmann aspiration psychrometer*. The use of a psychrometer for determining the evaporating power of the air (i.e. the theoretically possible evaporation under given atmospheric conditions) has, however, one very serious drawback. With this apparatus we determine evaporation at a given moment only, and cannot accurately calculate the evaporation over a more or less considerable interval of time. During such a period the temperature and humidity of the air may be subjected to numerous fluctuations; this is frequently the case

under natural conditions, especially in changeable weather. Under these conditions, atmometers and other evaporimeters —in spite of their many defects—have the decided advantage of integrating the changes in the rate of evaporation during the intervals of time between the readings. For this reason, in investigations in physiological ecology, it is scarcely possible to discard evaporimeters as indicators of the external conditions to which the transpiring plant is exposed. But in interpreting the results obtained, it must always be borne in mind that these results are to a great extent conditional, and represent an abstract magnitude which cannot, strictly speaking, be compared with the results obtained from other evaporimeters, and still less with evaporation from such a complicated evaporator as the transpiring plant.[1]

An examination of the dependence of "simple" physical evaporation on external conditions shows that this process is so complicated that as yet we cannot exactly calculate the quantity of water evaporated, from data respecting temperature, humidity, and air movements. We are compelled, therefore, to carry out direct determinations of evaporation by means of such imperfect apparatus as the evaporimeters in use at the present time. Still less can we calculate beforehand the amount of evaporation from the surface of the plant. Thus we must agree with **Burgerstein** (1920, p. 41) that attempts to do this are predestined to failure, and that up to the present the only possible method of estimating the amount of water lost by the plant is not by calculation, but by direct experiment.

There is an extensive literature regarding the influence on transpiration of individual meteorological factors and external conditions in general. Some authors have arrived at the conclusion that in the main transpiration follows the same course as physical evaporation. Others are of the opinion that the march of transpiration deviates considerably from that of

[1 **Briggs and Shantz** (1917a) have compared the rate of transpiration of *Medicago sativa* with the corresponding rates of evaporation from different types of evaporimeters, see p. 205.—ED.]

evaporation; and that this deviation is to be attributed to the regulatory activity of the stomata. The detailed discussion of these conflicting results may be preceded by a consideration of the daily march of transpiration as determined by the regular daily march of the meteorological factors. This will enable us to form a preliminary general conception of the transpiratory activity of the plant in response to environmental changes, and also a more correct objective idea of the limits of the regulatory capacity of the plant.

The Daily March of Transpiration and of Meteorological Factors

Until recently only two detailed investigations of the daily march of transpiration had been carried out: one by **Briggs and Shantz** (1916) at Akron, Colorado, during the years 1912 to 1914, the other by myself (**Maximov**, 1917) at Tiflis, 1914 to 1916. Later, **Žemčužnikov** (1924) and **Maximchuk** (1923) dealt with the same question, which may now be regarded as sufficiently elucidated, at least so far as the influence of the meteorological factors is concerned. Both Briggs and Shantz and I determined simultaneously the actual transpiration from the plants used in the experiments, and the daily march of "physical" evaporation from the surfaces of different kinds of evaporimeters. This permitted a direct comparison of transpiration and evaporation. The most interesting determinations of the daily march of transpiration are those made on clear days with a definite and regular march of the meteorological factors. Both Akron and Tiflis have a large number of clear days and are therefore favourable localities for such experiments. I will first deal with the results obtained by **Briggs and Shantz**, who employed more elaborate methods and a greater number of plants.

The objects of these investigators were to study the march of transpiration during the growth period, and as far as possible to determine the relative influence of various weather

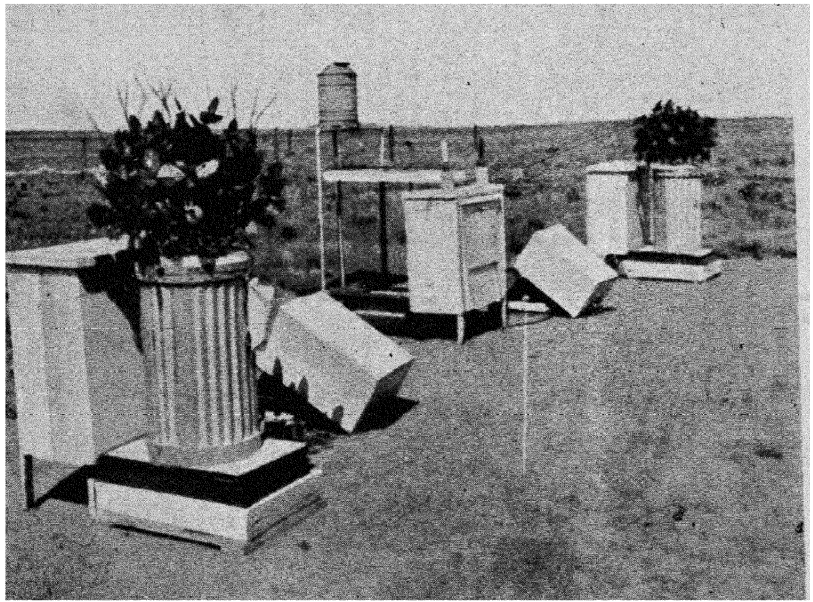

FIG. 22.—Determination of the daily march of transpiration and evaporation by means of automatic recording balances and atmometers (from Briggs and Shantz)

factors on transpiration. Accordingly, automatic records were made by means of self-registering apparatus of radiation intensity, temperature, depression of the wet bulb thermometer, wind velocity and evaporation from a free water surface. The evaporimeter used was a shallow, blackened copper tank 3 feet (91·3 cm.) in diameter and 2·5 cm. deep, mounted on the platform of an automatic scale. The potted plants were placed on similar recording platform scales. To allow of normal growth of the plants, very large pots were used, each holding about 115 kg. of dry soil. Evaporation from the surface of the soil was prevented by closely fitting metal covers sealed with wax. Fig. 22 illustrates the general arrangement of Briggs and Shantz's experiments. Two pots with plants (cowpeas) are seen on their automatic scales, and between them a copper evaporimeter (on a similar scale) and two Livingston atmometers —one white and one black.

As the march of transpiration for a single pot of plants for a single day usually shows slight irregularities, the authors based their conclusions on average figures obtained for the same plants during 15–20 clear days, at the period of greatest development of the plants. For convenience of comparison they calculated the results obtained during the separate hourly intervals as percentages of the maximum rate, treating the figures representing the march of the meteorological factors in the same way.

As an example, the daily march of transpiration of alfalfa (*Medicago sativa*) and of environmental conditions, for the period June 18–21, 1914, may be cited (Table VI on following page).

An examination of the above table shows a general agreement between the march of transpiration and of the meteorological factors during the day. Transpiration is low in the early morning hours; increases rapidly with the height of the sun above the horizon, the rise of temperature and increase of psychrometric difference; attains its maximum in the early afternoon hours and again falls rapidly with the setting of

the sun. There is no marked difference between the general march of external conditions and that of transpiration, such as might indicate active interference by internal factors with the rate of this process. It is true that different species exhibited slight differences in the rate of transpiration at different hours

TABLE VI

Daily March of Transpiration of Alfalfa and of Meteorological Factors (according to Briggs and Shantz).

Time	Transpiration [1]	Evaporation [1]	Solar radiation [1]	Air Temperature [2]	Wet-Bulb Depression [2]
3–4 a.m.	2	0	—	3	4
4–5	4	3	25	0	0
5–6	11	12	60	3	8
6–7	42	27	82	19	24
7–8	55	43	92	38	32
8–9	60	62	95	54	40
9–10	72	73	96	66	57
10–11	84	98	100	80	79
11–12 noon	88	100	100	88	86
12–1 p.m.	98	100	98	93	91
1–2	100	98	97	98	98
2–3	96	77	92	100	100
3–4	93	73	83	98	95
4–5	88	63	78	97	92
5–6	67	35	60	95	78
6–7	31	17	25	81	52
7–8	15	12	—	59	38
8–9	3	9	—	49	40

[1 In percentages of maximum. 2 In percentages of maximum range.—ED.]

of the day. For instance, in cereals the initial rapid rise of transpiration during the early morning hours was followed by a visible retardation (indicated by a flattening of the curve) in the forenoon, unaccompanied by corresponding changes in the meteorological factors. The maximum transpiration was attained comparatively late, i.e. between 2 and 4 p.m., after

which it fell rapidly. With dicotyledons and *Sorghum*, on the other hand, the march of transpiration corresponded more closely with that of the meteorological factors, the maximum occurring between 12 noon and 2 p.m. The authors are inclined to attribute this divergence to some internal change in the transpiring cereals, but do not indicate the nature of this supposed change.

All the experiments showed a considerable reduction of transpiration during the night, the total water lost during the night hours amounting to only 3–5 per cent of that lost during the daytime, so that for practical purposes the night transpiration may be regarded as equivalent to zero. From the ecological point of view this is very important, for it allows the plants to recover during the night from the effects of excessive transpiration in the daytime. Physiologically it indicates that the principal factor regulating the rate of transpiration is the intensity of sunlight.

Solar radiation is undoubtedly the chief factor determining the daily march of all other meteorological factors. Hence an increase or decrease in the intensity of radiation more or less precedes a rise or fall of temperature and of psychrometric differences, as well as a rise or fall of transpiration.

Briggs and Shantz further calculated the correlation coefficients between transpiration and the various environmental factors. The results showed that solar radiation, air temperature and wet-bulb depression are correlated with transpiration approximately to the same degree. Thus the correlation coefficient of transpiration with radiation (or more precisely with the vertical component of radiation, determined by the heating of a horizontal disc) ranges from 0·82 to 0·89; with air temperature from 0·77 to 0·86, and with wet-bulb depression from 0·75 to 0·85. These figures indicate the intercorrelations existing amongst the environmental factors, and in particular that transpiration shows the greatest dependence on the intensity of radiation. These correlations are well brought out in the numerous graphs presented by the authors.

Fig. 23 shows graphs of transpiration and of total radiation (and in the 1914 experiments, of the vertical component of radiation also), for experiments with wheat, oats, spring rye, *Sorghum*, alfalfa, and *Amaranthus*.

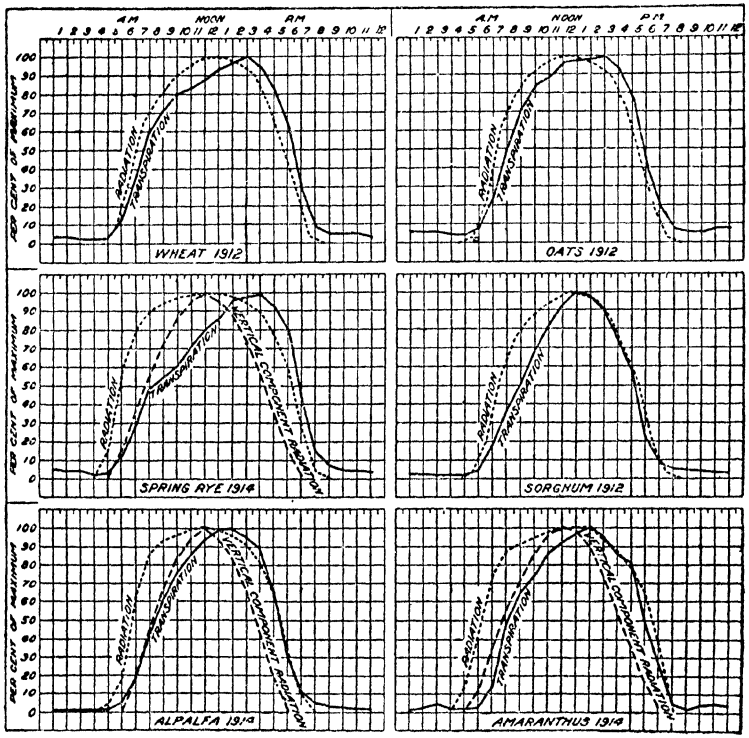

FIG. 23.—Comparison of the daily march of solar radiation and of transpiration from various plants (from Briggs and Shantz).

These are the most important and interesting results of Briggs and Shantz's investigations. The results show quite definitely that on the whole the daily march of transpiration follows the march of the meteorological factors, and especially that of solar radiation. Further, that even in very dry air (at Akron in summer-time the average psychrometric difference

for the noon hours was 15° C., rising in certain cases to 20° C.), the plant does not exhibit any marked decrease in transpiration as the result of internal regulation. This is true at least under the conditions of Briggs and Shantz's experiments, i.e. with constant and sufficient soil humidity—the significance of which will be readily seen.

My own investigations in Tiflis, carried out almost simultaneously with and independently of those of Briggs and Shantz, have led me to the same general conclusions as those arrived at by the American authors. Twenty-eight species were investigated; these included crop plants and native plants, and mesophytes as well as xerophytes. Transpiration was determined by periodical weighings (every one or two hours) of sealed pots with well-developed plants. Simultaneously, records were made of evaporation from porous cup atmometers of the Livingston type, of air temperature, saturation deficit, and wind velocity. Clear, cloudless days, on which the march of the meteorological factors was as regular as possible, were chosen for the experiments.

My experiments showed that all the species investigated had on the whole a similar daily march of transpiration, which was independent of the degree of xerophytism. Transpiration is very low during the night hours, rising rapidly after sunrise, and attaining its maximum soon after midday. It then falls rapidly, and soon after sunset returns to its initial low night rate. We may judge of this low rate from the following examples. *Zygophyllum Fabago*, which possessed the highest night transpiration, lost during one hour of the day the same amount of water as it transpired during the whole of the previous night, and corn (*Zea Mays*) five times as much. This sharp decrease in transpiration during the night is far from corresponding to the reduction of "physical" evaporation as determined by the atmometer. For instance, in one experiment, the atmometer loss during the night averaged 2·9 gr. per hour, and in the daytime 6·4 gr., the ratio of night to day evaporation being 1 : 2·2; at the same time corn showed a

ratio of night to day transpiration of 1 : 25. These figures show clearly how differently environmental factors may influence transpiration and evaporation respectively, and how much more the former is affected by solar radiation than the latter.

The only distinct and constant difference observed in the daily march of transpiration of plants of various ecological types was in plants with horizontal leaves or stems (sunflower, beans, *Zygophyllum*, *Portulaca*) as compared with plants with vertical leaves (wheat, *Stipa*, *Artemisia*). In plants with horizontal leaves transpiration rose more gradually in the morning and declined earlier and more rapidly in the evening than in plants with vertical leaves. The reason for this may be the better illumination of vertically placed leaves by the oblique morning and evening rays. If this is so, it affords additional evidence of the paramount rôle of solar radiation in determining the march of transpiration. Table VII (on opposite page) gives the results of an experiment carried out on June 12th and 13th. For purposes of comparison the figures, except those of temperature and wind velocity, are given, like those of Briggs and Shantz, as percentages of the maximum.

The march of transpiration in my experiments agrees in general with that observed by **Briggs and Shantz**, but it is otherwise with the evaporation of water. In their experiments evaporation attained its maximum and began to decrease prior to the maximum and decrease of transpiration, while the contrary was observed in my experiments (as also in the earlier experiments of **Livingston**). The cause of these divergent results lies in the different properties of the evaporimeters employed. I used a white porcelain atmometer, which is more sensitive to atmospheric humidity, and especially to wind, than to solar radiation. Briggs and Shantz, on the other hand, used a shallow, blackened copper tank, which must have reacted particularly to changes in the vertical component of radiation.

Apparently measuring one and the same "physical" evaporation, we actually measured quantities which are far from being

comparable. A comparison of our respective data clearly shows that the rate and march of evaporation of water does not depend wholly on meteorological conditions, but to a great degree (and possibly even more) on the shape, position, and other properties of the evaporating surface. This fact has long been known to meteorologists, but unfortunately is insufficiently recognized by ecologists and geobotanists, who frequently

TABLE VII

Daily March of Transpiration of Stipa and Sunflower, and of Meteorological Factors, June 12–13, 1916 (according to N. Maximov)

Time	Transpiration		Evaporation	Temp. in °C.	Saturation Deficit	Wind Velocity m/sec.
	Stipa	Sunflower				
10 p.m.–5 a.m.	12	2	18	16·2	33	4·8
5 a.m.–7 a.m.	23	14	15	15·9	25	4·95
7 –9	52	49	24	20·5	38	2·25
9 –10	72	65	36	24·6	65	1·8
10 –11	93	83	45	26·8	89	2·1
11 a.m.–12 noon	92	100	70	27·5	98	6·0
12 noon–1 p.m.	92	92	80	27·5	100	6·6
1 p.m.–2	100	98	70	27·4	99	4·5
2 –3	98	92	96	27·3	98	9·75
3 –4	97	84	100	27·0	99	13·5
4 –5	75	69	94	26·6	98	10·2
5 –7	54	27	53	24·9	88	6·6
7 –9	22	4	27	20·9	56	4·8

endeavour to apply to plants data obtained from one or another form of evaporimeter. **Livingston** (1906) in particular goes rather far in this direction, and is inclined to attribute every divergence between the march of transpiration and the evaporation of water from his atmometers to some regulatory mechanism of the plant. Livingston's opinions will be discussed later, in connexion with the question of the regulation of transpiration by the plant. For the present it is sufficient to say that

evaporimeters of different types—the living green evaporimeter represented by the plant amongst their number—are affected differently according to the properties of their evaporating surfaces, by changes in the environment (**Briggs and Shantz, 1917**[a]). The plant is particularly sensitive to light, the porous atmometer to wind. The latter fact is clearly brought out in Table VII, for a temporary calm between 1 and 2 p.m. did not affect transpiration, but decreased by nearly 25 per cent the loss of water from the atmometer.

To return to the daily march of transpiration, we may say that it is determined primarily by the march of solar radiation, which is responsible for the great difference between day and night transpiration. The degree of dryness, or moisture deficit, of the atmosphere, which can be calculated from the wet-bulb depression, is also one of the main factors. That wind must be relegated to the third place in order of importance is probably to be attributed to the structure of the evaporating surface of the plant. The vaporization of water takes place not on the cutinized outer surface, but on the surface of the intercellular spaces, which are protected from the wind. With regard to the internal regulation of transpiration during the day, so long as the soil contains abundant water such regulation either cannot be detected or only to a minimal degree. But under conditions of deficiency of soil moisture, considerable deviations from the normal daily march of transpiration may be observed. But these deviations, which are very important from the points of view of physiology and ecology, may be discussed after we have studied the means of regulating transpiration possessed by the plant organism.

The Effect of Individual Environmental Factors on Transpiration.

The daily march of transpiration represents the resultant of the influence of the individual meteorological factors. Many authors have endeavoured to study in detail the effect of each

of these factors separately. Much has been done by **Wiesner** (1877, 1887) and by later investigators, but it must be admitted that our knowledge of these factors has not yet been placed on a strictly scientific basis. The chief reason for this unsatisfactory state of affairs is that so far laboratories, in which one can scientifically regulate the external factors governing the process of transpiration, do not exist. In wealthy America, **Livingston** (1917) has dreamed of underground laboratories —isolated from climatic changes, and provided with devices for generating artificial sunlight, maintaining constant temperature, controlling atmospheric humidity, and creating artificial winds of required velocities, and it may be artificial rain as well. It is but now that such dreams begin to be partly realized. In the newly organized American "Boyce Thompson Institute for Plant Research" a room has been provided with artificial sunlight, though so far there are no special appliances for the study of our problem. Moreover, the difficulties connected with the application of artificial sunlight have not yet been completely overcome (see **Crocker, 1924; Maximov,** 1925). Thus exact studies of the effects of changes in environmental conditions on transpiration are still to be desired. Yet there is scarcely any physiological process so closely dependent on atmospheric conditions as the loss of water by the plant.

(*a*) *Atmospheric Humidity or Saturation Deficit*

Of all the environmental factors influencing transpiration, atmospheric humidity has been most thoroughly studied, for it can be comparatively easily regulated. It is unnecessary here to discuss in detail the numerous investigations of the nineteenth century (e.g. those of **Unger, Sorauer, Masure, Hellriegel, Shloesing, Leclerc du Sablon, Aloi, Wollny,** and others), as they are referred to in Burgerstein's monograph. For the most part these researches were qualitative in character, and the main conclusion to be drawn from them is that plants lose less water in a moist atmosphere than in a dry one.

Of greater interest are more recent investigations in which attempts have been made to establish exact quantitative relations between the humidity of the air and the rate of transpiration. Few investigations of this kind have been made, for they require both the external and the internal conditions affecting transpiration to be as constant as possible, a matter of great difficulty. Of the internal conditions, the greatest difficulties are occasioned by the so-called "play of the stomata", which by their movements can completely mask the direct influence of environmental factors. For instance, if there is a decrease in the humidity of the air, the stomata may close, in which case, instead of an increase of transpiration as a result of the drier air, we may find an actual decrease.

F. Darwin (1914[a]) devised an original method of eliminating the effect of stomatal movements. Taking leaves of cherry laurel (*Prunus laurocerasus*), which have stomata on the lower surface only, he covered this stomatal surface with vaseline or cacao butter, and then pierced the upper epidermis of the leaf by small incisions or pricks. By this means he placed the intercellular spaces once more in direct communication with the surrounding atmosphere. Varying humidity of the air was obtained by the use of a bell-jar, and the rate of transpiration was estimated by the potometer method, which, as seen above, is not a very accurate one.

By these experiments Darwin established the existence of a direct relation between transpiration and the relative humidity of the air. He also found that the zero point of transpiration coincided not with 100 per cent relative humidity, but with 105–110 per cent; that is, it occurred in an atmosphere supersaturated with water vapour. This second conclusion, however, was arrived at by the method of extrapolation, as the relative humidities used varied between 50 and 95 per cent only. Moreover, Darwin's experimental methods are not above criticism, so his conclusions can only be accepted as a first approximation. They are cited here on account of his original and ingenious method of eliminating the influence of stomatal movements.

I have found a very exact and detailed discussion of the question of the influence of air humidity on transpiration in an article not by a botanist, but by a physicist and meteorologist, **B. I. Sresnevski** (1905). As this paper is not readily available, it has probably escaped the notice of many physiologists. In his investigation Sresnevski starts with Dalton's formula for evaporation,

$$V = K(F - f)\frac{760}{P} \cdot S$$

where V is the rate of evaporation; S the area of the evaporating surface; P the atmospheric pressure in mm. of mercury; K a constant (diffusion coefficient); F the saturation pressure at the temperature of the liquid; f the vapour pressure in the surrounding atmosphere. $F - f$ will be the saturation deficit, a concept we have already met with. This formula shows, first of all, that if we compare transpiration with evaporation from a free water surface, transpiration must change proportionally to the deficit of saturation, and not to the relative humidity, as is, unfortunately, stated in many botanical works.

Now Dalton's formula only applies to evaporation from an absolutely plane surface. If the evaporation is from the surface of a liquid contained in capillary tubes, the vapour pressure over the curved surfaces will differ from the vapour pressure over a plane surface (this is associated with the rise of liquids in capillaries). As William Thomson (Lord Kelvin) has shown, the dependence of vapour pressure on the curvature of the surface may be expressed by the formula

$$F_r = F_\infty + \frac{2T}{r} \cdot H$$

where F_r is the saturation pressure above a curved surface with the radius r; F_∞ the saturation pressure above a plane surface with a radius ∞; T is the surface tension; H a constant depending on the density of the liquid. The formula shows that the narrower the capillary tube, and consequently the

smaller the radius of the surface curvature of the liquid meniscus, the smaller will be the saturation pressure (with a concave meniscus, r is a negative magnitude), and consequently the lower will be the process of evaporation.

Every hygroscopic substance or colloid capable of swelling may perhaps be regarded as a porous substance with very fine, narrow capillaries, the water menisci of which are more or less drawn in, according to the degree of saturation of the substance with water. This would explain the capacity of porous and hygroscopic substances to imbibe water with a considerable force, often overcoming resistances amounting to several atmospheres. It is obvious that the greater the resistance, the more concave will be the menisci in the capillaries or pores of the hygroscopic substance, and the more will the evaporation of water be impeded.

From these considerations Sresnevski worked out his theory of de Saussure's hygrometer, in which a hygroscopic human hair forms the sensitive part. The same considerations served to explain the deviations from Dalton's formula which Sresnevski found when studying evaporation from the surface of the human body, and from the leaves and flowers of different plants. Recalculating the data contained in an old work by **Unger** (1861) on the transpiration of leaves of *Digitalis purpurea*, he arranged these data in groups according to the saturation deficit. He found that transpiration augments with the increase of $F - f$, but more slowly than it should do according to Dalton's law, and that the quantity $\frac{V}{F-f}$, which should be constant, gradually decreased with the increase of the humidity deficit, and augmented with its decrease. Later Sresnevski obtained similar results in his own experiments with small plants of cherry laurel (*Prunus laurocerasus*) and hazel (*Corylus*), and with flowers of lilac (*Syringa*), and came to the conclusion that when the saturation deficit is either very great or very small, transpiration does not proceed as rapidly or as slowly respectively as one would expect from observations

under mean conditions. The result of this is a kind of regulation of transpiration, not of a physiological, but of a purely physical character. This may be explained by an increase of the concavity of the water menisci with the increase of the saturation deficit, and as a consequence a decrease in the rate of water loss.

It appears to me that this purely physical self-regulation of water loss from the surface of porous substances and capillaries, established by **Sresnevski,** is of extreme importance. We shall have occasion to return to this question when discussing the regulation of transpiration by the plant. Taking into consideration the investigations of Sresnevski, we can express in a general way the dependence of transpiration on the humidity of the air as follows: the rate of water loss by the plant obeys Dalton's law within a certain very narrow range of relative humidity of the air: with an increase of relative humidity (this means a lower temperature if the magnitude of deficit is maintained) the rate increases, with a decrease of relative humidity (accompanied by a rise of temperature) the rate diminishes.

Thus quite apart from possible stomatal movements the influence of atmospheric humidity on transpiration is exceedingly complicated and cannot be expressed by a simple formula. The influence of air movements is still more complicated.

(*b*) *Air Movements*

In the case of wind, even physical evaporation from a free water surface cannot be exactly expressed by a definite formula. In an absolutely still atmosphere evaporation is a process of pure diffusion, but this is no longer the case when air currents remove the particles of water vapour as they diffuse into the atmosphere. In general, even a very slight movement of the air completely suppresses the process of diffusion.[1] Air currents

[1 The process of diffusion is not really suppressed, but the relative importance of the rôles of diffusion and convexion respectively become more or less reversed. See footnotes 2, p. 135, and 1, p. 137.—ED.]

naturally increase evaporation, but it is by no means easy to establish an exact quantitative relation between wind velocity and evaporation. According to **Houdaille**, the rate of evaporation in an air current with a velocity of 0·25 m. per second is three times that observed under the influence of diffusion alone. With greater velocities, however, the effect of wind increases more and more slowly.

The effect of wind on the wet-bulb depression (which is dependent on the rate of evaporation of water from the surface of the moistened thermometer) has been carefully studied in connexion with the construction of a psychrometer, the readings of which would not be affected by wind. This end was achieved in the *Assmann aspiration psychrometer*. Investigations have shown that with a current of air of 2·5–3 m. per second, the wet-bulb depression becomes practically constant, any further increase of wind velocity scarcely affecting the reading of the wet bulb. This rate of air current has therefore been adopted as the standard rate for the Assmann psychrometer.

Direct observations show that the effect of wind on evaporation from different types of evaporimeters varies according to the shape and other properties of the evaporating surface. Thus **Livingston's** atmometer, with a vertical cylindrical evaporating surface, is more sensitive to air movements than evaporimeters with a horizontal water surface, slightly protected from the wind by the protruding edges of the cup. Hence the differences between the readings of evaporimeters of different types will vary according to the velocity of the wind.

These considerations must be borne in mind when estimating the conditions of evaporation in different habitats. In order to compare evaporation at different levels in the vegetation a series of atmometers are frequently arranged at different heights above the soil, and the amounts of water evaporated at the different levels compared (cf. **Yapp**, 1909; **Ramenski**, 1915; **Kiesselbach**, 1916). Such determinations undoubtedly serve to indicate the humidity at different levels in the vege-

tation under natural conditions. But too much stress should not be laid on the quantitative side of the results. Experiments of this kind can only yield figures of a very approximate value, which reflect the properties of the apparatus as well as the conditions of the environment.

It is also unsafe to base on such data definite quantitative conclusions as to the rate of transpiration of shoots at different levels and under different environmental conditions. As a general rule, the plant is less affected by air movements than are evaporimeters. This has been directly proved by the recent experiments of **Knight** (1917[b]). The special apparatus used was one described by **Blackman and Knight** (1917), by means of which transpiration experiments can be conducted in a current of air of constant velocity. Knight placed a filter-paper atmometer near his plants and determined the increase of both evaporation and transpiration at a definite wind velocity (7 m. per minute). The results of these experiments proved that evaporation from the atmometer increased under the influence of wind by 73–74 per cent, but transpiration only by 50–51 per cent. It is important to note that during these experiments the stomata were widely open, their apertures remaining constant. In this case, the smaller effect of wind on the plant as compared with that on the atmometer cannot be attributed to stomatal movements. The cause of this inferior sensitiveness of transpiration to wind must therefore be sought not in the "play of the stomata", but in the structure of the evaporating leaf surface.

Szymkiewietz (1924) has compared the evaporation of water from the cells of the mesophyll with the drying of linen in a room with open windows, but evaporation from an atmometer with the drying of linen in the open air. Naturally the influence of wind will be greater in the second than in the first case. Although wind cannot penetrate directly into the interior of the leaf through the minute stomatal openings, it may considerably accelerate transpiration in at least two ways. First, by the removal of humid air from the surface of the leaf,

thereby promoting diffusion through the stomata. Secondly, by causing bending movements of the leaf lamina: such movements bring about alternate contraction and expansion of the intercellular spaces, which facilitates the exit of saturated and the entrance of drier air (**Bernbeck**, 1924).[1] Bernbeck's suggestions agree with the experiments of **Eberdt** (1889), who observed that with the same wind velocity, an immobile, attached leaf transpired less water than a leaf free to move and bend with the wind. On the other hand, mechanical deformation, as well as increased loss of water under the influence of wind, may lead to a closing of the stomata, and consequently to a retardation of gaseous interchange between the intercellular spaces of the leaf and the surrounding atmosphere. These considerations greatly complicate the problem of the influence of wind on transpiration, and render more difficult the establishment of quantitative relations between the velocity of the wind and the rate of transpiration.

(*c*) *Light*

We have now become acquainted with the dependence of transpiration on those environmental factors which determine purely physical evaporation. There remains still another factor, i.e. *light*, which exercises a very important influence on transpiration, though it is mentioned neither by physicists nor by meteorologists as a factor in evaporation.[2]

In studying the daily march of transpiration we found that solar radiation is the principal factor determining the intensity of transpiration. But in experiments carried out under natural

[1 It has also been suggested (**Yapp**, 1912) that wind passing rapidly over the surface of a glabrous leaf would reduce the pressure at the entrances of the stomatal apertures, and so tend to suck air (and consequently water vapour) out of them. The action is similar to that of a hairdresser's sprayer or of a Gifford injector in sucking water into a boiler. This paper also discusses the effect of a covering of hairs in reducing transpiration when the plant is exposed to strong winds.—ED.]

[2 That is, presumably, light in the narrow sense, as distinct from solar radiation as a whole: cf. p. 206.—ED.]

conditions it is difficult, if not impossible, to distinguish between the effect of light and the effects of other environmental factors. An increase of radiation is accompanied by a rise of temperature, an increase of the wet-bulb depression, and so on—in fact, the daily march of transpiration is the result of the combined effect of the various environmental influences. Hence the need of exact physiological experiments under laboratory conditions, where one could change the light intensity only—keeping all other conditions constant—and thus be enabled to observe the results of changes in this one factor alone.

A considerable number of such experiments have already been made, but one must observe at the outset that as yet no such exact quantitative relations have been established between light intensity and the rate of transpiration, as between light and carbon assimilation. The question stands in need of further study. The first more or less exact experiments in this direction were those of **Wiesner** (1877), who showed that not only direct sunlight (naturally accompanied by a considerable heating of the plant), but also diffused daylight, and even the comparatively weak light of a gas lamp (of 6·5 candlepower), considerably increase the rate of transpiration.

That light has a considerable effect on transpiration has also been shown by the experiments of many other investigators. This led **Van Tieghem** (1886) and other French authors to the view that two distinct processes are to be distinguished in the loss of water by the plant. (1) An active elimination of water vapour by the plant, comparable to the exhalation of water from the lungs of higher animals, and like that process, proceeding in the dark as well as in the light. (2) *Chloro-vaporization*, i.e. the conversion of water into vapour under the influence of the radiant energy absorbed by the chloroplasts of the leaf. In its original form this hypothesis has few, if any, supporters at the present time. The Indian scientist **Bose** (1923) alone, in his recently published book on the *Physiology of the Ascent of Sap*, persists in a belief in the

active elimination of water vapour by the plant. The generally accepted view is that the chief cause of the loss of water is not the activity of the plant, but the saturation deficit of the surrounding atmosphere. Van Tieghem's hypothesis, however, had the advantage of drawing attention to the great significance of light in the process of transpiration, a fact often neglected in the past.

A plausible explanation of the accelerating effect of light on transpiration was put forward by **Wiesner** (1877) in the paper referred to above. Comparing the action of light on green and etiolated plants, Wiesner drew attention to the fact that transpiration increases *pari passu* with the amount of chlorophyll. This led him to the conclusion that the effect of light depends on its absorption by the tissues of the leaf, where the radiant energy is transformed into heat. This causes a heating of the leaf, in consequence of which there is an increase of the saturation deficit in the intercellular spaces and on the surface of the leaf, which in turn brings about increased evaporation.

Wiesner's "heat theory" has been widely accepted, and in a general way received confirmation from later investigations, of which the most detailed were those of **Comes** (1880) and **Henslow** (1887). These showed that transpiration is most intense under the influence of those rays of light that are most absorbed by the leaf.

Gradually, however, objections to Wiesner's interpretation began to accumulate. **F. Darwin** (1898) pointed out that sunlight, and in particular the red rays, induces the opening of the stomata, thus favouring an increase of transpiration. On the other hand, the fact, stated by Wiesner himself and confirmed by other investigators, that transpiration is greater in the blue than in the red rays, is contradictory to his own theory. We now know that the red rays of the solar spectrum possess (at the surface of the earth) considerably more energy than the blue rays, in consequence of which the assimilation of carbon dioxide is considerably greater in the red rays.

The first of these objections can be ignored in view of more recent experiments by **F. Darwin** (1914[b]). Darwin found that with constant temperature and humidity, transpiration in diffused daylight exceeded (on the average) that in the dark by 32 per cent (*Prunus laurocerasus*) or even by 36 per cent (*Hedera helix*). In these experiments he used the method of eliminating possible stomatal interference described above, i.e. blocking the stomata with vaseline or cacao butter, and then making incisions in the upper surface of the leaf. These results again prove the direct influence of light on transpiration.

The second objection is a more serious one. **Leclerc du Sablon** (1913) repeated Wiesner's experiments on the transpiration of leaves with and without chlorophyll, using *Pelargonium* and *Hedera helix*. He found that on transferring plants of *Pelargonium* from shade to direct sunlight, the transpiration of green leaves increased by 3 times, but that of white leaves only by 1·5 times. Under similar conditions, the transpiration of green leaves of *Hedera helix* increased by 2·26, of variegated leaves by 1·40, and of white leaves by 1·27 times. Leclerc thus confirmed Wiesner's results, but suggested a different interpretation of the facts. He concluded that light not only exerts a purely physical effect, but also a physiological effect, by causing an increase in the permeability of the protoplasm. Such increased permeability in light had, in fact, been shown several years previously by **Lepĕshkin** (1909) and **Tröndle** (1910). Leclerc's view was that on account of its osmotic properties, the living cell ordinarily possesses a certain capacity of retaining water, in spite of external conditions which may tend to promote evaporation. On the other hand, any increase of the permeability of the protoplasm, e.g. under the influence of light, lessens the power of the cell to retain water. Leclerc's experiments were inadequate to prove his hypothesis, but confirmation has recently been furnished by the investigations of **Ivanov and Thielman** (1923). The experiments of these authors were carried out partly in a prismatic spectrum and partly behind coloured screens. In the second case the quantity

of energy obtained by the leaf through the different screens was equalized by regulating the distance of the source of light. To measure the total light intensity the authors used a Rubens thermopile, placed beside the leaves. Potted plants, as well as living, detached leaves, and leaves previously killed by boiling in water, were used. These experiments proved that when living leaves are transferred from red-yellow to blue-violet light *of the same intensity*, their rate of transpiration always increases, often by 40 per cent or more. On being transferred back again to red-yellow light, the rate of transpiration decreases. Killed leaves showed practically the same transpiration in both regions of the spectrum. The authors conclude that the greater effect on transpiration of the blue-violet, as compared with the red-yellow rays, militates against **Wiesner's** hypothesis, and indicates, in all probability, that the blue-violet rays exert some specific influence on the living leaf. This specific influence cannot consist of the opening of the stomata, for these are most strongly affected by the red-yellow rays. A more probable explanation is that the increase in permeability of the protoplasm is greatest in the blue-violet region of the spectrum.

The results of the investigations outlined above lead one to suppose that the influence of light on transpiration is two-fold: (1) that conditioned by the absorption of radiant energy by the pigments of the cell, and in particular by the chlorophyll, and (2) its direct effect on the permeability of the protoplasm. If this is so, it is clear that plants differing in the structure of their leaves, in the quantity and concentration of their chlorophyll, and in the sensitivity of their protoplasm to the influence of light, must respond differently to changes in light intensity. It follows that it is impossible to find a formula of general application to express the precise relation between transpiration and the conditions of illumination.[1] Further, one

[1] With regard to the effects of radiant energy on transpiration, Prof. Maximov's arguments in this chapter may perhaps be summarized as follows. Solar radiation has the most profound influence of all the meteorological factors because—(*a*) it affects transpiration *indirectly*, by deter-

can readily understand the impossibility of constructing an evaporimeter which will respond in the same way as a green plant to the influence of light. Hence such attempts as that of **Livingston** (1911) to obtain parallel readings between the transpiration of a plant and evaporation from an atmometer, by painting the evaporating surface of the latter brown, or even green, cannot be other than unsuccessful.

* * *

The influence of other environmental factors on transpiration (e.g. atmospheric pressure or the amount of carbon dioxide in the air) is too insignificant, in comparison with the factors discussed above, to be worth studying in detail. A low atmospheric pressure must increase the transpiration of plants in the alpine and subalpine zones (cf. Dalton's formula). Other peculiarities of the high mountain climate, however, affect the transpiration of alpine plants to a still greater extent, and completely mask the effect of low pressure. Such are the great humidity, low temperatures, increased intensity of insolation, especially of the violet and ultra-violet rays, and the frequently high velocity of the wind. For this reason the published data concerning the rate of transpiration at high altitudes are very contradictory (**Bonnier**, 1890; **Sampson and Allen**, 1909). The experiments of L. Kochanovsky, carried out at my suggestion in the Bakuriany mountains of the Tiflis Botanic

mining the diurnal march of such factors as temperature and humidity, which themselves directly influence the rate of transpiration. (*b*) In the form of light it appears to exert in addition a more *direct* effect of a twofold nature (see text).

How far the two supposed direct effects of light are ultimately distinct may be problematical. It seems possible, however, that the rays of longer wave-length absorbed by the chlorophyll may produce a heating effect such as that required by **Wiesner's** hypothesis. This would not be incompatible with a specific influence of a different nature exerted on the protoplasm by the shorter rays at the blue end of the spectrum, as suggested by **Ivanov and Thielman.** In other words, heat energy as such, as well as some form of molecular energy connected with a particular range of wave-length, may both play an important part. If so, the rival interpretations mentioned in the text may not necessarily prove to be antagonistic (see also **Darwin**, 1914[b]).—ED.]

Garden, at an altitude of 6,000 feet (**Kochanovsky**, 1926) have shown that the absolute rate of transpiration of plants in high mountains does not differ from that of mesophytes of the usual type in Tiflis.

A considerably greater influence is exerted upon transpiration by the water content of the soil. As, however, this influence is closely connected with the question of the regulation of transpiration by the plant, which is closely related to that of the movements of the stomata, we may study these two questions first.

CHAPTER VI

THE STOMATAL APPARATUS OF THE PLANT

The stomatal apparatus of the plant. The static diffusion of gases through small apertures. The mechanics of stomatal movements. Methods of investigating the movements of stomata. The diurnal march of stomatal movements. Effect of light and other factors on stomatal movements.

The Stomatal Apparatus of the Plant

The intercellular spaces of the leaf, the atmosphere of which is saturated, or nearly so, with water vapour, communicate with the surrounding air through microscopically small but very numerous openings called stomata. A typical stoma consists of two crescent- or kidney-shaped guard cells, the concave sides of which face each other and thus enclose the oval pore or aperture of the stoma. It is by means of this aperture that communication between the internal and external atmospheres is effected.

The stomatal pores thus form the pathway of the outward diffusion of water vapour in transpiration, and of the gaseous exchanges which accompany the processes of photosynthesis and respiration. These three dissimilar processes, then, are linked together by the possession of a common pathway, and we shall find that this apparently external connexion between them leaves a deep impress on the whole structure and development of the plant.

Diffusion is not the only process by which exchanges between the external and the internal atmosphere are effected. Mass movement also is concerned, if the pressure in the intercellular spaces is either higher or lower than that of the external atmosphere. Such differences of pressure may be caused either by the contraction or expansion of the intercellular spaces, as the leaf is bent by the wind, or by the heating of the internal air by strong sunlight. But in still air and moderate illumination, diffusion is the more important process. We may therefore study in the first place the phenomena observed when gases diffuse through a great number of very

minute openings such as the stomata on the surface of a leaf. The number of stomata per unit area of leaf surface is very great, usually between 50 and 300 per sq. mm., but in exceptional cases they may even exceed 1,000. Thus **Yapp** (1912) found on the lower surface of the upper leaves of *Spiraea Ulmaria* up to nearly 1,300 per sq. mm. The dimensions of the stomatal aperture are very inconsiderable, usually not more than several microns (i.e. thousandth parts of a millimetre).

The Static Diffusion of Gases through Small Apertures

Important detailed investigations on the static diffusion of gases and liquids through small openings were carried out by **Brown and Escombe** (1900). These investigations proved that the rates of diffusion through small single apertures are proportional to the diameters and not to the areas of the openings (this agrees with the results previously established by **Stefan** for the converse case of evaporation from circular surfaces of water, see p. 136). **Brown and Escombe** found that their "diameter law" holds good also for the case of diffusion through a number of small openings, i.e. through a "multi-perforate septum". From this it follows that more water vapour will diffuse in unit time through several small apertures than through a single larger opening with an area equal to the combined areas of the smaller ones. If, however, the perforations in a septum separating two mixtures of gases of different composition (e.g. dry and moist air) are very close together, the rate of diffusion is modified. The "lines of flow" of the diffusing molecules, which normally tend to diverge fan-wise as they issue from the apertures (cf. Fig. 24), now interfere with one another, and mutually hinder the spread of the diffusing particles, thus slowing down the rate of diffusion. Brown and Escombe showed experimentally that such interference begins when the distance between the apertures is somewhat less than ten times the diameter of the holes. The

fact that the rate of diffusion through small openings is proportional not to the area but to the diameter of the opening, greatly increases the possible amount of diffusion which can take place through a multi-perforate septum.

Though such a septum must obstruct diffusion to some extent, the amount of obstruction is surprisingly small, and

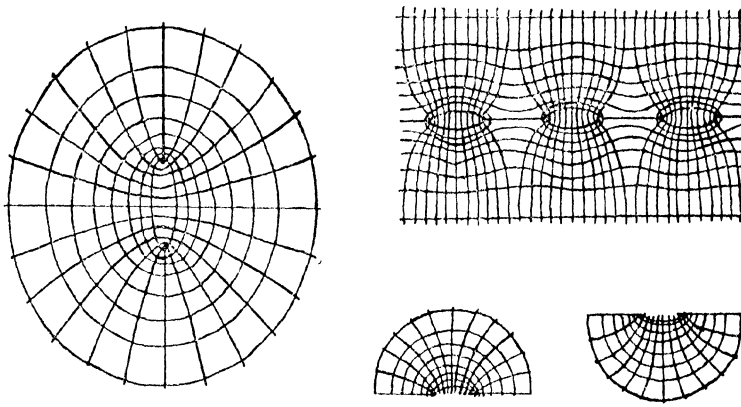

FIG. 24.—Diagrammatic representation of the diffusion of water vapour through small openings. *Left*—diffusion through a single opening in a vertical septum; the fan-like diverging lines show the courses of the diffusing particles; perpendicular to them are concentric lines of equal vapour density. *Right* (*above*)—diffusion through a horizontal multi-perforate septum (three openings are represented); (*below*)—diffusion through single openings of the same size (from Jørgensen and Stiles).

under certain conditions the diffusive flow may be almost as great as if the septum were entirely absent.[1]

[1 In one experiment a septum with 100 perforations (each of 0·38 mm. diameter) per sq. cm. was fixed (with paraffin luting) over the end of a glass diffusion tube about 3·4 cm. in diameter. In spite of the fact that 88·66 per cent of the cross-sectional area of the tube was blocked by the solid part of the septum, the increased velocity of diffusion through the remaining 11·34 per cent was sufficient to maintain a flow practically equal to that through an open tube of the same dimensions. In another septum, with 6·25 holes per sq. cm., the combined areas of the perforations only amounted to 0·7 per cent of the sectional area of the tube, 99·3 per cent being blocked. Yet in this case septum diffusion amounted to nearly one-third (i.e. 31·1 per cent) of that when the septum was absent. —ED.]

Such are the more important results of **Brown and Escombe's** experiments with artificial septa. The results of observations on the plant epidermis, with its numerous minute stomata, agree with these experiments. For instance, the rate of transpiration from the surface of a leaf is comparable with the rate of evaporation from an open water surface. Yet the surface of the leaf is almost entirely covered with a nearly impermeable cuticle, the combined area of the stomatal apertures, in spite of their great number, not exceeding 1–2 per cent of the total leaf surface. In fact, an epidermis with open stomata possesses the physical properties of a multi-perforate septum.

Such a structure is doubtless very advantageous to the plant. With widely open stomata, and other conditions favourable, the diffusion of gases through these numerous minute apertures may proceed almost at the same rate as if the cutinized epidermis were entirely removed, and the cells of the mesophyll in direct contact with the external atmosphere. This free gaseous exchange is of great importance in the carbon nutrition of the plant, for practically the only available source of carbon is the small amount of carbon dioxide scattered through the air. In the event of a deficiency of moisture, on the other hand, the closing of the stomata enables the plant almost completely to block the lines of communication between the intercellular spaces and the surrounding atmosphere. This movement, which requires only a slight displacement of the guard cells, materially assists in preventing a dangerous loss of water. In most cases, however, the actual amount of water vapour or other gas which diffuses through the stomata is very much less than the amount theoretically possible under the "diameter law". One reason for this is that, in addition to the diameter of the apertures, the rate of diffusion is strongly influenced by the thickness of the septum, or, in other words, by the length of the perforating canals. In the case of diffusion through stomata, this length is the depth of the stomatal pore. The following equation (adapted from Brown and Escombe) gives the rate of

diffusion of water vapour, when the canals are of a definite length:

$$V = \frac{k \,.\, p \,.\, \pi r^2 \,.\, n}{l + \frac{1}{8}\pi r}$$

where V is the amount of water evaporated in unit time; k a constant (the diffusivity of water vapour in C.G.S. units); p the moisture deficit; r the radius of the aperture (and this being of irregular shape—the radius of a circle the area of which is equal to that of the opening); n the number of apertures; l the thickness of the septum or length of the canal. The formula shows that with a very thin septum, when l may be taken as zero, it may be expressed thus:—

$$V = 8\, k \,.\, p \,.\, r \,.\, n \,.$$

i.e. evaporation will be actually proportional to the sum of the radii of the openings. But if, as pointed out by **Bachmann** (1922) in an interesting paper, l is so large that the value $\frac{1}{8}\pi r$ may be neglected, evaporation is proportional not to the sum of the radii, but to the sum of the areas of the openings, and will in consequence be considerably slower. To this influence of the value of l is probably due the fact that the actual loss of water through the stomata always proves distinctly less than that calculated from the "diameter law" alone. **Brown and Escombe** give an example in which they compare the possible with the actual diffusion of water vapour through the epidermis of a leaf of *Helianthus annuus*. The leaf had 330 stomata per sq. mm., the distance between them being 8–10 diameters, so that mutual interference is reduced to a minimum. In a still atmosphere, with a relative humidity of 25 per cent, the theoretically possible transpiration which could take place by diffusion alone amounts to 1·73 gr. per sq. m. of leaf surface per hour. But the maximum transpiration actually obtained in any of their experiments, from detached leaves with the petioles in water, and exposed to bright sunshine, was 0·276 gr., i.e. less than one-sixth of the

calculated amount. Similar results were later obtained by **Lloyd** (1908, p. 33), who compared the possible intensity of transpiration, as calculated from Brown and Escombe's formula, with the actual intensity observed in *Fouquieria splendens*, an Arizona desert plant. A still slower transpiration must occur in plants with sunken stomata, where the length of the canals leading to the intercellular spaces is very considerable. Those interested in the question of sunken stomata should consult the detailed papers of **Renner** (1910) and **Gradmann** (1923).

The diffusion of water vapour—and of other gases—through the stomatal pores is considerably complicated by the fact that the diameter of these openings is not constant, but shows a wide range of variation. This variation is conditioned by the degree of curvature of the guard cells. With maximum curvature the "split" of the stoma approaches a circular shape, while with minimum curvature the guard cells closely touch throughout their whole length. The stoma is now completely closed, and diffusion of carbon dioxide and water vapour checked.

The Mechanics of Stomatal Movements

The results of the investigations of **Hugo von Mohl** (1846) and **Schwendener** (1881) on the mechanics of stomatal movements are described in textbooks of plant physiology, so need not be dealt with here. These movements depend on fluctuations of the turgor of the guard cells, such fluctuations being closely connected with chemical changes occurring in the cell contents. **Lloyd** (1908) pointed out that simultaneously with variations in the width of the stomatal aperture, changes occur in the contents of the guard cells. When the stomata are closed, the guard cells are full of starch, but as the stomata open the amount of starch diminishes, sugars being accumulated instead.[1] Lloyd's observations were extended later by

[1 **Strugger and Weber** (1926) state that in *Galium Mollugo* the starch content, not only of the guard cells, but also of the subsidiary and other epidermal cells, varies according to the degree of opening of the stomata. When the stoma is widely open the guard cells contain no starch (or only

Iljin (1914[a]), who investigated the magnitude of the osmotic pressure in the guard cells of the stomata and in the surrounding epidermal cells. Iljin found that with a widely open aperture the osmotic pressure in the guard cells attains the enormous strength of 90–100 atmospheres. With a closed aperture, however, the pressure does not exceed 10–20 atmospheres, and does not differ essentially from the pressure in the neighbouring cells of the epidermis.[1] Iljin attributes these changes of pressure to the action of diastatic enzymes in the guard cells. Later, Iljin's observations on the fluctuations of osmotic pressure during stomatal movements were confirmed by **Wiggans** (1921) and **Steinberger** (1922), though these authors found considerably smaller fluctuations than those given by Iljin. Quite recently, **Kiselëv** (1925) and **Nicolič** (1924) have suggested that in addition to enzyme action, another mechanism is also concerned in stomatal movements, i.e. changes in the permeability of the guard cells. With increased permeability, turgor diminishes and the guard cells approach each other; conversely, when impermeability is again restored, turgor increases and the stoma opens.[2] The actions of these two mechanisms may overlap, giving rise to the capricious "play of the stomata" which renders the study of their movements so difficult.

traces), while the subsidiary and other cells are rich in starch. As the stoma closes starch appears in the guard cells (attaining a maximum during complete closure), at the same time disappearing from the other cells. The authors regard these results as evidence that (in this species) not only the guard cells, but also the subsidiary and other epidermal cells play an active part in regulating the stomatal pore. Determinations of osmotic pressure supported their hypothesis, for during closure the osmotic value of the sap in the subsidiary cells rises considerably higher than that in the guard cells. This contradicts, for the species in question, the statement of **Kiselëv** (1925) that the osmotic pressure in the guard cells is higher than in the epidermal cells, whether the stomata are open or closed. Cf. **Iljin** (1914[a]), see text.—ED.]

[1 See previous footnote.—ED.]

[2 In this connexion the discussion on pp. 164–169 on the effect of light on transpiration is suggestive. There appears to be some ground for the supposition that the permeability of the protoplasm is greater under the influence of rays in the blue-violet region than of those at the red-yellow end of the spectrum. At the same time the red rays are the most effective in inducing the opening of the stomata.—ED.]

Such is the peculiar and rather complicated mechanism of stomatal movements. It is important to note that these movements are not autonomic, but are induced by changes of environmental conditions. The chief factors concerned are illumination and moisture. The carbon dioxide of the air is also not without influence. Before dealing with the effect of the separate external factors on stomatal movements, we may examine the methods at our disposal for studying these movements. This is advisable in view of the connexion that exists (or is supposed to exist) between stomatal movements and the intensity of transpiration.

Methods of Investigating the Movements of Stomata

The simplest and most reliable method would appear to be the *direct observation of stomatal movements* in an uninjured leaf under the microscope. It is difficult, however, to apply this method except in a few cases, on account of the small size of the stomata and the lack of transparency of the leaves. **Kohl** (1886) and **Eberdt** (1889) observed stomatal movements in living leaves of *Alisma Plantago* and *Trianea* (= *Limnobium*) *bogotensis*. According to Eberdt, the last-named plant is especially well adapted to such direct observations. More recently this method was used by **Lloyd** (1913) with the cotton plant, and by **Gray and Peirce** (1919) in observations on the stomata of oats, wheat, and other cereals. Nevertheless, in the vast majority of cases this method cannot be applied, and its use is in any case attended by considerable difficulties. We have usually, therefore, to avail ourselves of less direct but more convenient methods.

A number of such methods have been described, but each has its drawbacks. The one which most nearly approaches the method of direct observation on the living leaf is the microscopical examination of rapidly fixed stomata. **Lloyd** (1908) uses *absolute alcohol* as a fixative: this, it is claimed, dehydrates and hardens the walls of the guard cells so rapidly that the

stomata undergo no further change of shape or dimensions. An incision is made in the leaf with a scalpel or razor, and a strip of epidermis removed with forceps and instantly plunged into absolute alcohol. According to **Loftfield** (1921) speed is essential to success, and the whole operation must not occupy more than 1–2 seconds.

The advantage of this microscopic method is that we can directly observe the condition of the stomata. The drawbacks are the complication of the method and the damage involved to the leaf, which cannot be used for further experiments. It is, moreover, somewhat laborious, for, on account of the fact that neighbouring stomata are often in very different states, a great number of exact measurements must be carried out. Attempts have therefore been made to devise indirect methods which would indicate simultaneously the average condition of a great number of stomata, and at the same time avoid serious injury to the leaf.

We are indebted to **Francis Darwin** for the introduction of most of these indirect methods. In his early investigations on stomata and transpiration (1898) he started with the assumption that the intensity of transpiration must be strictly proportional to the degree of opening of the stomata, and that therefore the amount of water vapour transpired would indicate the condition of the stomata. Darwin employed small, cleverly constructed hygroscopes, in which the hygroscopic substance was either a thin shaving of horn (*horn hygroscope*) or a strip of dried epidermis of *Yucca aloifolia* (*Yucca hygroscope*). With these instruments he determined the relative rates of water loss, and from these deduced the degree of opening of the stomata. At the present time, however, when the relations between stomatal opening and transpiration are known to be more complicated than was formerly supposed these methods are chiefly of historical interest. Together with **Stahl's** cobalt method they may be regarded as methods of studying transpiration rather than stomatal movements.

Darwin's latest apparatus, the *porometer* (**Darwin and**

Pertz, 1911) is based on a different principle. The size of the stomatal pores is estimated by the velocity of a current of air drawn through them in the living leaf. A glass chamber (*C*, Fig. 25) with a broad flange is glued to the stomatal surface of a leaf. This leaf-chamber is connected by a rubber tube with a T-tube, the long limb of which is graduated and dips

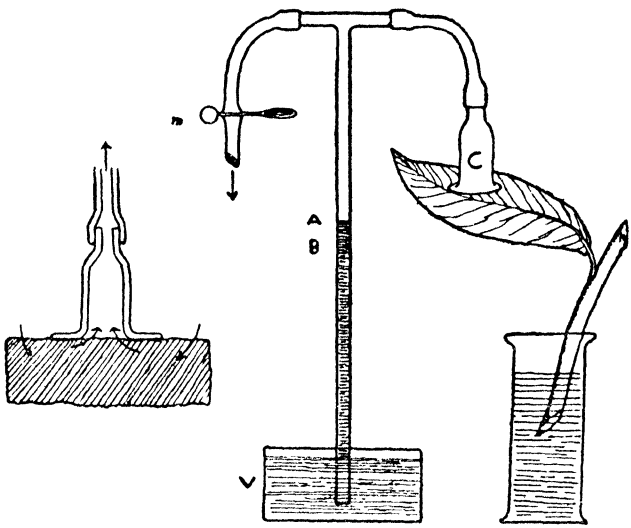

FIG. 25.—Darwin's porometer. *Right*—diagram showing the arrangement of the parts of the porometer; *left*—course of the air current through the stomata and the intercellular spaces of the leaf into the chamber of the porometer (after Darwin and Pertz).

into a vessel of water (*V*). The other short limb may either end in a rubber tube controlled by a clamp (*m*), or may be provided with a glass stopcock.

To start an experiment, the clamp is opened and air sucked through in the direction of the arrow, until the water column is raised to a point *A*, when the clamp is again closed. Owing to the now reduced pressure in the apparatus, air enters through the stomata enclosed in the leaf-chamber, being

replaced by air drawn in through stomata on the free surface of the leaf. The path of the air current is shown in the left-hand diagram in Fig. 25. As air enters the leaf-chamber the water column gradually falls, the time taken for the meniscus to travel from *A* to a second point *B*, giving the velocity of the current of air passing through the leaf.[1] This velocity depends on the resistance met with as the air traverses the intercellular spaces and the stomata. The resistance is naturally increased by the narrowing and decreased by the widening of the stomatal pores. If the stomata are completely closed the water column remains stationary at the height to which it was raised, but if widely open it falls rapidly. Hence the rate of the current of air is regarded as an indication of the degree of opening of the stomata.

Knight (1916) carried out a series of critical experiments in order to determine the limitations of the porometer, and the precautions necessary in its use. He found that differences of pressure may cause temporary curvature of the portion of leaf under the porometer chamber, and thinks that this may possibly affect the stomatal pores. To minimize the effect, small differences of pressure should be used. Further, the stomata of some plants tend to close when a continuous current of air is passed through them. To avoid this, the porometer chamber should be placed, between readings, in direct communication with the outer air. For this purpose, both short limbs of the T-tube may be provided with stopcocks, or a three-way stopcock may be inserted at the junction of the limbs of the T-tube.[2]

[1 Darwin used a graduated tube in which 1 cm. in length = 0·1 c.c., the points *A* and *B* being from 1 to 3 cm. on either side of a mean height of 20 cm. In this case the reciprocals of the time readings of the porometer are proportional to the rate of passage of air through the leaf, when the mean pressure difference between the two sides of the leaf is 20 cm. of water. Later, **Darwin** (1916) employed lower average pressures (e.g. 10 cm.) when the stomata were widely open.—ED.]

[2 **Knight** (1915) has described a modified form of porometer, in which, amongst other improvements, the air is drawn through the leaf under practically constant pressure. Automatic recording porometers have been described by **Balls** (1912), **Neilson Jones** (1914), and **Laidlaw and Knight** (1916).—ED.]

Knight devoted special attention to the effect of the resistance to the air stream due to friction against the walls of the intercellular spaces. This effect is considerable, as is shown by the porometer readings when the total length of the intercellular spaces traversed by the air stream is increased. In Knight's experiments this was done by blocking the stomata immediately outside the leaf-chamber, either with vaseline or by using a broad flange to the chamber, or by the use of a special "double leaf-chamber". With hypostomatous leaves, therefore, it is advisable to reduce the length of the path of the air through the mesophyll by using leaf-chambers without a definite flange. It may be mentioned here that **Neger** (1912), using another method (i.e. injection of the intercellular spaces under reduced pressure), has found that in the leaves of certain plants the veins completely separate the intercellular spaces of one portion of mesophyll from those of adjacent portions. Such leaves he terms *heterobaric*, in distinction to *homobaric* leaves, in which the intercellular spaces of the mesophyll communicate round the veins, thus forming one continuous system throughout the leaf. The use of the porometer with heterobaric leaves (e.g. oak, beech, maple, and many other mesophytic trees) would obviously lead to erroneous results.

One of the chief practical difficulties in the use of the porometer is how to ensure an airtight joint between the chamber and the leaf-blade, at the same time avoiding injury to the leaf. **Darwin and Pertz** found ordinary glue the best medium, but in some cases used perforated discs of 20–25 per cent gelatine. Other workers have used glue (the consistency is important), paraffin of low melting point, "syndeticon", etc. The most satisfactory joints are obtained with flat, glabrous leaves such as those of *Ficus elastica*. Strong pressure when fixing the chamber must be avoided, as with some leaves shock may cause the stomata to close. In any case Knight advises that readings should not be taken until two hours after fixing the chamber, during which time the leaf should be undisturbed. The last precaution is difficult in field experi-

ments, where the leaves may be exposed to wind; it must indeed be admitted that the porometer is scarcely adapted to observations under natural conditions. **Iljin** (1917) used, in field experiments, a porometer with a leaf-chamber of rubber pressure-tubing. He cut small circular discs from the leaves, fixing them with "syndeticon" to the ends of the rubber chambers. Readings were taken immediately after fixing a disc, in order to avoid possible alterations in the size of the stomatal pores. This method is simple and convenient, but doubts arise as to whether the degree of opening of the stomata really remained unaffected by the previous manipulation. For plants with very sensitive stomata the method is impracticable. Even with other plants control experiments are necessary in order to make sure that the cutting and cementing have not altered the condition of the stomata. Suitable controls would be afforded by **Lloyd's** absolute alcohol method, or even better, by the direct observation of living stomata under the microscope.

The readings of the porometer are usually expressed as the number of seconds required by the meniscus in the vertical tube to fall a given distance (the same for all experiments in any series). It would be a mistake, however, to suppose that the number of seconds taken either indicates the precise degree of opening of the stomata, or shows a simple relation to the intensity of transpiration. If we assume (cf. **Darwin,** 1916, p. 415)—(*a*) that the rate of diffusion through small apertures obeys **Brown and Escombe's** "diameter law" (or **Stefan's** "law of radius"), and (*b*) that the rate of a current of air drawn forcibly through such openings (as in the porometer) is proportional to the area (or sum of the areas) of the openings,[1] or, in other words, to the square of the radius; then, other conditions being equal, we should expect to find transpiration proportional to the square root of the observed

[1 If the effect of viscosity can be neglected, but proportional to the 3/2 power of the area if viscosity is preponderant. See Larmor in **Darwin** (1916).—ED.]

rate of fall of the water meniscus of the porometer. Darwin (**Darwin and Pertz**, 1911; and **Darwin**, 1916) actually found that the curve constructed from the square roots of the porometer rates of air-flow through the leaf closely followed the potometer curve of transpiration. But all such calculations are merely rough approximations. As **Bachmann** (1922) has rightly pointed out, the porometer readings may be strongly influenced by variations of the diameter of the intercellular spaces. According to **Poiseuille's** law, the rate of a steady flow of liquid through narrow tubes (or of a gas if, as in the porometer, the difference of pressure is not too great) is proportional to the fourth power of the diameter of the tube. Hence, with contraction of the intercellular spaces, which is very pronounced during wilting, the porometer readings may change independently of the size of the stomatal pores. On the other hand, as shown by calculations which cannot be given here, with very marked narrowing of the stomatal aperture, transpiration may be proportional not to the square root of the rate of the current of air through the stomata, but to the cube root or even the sixth root. At the present time, however, it is impossible to treat the data obtained from the porometer with any degree of mathematical exactitude. The porometer, in fact, cannot be regarded as an apparatus capable of yielding exact quantitative information regarding the degree of opening of the stomata. As a qualitative method it is inferior to the absolute alcohol method or to exact measurements obtained directly from the living leaf.

Still less exact, but simpler, and better adapted for use under natural conditions, is **Molisch's** *injection method* (1912) of investigating the condition of the stomatal pores. If a drop of liquid capable of wetting the cuticle and cell walls generally (e.g. absolute alcohol), is placed on the surface of a leaf with open stomata, it will be immediately absorbed by capillarity, and will inject the nearest intercellular spaces. Dark spots appear (transparent with transmitted light) which gradually fuse into a larger patch. If the stomata are nearly

closed, the spirit cannot penetrate, and no injection takes place. Other liquids, however, e.g. benzol, and xylol to a still greater degree, can penetrate even partially closed stomata.

The injection method is simple and convenient, the only apparatus required being three bottles—fitted with small brushes or glass rods—containing respectively absolute alcohol, benzol, and xylol. The method enables us to determine not only whether the stomata of a given leaf are open or closed, but also roughly the approximate degree of opening. If the alcohol will penetrate the leaf, the stomata are widely open; if benzol enters but not alcohol, the pores are considerably narrowed; if xylol alone will inject the leaf, the stomata are nearly closed, and finally, if none of the liquids will enter, the stomata are completely closed.

When Molisch's paper appeared, **Emmy Stein** (1912) pointed out that what is essentially the same method was in use in Stahl's laboratory at Jena. In this case liquid paraffin, petrol, and petroleum ether were used instead of absolute alcohol, benzol, and xylol. Subsequently, **Kamerling** (1913) somewhat improved the method, using an alcoholic solution of fuchsin instead of pure alcohol. This clearly indicates even a slight degree of injection.

Stålfelt (1916) critically examined the injection method, pointing out that this method is reliable when applied to amphistomatous leaves, as the air displaced by the liquid readily escapes through the stomata of the opposite side of the leaf. In the case of leaves with stomata only on the under side (hypostomatous leaves), however, only a very small drop of liquid must be used if the air is to escape through the neighbouring stomata. If the drop is large, it may either not penetrate at all, or injection may be confined to the edges of the drop, and so be easily overlooked.

Owing to its simplicity and convenience, this method is widely used and must be recognized as the most suitable for approximate observations regarding the condition of the stomata. It is true that the differences of behaviour of the different

liquids is only relative, and that, strictly speaking, injection only answers the question of whether the stomata are open or closed. But as we have already seen, the porometric method, which is regarded by many as strictly quantitative, is valuable chiefly as a qualitative method. It seems to me, therefore, that the simplicity of the injection method is no reason for underrating it.

Such are the methods at present available for the study of stomatal movements. They have all been elaborated within the last 10–15 years, and it is therefore not surprising that during this period our knowledge of the behaviour of the stomata, and of the influence on them of environmental conditions, has been considerably extended. Up to that time the prevalent view was that the stomata are open during the day and with a sufficient water supply, and closed during the night or when the water supply is deficient. But this original concept requires to be modified in the light of the more exact data now available, regarding the daily march of stomatal movements and the influence of various external and internal factors.

The Diurnal March of Stomatal Movements

In the first place, there are many exceptions to the general rule that the stomata are closed during the night. As early as 1886, **Leitgeb**, in his classical work on stomata, stated that the stomata of a considerable number of plants do not close at night. This statement has since been confirmed by other investigators. **Stahl** (1919), for instance, by means of injection with benzol, proved that out of 60 Central European species (chiefly wild plants), 35 had closed and 25 open stomata at night. In tropical rain forests at Tjibodas (Java) **Faber** (1915) often observed plants with stomata that were open both by day and by night, guttation in some cases taking place through the stomata. **Molisch** (1912), again, when testing his injection method, observed that though the

majority of plants tended to close their stomata by night, there were many which kept them open, for instance, the cucumber (*Cucumis sativa*), *Ranunculus acer*, *Melandryum album*, etc.

On the other hand, the stomata of some plants open in the morning, but soon close again. **Lloyd** (1908) was the first to discover this fact, **Iljin** (1914[a]) observing the same phenomenon a few years later. Both authors worked under the conditions of a hot, dry climate, the first in the Arizona desert, the second on the steppe of Voronezh. The reliability of their results, however, is considerably impaired by the fact that the observations were made on cut branches placed in water. But these observations were confirmed later for plants rooted in the soil (**Iljin and Sabinin**, 1917; **Maximov**, 1917), and it may now be regarded as an established fact that in a dry climate stomata not infrequently close, or at least narrow their apertures during the noontide hours. This closure may begin as early as 9 or 10 a.m., and the stomata may or may not open again after noon.

The most detailed investigation of the daily march of stomatal movement is that of **Loftfield** (1921), who studied the behaviour of the stomata during the whole 24-hour period, in a series of wild and cultivated plants. In addition to the weather conditions, the degree of soil moisture was taken into consideration. Lloyd's alcohol method was used in the investigation, and the results were from time to time verified by direct observations on living stomata. Loftfield's investigations have shown that the daily march of stomatal movement is not entirely regular,[1] but varies according to the conditions of weather and soil moisture. Loftfield divides the plants investigated by him into three main groups, according to their stomatal behaviour, which varies considerably in different cases.

(1) To the first group belong the cereals, in which the stomata, under ordinary conditions, are always closed at night.

[[1] The movements of the stomata, however, tend to follow a regular course under optimum conditions.—ED.]

Opening during the day is dependent, as regards both duration and degree, on favourable conditions of evaporation, temperature, and soil moisture. Deficiency of moisture greatly reduces the period of opening, and under steppe conditions cereals open their stomata only from about 5 to 10–11 a.m., and only from 10–20 per cent of the full width of the aperture.

(2) The second group embraces most thin-leaved mesophytes, a typical representative being alfalfa (*Medicago sativa*), which Loftfield studied in great detail. Other plants in this group are peas, clover, sweet clover (*Melilotus alba*), beans, beetroot, turnip, poppy, sunflower, etc., and such weeds as *Chenopodium album*, *Rumex Patientia*, *Amaranthus retroflexus*. Under favourable conditions the stomata of plants of this group are open all day and closed all night. With less favourable conditions, a partial or even complete closing of the stomata is observed during the middle of the day. As the environment becomes still more unfavourable, the period of closing sets in sooner and is more prolonged, at the same time night opening of the stomata being observed. Finally, under conditions of maximum heat and dryness, the stomata are closed all day and open all night, the degree of opening depending on the water content of the soil.

(3) The third group includes the potato and most other plants with fleshy leaves, such as cabbage, tulip, cowbeet, *Portulaca*, etc. Under optimum conditions (especially of water content of the soil) the stomata tend to remain open throughout the day and night. As evaporation increases a temporary closing is observed, which in the potato first occurs after sunset, but with still greater evaporation closure begins earlier, and the stomata may even close for a time during the day. Finally, with very great dryness, the plant spends the day in a half-wilted condition with closed stomata, the latter opening during the night as in group (2). It is interesting to note that the stomata of the upper side of the leaf open later and for a shorter time than those of the lower surface.

Such is the march of stomatal movements under natural

conditions, under the influence of the complex diurnal march of light, temperature, atmospheric humidity, water content of soil and leaves, etc. The study of the effect of each separate factor is of great importance, and many such investigations have already been carried out.

Effect of Light and other Factors on Stomatal Movements

The most important rôle in the opening of stomata, as well as in transpiration, is played by light. It has long since been established that, as a general rule, light promotes the opening of the stomata, while darkness leads to closure. The explanation of this fact was formerly sought in the presence of chloroplasts in the guard cells. The chloroplasts were supposed to form, under the influence of light, osmotically active substances, which increased the concentration of the cell sap. At the present time, when it seems more probable that the mechanism of stomatal movements may be connected with enzyme action, this explanation is no longer satisfactory. **Kümmler** (1922), for instance, has shown that in plants with variegated leaves, normally functioning stomata may be entirely devoid of chlorophyll. Thus it may be supposed that light influences the enzymatic processes in some indirect way.

Whatever the nature of the action of light on stomata may be, the importance of this action is beyond doubt. The stomata are the gateways through which carbon dioxide enters the leaf, and therefore their opening is essential for the process of carbon nutrition. No wonder, then, that modern authors, in studying the influence of external factors on stomatal movements, assign the first place among these factors to light.

It must not be supposed, however, that a change from light to darkness or from darkness to light induces an immediate closing or opening of the stomata. The opening or closing is a slow and gradual process, usually taking half an hour or more; the closing of stomata in darkness is especially

slow. That light acts as a specific stimulant is shown by some interesting experiments by **Loftfield**. He illuminated a plot of alfalfa on a dark night, from 10 p.m. to midnight, by a strong electric lamp (250 watt, 1 m. above the plants). The stomata were examined at intervals of half an hour. The illuminated stomata, which were closed before the experiment, began to open at 11 p.m. By midnight they were far more widely open than stomata from a dark control plot, which also showed a slight night opening (beginning at 11.30). In a similar experiment on a moonlit night, the stomata, under the influence of the moonlight, were partially open throughout the experiment. The addition of artificial light, however, apparently did not cause the stomata to open more widely. Loftfield found further that the response of the stomata to light is more rapid the nearer the experiment to the normal time of opening in the morning.[1]

Linsbauer (1916) found that in the case of light (as in many others), there may be an optimum intensity for promoting the opening of stomata, an excess of light actually leading to closure. This may be so in shade plants which close their stomata under the influence of strong light. It is possible, however, that in this case the effect is partly due to the water content of the leaf, a factor which also influences stomatal movement.

That stomata tend to close with reduced water content of the leaf, and especially during wilting, has long since been established. But the widespread belief that this is a means of protecting the plant against excessive loss of water needs revision. In the first place it must be noted that the stomata of many plants do not close during wilting. **Molisch** (1912), for instance, studied (by the injection method) the behaviour of stomata during wilting. Out of 38 species investigated, only 23 had completely or nearly closed stomata. In the other

[1 **Loftfield** is inclined to attribute this to progressive changes in the carbohydrate content of the guard cells occurring during the night in preparation for the morning opening of the stomata.—ED.]

15 species the stomata remained open even in perfectly dry leaves. Similar results were obtained by **Burgerstein** (1920[b]). Of 110 species of herbaceous plants, 48 had completely closed stomata, 44 partially open, and 18 fully open stomata, when in the wilted condition. Of 140 species of trees, wilting resulted in complete closure in 94, partial closure in 32, only 14 species retaining open stomata. From these results Burgerstein concludes that the closing of stomata during wilting is more frequent in trees than in herbaceous plants.

The behaviour of the stomata during wilting may depend on a number of circumstances. Thus, in view of the fact that the stomata not infrequently take one or two hours to close, the leaf may have time to wilt before closure occurs. Or if wilting experiments are conducted in sunlight, the "opening effect" of light may counteract the "closing effect" of loss of water, and the plant even become air-dry with widely open stomata. Phenomena of this kind were observed by **Iljin** (1911). On the other hand, even in plants which unquestionably close their stomata, complications may be observed during the process of closing. **Darwin** (1898) found, by means of his horn hygroscope, that the decrease of transpiration in wilting is preceded by a transient increase, and attributed this increase to a temporary widening of the stomatal aperture. This observation was confirmed later by various authors, and finally **Laidlaw and Knight** (1916), by using an automatic recording porometer, succeeded in proving the reality of this temporary widening of the stomata at the commencement of wilting. Whether the widening is due to an earlier loss of turgor by the adjacent epidermal cells, which by their contraction mechanically distend the stomatal pore, or to some other cause, it is difficult to say.

In addition to the temporary opening at the outset of wilting, there may be another opening at its close. **Molisch** found that in dried-up leaves the stomata are often open, though closed earlier during wilting. **Burgerstein** also observed the same phenomenon, and regarded it as posthumous.

It may be that it is brought about by the contraction of the drying epidermal cells, accompanied by a passive distension of the stomatal pores. Mme. **Krasnoselsky-Maximov** has observed such passive opening of the stomata in contracting petals of lilac and other plants (these observations are as yet unpublished).

We have seen that the influence on the living stomata of a deficiency of soil moisture, involving a decrease in the water content of the plant, has been distinctly observed by **Loftfield** (1921). Extremes of drought may, in fact, entirely reverse the normal daily march of stomatal movements, so that the stomata are open at night and closed by day.

The effect of other external factors, such as atmospheric humidity, wind, etc., is in most cases indirect, being mainly due to a decrease in the water content of the plant. The influence of temperature is somewhat more complex. A higher temperature markedly accelerates plant movements in general and those of the stomata in particular. **Loftfield** (1921), for instance, observed that in alfalfa, on transferring the plant from darkness to light, the stomata opened in 8 hours at a temperature of 0° C. At 10° C., the maximal opening was reached in 4 hours; at 20° C., in rather less than 2 hours; and at 30° C., in approximately one hour. Broadly speaking, this accelerating effect of temperature obeys van't Hoff's law, according to which the rate of a chemical reaction is doubled with each rise of temperature of 10° C. But a rise beyond certain limits involves, in addition, definite pathological changes in the stomata. As **Zalenski's** (1921) experiments have shown, a temperature of 38–40° C. induces intense hydrolysis of the starch in the guard cells. Consequently, there is a great increase of osmotic pressure in the stomata, which not only open widely but also lose their capacity of closing. A plant unable to close its stomata naturally loses water very quickly. It is by this effect on the stomata that Zalenski explains the injurious results of dry fog[1] and desiccating winds

[1] See p. 389.—ED.]

when accompanied by a temperature of 40° C. and more. Under these circumstances a plant, even though rooted in the soil, may be reduced to an air-dry condition. The temperature and rate at which these pathological changes occur differ in different species, and Zalenski is inclined to connect this with the varying capacity of plants for drought resistance. We shall return to this subject in the last chapter of this book.

Lastly, a very considerable and at the same time complex effect is exerted on stomatal movements by salts (or more precisely by their ions) and the corresponding acids. The influence of salts has been studied in detail by **Iljin** (1922 [a, b, c]). This author immersed small portions of epidermis in hypertonic solutions of various salts, and observed that plasmolysis took place, owing to the withdrawal of water from the cells. The stomata closed in consequence of this loss of water, but in an hour or less turgor was again restored, and the stomata opened widely. Iljin explains this phenomenon by supposing that the ions of the salt gradually penetrate the guard cells and induce the hydrolysis of starch. The action of different ions varies considerably. Univalent cations, especially sodium, produce the most vigorous hydrolysis, while bivalent cations (calcium, magnesium) are not only inactive, but inhibit the action of sodium and potassium. The most active anions are those of organic acids, especially acetic and citric. Inorganic anions, on the other hand, have no particular effect.

Iljin's results on the hydrolysing effects of salts were independently confirmed by **Weber** (1923). These discoveries must be regarded as some of the most important hitherto made in the field of the chemistry of stomatal movements.

CHAPTER VII

THE REGULATION OF TRANSPIRATION BY THE PLANT

Regulation of transpiration by the plant. Attacks on the theory of stomatal regulation. Relative transpiration and incipient drying. The mechanism of regulation—stomatal and non-stomatal.

The Regulation of Transpiration by the Plant

As the plant spends an immense quantity of water in the process of transpiration, and at the same time must replenish its supply, often with great difficulty, from the soil, it must needs regulate its water loss in conformity with its water absorption. To balance the expenditure and receipt of water is indeed one of the most necessary conditions of existence for land vegetation, and plants of arid regions are faced with this problem in its most acute form.

When we speak of the ability of the plant to regulate tran spiration we naturally think first of the stomata, the importance of which in such regulation seems obvious. The stomata are the outlets through which water vapour diffuses from the intercellular spaces to the external atmosphere. We have also seen that the amount of water lost by cuticular transpiration is insignificant as compared with that transpired through the stomata. This makes the mechanism of stomatal regulation of transpiration easy to understand. In fact, when the stomata are closed, water can no longer escape from the intercellular spaces, but only directly through the cuticle. If **Unger's** (1861) figures are accepted, this must decrease transpiration to a small fraction of its former value. With the opening of the stomata, transpiration must again correspondingly increase.

Until recently, the prevalent view was that the fundamental factor regulating the water expenditure of the plant is the movements of the stomatal apparatus. This view is still accepted by most botanists, and has been upheld consistently by **Francis Darwin** (1898, 1916) in particular. Amongst

Russian authors it has been especially emphasized by **V. S. Iljin.** If this point of view is carried to its logical conclusion, it would follow that all external factors only influence transpiration indirectly, i.e. by their effect on the stomatal movements. If, for instance, the stomata open under the influence of light, transpiration increases. If they close, transpiration must decrease notwithstanding the fact that solar radiation tends to heat the leaf, and thereby to accelerate the evaporation of water. Similarly the effect of wind may depend on the behaviour of the stomata. If they close, owing to battering by the wind or through local loss of water, transpiration will decrease, though the wind as such would increase it. If, on the other hand, the stomata remain open in spite of the wind, the direct effect of the air movements may be manifested. But since the movements of the stomata have been studied in greater detail, it has become clear that they are not necessarily either widely open or completely closed, but may show various intermediate states between these two extremes. Moreover, even the degree of opening can be calculated either by direct measurements of the width of the pore under the microscope or from the readings of the porometer. From this it has been inferred that every narrowing of the stomatal aperture must lead to a decrease, and every widening to an increase in transpiration.

Attacks on the Theory of Stomatal Regulation

It is true that as long ago as 1883, **Schwendener,** in his classical work on the mechanism of stomatal movements, raised a warning voice against the over-estimation of the rôle played by these movements in regulating transpiration. As he pointed out, the fact that the stomata open during the day, when the loss of water is greatest, and close during the night, when it is usually least, precludes the view that the chief function of stomata is the control of transpiration. The stomata, in fact, are concerned with assimilation at least as much as

with transpiration. Nevertheless, the belief that stomatal movements are of paramount importance in regulating transpiration continued to command acceptance, until it was subjected to a series of assaults, chiefly from American investigators.

Lloyd (1908) was the first to open the contest. In a comprehensive monograph on "The Physiology of Stomata" he gave the results of a detailed study of the march of stomatal movements and transpiration in two desert plants, *Fouquieria splendens* (the ocotillo) and *Verbena ciliata*.

In the first place Lloyd compared the normal daily march of transpiration with that of stomatal movements. He showed that during the course of the day the curve of intensity of transpiration by no means coincides with the curve of stomatal movement. In the morning the maximal width of the stomatal apertures is usually reached some two hours before the maximal transpiration rate. In the evening, when the stomata have practically closed, transpiration still continues to fall. In some cases the rate of transpiration actually increased while the stomatal pores were becoming narrower.

From measurements of the diameters of the stomatal pores of *Verbena ciliata*, **Lloyd** calculated (by Brown and Escombe's formula) the diffusion capacity of the stomata, when open to different degrees. He then compared the range of diffusion capacity during the day with the range of transpiration. In one experiment the ratio of maximal to minimal transpiration was 6·22, and that of maximal to minimal diffusion capacity 2·50. In another case the corresponding ratios were 6·43 and 4·00. Lloyd thinks that the fact that the respective ranges of transpiration and capacity for diffusion are more or less independent of one another indicates that some factor other than stomatal movement is concerned in determining changes in the rate of transpiration.

Lloyd further studied the responses of transpiration and stomatal movement to sudden changes in illumination. He found that when a plant is transferred from light to darkness,

or vice versa, the amount of water transpired may alter considerably without any appreciable change in the size of the stomatal pores, provided that the experiments are of short duration. In more prolonged experiments, however, the stomata begin to close or open, but such changes of size are incommensurable with the fluctuations in intensity of transpiration. For example, in certain plants transferred from darkness to light, Lloyd observed that without any changes in the stomatal apertures, transpiration increased in one hour[1] by 1·7, 2·3, 2·5, or even by 4 times. In similar experiments of varying duration (15 minutes to 2 hours), the diffusion capacity of the stomata increased by 2·2, 2·9, 4·5, or even by 5·5 times. Briefly, the changes in the rate of transpiration always exceed the changes in diffusion capacity, and therefore, in Lloyd's opinion, the rate of transpiration cannot be conditioned by stomatal movements alone. But Lloyd goes still further. He thinks that changes in the rate of transpiration caused directly by variations in the size of the stomatal pores are so insignificant, that the influence of these changes on the general water budget of the plant may be entirely neglected. Finally, Lloyd comes to the conclusion that, at least in *Fouquieria* and *Verbena*, the regulating effect of the stomata on transpiration is nil.

Lloyd's attempt to discredit the theory that the stomata are the regulators of transpiration met with a somewhat hostile reception, especially on the European Continent. **Renner** (1910) criticized Lloyd's view in detail, pointing out in the first place a serious error of logic in his argument. Lloyd's argument is really an elaborate attack on the assumption that the diameter of the stomatal aperture is the only variable quantity determining the rate of transpiration under different external conditions. But, *a priori*, it is evident that even if stomatal regulation be fully admitted, external factors also (e.g. light) must influence the amount of water transpired by the plant. The actual oscillations of transpiration must, indeed, represent

[1 Twenty-five minutes in the case of the last experiment of this series.—ED.]

the successive resultants of the effects of all the factors operative—external as well as internal, including the diameter of the stomatal pores.

Objections were also raised to some of **Lloyd's** methods. Transpiration was usually determined indirectly by means of somewhat crude burette potometers. The cut ends of branches were inserted into the rubber tubes attached to the burettes,

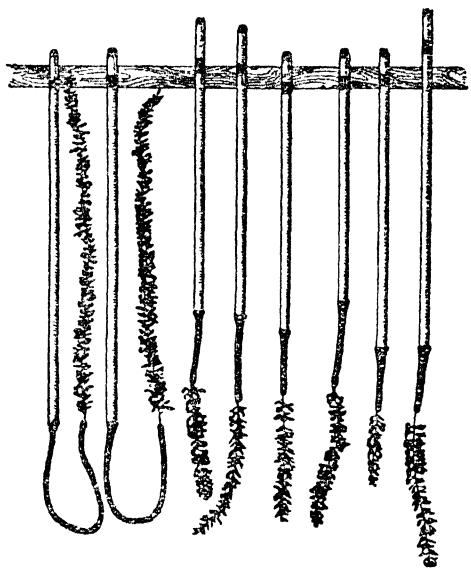

FIG. 26.—The use of burettes as potometers (from Lloyd).

which were suspended vertically. The branches were either tied to the burettes in an erect position or else allowed to hang downwards (Fig. 26). But while usually studying transpiration from cut branches, Lloyd observed stomatal movements in intact plants rooted in the soil. The march of these movements may have been quite different from that in the leaves of cut branches, as recently shown by **Loftfield** (1921). Further, the method of calculating diffusion capacity from the linear measurements of the stomata must be regarded as only an

approximation (**Burgerstein** lays stress on this in his monograph). Hence, complete agreement between the calculated diffusion capacity and the observed rate of transpiration is not to be expected.

In spite of these objections Lloyd adhered to his opinion that at most the stomata play but a very minor part in the regulation of transpiration. In subsequent papers he made an attempt to attack the problem from another side (**Lloyd,** 1912, 1913). Calculating simultaneously the absorption and loss of water by cut branches of *Fouquieria splendens*, he found that during the earlier part of the day the loss of water exceeds absorption, while at night absorption is greater than transpiration, and the daytime deficit is made good. Comparing these observations with the movements of the stomata, Lloyd points out that the diminution of the water content of the plant more or less coincides with the period of opening of the stomata. Hence he concludes that there is no very close connexion between stomatal movements and the water content of the leaf, and that the stomata are unable to maintain the water content (relative to dry weight) at a constant level.

Relative Transpiration and Incipient Drying

Livingston and Brown (1912) have treated the question of the relation between the intensity of transpiration and variations of the water content of leaves in much greater detail. Livingston had been interested in the question of the regulation of transpiration ever since his work on desert plants (**Livingston,** 1906), in which for the first time he attempted to give quantitative expression to the regulatory capacity of the plant. For this purpose he introduced the concept of *relative transpiration* (cf. p. 129), by which is meant the ratio of the rate of transpiration to the rate of evaporation (under properly defined conditions) from a free water surface or from the evaporating surface of an atmometer. These rates are calculated in grammes per hour per square centimetre of surface. If T is

the rate of transpiration and E the rate of evaporation per unit area, then $\frac{T}{E}$ is the relative transpiration. **Livingston** (1906) stated that the magnitude of relative transpiration is not constant for a given plant, but is subject to considerable variation during the day. For example, he obtained the following maximum and minimum values for relative transpiration in certain Arizona desert plants:—

	Maximum	Minimum
Euphorbia sp.	0·068	0·008
Tribulus brachystylis	0·193	0·009
Allionia incarnata	0·371	0·029
Boerhavia sp.	0·609	0·054

The maximum of relative transpiration usually occurs in the daytime and the minimum at night. Livingston regards these variations as an indication of the regulatory activity of the plant, and even calculates the efficiency of regulation from the relation between the maximum and minimum values. Thus for *Euphorbia* he gives the value of the efficiency of regulation as 1/9, and for *Tribulus*, *Allionia*, and *Boerhavia*, 1/12.

In his earlier work Livingston does not deal with the question of the mechanism of regulation, but confines himself to suggesting the possibility of "stomatal or some internal foliar responses". Later, however (**Livingston and Brown, 1912**), he gives the preference to non-stomatal regulation, assigning to the stomata a comparatively modest part in the regulation of transpiration. Livingston thinks that this non-stomatal regulation may explain an interesting phenomenon referred to in his earlier paper, i.e. that the daily march of transpiration does not coincide with that of evaporation. During the noontide hours the rate of transpiration always begins to fall somewhat earlier than that of evaporation from an atmometer. For this reason, relative transpiration, which

attains its maximum in the morning, rapidly falls during the afternoon. Since, according to Lloyd, a fall in transpiration may begin before there is any perceptible closing of the stomata, Livingston considers that the decrease of relative transpiration is a factor of great importance in the regulation of water loss. Under conditions of high evaporation, Livingston found a marked decrease in the water content of leaves during the day, owing no doubt to excess of water loss over water supply. This decrease of water content, though not sufficient to induce definite wilting, is not infrequently accompanied by a perceptible loss of turgor, and has been termed by Livingston and Brown *incipient drying*.

Livingston and Brown suppose that "incipient drying" proceeds as follows. With a moderate rate of water loss, the cell walls lining the intercellular spaces of the leaf are saturated with water, and the air filling these spaces is saturated with water vapour. Under these conditions, the external atmosphere is in contact with a saturated internal atmosphere at the entrance to the stomatal pores, and the outward diffusion of water vapour is more or less rapid. As transpiration increases, however, and the leaf begins to lose more water than it receives, the surfaces of the cell walls bounding the intercellular spaces begin to dry out, the water films gradually retreating into the pores of the cellulose. The partial pressure of water vapour in the intercellular spaces is now reduced, and the internal atmosphere in contact with the external atmosphere is unsaturated; accordingly, the rate of diffusion decreases, and with it the rate of transpiration.

It is of interest to note that some years previously a similar view regarding the dependence of the rate of evaporation from the surface of moist bodies on the water content of the evaporating surface was put forward by **B. J. Sresnevski** (1905). This author, in the paper referred to above (p. 159), found that transpiration obeys Dalton's law of evaporation only within a certain narrow range of relative humidity of the air. If the atmospheric humidity falls outside this range, i.e. is

either greater or less, the rate of transpiration is automatically modified by purely physical processes. With greater humidity the rate becomes more rapid, and with lower humidity less rapid, than is required by Dalton's law. Sresnevski maintains that this physical self-regulation of evaporation is due, not to stomatal movements, but to changes in the water relations of the evaporating surface. According to Sresnevski the course of events may be somewhat as follows: (1) atmospheric humidity determines the initial rate of evaporation; (2) this rate of evaporation determines the degree of saturation of the evaporating surface; and (3) this in turn affects the subsequent rate of evaporation.

The work of **Lloyd** and **Livingston** seriously weakened the position of those who held the then prevailing opinion that stomatal movements are the chief, if not the only means of regulating transpiration. Their attacks were followed by others, again mainly by American investigators. **Edith Shreve** (1914) at the same Desert Laboratory, studying the daily march of transpiration in the shrub *Parkinsonia microphylla*, obtained results which on the whole agreed with Livingston's data. The maximal transpiration is always considerably earlier than the maximal evaporation from the surface of an atmometer. Studying simultaneously the degree of opening of the stomata, she discovered that during the morning the curves of absolute as well as relative transpiration nearly coincided with the curve of opening of the stomata. In the afternoon, however, transpiration begins to decrease though the stomata continue to open. But the explanation of these results presented some difficulty, inasmuch as the morning readings appeared to indicate a close connexion between transpiration and stomatal movements, which was contradicted by readings taken later in the day.

The problem of the rôle of stomata in the regulation of transpiration was approached in an original way by **Muenscher** (1915). Eight species, with a wide range in size of stomata, were selected, i.e. *Phaseolus vulgaris*, *Zea Mays*,

Ricinus communis, *Helianthus annuus*, *Triticum sativum*, *Primula sinensis*, *Pelargonium zonale*, and *Impatiens Sultani*. Seedlings were planted in large stone pots, which were sealed with wax when the plants had attained a sufficient size. The total amount of water lost from each pot was determined by weighing, the length of individual experiments varying from 5 to 60 days. At the end of each experiment the leaf area of the plants used was measured. The actual experiments were made between November 1914 and January 1915, at Lincoln (Nebraska).

Muenscher calculated for each species the average intensity of transpiration in milligrams per hour per square decimetre of leaf surface, and also ascertained the numbers of stomata per square millimetre and the lengths of the stomatal pores. He was unable to establish any constant relation between the amount of water lost and either the number of stomata per unit area of leaf surface or the size of the stomatal pores. This was so whether size was calculated as the sum of the areas or the sum of the lengths of the pores per unit area. From these results Muenscher concluded that the amount of transpiration is not regulated entirely by the stomata, and that variations in different species are probably due to a complex of several factors rather than to the size and number of the stomata.

These results are anything but unexpected. It is self-evident that the number and size of the stomata alone cannot determine the intensity of transpiration. So far as the leaf itself is concerned, the structure of the mesophyll, the dimensions of the intercellular spaces, the area of the leaf surface, the behaviour of the stomata, and other peculiarities must also affect the amount of water lost. The experiments, moreover, were conducted during the winter. We have therefore only to suppose that the more heliophilous plants had their stomata closed owing to the deficient light, and that those more tolerant of shade kept them open during the greater part of the day, and the author's whole theory falls. Some of Muenscher's methods too are open to criticism.

When studying the march of transpiration in plants of different ecological types, in the arid climate of Tiflis, I, too, (**Maximov**, 1916 and 1917) was faced with the problem of the regulation of transpiration in plants. From a physiological point of view, the principal questions are (1) whether the plant actually possesses a regulatory mechanism which enables it considerably to reduce the loss of water during the hours when such loss threatens to exceed the limit of safety; and (2) what is the nature of this mechanism (if any), and how far reaching is its action. Since the stomata are usually considered to constitute such a regulatory mechanism, I endeavoured to choose for my experiments plants showing a widely different march of stomatal movements. The sunflower and alfalfa were found to meet this requirement. Under the conditions of my experiments, the stomata of the sunflower—as shown by Lloyd's absolute alcohol method and by that of injection with alcohol and xylol—remained open during the whole day, closing only towards sundown. In the thin, delicate leaflets of alfalfa, on the other hand, the stomata began to close as early as 11 a.m. With such differences of stomatal behaviour, corresponding differences in the daily march of transpiration might be expected. The experiments, however, showed no substantial difference in this respect between the two plants.

The results of my own experiments, and especially a comparison of these with the data obtained by **Briggs and Shantz** (1916), appear to me to indicate that Livingston's concept of "incipient drying" is of very limited importance. The fact that the water content of plants decreases considerably during the noontide hours has been fully confirmed by the experiments of **T. A. Krasnoselsky-Maximov** in Tiflis (1917), and later in Leningrad (**Maximov and Krasnoselsky-Maximov**, 1924). This work has shown that a decrease in the water content of leaves about midday occurs in clear weather in different climates, and even with a high moisture content of the soil.[1] That the transpiration maximum is attained earlier

[1 See p. 225.—ED.]

in the day than the maximal evaporation from an atmometer, on which fact Livingston based his theory, was also observed in most of my experiments. This, however, in my opinion indicates not a regulatory activity on the part of the plant, but simply the different ways in which the white porcelain atmometer and the green plant respectively respond to the same external factors. The plant is more sensitive to the influence of solar radiation (see p. 154), which reaches its climax at noon, and therefore the transpiration maximum occurs about this hour. The atmometer, on the other hand, with its vertical evaporating surface, responds more readily to changes of temperature, atmospheric humidity, and wind velocity. These meteorological factors normally reach their maxima not at noon but at 2–3 p.m., hence the difference between the march of transpiration and that of physical evaporation. It is significant that such differences between the daily march of transpiration and evaporation as were obtained by **Briggs and Shantz** (1916) were in the opposite direction to that observed by **Livingston**, i.e. the transpiration maximum was later (not earlier) than the evaporation maximum. This is probably due to the fact that the shallow, blackened evaporation tank used by Briggs and Shantz is still more sensitive to solar radiation than the plant, and therefore much more so than the porcelain atmometer.

In a later paper, **Briggs and Shantz** (1917[a]) compared the hourly rate of transpiration of *Medicago sativa* with the corresponding rates of evaporation from different types of evaporimeters during a period of hot weather in July. The closest agreement between transpiration and evaporation was obtained with a shallow, blackened evaporation tank (depth of water about 1 cm.). The following are the average hourly departures (for the total period) of the evaporation rate from the transpiration rate in percentages of the mean evaporation rates: shallow tank, 17 per cent; filter-paper evaporimeter, 31 per cent; porous cup atmometers (brown cylinder, white sphere, and Bellani plate), about 41 per cent; white cylinder atmo-

meter, 49 per cent; and deep evaporation tank (depth of water about 50 cm.), 89 per cent. For the day periods only (i.e. 6 a.m. to 6 p.m.) the corresponding percentages are 12, 22, about 30, 38, and 93 (see pp. 141-3 and 149 for illustrations of the atmometers used and of Briggs and Shantz's experiments). Briggs and Shantz attribute the observed deviations to differences in response of the various evaporating systems to wind velocity and solar radiation. In point of fact, different evaporimeters show much greater divergence in their respective rates of evaporation than do the most diverse plants in respect of their rates of transpiration. Hence it is evident that the magnitude and course of "relative transpiration" are determined not merely by the regulatory processes of the plant, but probably even more by the properties of the evaporimeter used.

In recent years the concept of "relative transpiration" and the question of the regulation of transpiration by the plant have been investigated by **Knight** (1917[a, b], 1922). In his first paper Knight dealt with the interrelations of stomatal aperture, the water content of the leaf and the rate of transpiration. Transpiration was determined either from rooted plants or from cut shoots mounted in potometers, which were weighed at intervals of 30 minutes. Simultaneous readings of the potometers gave the amount of water absorbed, and the difference between this and the amount transpired indicated changes in the water content of the plant. Physical evaporation was determined by atmometers, the loss of water again being measured by weighing. Livingston's atmometer and a modified form of the Piche atmometer were used, the latter being found more convenient, as it responded more rapidly to changes of temperature. The porometer was employed to indicate the degree of opening of the stomata, the author adopting Darwin's method of representing the size of the apertures by taking the square root of the porometer readings.

In order to investigate the relations between stomatal opening and transpiration, Knight carried out some twenty-six experiments, but the results obtained were inconsistent. In

some experiments the curves of "relative transpiration" and stomatal aperture were closely parallel, the maximum of one coinciding with the maximum of the other. But in many cases there appeared to be no correlation whatever between the two curves, a decreasing transpiration rate being accompanied by stomatal opening, and vice versa. From this Knight infers that at any rate the stomata do not strictly regulate transpiration.

Knight also investigated the relation between the rate of transpiration and the water content of the leaf, as calculated from the difference between the absorption and the loss of water. He found that the water content of the leaf played an important part in the control of transpiration, a high water content tending to increase transpiration, and a lower one to decrease it. At the same time, the stomatal aperture is not reduced by a slight water deficit. Hence the current view that the stomata, by their response to incipient drying, tend to maintain a constant supply of water in the leaf is untenable.

In one instructive experiment Knight placed a cut shoot of *Eupatorium adenophorum* in a current of air produced by an electric fan fitted to an air-flue. Under these conditions transpiration exceeded absorption. From 3.30 to 4 p.m. the air current was stopped, and transpiration at once fell abruptly—absorption now exceeding transpiration. On restarting the fan, transpiration again increased, being even greater than immediately before the stoppage of the air current. During this experiment (from 12 noon to 5.30 p.m.) the total water content of the shoot decreased by 413 mg.; yet the stomatal apertures, instead of closing, showed a slight tendency to open more widely as the experiment proceeded. Fig. 27 (on following page) reproduces Knight's curves for this very interesting experiment, which shows conclusively, perhaps for the first time, the existence of non-stomatal regulation of transpiration.

In a later paper **Knight** (1917[b]) criticized Livingston's concept of relative transpiration (cf. p. 129), which the latter regarded as the expression of the *intrinsic transpiring power* of the plant. The concept is based on the assumption that changes

in the atmospheric environment have the same effect on the rate of transpiration as on the rate of evaporation from a water surface, and therefore do not affect the ratio between them. Knight shows that this assumption is erroneous, for the structure of the leaf is such that wind must affect evaporation from the surface of an atmometer much more than it does transpiration. He brings forward ample experimental evidence in support of his contentions.[1] **Briggs and Shantz** (1917[a])

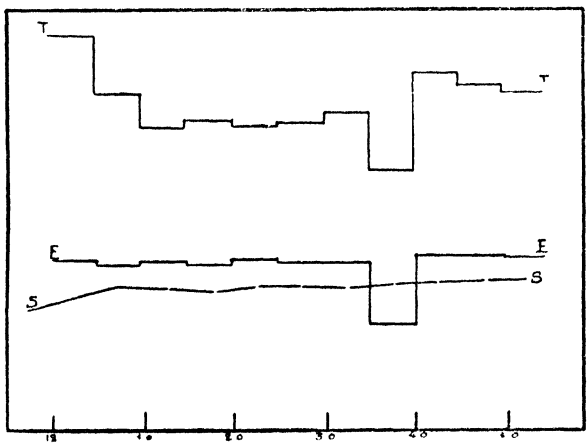

FIG. 27.—Comparison of the march of transpiration (*T*), evaporation of water from an atmometer (*E*), and the condition of the stomata (*S*) (from Knight).

came to similar conclusions (see above), and the question was also treated in detail by myself at about the same time.

Huber (1924) also has recently discussed in detail the concept of relative transpiration, which he prefers to call "Transpirationsvermögen" (the transpiring power of Livingston). Huber, too, points out the extreme variability of this quantity,

[[1] From his experiments Knight concluded, however, that temperature and relative humidity do act equally on the rate of transpiration from a plant and the rate of evaporation from an atmometer. He therefore regards "relative transpiration" as a valid measure of the intrinsic transpiring power of a plant *provided that wind velocity is constant.*—ED.]

and that transpiration from the plant and evaporation from the atmometer react quite differently to environmental changes. He maintains, therefore, that changes in relative transpiration cannot serve as a measure of the regulatory activity of the plant. At the same time Huber rightly points out that great credit is due to Livingston for introducing this concept into botanical science. A determination of the transpiration capacity at least enables us to form some idea of the combined effect of factors influencing the rate of water loss, as modified by the specific anatomical structure of the plant. For instance, if the mean transpiration capacity during the daytime of the birch (*Betula*) is 0·59, of the oak (*Quercus*) 0·16, the pine (*Pinus*) 0·06, and of *Opuntia* 0·006, these figures serve to illustrate the degree of protection against loss of water possessed by these plants respectively.

The Mechanism of Regulation—Stomatal and Non-Stomatal

The inadequacy as regulatory mechanisms, both of the stomata and of a reduced water content of the plant, suggested to me the idea of seeking some other means by which the plant could, in case of need, considerably reduce its transpiration. The method adopted of investigating this problem was to compare the march of transpiration in two sets of plants: one suffering from a shortage of water, and the other plentifully supplied with water.

A particularly convenient plant for these experiments was maize, in which the stomata usually closed during the noon-tide hours on hot days, even though the plant was well supplied with water. In comparing, therefore, the march of transpiration in watered and unwatered plants, the question of the behaviour of the stomata in the second half of the day could be regarded as a subordinate one. The following are the results of one experiment with this plant. Three pairs of maize plants, grown in comparatively small pots, were selected, each pair

being as uniform in size as possible. Of each pair one pot was watered regularly after weighing, the other receiving no water at all on the day of the experiment. The pots were weighed every two hours. As the experiment progressed, the plants in the unwatered pots began to suffer from an ever-increasing water deficit, which manifested itself externally in a certain degree of rolling of the leaves. Table VIII gives the results of this experiment. For convenience of comparison the amount transpired by each of the watered plants in the midday hours is taken as 100: all other figures are given as percentages of this arbitrary value.

TABLE VIII

March of Transpiration in Maize Plants when continually supplied with Water, as compared with Plants suffering from Water Shortage (according to N. Maximov)

Hours	7–9 a.m.	9–11 a.m.	11 a.m.–1 p.m.	1–3 p.m.	3–5 p.m.
No. 105, watered ..	51	87	100	106	100
No. 104, unwatered ..	50	90	75	52	20
No. 107, watered ..	62	93	100	114	81
No. 106, unwatered ..	62	93	90	72	23
No. 109, watered ..	46	74	100	109	83
No. 108, unwatered ..	42	78	83	47	31

We see that the figures, at first very similar, begin to diverge from about 11 a.m. In the watered specimens, transpiration continued to increase up to between 1 and 3 p.m. The transpiration of the unwatered plants, on the other hand, showed a marked diminution during these hours, while by 5 p.m. it had decreased to $\frac{1}{3}$–$\frac{1}{5}$ of that of the control plants. Thus a deficiency of soil water caused the intensity of transpiration to decrease by 3–5 times. Experiments with other plants yielded similar results. In some cases I observed a decrease of transpiration, in plants wilting in drying soil, of 8–10 or even more times, as compared with watered controls.

Such is the powerful regulator at the disposal of the wilting plant, far surpassing, in its effect, the regulative action of a mere closing of the stomata. The actual mechanism of regulation has yet to be explained, but it is connected, at all events, with the conditions of water supply of the plant. My experiments have shown that if the soil moisture is maintained at a low level, and the plants not allowed to wilt completely, the intensity of transpiration is diminished, the decrease being distributed fairly equally throughout the day. But the investigations by which I hope to elucidate the nature of this regulative action are not yet completed. I will, therefore, not enter into a detailed discussion of the possible explanations of this regulation, but will confine myself to quoting certain considerations which I advanced some years ago when dealing with these experiments (**Maximov**, 1917, p. 90). "This regulation can be explained neither by the stomatal movements, since the relation between the respective amounts of transpiration remains constant during the whole day, and is not affected by the closing of the stomata in the evening; nor by the decrease of the water content in the leaves alone, for the effect of this decrease should be particularly marked during the daytime, and gradually lessen towards evening. The cause of this regulation... I am inclined ... to seek in a change of the conditions of water supply and of the movement of water through the plant. For the drier the soil, the less readily does it yield up its moisture to the root system of the plant, and the greater is the resistance which the ascending current of water (drawn upwards chiefly by transpiration) meets with in the lower part of its course. Owing to the cohesion between the particles forming the water columns which run through the plant organism from top to bottom, the retardation of the water current at the bottom inevitably involves a similar retardation at the top. In the walls of the evaporating cells ... the water menisci retreat into the pores, the pressure of water vapour at the surfaces of the cells diminishes, and transpiration decreases. Such is my hypothesis (based to a considerable extent on

Dixon's work) regarding the regulation of transpiration through the activity of the root system."

This hypothesis of "root regulation" has not been advanced in any of my papers published in foreign periodicals, and has not as yet been discussed in detail by other authors. I propose to devote a special paper to a detailed working-out of my hypothesis, based on material accumulated during recent years. All I need say here is that at the present time the hypothesis in question appears to me to offer the most probable explanation of the marked decrease in transpiration observed when there is a shortage of water in the soil, or during the wilting of the plant in general. A series of papers published since the hypothesis was first put forward has strengthened my conviction of its correctness.

Loftfield (1921) has devoted part of his comprehensive investigation of stomata to the question of the influence exerted by stomatal movements on transpiration. Many of his experiments afforded indirect evidence that stomatal movements do affect transpiration. He therefore subjected Lloyd's and Muenscher's data to the test of critical experiment. As a result Loftfield found himself compelled to dissent from the "commonly accepted view" (in America though not in Europe!) that the stomata do not act as regulators of transpiration.

In one series of experiments with alfalfa he found that the stomatal movements were strikingly different in cut shoots and plants rooted in the soil respectively. In well-watered field plants the daily march of stomatal movement was normal, the stomata remaining widely open from 9 a.m. to 2 p.m. In cut shoots, on the other hand, the stomata opened in the morning, but on attaining their maximum aperture at 9 a.m., immediately began to close again. By 11 a.m. they had closed to 10 per cent, and by 2 p.m. to 5 per cent of the maximum.[1]

[1] The march of stomatal movement in *unwatered* field plants differed considerably from the two cases mentioned in the text. The stomata were more widely open during the early morning hours, attaining their maximum aperture at 7 a.m., when they rapidly began to close. By 9 a.m. the

There was marked correlation in these cut shoots between stomatal movements and the rate of transpiration, as measured by potometers. More or less similar results were obtained with cut shoots of potato. In this case the stomatal movements in the cut shoots were compared with those of potted plants and of watered and unwatered field plants.

These and other observations led Loftfield to the conclusion that the stomata regulate transpiration to a considerably greater degree than was supposed by Lloyd. He attributes the divergence between the curves of stomatal movements and transpiration in Lloyd's experiments to the fact that while Lloyd studied stomatal movements in plants growing in the soil, he used cut shoots for his transpiration experiments. Even so, Lloyd did not actually measure transpiration itself but merely absorption. Loftfield rightly insists that results obtained from cut shoots or separate leaves cannot be applied to plants growing either in pots or in the field, since the stomata in these cases differ markedly in their behaviour.[1] Nor is it possible to establish any general rule regarding the influence of cutting, for while in some plants (alfalfa, potato) the stomata of cut shoots are often less widely open than those of plants growing in the soil, in others (*Fouquieria*, *Verbena*) they are more open.

While recognizing the existence of stomatal regulation, Loftfield does not deny the direct influence of external factors. He considers that when the stomata are fully open, or nearly so, the rate of transpiration is the direct result of the effect of external factors, the stomata taking no part in its regulation. As the stomatal apertures narrow, the influence of external factors becomes less, but until closure has reduced the pores to less than one-half of their maximum width, stomatal regulation is largely masked by the influence of these factors. When the

stomata of both watered field plants and cut shoots had reached their maximum aperture, but those of the unwatered field plants were completely closed.—ED.]

[1 Loftfield concludes that deductions drawn from potometer readings as to the transpiration of rooted plants must inevitably lead to serious error, for the respective rates of water loss of cut shoots and rooted plants differ considerably, as do their stomatal movements.—ED.]

slits are still narrower, and closure almost complete, stomatal regulation plays an important rôle, even very slight changes in the width of the pore overshadowing the effect of external factors. Similar views have been put forward by **H. Walter** (1925) in his survey of the water régime of plants. In this connexion it must be pointed out that **Lloyd** himself (1908, p. 63) had previously admitted the possibility that stomata with very minute openings, and perhaps larger stomata when nearly closed, may exert a regulatory effect on transpiration.

Loftfield has thus introduced an essential correction into the original theory that the stomata are the chief if not the sole means of regulating transpiration. In this modified form the theory appears considerably more probable. At the same time it must be recognized that, strictly speaking, Loftfield's investigations as well as the still more recent work of **Žemčužnikov** (1923–1924) have only actually proved the existence of a far-reaching parallelism between the width of the stomatal apertures and the intensity of transpiration. Both these quantities increase or decrease more or less simultaneously according to the time of day and the conditions of water supply. But this parallelism by no means excludes the possibility that the size of the stomatal pores and the rate of transpiration are linked together, not as cause and effect, but as two effects of a common cause.

That neither stomatal regulation nor a lowered water content of the leaf alone is sufficient to explain the decrease of transpiration which occurs with a shortage of water in the soil, is also suggested by the interesting data obtained by my collaborator, **Mme. Kokin** (1925).

The object of her investigation was to study the relations between the amount of available water in the soil and the rate at which this water is absorbed by the roots of the plant. The rate of absorption was measured indirectly by the intensity of transpiration, as the rates of the two processes are more or less proportional. The results proved that the rate of water loss and

therefore also that of absorption are to a large extent independent of the water content of the soil. It is only when the quantity of available water begins to fall below a certain level (for the majority of plants 6–8 per cent of the air-dry weight of the soil) that a slowing down of transpiration is observed. In attempting to determine the cause of this reduced rate it was found that the decrease began while the stomata were equally widely open in both the plants under experiment and in the controls. The cause of the decreased rate of transpiration, therefore, was not the closing of the stomata. Similarly, the water content of the leaves at the beginning of the reduction of transpiration had decreased to such a slight extent that this alone could not explain the considerable retardation of water loss. There remains, therefore, the assumption that the slowing down of transpiration, the simultaneous decrease of the water content of the leaf, and the closing of the stomata which occurs somewhat later, are not directly related as cause and effect, but that all three phenomena are due to the operation of some common cause.

This common cause is, in my opinion, the conditions of the water supply of the plant. According to the cohesion theory, as soon as the loss of water begins considerably to exceed the intake, the resistance to the yielding up of water vapour to the intercellular spaces increases. Almost simultaneously both the water content of the cells of the leaf and transpiration begin to decrease, the former, however, somewhat earlier. This decrease of the water content involves the gradual closing of the stomata, which in turn leads to a further reduction of transpiration, and may finally result in a decrease of the water deficit which started this complex chain of phenomena. If, on the contrary, the plant experiences no shortage of water, the whole regulating mechanism remains inactive, and the march of transpiration passively follows that of the meteorological factors.

PART III

THE WATER BALANCE AND DROUGHT RESISTANCE OF PLANTS

CHAPTER VIII

THE WATER BALANCE OF PLANTS

The water balance of the plant. The diurnal water deficit in plants. Transient and permanent wilting. The behaviour of plant cells during wilting. Movements of water in the plant. Effect of wilting on carbon nutrition. Death of plant cells and tissues from desiccation.

The Water Balance of the Plant

Only an inappreciable part of the water required by the plant for its growth and development is actually assimilated in the process of photosynthesis. By far the greater part absorbed from the soil is eliminated unchanged, being either dispersed as vapour in the process of transpiration, or, more rarely, exuded as drops of liquid in the process of guttation. A land plant, indeed, represents as it were a kind of wick along which a continual stream of water ascends from the soil and escapes into the atmosphere. The total water content of a plant at any given moment is small in comparison with the quantity that may pass through the plant in twenty-four hours, for we have seen above that, even under shade conditions, the leaves of some plants are able to replace the whole of their water in the short space of an hour.

The question of what constitutes a "sufficient" water supply must therefore be approached differently from questions concerning the supply of carbon, nitrogen and mineral salts. In the latter cases the plant has only to secure a quantity of these substances sufficient to build up its body. It is true that a small amount of carbon is lost in the process of respiration, but this cannot be compared with the great quantities of water liberated during transpiration.

The close connexion between the absorption and loss of water and the passage of large quantities through the body of the plant, remind us of the relations between income and expenditure and the circulation of money in the course of business transactions. Hence in botanical works we not infre-

quently find terms borrowed from book-keeping—e.g. income and expenditure, profit and loss, balance sheet—applied to the water relations of the plant.

Montfort (1922) has recently employed this terminology in a very consistent manner. He points out that two chief methods, i.e. subtraction and division, may be used to express the water balance of plants. In the first, absorption and loss of water are compared by merely subtracting one value from the other. If absorption is greater than transpiration, there is a resulting "profit"; if less, there is a "loss". In the second method, the "loss"—or "profit", as the case may be—is divided by the transpiration, the result being expressed as a percentage of the latter value. By this method we obtain the *relative loss* (or, in the converse case, the *relative profit*), i.e. the percentage of the total water lost by the plant which remains uncompensated by absorption. If T = transpiration and A = absorption, then: $T - A$ = loss; $A - T$ = profit; $\frac{T-A}{T}$ = relative loss; and $\frac{A-T}{T}$ = relative profit. The relation between absorption and transpiration may also be expressed as a ratio, $\frac{T}{A}$, which Montfort terms the "Bilanzquotient", indicating it by the letter Q. If $Q > 1$ we have an "Unterbilanz"; if $Q = 1$ an exact balance, and if $Q < 1$ an "Ueberbilanz". A decrease in the value of Q owing to altered external or internal conditions, means that the water balance changes for the better; an increase of the ratio, on the other hand, involves a change for the worse. This second method of calculating the water balance has not as yet been widely adopted, the simpler subtraction method being the one commonly used.

One of the chief reasons for our lack of knowledge of the water balance of plants is the difficulty of determining this balance experimentally. The only apparatus by which we can measure, with reasonable accuracy, absorption and transpiration simultaneously is the potometer adapted for weighing.

This was first used by **Vesque** (1878), who fully realized the importance of a direct comparison of absorption and transpiration. The potometer, however, can only be used conveniently for experiments with cut shoots or small seedlings. In neither case do the results furnish a reliable indication of the water balance of adult plants. Experiments with adult plants themselves, on the other hand, involve the use of such large containers that the error due to the inevitable fluctuations of temperature is increased. But the chief drawback of the potometric method, as applied to rooted plants, does not lie so much in the difficulty of obtaining accurate readings, as in the changes which take place in the root system when the plant is dug up and transferred from soil to water. After some time the normal roots die, being replaced by new roots adapted to life in a liquid medium. The original "soil roots", on removal to water, show signs of disturbance and a retardation of absorption must ensue. Moreover, in digging out the root systems, mechanical injury to and rupture of the slender roots is inevitable. In potometer experiments, therefore, it is necessary to use plants grown in water cultures. Here we are confronted by a new difficulty. During their development, plants grown in water cultures become adjusted to special conditions as regards both water balance and mineral nutrition. Hence considerable caution is necessary in applying the results obtained to plants growing naturally in soil. In addition, many plants cannot be grown successfully in water cultures.

Potometer determinations, then, though not infrequently affording very valuable information, cannot be substituted for a direct study of the water balance of plants normally rooted in the soil. But how are we to determine the amount of water actually absorbed by the plant from the soil? At first sight the simplest method would appear to be to determine the water content of the soil. This method is used under field conditions, but is not adapted for exact determinations, as the moisture is far from being uniformly distributed through the soil used in an experiment. During a period of rapid transpiration, for

example, a zone of dry soil is formed in the neighbourhood of the roots (pp. 78–82). Moreover, the roots are easily damaged when taking the samples.

An interesting attempt to investigate simultaneously transpiration from the plant and changes in the water content of the soil was made by **Livingston and Hawkins** (1915) by means of their so-called auto-irrigator (cf. Chapter II, p. 80). We have already seen that during the daytime the plant loses more water than the auto-irrigator can supply. As a result of this the water content of the soil decreases and root absorption becomes considerably more difficult. Assuming, however, that the rate of supply of water from the surface of the porous cylinder is at least equal to the rate of translocation of water through the soil capillaries, we may conclude that difficulties of absorption may occur even when the soil is fairly moist. During the period of maximal transpiration, then, absorption may be retarded, and the water balance of the plant changed for the worse. We may, therefore, expect to find a more or less considerable water deficit in the plant during the midday hours.

The Diurnal Water Deficit in Plants

The actual existence of a water deficit in desert plants growing under conditions of intense insolation and strong evaporation was proved by **Livingston and Brown** (1912), who measured directly the water content of leaves at different hours of the day. This determination of the fluctuations in water content is, indeed, the most direct method of investigating the water deficit.

On taking samples in the early morning, when absorption is at all events not less than transpiration (the tissues in consequence being fully turgid), and again during the period of maximal transpiration, we find that the water content of the later is considerably less than that of the earlier samples. In the desert plants investigated by Livingston and Brown, the difference between the maximal and minimal water content

reaches on an average about 30 per cent of the total water content of the plant. Table IX is compiled from the results obtained by these authors with various species.

TABLE IX

Fluctuations during 24 Hours of the Water Content of Leaves of Arizona Desert Plants (according to Livingston and Brown)

Species	Water Content in per cent of Dry Weight		Decrease of Water in Percentage of Maximal Amount
	Maximal	Minimal	
Amaranthus Palmeri	601·9	366·6	39·1
Martynia louisiana (=*M. proboscidea*)	551·6	338·4	38·6
Trianthema Portulacastrum	1203·9	758·0	37·0
Sida angustifolia	484·3	307·3	36·5
Physalis angulata	781·1	566·2	28·9
Covillea glutinosa	139·3	116·7	16·0
Prosopis velutina	168·4	144·3	14·3

The least decrease was shown by the two last-named plants, which have hard, leathery leaves and small water storage. The succulent *Trianthema*, on the contrary, displayed almost the maximum water impoverishment during the midday hours.

The chief object of Livingston and Brown's work was to investigate the probable causes of the diurnal retardation of transpiration. Hence, as in the case of **Lloyd**, the question of the water balance of desert plants is only touched upon incidentally in the work of these authors. Mme. **Krasnoselsky-Maximov** (1917) has treated this question in much greater detail. Her investigations dealt with the daily fluctuations of water content in the leaves of plants of different ecological types growing in the neighbourhood of Tiflis. This work showed that in plants of a definitely xerophytic type, such as *Zygophyllum Fabago*, *Artemisia fragrans*, and *A. fasciculata*, a marked water deficit occurs during the midday hours. This deficit may reach 20–25 per cent of the total water content.

By night the deficit is gradually made up until in the morning the leaves of the plants once more exhibit a maximal water content. Similar fluctuations, though on a somewhat smaller scale, were observed in the springtime in more mesophytic plants. These plants were for the most part winter forms which terminate their cycle of development in early summer, being scorched by the summer heat. Table X gives some of the figures obtained by Mme. Krasnoselsky-Maximov; the water deficit is expressed in percentages of the maximal water content at sunrise.

TABLE X

Water Deficit in Semi-desert Plants during the Midday Hours (according to Krasnoselsky-Maximov)

Species	Water Deficit
Zygophyllum Fabago	20–28 per cent
Artemisia fasciculata	27–28 per cent
Artemisia fragrans	12–19 per cent
Artemisia scoparia	13–18 per cent
Salsola Kali..	14–23 per cent
Gypsophila acutifolia	12–13 per cent
Erodium ciconium	9–14 per cent
Hirschfeldia adpressa	17–19 per cent

These fluctuations in water content naturally vary from day to day. In a three days' experiment Krasnoselsky-Maximov observed distinctly that on hot days, with a high moisture deficit of the air, the fluctuations were more pronounced, while on cooler days they were less perceptible. If the march of the water content of the plant and that of the moisture deficit are represented graphically, one curve appears to be a reflection of the other, as if seen in a mirror (Fig. 28). These investigations also proved that during the daytime, the excess of transpiration over absorption causes the more vigorous parts of the plant, namely the upper leaves, to abstract water from the lower, less active leaves. For this reason the upper

leaves, though subjected directly to the drying influence of sun and wind, exhibit smaller variations in water content than the lower leaves, which are more or less shaded and nearer to the roots. For instance, in one experiment with *Zygophyllum Fabago*, the greatest deficit in the upper leaves was 19·3 per cent, but in the lower 27·2 per cent; in another experiment the corresponding figures were 13·2 per cent and 21·7 per cent.

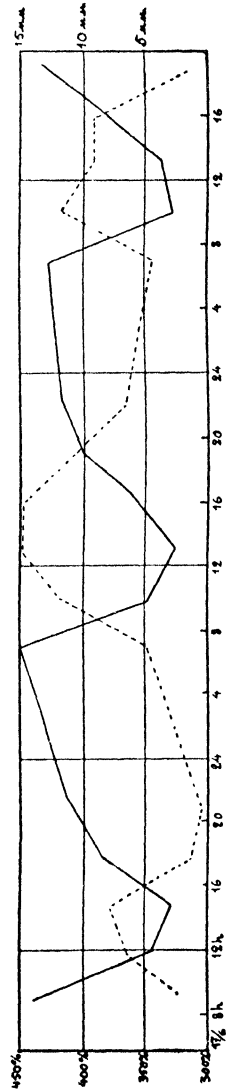

FIG. 28.—Fluctuations in the water content of leaves of *Zygophyllum Fabago* (continuous line) and the march of moisture deficit (dotted line) during three days (from Krasnoselsky-Maximov).

It would be a mistake, however, to suppose that such considerable variations in water content occur only in dry climates such as those of Tiflis and the Arizona desert. Later investigations by Krasnoselsky-Maximov in the summer of 1922 in Leningrad (**Maximov and Krasnoselsky-Maximov**, 1924) have shown that even in the cool, moist climate of North-Western Russia, during the midday hours on bright sunny days, plants lose considerably more water than they can absorb from the soil. Hence in this case also there is a marked water deficit, which in the sunflower reached 28 per cent of the maximum water content, in the potato 22–26 per cent, in *Impatiens parviflora* 13 per cent, in *Tussilago farfara* 15 per cent, and so on. The single exception amongst all the plants investigated was *Alisma plantago*, growing in water near the bank of a pond;

this showed no definite water deficit during the midday hours.[1]

Considerable fluctuations in the water content of leaves of crop plants (millet, wheat, corn, buckwheat, sugar-beet, pumpkin, cucumber), ranging up to 20 per cent, were observed under the climatic conditions of Kiev by **Mina and Butovski** (1923), who worked with Professor Kolkunov. On very dry, hot days the water content showed two minima, i.e. in the hours before and after noon, while about noon a temporary increase was recorded. The reasons for this increase are obscure, and the whole question needs further investigation. In these experiments the leaves of the more drought resistant plants showed a wider range of water content; this, however, was true only on hot days—on cooler days the reverse was found to be the case.

By means of a peculiar, but very sensitive method, **Bachmann** (1922) found a diurnal water deficit even in plants growing under conditions of optimum water supply and inconsiderable transpiration. The method employed was that of

[1 It appears to be a more or less general phenomenon that, so far as land plants are concerned (whether mesophytes or xerophytes), during the hours of maximal transpiration in the summer, water loss exceeds water supply. This manifests itself in a reduction of the water content of the leaves. The actual differences in water content between day and night may vary considerably. **Livingston and Brown** (1912), in the dry climate of Arizona, found a maximal difference of 8 per cent (of the fresh weight of the leaves), the average being about 4·5 per cent. In the similar climate of Tiflis, **Krasnoselsky-Maximov** (1917) obtained differences up to 7·7 per cent. On the other hand, in the more humid climate of England, **Knight** (1922) found a maximal diurnal change of 1·3 per cent, while **Yapp and Mason** (results not yet published) obtained a maximum of 2·77 per cent, with an average for a number of experiments of 1·01 per cent. These results illustrate the effect of differences of climate. The daily fluctuations of water content, however, may vary in different leaves on the same shoot. For instance, Krasnoselsky-Maximov found (in Tiflis) that upper leaves had a smaller diurnal range than leaves lower on the stem (see text). Yapp and Mason, on the other hand, frequently found the greatest range in partly developed leaves near the apex of the stem. These apparently conflicting results are readily explicable in terms of the effect of environmental differences on the water balance of the plant, and will be dealt with in a forthcoming paper by the last-mentioned authors.—ED.]

measuring the thickness of the leaves. Bachmann constructed a very sensitive "Hebelpachymeter", which enabled him to measure the thickness of the leaf with an accuracy of 1·35–1·9 microns. With this instrument the smallest changes in thickness of the leaf (these changes depending on variations in the turgor of the cells) could be detected. Bachmann found that even with very small fluctuations of the moisture deficit of the atmosphere, clearly perceptible variations in the thickness of the leaf—up to 5–6 per cent of the original dimensions—could be observed. If a decrease in atmospheric humidity were accompanied by a decrease of soil moisture, the thickness of the leaf was still further reduced.

The decrease of turgor in the daytime, involving as it does a decrease of water content, is even more readily perceived if the reduction in area—rather than in thickness—of the leaf blade is measured. This reduction in area was first definitely pointed out by **Thoday** (1909), in a very careful and critical examination of Sachs's well-known "dry weight" method of determining the rate of assimilation. Thoday's measurements have shown that during the midday hours the area of the leaf is considerably reduced, and that in bright weather this reduction may reach 5–7 per cent (2–3 per cent with somewhat feebler insolation). The method proved so sensitive that even the slight changes of turgor caused by the shade of passing clouds could be recorded.[1] Still greater reductions of leaf area, up to 20–25 per cent, were observed in Tiflis by **Alexandrov** (1923) in *Helianthus annuus*, *Amaranthus retroflexus*, and *Atriplex hortensis*. Alexandrov found the greatest fluctuations in the upper leaves, those of the lower leaves being less marked.[2]

[1 Thoday's method was to mark, with waterproof ink, fine black crosses on flat areas of the lamina. The distances between the centres of these crosses were measured with a millimetre scale, the leaf being supported on a flat rule covered with plush. He found greater shrinkage, and less rapid recovery, towards the tip of the leaf (which is more remote from the water supply) than nearer the base. Variations along the midrib were comparatively small.—ED.]

[2 **Thoday** (*loc. cit.* p. 25), on the other hand, found greater variations in area in the lower (older) than in upper leaves.—ED.]

We see, then, that data obtained by various methods and by different investigators yield similar results. During the midday hours a more or less considerable water deficit occurs in the leaves of plants, even under conditions of an abundant supply of soil water. This leads us to the conclusion that during periods of maximal transpiration, the rate at which water is translocated through the plant is insufficient to make good the whole of that lost by transpiration. The normal daily water balance of a plant, then, may be represented as follows. Before sunrise the plant is in the condition of maximal saturation with moisture. The rays of the sun bring about a rapid increase of transpiration, which increase is further facilitated by the now widely open stomata. During the forenoon hours the loss of water exceeds absorption and the water content of the leaves begins to fall. In spite of the partially closed stomata the water deficit continues to increase until the early evening hours, when, owing to the less severe meteorological conditions, the water balance is improved. Later in the evening, and especially during the night, absorption prevails over transpiration. This results in an increase of the water content of the leaves, which again reaches the maximum by daybreak. Sometimes the maximum is attained earlier, the excess of water supplied by the roots being exuded in the form of drops in the process of guttation. After very hot, dry days the water deficit may be so considerable that the plant is unable to make good the deficiency during the night. In such cases no guttation is observed, and the plant begins the work of the following day with an adverse water balance.

Transient and Permanent Wilting

With continuous drought and insufficient soil moisture, the diurnal water deficit will naturally become more and more pronounced, and finally the point may be reached where incipient drying gives place to actual wilting. The one condition passes into the other when the decrease in the water

content of the cells results in a loss of turgor. The whole leaf or even the shoot now loses the relatively rigid appearance which characterizes it when fully saturated with water. Different species of plants vary in respect of the amount of water loss necessary to produce a perceptible loss of turgor (**Maximov and Krasnoselsky-Maximov**, 1924). It has long been known that shade plants very soon wilt when exposed to bright sunlight, while under the same conditions plants of exposed habitats may remain fully turgid. It is often assumed that ombrophilous plants possess no protective adaptations against excessive transpiration, and therefore rapidly lose water and wilt when exposed to direct insolation. On the other hand, the better-protected heliophilous species are supposed to have means of conserving their water supply. We shall see in Chapter XI that this so-called explanation is erroneous. In point of fact, shade plants actually transpire considerably less—not more—than sun plants. There can, therefore, be no question of a greater expenditure of water by shade plants under these conditions. Our experiments have shown that the true explanation of this rapid wilting of shade plants when exposed to insolation is that these plants wilt when the water deficit in the leaves does not exceed 3–5 per cent of the total water reserve, while sun plants can endure a loss of 20–30 per cent without wilting. To bring about this greater water deficit, more time and a greater intensity of the external factors which accelerate transpiration are required.

The results of our investigations were in complete agreement with those of **Knight** (1922). In determining the water content during the wilting of leaves of the shade plant, *Eupatorium adenophorum*, Knight was surprised to find that extreme flaccidity resulted from a decrease in the water content of approximately 1 per cent of the fresh weight. Indeed, in such plants the early stages of wilting are more readily detected by direct observation than by determining the decrease in water content. The loss of water is naturally accompanied by a corresponding decrease in volume of the cells.

The fact that ombrophilous plants lose their turgor with only a slight decrease of water content, and therefore of cell volume, suggests that the cell walls in these plants can be but little distended by internal pressure. The cell walls of heliophilous plants, on the other hand, would appear to be distended to a much greater degree when the cells are turgid. This supposition was confirmed later by Mme. **Krasnoselsky-Maximov** (1925), by means of direct measurements of the reduction in volume of the cells of various plants during plasmolysis. This author compared the volumes of mesophyll cells when fully saturated with water and when plasmolysed. She found that in heliophilous plants such as the sunflower and potato, the reduction of cell volume during plasmolysis amounted to 25–30 per cent. In ombrophilous plants, on the other hand, e.g. *Impatiens parviflora*, the reduction did not usually exceed 1–3 per cent, often, indeed, being nil.

Two types of wilting may thus be distinguished. In the first a rapid loss of turgor is accompanied by an insignificant decrease in the water content of the leaf: this type is confined to tender shade plants. In the second there is a slow and gradual transition from incipient drying to actual wilting, during which a considerably greater loss of water takes place: this type is characteristic of the majority of plants, especially of those of dry, exposed habitats. Little is known as yet of the first type, which is peculiar to plants not usually exposed to the danger of shortage of water. We may, therefore, confine our attention chiefly to the second type.

As wilting indicates a more or less considerable water deficit in the plant, it must be regarded as the result of an excess of water loss over water absorption. This excess, however, may be due to various causes: either to so great an increase of transpiration that even rapid absorption is unable to cover the loss, or to such a decrease of absorption that even a slow rate of transpiration is sufficient to bring about a water deficit in the plant.

The former occurs at times when the external factors

influencing evaporation, such as solar radiation, temperature, dryness of the air and wind, are especially intense. Under these conditions, as we have seen already, even with optimum soil moisture, a water deficit in the leaves is observed, which manifests itself by incipient wilting. The rapid escape of water leads to vigorous leaf suction. Owing to the force of cohesion, which governs the translocation of water through the plant, this suction is transmitted downwards to the roots, thereby bringing about increased absorption from the soil. But before the water can reach the transpiring cells of the leaf, it encounters a series of resistances, which increase with the rate of translocation. First of all the water meets with resistance during its passage through the soil, again as it enters the root, and later as it passes through the parenchyma of the root into the vessels and during its translocation along the vessels of the root, stem, and leaves. Finally, there is the resistance to the passage of the water from the vessels of the leaf into the parenchyma cells, and from cell to cell of the mesophyll—for the majority of these cells do not abut directly on the vessels. Such resistance to the flow of water through the plant may itself give rise to a deficit of water. But with a decrease in the rate of transpiration these various resistances diminish, and if the retardation of the transpiration current has caused a sufficient deficit of water in the leaves to bring about wilting, this wilting is but transient. As transpiration is reduced, owing to changes of weather, the fall of night, or to artificial shading, the plant recovers completely, no injurious after-effects being discernible. During such transient wilting, at least in its earlier stages, the greatest water deficit occurs in those organs which transpire most energetically. The other portions of the plant, and especially the absorbing cells of the root, which are extremely susceptible to the loss of water, do not to any extent suffer from a shortage.

The state of affairs is different when the moisture reserve of the soil is so far exhausted that the plant is no longer able to draw water from the surrounding soil particles. No matter how

slowly, the plant inevitably loses water—there is nothing to compensate the loss. The leaves, which transpire most rapidly, show the greatest water deficit. They also possess the greatest power of suction, and so draw water from other portions of the plant. In the first place the younger leaves withdraw water from the older, then from the growing points of the stems and from the absorbing region of the roots; hence all these parts, though not transpiring themselves, are to a considerable extent deprived of water. The water content of the embryonic tissues of the stem and of the delicate absorbing zone of the root does not usually fluctuate very greatly. These tissues are evidently more sensitive to shortage of water than are those of the leaves, and prolonged wilting, the *permanent wilting* of American authors, induces as yet little understood changes in the protoplasm of their tender cells, which in consequence are injured or even die. As a result, permanent wilting produces a lasting effect on the plant, though the latter may again recover if the soil moisture is increased by watering or rain. Recovery, however, is very slow, for new root hairs or even new rootlets require to be developed. For this reason, plants which have been subjected to "permanent wilting" are deficient in growth and yield as compared with normal control plants.

The phenomenon of permanent wilting was carefully studied by **Caldwell** (1913), who regards it as a physiological condition in which the water content of the plant falls to such an extent that the plant can only recover slowly. Permanent wilting is readily distinguished from transient wilting by a simple practical test. In the case of transient wilting (induced, as we have seen, by an excess of loss over intake of water) the plant, when removed to a moist, dark room, soon recovers without being watered. With permanent wilting, on the other hand, even an atmosphere saturated with water vapour will not restore turgor, so watering is required.

Permanent wilting differs from transient wilting also in the fact that in the former the water content of the leaves falls to a much lower level. The following table gives the results of

several hundreds of determinations by Caldwell of the water content of leaves of six-week-old plants of corn, beans, *Martynia Louisiana* (= *M. proboscidea*) and *Physalis angulata.*

TABLE XI

Water Content of Leaves of (a) *Normal Plants,* (b) *Plants showing Incipient Wilting, and* (c) *Plants in a state of Permanent Wilting (according to Caldwell)*

Species	Condition of the Plant	Water Content in Percentages of Dry Weight	Water Deficit in Percentages of the Original Content
Physalis angulata ..	(*a*) turgescent	598	—
	(*b*) incipient wilting	503	10·6
	(*c*) permanent wilting	352	42
Zea Mays	(*a*) turgescent	804	—
	(*b*) incipient wilting	675	15·6
	(*c*) permanent wilting	472	40
Martynia Louisiana (=*M. proboscidea*)	(*a*) turgescent	529	—
	(*b*) incipient wilting	437	17·5
	(*c*) permanent wilting	347	34
Phaseolus vulgaris ..	(*a*) turgescent	694	—
	(*b*) incipient wilting	569	18·0
	(*c*) permanent wilting	486	30

The table shows that permanent wilting is characterized by a water deficit nearly double that found in transient wilting, at least in its early stages. This greater loss of water is correlated with a more profound disturbance of the activities of the plant. In Caldwell's experiments this manifested itself in the decreased capacity of the plant to avail itself of the soil moisture. With repeated wilting more unavailable water remained in the soil than was the case during the initial wilting. This is probably the result of the diminished contact between soil and plant due to the dying off of the root hairs. In my own experiments (**Maximov**, 1917) I observed a reduction of the water supply after permanent wilting. When plants which had

suffered permanent wilting were again watered, they showed at first a considerably reduced intensity of transpiration, only gradually regaining the normal rate. For example, in an experiment with *Artemisia scoparia*, on the first day after watering, the wilted plants transpired 50 per cent less than the controls, on the second day 20 per cent, and on the third 10 per cent; only on the fourth day did the previously wilted plants and the controls transpire at the same rate. As a result of numerous experiments (some of them as yet unpublished), I have found that, so far as this after-effect is concerned, the difference between transient and permanent wilting is one of degree rather than of kind. Both sorts of wilting involve a temporary decrease of transpiration, indicating a reduced absorption of water by the root system.

The Behaviour of Plant Cells during Wilting

The opinion is widely spread that plasmolysis of the cell contents occurs during wilting. **Livingston**, for instance, himself a specialist in the subject of the water relations of plants, holds this view. **Caldwell** also speaks of the plasmolysis of root hairs. But this use of the term plasmolysis is inexact. Wilting has this in common with plasmolysis, that in both cases water is withdrawn from the cell contents. The early stages of both are similar, so long as the cell wall is even slightly distended by turgor pressure. But from the moment that the cell wall completely ceases to be under tension, the paths of wilting and plasmolysis diverge. In plasmolysis the still shrinking protoplasm separates from the cell wall, which has ceased to contract, the space between protoplast and wall being filled with the concentrated external solution. This is the phenomenon of plasmolysis in the strict sense of the word. In wilting, on the other hand, the protoplasm cannot separate from the cell wall, as the place of the external plasmolysing solution is taken by air, which is unable, in a gaseous condition, to pass through the wall. By virtue of the cohesion between the

particles of water permeating protoplasm and cell wall alike, the contracting cell contents draw with them the wall, which thus becomes compressed. As the cell wall, however, is only capable of slight compression, it becomes folded and wrinkled, owing to the shrinking of the cell during wilting. This has been observed by **Holle** (1915). If the large cells of *Rhoeo discolor* (better known by its former name of *Tradescantia discolor*) are viewed from above, this infolding of the lower wall produces the effect of a light centre surrounded by a dark red ring. Similarly, the infolding of the upper and lower walls of cells of the mosses *Mnium* and *Funaria* pushes the numerous chloroplasts towards the periphery, forming a green ring round a colourless centre. **Thoday** (1921) describes strong shrinkage in wilted cells of certain African evergreen plants (*Passerina* spp.), which during the dry season enter the state of permanent wilting. To estimate the degree of expansion after shrinkage Thoday mounted sections cut dry, some in oil and others in water, and compared the camera lucida outlines.[1] Direct determinations of the volume of wilted cells have been made by Mme. Krasnoselsky-Maximov, first in paraffin oil and afterwards in a strong plasmolysing solution. The measurements show that when removed to the plasmolysing solution, the volume of a wilted cell actually increases, as the cell wall, which had contracted during wilting, imbibes liquid from the solution.

The erroneous belief that wilting cells become plasmolysed is probably based on the fact that when such a cell is immersed in water, its wall rapidly expands, while the protoplasm may be coagulated (owing to a sudden disturbance of the osmotic conditions), and shrink rather than swell. Thus a space filled with water may be formed between the cell wall and the protoplast, an effect closely resembling that seen in true plasmolysis. Observations of desiccating microscopical sections may also

[1 **Thoday** (1921) found that during the contraction in volume, the lateral walls of the epidermal and palisade cells were thrown into fine "bellows-like" folds.—ED.]

have fostered this belief. The sap exuding from the cut cells gradually becomes more concentrated, and may then induce actual plasmolysis of neighbouring uninjured cells.

Iljin (1927) has recently investigated the behaviour of the cell contents during prolonged wilting. According to this author, the following is the sequence of events during the wilting and desiccation of microscopical preparations. First of all the whole cell shrinks slightly; then the cell sap, continuing to decrease in volume, drags with it the protoplasm, tearing it from the cell wall, which has already ceased to shrink. The protoplasm is mechanically deformed and lacerated by the tension, and fragments of torn protoplasm may often be observed still adhering to the cell walls. This mechanical injury to the protoplasm Iljin regards as the chief cause of the death of cells during desiccation. Death occurs considerably before the cell sap has entirely evaporated. Iljin never observed actual plasmolysis during wilting.

Very interesting data regarding the increase of suction pressure in a detached ivy leaf (*Hedera helix*) are given by **Ursprung and Blum** (1919). These authors determined the suction pressure of the cells of the various tissues day by day as the leaf wilted, until it had completely died off. Table XII, opposite, summarizes their results.

In all tissues of the leaf, with the exception of the palisade cells most distant from the veins, there was a considerable increase of the suction pressure during wilting. The greatest increase (64 per cent) is in the cells of the upper epidermis, which may justly be regarded as a water-carrying tissue supplying the assimilating tissues of the leaf with water. A considerable increase of suction pressure was shown by the cells of the bundle sheath (46 per cent) and the spongy mesophyll (38 per cent). As regards the palisade mesophyll, an interesting and quite unexpected phenomenon was noted. The suction pressure of the cells nearest to the veins increased strongly (by 55 per cent), but that of the palisade cells remote from the veins remained unaltered until the death of the cells.

The authors explain this by the fact that even in the fresh leaf these distant palisade cells possessed the maximum suction pressure, and suppose that during wilting they formed centres which abstracted water from all other tissues. When this influx ceased, owing to the differences between the suction pressures in the various tissues becoming less and less, these palisade cells, unable to endure further impoverishment in respect of water, began to die.)

TABLE XII

Variations in the Suction Pressure of the Cells of a Wilting Ivy Leaf (according to Ursprung and Blum)

	Upper Epidermis	Palisade Parenchyma		Spongy Parenchyma	Parenchyma of Bundle Sheath	Lower Epidermis
		Near the Veins	Distant from the Veins			
Normal suction pressure (in atmospheres)	7·8	9·7	15·6	8·6	7·4	7·5
Maximal suction pressure before dying off	12·8	15·0	15·6	10·9	11·8	9·9
Maximal increase (in atmospheres) ..	5·0	5·3	0·0	3·3	3·4	2·4
Maximal increase (in percentages) ..	64	55	0	38	46	32

It is interesting to note that having regard to the absolute magnitude of their osmotic pressure—corresponding to 0·9 to 1·1 *N* saccharose solution—the palisade cells could, by a complete loss of turgor, develop a suction pressure equal to 30 atmospheres. Yet these cells begin to die while their suction pressure is still only about 15 atmospheres. I have no reason to doubt the correctness of Ursprung and Blum's results, but regard it as premature to generalize too widely from them. Ivy, the plant used by these investigators, is a typical shade plant, and may probably be classed with those

plants which wilt without losing a great deal of water (cf. **Maximov and Krasnoselsky-Maximov, 1924**). It would be interesting to investigate, from this point of view, some of the more resistant xerophytes or even mesophytes of the type of the sunflower. I am confident that with such plants as these we should find another state of affairs, i.e. an increase of the suction pressure of the wilting cells up to, or even beyond, the limits of the suction pressure (i.e. the concentration) of the cell sap. With the ever increasing loss of water and decrease of volume the cell walls must be elastically compressed. In the cells of the annulus of the fern sporangium—drying, dead, but filled with water—the suction pressure of the elastically compressed cells may attain 300 and more atmospheres. In the living cells of a leaf such high tension is impossible, owing to their different anatomical structure. In any case, the suction pressure of the wilting cell not only can but must be greater than the suction pressure of the cell contents only. The magnitude of this suction pressure will be the greater, the thicker the cell wall and the greater its resistance to influences tending to compress it.

Movements of Water in the Plant

On the basis of the cohesion theory we may draw the following picture of the internal condition of a wilting plant. Owing to the progressive loss of water and the stoppage or deficiency of the supply, the parenchymatous cells of the leaf lose their turgor. These cells still continue to decrease in volume, their walls gradually become compressed, and a tension equivalent to a pressure of many atmospheres arises in the cells. This tension is transmitted to the contents of the vessels, which give up a portion of their water to the parenchyma of the leaf. In doing so the vessels also become compressed, but are prevented from collapsing by the resistance offered by the thickenings of their walls. By way of the vessels, the tension is transmitted to all other tissues of the plant. Thus the mesophyll

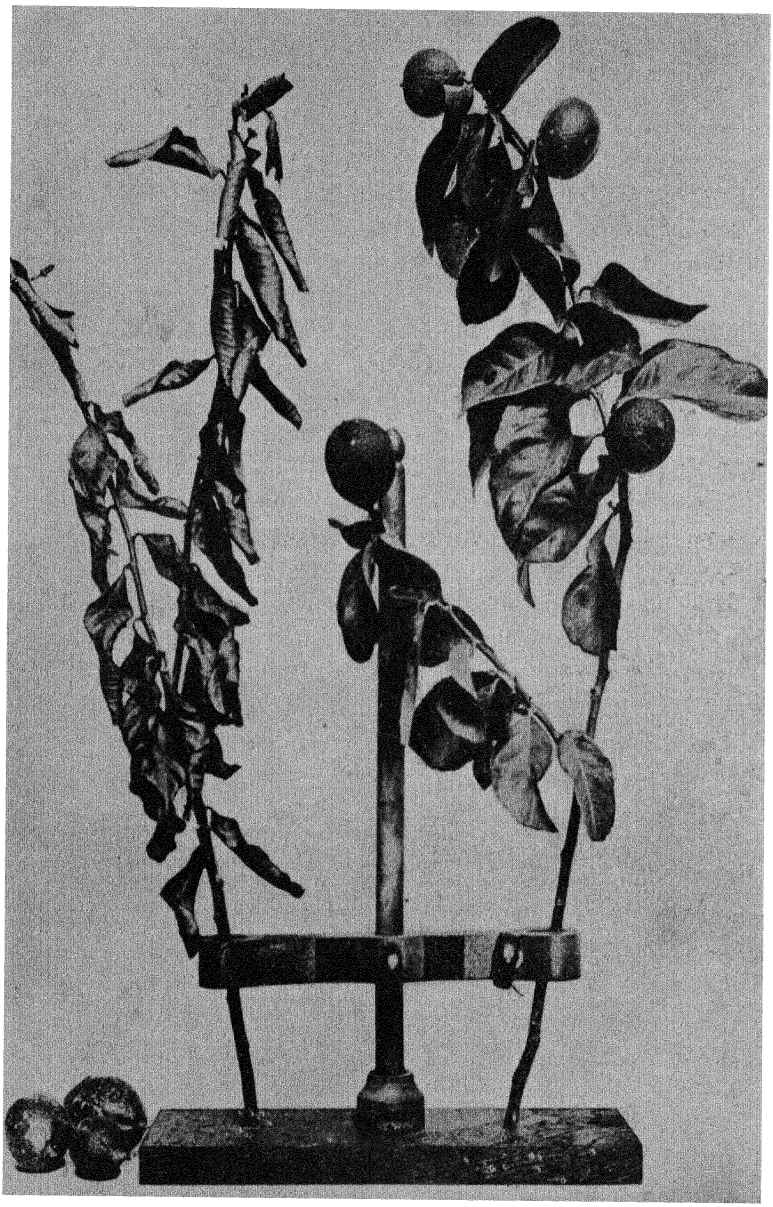

FIG. 29.—Abstraction of water by wilting leaves from lemon fruits. *Left*—branch from which the fruits were removed at the beginning of the experiment. *Right*—branch with attached fruits (Photo. by Bartholomew)

of the leaf may draw water from the absorbing layer of the root, the phloem adjacent to the vessels, and the meristematic tissues of young growing points, as well as from developing or opening flowers, and from setting or ripening fruits. In brief, owing to the cohesive power of the water permeating the plant, the suction developed in wilting leaves—provided that the plant wilts sufficiently slowly and deeply—is transmitted to all parts of the plant organism. Under these conditions the transpiring leaves draw upon such reserves of water as the other organs may contain.

This transference of water from one part of the plant to another was observed by **Meschayev** in 1882, and was afterwards investigated in detail in succulent plants by **Pringsheim** (1906). A similar internal translocation of water was found by Mme. **Krasnoselsky-Maximov** (1917) in intact rooted plants of the semi-succulent *Zygophyllum Fabago*. The photograph reproduced in Fig. 29 (kindly supplied by Dr. Bartholomew: see **Bartholomew,** 1926) illustrates the withdrawal of water by wilting leaves from lemon fruits. Two lemon branches were cut and kept without water for several days in a laboratory, the fruits being removed from one of the branches (left) at the beginning of the experiment. At the close of the experiment this fruitless branch was completely wilted, the leaves being dry and brittle, while the branch with fruits was still fresh and healthy. Owing to the amount of water abstracted by the leaves, the attached lemons decreased in diameter (during the first forty-eight hours of the experiment) some two or three times as much as the detached fruits.

In consequence of this change in the direction of the water stream the growth of shoots is checked, the as yet unopened buds are shed (a phenomenon leading to considerable losses in the yield of cotton, cf. **Lloyd,** 1920), and the grain of cereal crops is poor and sparsely filled.[1]

[1] Such internal movements of water in various directions through the plant, largely determined by local differences in the intensity of transpiration, are of common occurrence and have far-reaching consequences. Actively transpiring organs, such as strongly insolated leaves, may not

Effect of Wilting on Carbon Nutrition

It must be pointed out that although, broadly speaking, wilting is one of the most efficacious means of reducing transpiration, when this threatens to overstep the limits of safety, it is by no means without injurious effects. One of the first consequences of wilting, viz. the closing of the stomata, causes considerable loss to the assimilatory activity of the plant. If the stomata do not play the all-important part in the regulation of transpiration formerly ascribed to them, they are at all events essential for the absorption of carbon dioxide by the leaf, as has been proved by **Blackman** (1895) and **Brown and Escombe** (1900). Therefore the closing of the stomata, which usually takes place at the beginning of wilting, immediately checks carbon nutrition. A plant with continually closed stomata, indeed, soon begins to starve, as the process of respiration continues in spite of the closed stomata. Interesting experiments showing how great the loss of dry substance may

only withdraw water from less active parts, but also deflect supplies which might otherwise reach them. There is no doubt that under conditions favouring intense transpiration, severe competition for water may occur between different parts of an "individual" plant. For example, during the long drought (in England) of the summer of 1921, I noticed in a weeping ash in my garden that the inner, more sheltered "shade" leaves wilted during the hotter hours of the day. The exposed "sun" leaves on the outer part of the tree, on the other hand, remained perfectly fresh. This inadequacy of the water supply to the more shaded leaves apparently caused most of them to fall prematurely, and many of the sheltered branches to die.

If such competition occurs at an earlier stage, e.g. between mature and developing leaves, or between developing leaves alone, it may profoundly influence the course of development itself. The mature size, form, and structure of leaves may all be affected by competition for water (or of course by a general shortage of water) during the early stages of development. **Wiesner** (1905), for example, found that unilateral illumination of opening buds of the horse-chestnut resulted in marked anisophylly. The more strongly illuminated leaves or leaflets partially deprived the others of water, thereby hindering their development. In the case of cut shoots, the smaller, less developed shade leaves withered much earlier than the others. Wiesner suggests the term "correlative transpiration" for this and other cases in which actively transpiring organs reduce the amount of water available for other parts. He regards such displacements of water as of considerable importance in respect of various vital phenomena. Many other instances of correlative transpiration might be given.—Ed.]

be in a plant suffering from starvation induced by drought were made by **Iljin** (1922), at the Ekaterinoslav Agricultural Experiment Station. From a field sown with pure line wheat "Poltavka" (*Triticum vulgare*, var. *lutescens*), a sample consisting of 500 or even 1,000 specimens was taken every day. These samples were dried and weighed, and thus, by comparing the figures for each two consecutive days, the daily increment of dry substance was ascertained. As the plants grew and developed, a gradual increase in the weight of the sample was observed. The daily increase was very variable in amount; sometimes, indeed, on particularly dry days, there was an actual decrease of dry weight amounting to 15–20 per cent, or even to 30 per cent or more. For instance, on July 4th the average dry weight of a specimen of wheat was 1·65 gr., by July 8th, drought having set in, the weight fell to 0·93 gr. By July 19th it rose to 2·14 gr., but once more fell at the time of ripening and harvest to 0·83 gr. In my opinion, however, this rapid final decrease may be explained by the partial dying off and shedding of the leaves. At all events, my co-worker, **Tumanov**, was unable to find any significant decrease of the dry weight of plants of wheat and millet in his pot experiments carried out in 1927 (results as yet unpublished) under more exact conditions than **Iljin's** field experiments. A considerable loss of dry substance during permanent wilting was established by my joint work with Mme. **Krasnoselsky-Maximov** (1924). During five days of wilting the leaves of *Impatiens parviflora* lost about 40 per cent of their dry weight.

The significance of the closing of the stomata during wilting, however, must not be overrated, for the unfavourable consequences of wilting cannot be wholly ascribed to the checking of the supply of carbon dioxide to the leaf. It must be borne in mind that for the normal functioning of the cell a certain degree of swelling of the plasma colloids is required (**Walter**, 1924). For assimilation in particular a definite degree of swelling of the plastids is necessary. In a very interesting paper Mme. **Brilliant** (1924) has shown that as the water content

of the leaf decreases the assimilating capacity of the latter rapidly falls. This author cut pairs of symmetrical pieces from the leaves of various plants, placing one piece in water and leaving the other to dry. Subsequently she compared the relative amounts of carbon dioxide decomposed by the two pieces. The water lost by the drying piece was expressed as a percentage of the fresh weight, the water content of the piece kept in water being taken to represent complete saturation.

In one experiment with ivy the following results were obtained:—

Loss of water, per cent	5–15	15–25	31–39	41–52	53–65
Amount of carbon dioxide decomposed	127·4	142·0	37·0	1·5	1·4

As soon as the water deficit exceeds 25 per cent there is a sharp fall in the assimilating capacity of the leaf. Apparently an excess of water somewhat delays assimilation, but this observation needs confirmation.

The observations of **Bernbeck** (1924) also showed that, independently of the closing of the stomata, a deficiency of water retards the rate of assimilation. Bernbeck found that assimilation always decreased under the influence of wind, though the latter often leads to a mass movement of air through the stomata and intercellular spaces of the leaf, thus facilitating rather than impeding the access of carbon dioxide to the assimilating cells.

Such are the various direct and indirect consequences of wilting. It must be pointed out, however, that our knowledge of the phenomena accompanying wilting is as yet very incomplete. Probably the reason for this is that wilting has usually been regarded as a pathological phenomenon, and not as one of the most important means of protecting the plant against excessive loss of water. It is only in recent years that an interest in the study of wilting has been aroused, and it may be hoped that in the near future more light will be thrown on this phenomenon than has hitherto been the case.

Death of Plant Cells and Tissues from Desiccation

Still less attention has been paid to the death of plant cells and tissues under the influence of loss of water. We know that different plants and plant organs respond differently to a deficiency of water. For instance, **G. Schröder** (1886) in Pfeffer's laboratory in Tübingen, investigated the capacity for drought resistance of various plants and parts of plants—seeds, fern spores, mosses, algæ, fungi, lichens, and the vegetative organs of higher plants. He found that seeds, as well as many cryptogams, such as lichens, mosses, and terrestrial algæ, readily endure desiccation even to the extent of being reduced to an air-dry condition. The leaves of higher plants, on the other hand, perish before this state is reached. The leaves of *Parietaria arborea*, for instance, suffered greatly from a loss of 50 per cent of their total water content, and died with a loss of 70–75 per cent. The corresponding percentages for the leaves of *Fuchsia* were 54–59 per cent and 77 per cent. The leaves of the water plant *Limnanthemum nymphaeoides* showed a very similar susceptibility.[1]

D. Schröder (1909) gives detailed data regarding the progress of wilting and the preservation of vitality by leaves during desiccation. The leaves of elder began to die with a loss of 82 per cent of their water content; those of pumpkin (*Cucurbita Pepo*) with 81 per cent, of sunflower with 80 per cent, birch 75 per cent, alder 74 per cent, beech 70 per cent, plane (*Platanus orientalis*) 48 per cent, and buckwheat (*Fagopyrum vulgare*) 46 per cent. The following percentage losses

[1 The power of recovery after severe permanent wilting of plants of arid regions, however, is often remarkable. I myself collected twigs of *Myrothamnus flabellifolia* from crevices in granite rocks on the Matoppo Hills in Rhodesia (Africa) in August 1905. The plants had then been exposed to about four months of drought, and were dry and brittle. The twigs were kept in an air-dry condition for thirteen months, and in September 1906 some were soaked for a night in water: in the morning they were fully expanded, fresh and green. **Thoday** (1921) also collected living twigs of the same species from the Matoppo Hills in July 1920, and determined their water content: this was only about 7 per cent of the original weight.—Ed.]

were required to induce the dying off of about half the entire leaf blade: in elder (*Sambucus niger*), a loss of 85 per cent of water; in pumpkin and sunflower, about 87 per cent; in birch, 83 per cent; alder, 79 per cent; beech, 80 per cent; plane, 63 per cent; buckwheat, 57 per cent; and in *Impatiens*, 44 per cent.

According to Schröder, this varying capacity of different plants for drought resistance is in no way related either to the structure of the leaves or to the rate at which water is transpired. The more resistant plants, for instance, include species with thin and others with leathery leaves. Again, both *Impatiens*, which loses water very slowly, and buckwheat, which wilts rapidly, are characterized by an equally low degree of resistance.

The causes which bring about the death of protoplasm on drying cannot be definitely stated at the present time. Such cases as those of ripe seeds, lichens, mosses, and even some ferns, show that plant protoplasm itself may be capable of almost complete desiccation without loss of vitality.[1] Even germinating seeds may endure desiccation provided that the embryos have not attained any considerable size, a phenomenon not infrequently observed in cereals. Schröder found that in higher plants the cells of the leaf die before the whole of the "liquid" water has disappeared from the vacuole. The injurious consequences of loss of water, therefore, might possibly be explained as due to an undue decrease of the swelling of the protoplasm, leading perhaps to a partial coagulation of its constituents. This opens a wide and interesting field for future experimental research. According to modern views (**Maximov**, 1914; **Schander and Schaffnit**, 1919), the cause of the death of plants from freezing is supposed to be the formation of ice crystals in the intercellular spaces, with consequent desiccation of the cells. We may naturally, then, seek to trace an analogy between death from drought and death from freezing. We know that frost resistance is conditioned not only by the specific properties of the protoplasm, which

[1 Cf. footnote, p. 26.—ED.]

enable it after thawing to return to its former condition, but also by the accumulation of protective substances in the cell: of these sugars are the most important (**Lidforss**, 1906; **Maximov**, 1912). The question naturally arises—does the plant form substances capable of protecting it against the injurious changes occurring in the protoplasm during desiccation? Hitherto, unfortunately, perhaps on account of the great experimental difficulties encountered in determining the limits of desiccation which can be endured by a cell, no work has been carried out on these lines.

Some indirect evidence bearing on this question is, however, already available. In attempting to devise means of protecting plants against the injurious effects of frost, American authors have recently paid considerable attention to the so-called "hardening" process, by which the plant becomes more resistant to frost (see **Rosa**, 1921). Most frequently "hardening" is brought about by keeping the plant at a low temperature, i.e. about 0° C. or slightly higher. Apparently, however, a decrease in the water content of the plant, such as occurs in temporary wilting, may also increase its hardiness. Rosa investigated the relation between the "free" water and the "bound" water, i.e. that intimately associated with the colloid substances of the plant. He found that in hardened plants a relatively greater amount of water is bound: this suggests an accumulation of colloids, which may prevent complete freezing. A similar decrease of the amount of free water during hardening has been observed by **Newton** (1922, 1924) in his interesting experiments with winter wheats. **Tumanov** (1927), too (see Chapter XII), observed that a single severe wilting not only retarded subsequent growth and diminished the yield of dry substance, but also effectively increased the drought resistance of plants. These facts afford further evidence of a close internal connexion between the phenomena of freezing and desiccation.

The factors which enable the protoplasm to resist desiccation will not be discussed here, as we possess too few reliable data on the subject. There is no doubt, however, that a funda-

mental investigation of this question would bring us appreciably nearer to a solution of the problem of the drought resistance of the whole plant organism. But one important fact—usually overlooked—may be pointed out, i.e. that drought may cause permanent or even irremediable injury to the plant as a whole much earlier than to the cells of the leaf itself. For example, we have seen that **Caldwell** (1913) observed permanent wilting, accompanied by destruction of the root hairs, when the leaves had lost 40 per cent of their water content. On the other hand, **Schröder** (1909) found that the leaf cells themselves did not usually begin to die until they had lost 70–80 per cent of their water. Evidently the roots are injuriously affected by drought considerably earlier than the leaves, and under natural conditions a plant with desiccated roots but still living leaves is doomed to perish. In my own experiments I have observed more than once that after very severe wilting—usually termed the *utmost limit of wilting*—all the leaves, with the exception of the uppermost ones, died in spite of profuse watering. But the leaves when cut off and placed in water after a considerable time recovered their turgor and vitality.

Considerable progress in the understanding of the factors conditioning the endurance of desiccation by the cell has been made by **Iljin** (1927), in the recent paper mentioned on page 236. As we have already seen, Iljin considers that the death of the cell during desiccation is caused by the mechanical rupture of the protoplasm in consequence of a considerable decrease of the volume of the evaporating vacuole. From this he draws the conclusion that any factor which can hinder this rupture of the protoplasm must increase the resistance of the cell to desiccation. Of such factors one may first of all mention plasmolysis. Repeating my experiments (**Maximov**, 1912) on the chemical increase of resistance to freezing caused by placing cut portions of plant tissues in solutions of various salts and non-electrolytes, Iljin observed that by this means it is also possible to increase considerably the resistance of the

cells to desiccation. In one experiment, for instance, cells of the mesophyll of *Iris*, previously washed in water, died when placed permanently in an atmosphere with 99 per cent of relative humidity. Similar cells, previously soaked in a 0·1 mol. solution of glucose, could endure a relative humidity of only 97 per cent; in a 0·2 mol. solution, 93 per cent; and in a 0·5 mol. solution, 90 per cent. During the gradual desiccation of the solution the cells are plasmolysed. By carefully transferring the desiccating preparations to containers with air of increasing dryness, Iljin succeeded in communicating to the cells such a degree of endurance that they could remain alive for months in a desiccator over concentrated sulphuric acid.

From these results Iljin concludes that desiccation of the protoplasm, as such, is not injurious. The cell is killed by the mechanical rupture of the protoplasm lining the cell wall due to a rapid loss of water from the vacuole. A careful separation of the protoplasm from the cell wall, such as takes place during gradual plasmolysis (e.g. when a tissue is drying gradually in a drop of solution, the concentration of which is continually increasing), preserves the cells from death. According to Iljin, the protoplasm of every plant cell can endure complete desiccation, provided that rupture of the protoplasm during the shrinkage of the vacuole is prevented. The best means of prevention is the complete absence of a vacuole. This condition may be actually observed in embryonic cells, which are generally more stable than adult cells. Or the vacuoles may be filled with various substances, e.g. starch, fats, proteins, etc., as is the case in the reserve tissues of seeds (cotyledons or endosperm), which are well adapted to endure complete desiccation. Iljin even goes so far as to suggest that these substances function less as reserves than as a protection against desiccation.

Iljin's experiments involving the complete desiccation of plasmolysed cells are of great importance, and his suggestions regarding the significance of the vacuole and of the mechanical injury to the protoplasm during the death of wilting cells are

very interesting. Further investigations alone can prove to what extent these experiments and suggestions will suffice to explain the varying capacity to endure wilting of plants of different ecological types. I myself have already (**Maximov**, 1914) indicated that in death by freezing a significant rôle must be attributed not only to desiccation, but also to a mechanical compression accompanying freezing. Iljin's theory, which attributes the death of desiccating cells also to mechanical causes, emphasizes the points of similarity between these two causes of death, and thereby facilitates the study of the colloid-chemical phenomena which form the basis of the resistance of plants both to frost and to drought.

CHAPTER IX

XEROPHYTES

Ecological classification of plants according to their water relations. The group of xerophytes. The succulent type. Desert ephemerals. The true xerophytes. Structural peculiarities of xerophytes. High osmotic pressures and their significance. Are xerophytes truly xerophilous? Recent American work on the physico-chemical properties of plant saps.

Ecological Classification of Plants according to their Water Relations

The plants which cover the greater part of the land surface of the globe with a green carpet of vegetation are exposed to very varied conditions of water supply and transpiration. Accordingly, this carpet varies in thickness and density, sometimes even being discontinuous, thereby exposing bare rocks, sands, or deserts. Such differences in the conditions affecting the water balance leave their mark on the structure of plants; hence arose early in the history of ecology the idea of classifying plants in ecological groups according to their water relations. *Hygrophytes* are plants growing under conditions of abundant water supply, *mesophytes* are found under average or normal conditions of water supply, while *xerophytes* are plants exposed to conditions of a deficient water supply. The limits of these groups are naturally ill-defined, and in practice it is sometimes difficult to decide to which group a given plant shall be assigned. Nevertheless this classification has been widely accepted, and has even found its way into elementary textbooks of botany.

The Group of Xerophytes

In studying the various ways in which plants protect themselves from drought, the peculiarities of xerophytic vegetation are of especial interest. By means of these peculiarities, many xerophytes are enabled to inhabit dry, hot regions, where meso-

phytic plants from more moderate climates would inevitably perish from lack of water. The interest of the problems presented by xerophytic vegetation has stimulated research on the anatomy and physiology of desert plants. In the early part of the present century, indeed, the Carnegie Institution of Washington founded a special Desert Botanical Laboratory near Tucson in the Desert of Arizona. From this laboratory have already issued many important works which have thrown considerable light on the life of the highly peculiar desert vegetation.

It is unnecessary to give here a detailed description of the curious morphological and anatomical peculiarities which distinguish typical desert xerophytes. Such descriptions may be found in textbooks by **Nathansohn** (1912), **Keller** (1923–24), and others. Keller's work is especially valuable on account of the original examples given of the xerophytes of South-Eastern Russia, which the author has studied for many years. More detailed descriptions are contained in books dealing with biology and ecology, e.g. **Kerner von Marilaun** (1893), **Lubimenko** (1924), **Neger** (1913), **Schimper** (1903), **Warming and Graebner** (1918). Amongst works of a more special character may be mentioned: **Volkens** (1887), **Holtermann** (1907), **Marloth** (1908), **MacDougal and Spalding** (1910), and **Cannon** (1911), as well as **Renner's** article on "Xerophyten" in Vol. X of the *Handwörterbuch der Naturwissenschaften* (1915[b]).

A very interesting description of the whole problem of xerophytism from the point of view of physiological ecology is to be found in **H. Walter** (1926). This book, though small, is very suggestive, and is provided with an extensive list of literature. It appeared shortly after the Russian edition of the present work, which the author was therefore unable to utilize. Walter, however, is well acquainted with the Russian language, and has studied the Russian literature thoroughly; his fundamental point of view coincides with my own.

In the present book I propose to deal with some of the

general features of xerophytes, and to put forward certain physiological considerations which may enable us to judge of the correctness or otherwise of the views now current, as to which of these features are to be regarded as truly characteristic. This is the more necessary as many authors have assumed that features peculiar to some special class of xerophytes are characteristic of the group—in reality a very diverse one—as a whole.

The Succulent Type

The necessity of reducing transpiration is usually regarded as one of the chief physiological peculiarities of xerophytes living under conditions of extreme drought. Thus the cactus form, with its insignificant transpiring surface, and great amount of stored water, which may suffice for several months or even for years, is often cited as a characteristic xerophyte. In order to demonstrate the physiological differences between, e.g. xerophytes and mesophytes, it is customary to compare the intensity of transpiration of a cactus with that of an ordinary mesophyte. **Burgerstein,** for instance, has found that the ratio of transpiration from the stem of *Opuntia* and the leaf of *Hydrangea*, or a similar plant, is about 1 : 32. From this the conclusion is drawn that a very low intensity of transpiration is characteristic of xerophytes.

It would be a mistake, however, to assume, from what occurs in succulents, that xerophytes as a class are compelled to reduce transpiration. Amongst the plants of deserts and semi-deserts succulents are not abundant. It is true that in American deserts they often form a striking feature of the vegetation, but in the deserts of the Old World, e.g. the Sahara, or the Desert of Gobi, succulents are very rare.[1] Here

[1 Succulents are, however, very characteristic of the semi-deserts of South Africa, where they are numerous as regards both species and individuals. According to **Warming** (1909), in certain parts of the Karroo, succulent plants (including *Euphorbias*, *Mesembryanthemums*, and many others) form about 30 per cent of the vegetation.—Ed.]

dry, hard-leaved plants are dominant. It is also erroneous to suppose that desert plants of necessity transpire very slowly. Many investigators (e.g. **Fitting**, 1911, and **Kamerling**, 1914) state that branches of such typical desert plants as *Alhagi camelorum* or *Citrullus colocynthis* wilt immediately on being detached from the plant.

In order to obtain a complete picture of the peculiar mode of life of desert xerophytes, one must take into account, not only their water expenditure, but the entire water balance—including the intake, expenditure, and storage of water. Moreover, it must be borne in mind that a mere reduction of gaseous interchange (including transpiration) between the plant and the external air will not solve the difficulty. Complete isolation from the surrounding atmosphere would lead to difficulties of nutrition, and a plant such as a cactus, the surface of which is well protected against loss of water, is often characterized by an extremely slow rate of growth. But in the cacti, even this slow growth can only be accomplished by the aid of a special peculiarity of their metabolism. The respiratory processes of these succulents differ from those of other plants. In the dark, respiration results in the formation of organic acids, which only later (in daylight) decompose to form carbon dioxide. Thus the important ultimate product of night respiration, carbon dioxide, which in ordinary plants is given off and lost, is, in the case of the cacti, again utilized in the process of carbon assimilation, without leaving the chlorenchyma.

It is possible that this peculiar type of respiration and assimilation is not unconnected with a curious anomaly in the transpiration of the cacti, first noticed by **Livingston** (1907) and later studied by **Edith Shreve** (1916). Contrary to what is found in other plants, the relative transpiration of these desert succulents is lower in the daytime and higher during the night. This anomaly is probably due to the closure by day and opening at night of the stomata. Further, on the hot, clear days so characteristic of deserts, the capacity of retaining water increases in the tissues of cacti. This phenomenon, which

needs further study, results in a decrease of transpiration and an acceleration of absorption of water by the roots.

These peculiarities of respiration, assimilation and transpiration are by no means characteristic of other types of desert plants. The cacti and similar succulents, indeed, constitute a special ecological type, which includes also certain of our temperate succulent plants, such as species of *Sedum* and *Sempervivum*. The physiological peculiarities of these plants are more akin to those of epiphytes, which are dependent on water absorbed during rains, than to those of the genuine xerophytes.

The cacti are further distinguished from other xerophytes, and resemble epiphytes, by their low osmotic pressure (this will be dealt with in detail later), and by sparse and superficial root systems. According to **Cannon** (1911) cacti—like epiphytes—are plants adapted to existence in regions with infrequent rainy periods. Their superficial, widely spreading root systems rapidly absorb the water which penetrates the surface layers of soil, transferring it to the enormous reservoirs which form the main part of the plant body. This water is expended very slowly by the green stems, which possess in proportion to their volume a very small transpiring surface. The interesting experiments of **MacDougal and Spalding** (1910) show how extremely slowly such plants lose water. A very large specimen of the cactus *Carnegiea gigantea*, weighing 40 kg., lost in one year only 28 per cent of its weight; another specimen of 45 kg., 23 per cent. An *Echinocactus* weighing 37·3 kg. was kept unwatered in the laboratory for six years and periodically weighed. During the first year it lost 3,443 gr.; the second, 2,080 gr.; the third, 1,535 gr.; the fourth, 1,400 gr.; the fifth, 1,165 gr.; and the sixth, 1,280 gr. It is interesting to note the gradual decrease in the rate of water loss, which is connected with the increasing water deficit. This affords a striking example of the non-stomatal regulation of transpiration.

Notwithstanding their great economy in the expenditure of water, cacti do not thrive in the Sahara Desert, where the

precipitation is only half that in Arizona. According to the observations of **Fitting** (1911) on a species of *Opuntia*, these plants can only grow in the Sahara if irrigated.

These observations may be compared with those of **Shantz and Piemeisel** (1924), that the driest and hottest localities in the south-western desert region of the United States are occupied by the hard-leaved creosote bush (*Covillea glutinosa* Vail.), while the giant cactus (*Carnegiea gigantea*) so very characteristic of the Arizona Desert is found only under somewhat moister conditions.

At the present time far less is known of the physiological peculiarities of desert plants other than succulents, but these must now be considered.

Desert Ephemerals

In the first place we must exclude from the xerophytes proper yet another group of desert plants, namely the ephemerals. These plants are active only during the brief rainy season which occurs in nearly all deserts. Where such a season is absent there is no vegetation. **Volkens** (1887), in describing the vegetation of the Egypto-Arabian desert, mentioned that at the commencement of the rainy period the soil is very soon covered with a green carpet, composed for the most part of annuals. On the advent of the rains, the seeds germinate, and leaves, flowers, and fruits follow in rapid succession. The life-cycle is now complete, and the seeds alone survive during the ensuing drought. In this case, the only adaptation to desert conditions is the rapid development, accomplished in the brief period of 4–6 weeks; this explains the small dimensions of the plants. Otherwise these desert ephemerals do not differ from ordinary mesophytes, for they have none of the peculiarities of a xerophytic organization. If they develop late, or if the drought sets in before its usual time, these plants inevitably perish. Such ephemerals are abundant in the semi-deserts of South-East Russia, in the Caucasus and Transcaspia (**Keller,**

1923–1924), etc. In a recent publication **Shantz** (1927) terms these plants "drought-escaping". To the same ecological type belong many winter annuals which persist through the comparatively warm winter of these regions. They begin their development in autumn, pass the winter in the form of slowly growing rosettes, and rapidly complete their life-cycle in the spring.

THE TRUE XEROPHYTES

After the exclusion of the ephemerals and the succulents, there yet remain several different types of true xerophytes. In order to understand their diversity we must see how these plants can maintain their water balance under conditions of drought.

There are various ways in which this end may be achieved. The first and most usual method consists in a decrease of the transpiring surface, accompanied by a considerable development of the absorbing root system. In this case the greater part of the vegetative body of the plant remains underground. The result is a type of vegetation with widely spreading, closely matted subterranean parts, represented at the surface by isolated bushes separated by wide spaces of bare soil. This type is prevalent in semi-deserts. Examples are *Artemisia* (which covers many thousands of acres of the Ciscaspian steppes), *Festuca ovina*, *Astragalus*, *Peganum*, *Zygophyllum*, *Kochia*, and many other xerophytes (see **Keller**, 1923–24, ii). The vegetation of the semi-deserts of North America, where the most common plant is the sage brush (*Artemisia tridentata*), is similar in character. The root systems of plants of this type have been studied by **Weaver** (1919). Fig. 30, on the following page, reproduces one of his drawings, which shows the relative development of shoots and roots. In spring the bare spaces between the perennials are occupied by ephemerals which are scorched at the beginning of summer, the drought resistant xerophytes alone surviving. Many shrubs and under-

shrubs belong to the same type. Similar plants may be found growing on rocky mountains and gravel slides, where their spreading roots penetrate the interstices, and assist in the consolidation of these slides.[1]

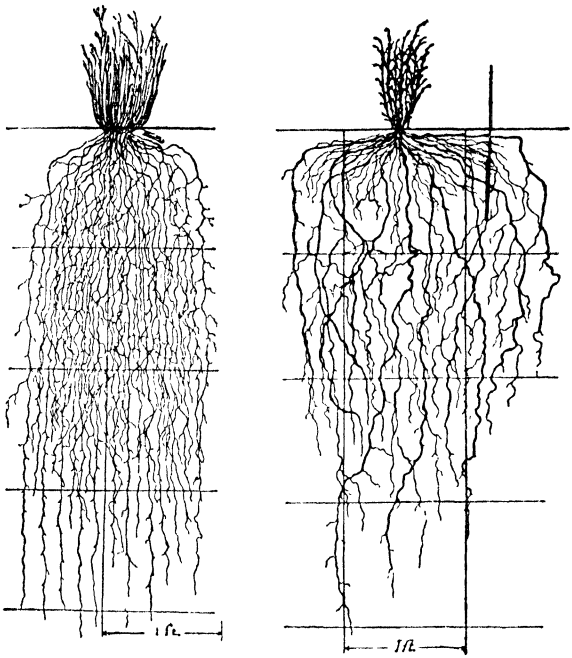

FIG. 30.—Semi-desert plants with root systems considerably larger than the aerial organs. *Left—Aristida purpurea. Right—Artemisia frigida* (from Weaver).

[1 Herbaceous (as well as woody) plants of an essentially similar though less extreme type are not infrequent in many habitats characterized by a highly porous substratum, even in climates with a considerable rainfall. Certain old shingle beaches on the Norfolk coast (England), for example, maintain an open vegetation dominated by *Statice binervosa*. The rosettes of the *Statice* are often small and stunted, while the highly developed root systems form a dense tangled mass which firmly binds the superficial layers of shingle and scanty soil. In times of drought there must be intense root competition for water, as also in the cases referred to in the text. Such competition, in fact, must in many cases determine the openness of the vegetation. Cf. **Yapp** (1925) and **Eugen Hess** (1910).—ED.]

A variation of this general type of semi-subterranean xerophytes includes plants "adapted" to the absorption of the "subsoil water". Such plants occur where the water level is not too far from the surface of the ground. Typical representatives of this sub-type are *Alhagi camelorum*, *Citrullus colocynthis*, and in part alfalfa (*Medicago sativa*). Provided that the substratum is sufficiently loose, the long roots may penetrate to a depth of 10 metres and more, and it is only after reaching the subsoil water that these roots begin to branch and develop their absorbing surface. Such plants do not suffer from drought even in the hottest and driest period of the year. Their chief problem is how the roots of the seedling, after germination, are to reach the level of the subsoil water before the effect of the rainy season dies away. Evidently the difficulty is a real one, for in dry years the seedlings often perish before reaching the necessary subterranean water. But once having reached the water they continue to grow without hindrance for many years.

It is useless to look for structural peculiarities in the aerial organs, and especially in the leaves of these plants, such as would protect them from excessive transpiration. Their leaves are frequently thin and delicate (e.g. alfalfa), and the amount of water transpired is often enormous. We can, indeed, regard the transpiring organs as powerful pumps which raise water from a great depth. Thanks to the activity of these pumps the plants are not obliged to economize water, but can transpire freely, obtaining at the same time carbon dioxide for their nutrition.

Many investigators have followed **Volkens** in referring all non-succulent desert plants with extensive root systems to the sub-type just described, i.e. that which makes use of subsoil water. This, however, is erroneous. **Fitting** (1911) states that many such plants occur in the rocky Sahara, though the subsoil water lies at an unavailable depth. **Keller** came to a similar conclusion with regard to certain typical semi-desert plants, e.g. *Artemisia* and *Festuca ovina*. The extensive development

of the roots of desert plants must in these cases be regarded as a means of absorbing a sufficient amount of water from as large as possible a volume of soil poorly provided with moisture.

In the absence of subsoil water, however, the greatest development of the root system cannot always provide the plant with sufficient water. We have already pointed out that if the moisture of the soil falls to the level of the wilting coefficient, no root system whatever is capable of absorbing water.

Plants which live under these very severe conditions of deficient water supply—often compelled to exist for months on their own stored water—develop a series of peculiarities which enable them to survive this dangerous period. Many, like our northern deciduous trees in winter, shed their leaves, the bare branches alone remaining above the soil. Examples are the desert shrub *Astragalus*, the American *Fouquieria*, and the cork-covered tubers of the African *Testudinaria Elephantipes*. These plants pass the driest part of the year in a state somewhat resembling anabiosis. Again, in the semi-deserts of Russia, many plants, such as the white *Artemisia* (according to the observations of **B. A. Keller** in the Ciscaspian steppes, and of myself near Tiflis), have two resting periods. During the winter rest all the aerial organs become dried up, but in the summer resting period growth ceases, though only some of the leaves are desiccated.

Similarly, the creosote bush (*Covillea glutinosa*), the most resistant of the North American desert xerophytes, passes the summer in a state of rest. This plant is dominant in the hottest parts of the desert and, according to the observations of **Shantz and Piemeisel** (1924), at the beginning of summer its small leathery leaves, covered with sticky resin, become brownish and enter into a state of permanent wilting. During the months prior to the October rains, the soil under these bushes dries out to such an extent that its water content falls 2–3 per cent lower than the wilting coefficient. Consequently during these months the creosote bush obtains no water from

the soil, and at the same time contains practically no internal reserve of water. Plants of this type **Shantz** (1927) terms "drought-enduring"; he regards them as the most characteristic type of the semi-deserts and deserts of North America.

During my visit in the autumn of 1926 to the Imperial Valley in the Colorado Desert (Southern California), where sometimes no rain falls for more than a year, I had an opportunity of observing the creosote bush in a curious state of anabiosis. Its leaflets were brown and shrivelled and some of the lower leaves had been shed; nevertheless, the plants remained alive. On the advent of rain the plant immediately recovers and so can utilize the first humid days for assimilation. The absence of a laboratory in the neighbourhood prevented my determining the water content of this interesting plant when in a condition of permanent drought. I only visited the Arizona Desert after the first rains, so that I was unable to make use of the hospitality of the Desert Laboratory of the Carnegie Institution in making such determinations. Nevertheless, even in the absence of precise observations, I am quite convinced that during the dry season of the year, the leaves of the creosote bush and similar desert plants contain no free water whatever; all the water remaining in them being firmly retained by the cell colloids.[1] The increase of the water retaining power of the leaves of another American desert plant, i.e. *Encelia farinosa*, is described in an interesting paper by Mrs. **Edith Shreve** (1924).

Thus semi-desert plants which remain green pass the period of greatest heat in a state of permanent wilting. We can find in their structure a series of modifications which help them to endure this severe trial.

Structural Peculiarities of Xerophytes

Among these peculiarities may be included the various means of protection against water loss developed at the sur-

[1 Cf. footnote, p. 243.—Ed.]

faces of the aerial and subterranean organs. Now a completely dry soil itself possesses an enormous sucking power (see the reference to the work of **Shull** in Chapter III), and can actually draw from a plant any water remaining in its tissues. This abstraction of water from the subterranean organs is rendered more difficult by the thick layer of cork which usually covers them, and especially their upper parts. A similar protection is usually found also in the aerial organs, the stems of xerophytic undershrubs being often thickly covered with cork. The stems of many plants too are protected from desiccation by a dense

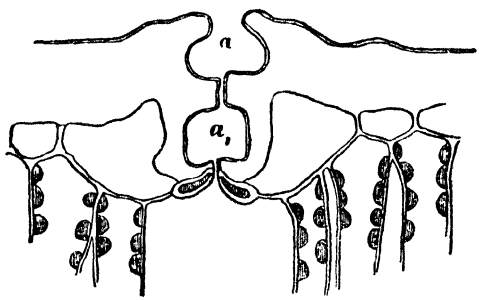

FIG. 31.—Deeply sunken stoma of *Dasylirion filifolium*. External air-chamber divided into two compartments (a and a_1) by projecting ridges (from Haberlandt).

covering of dead, dry leaves. This may be observed especially in the grasses of steppes and semi-deserts (*Stipa*, *Festuca*), as well as in plants of sandy soils (*Elymus arenarius*).

For plants that retain, during the driest season, their assimilating organs covered only by an epidermis, a new problem arises, i.e. how to protect this tissue, and especially its weakest part, the stomata. The closing of the stomata alone is insufficient, for this does not entirely check transpiration in strong sunlight. We find, however, in xerophytes various types of structural modifications which afford additional protection to the stomata. For instance, in *Dasylirion* (Fig. 31) the stomata are sunken in cavities below the level of the epidermis, and communicate with the external air by narrow ducts. In

Xanthorrhoea (Fig. 32) and in many Restionaceae the respiratory cavity is bounded by thick-walled cells with cutinized

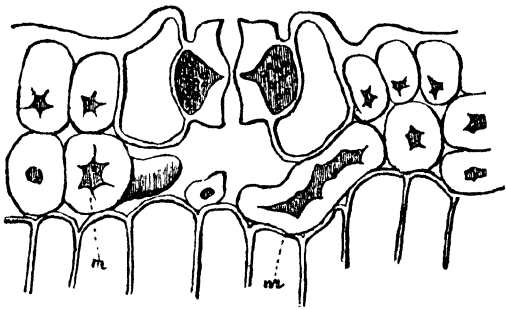

FIG. 32.—Stoma of *Xanthorrhoea hastilis* with ventilating cavity surrounded by thick-walled cells, *m* (from Tschirch).

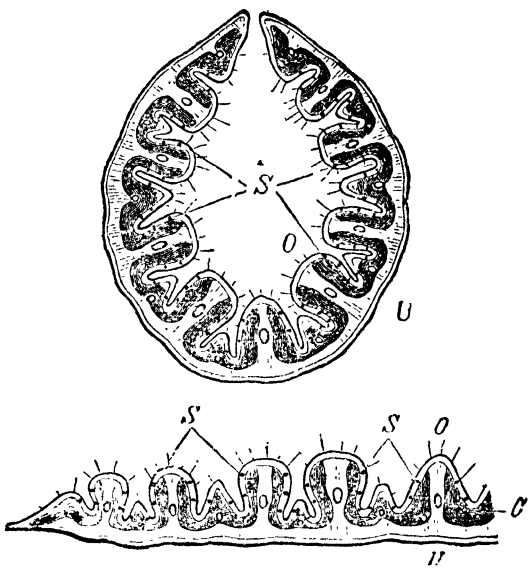

FIG. 33.—Cross-sections through the leaf of *Stipa capillata*. *Above*—leaf rolled into a tube during wilting; *below*—half of a similar section in a state of saturation with water. *S*, stomata; *O*, upper; *U*, lower side (from Kerner).

walls. In some of the Gramineae, e.g. *Stipa capillata* (Fig. 33) the leaves roll into a tube, with the stomatal surface inside. In

other cases the pores of the stomata are blocked by wax or resin. Cuticular transpiration, too, may be diminished by a series of "adaptations": the cuticle becomes very thick; it is covered by a deposit of wax; the surface is glossy, thus reflecting a considerable quantity of light, or it may be covered by a thick coating of hairs, forming a screen which decreases the heating effect of radiation. Many other means of protection are described in the publications mentioned above.

It is customary to associate such "adaptations" with a decrease in transpiration, but this generalization requires to be modified. A thick cuticle, a deposit of wax, or a covering of hairs, has little or no influence on transpiration when the stomata are open, just as the thickness or density of the walls does not affect the exchange of air in rooms with open windows.[1] The protecting influence of these additional epidermal developments can only take effect after the cessation of direct diffusion of water vapour consequent on the closing of the stomata, or the blocking of the stomatal pores by wax or resin. Hence these structures have little effect at times when the plant can obtain water from the soil and carry on its normal functions. On the other hand, they do assist in protecting the plant from excessive transpiration during the longer (in deserts) and more dangerous periods when the plant has entered on the state of permanent wilting, and it becomes essential to conserve what water remains in order that the vital processes may continue. An important adjunct is the accumulation of a store of water. Such stores are found not only in succulents but also in other plants in which they may be less obvious. In many cases

[1 This is no doubt largely true as regards a thick cuticle or a coating of wax, which renders the outer epidermal walls themselves less permeable to water, thereby affecting cuticular transpiration only. A dense covering of cutinized hairs, however, may affect stomatal as well as cuticular transpiration. In still air, with open stomata, the effect of hairs on stomatal transpiration is probably negligible. But in cases where a leaf with open stomata is exposed to wind, a dense covering of hairs may be supposed to have an essentially similar effect to that of sunken stomata or "rolled" leaves. In all these cases the accelerating effect of wind on transpiration is lessened by diminishing the gradient of density of water vapour outside the actual stomatal pores. (Cf. Yapp, 1912.)—ED.]

subterranean organs such as fleshy roots, tubers, and bulbs, which are widely distributed amongst xerophytes, serve for the storage of water. Sometimes these structures act, so to speak, as water buffers placed between the leaves, which transpire copiously when actively assimilating, and the tips of the absorbing roots, which are very sensitive to wilting. During periods of anabiosis these absorbing parts of the roots die, the plant passing

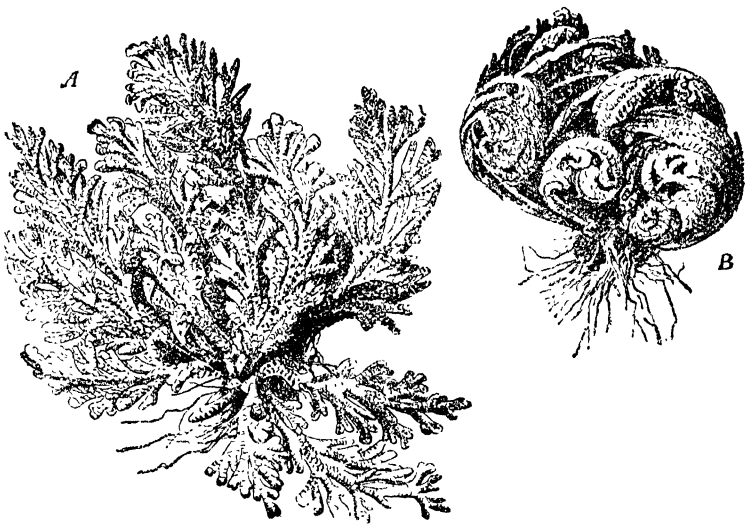

FIG. 34.—*Selaginella lepidophylla: A*, in a turgescent, and *B*, in a wilted state (from Hieronymus).

the dry season in the form of a bulb or tuber, as in many prairie and desert plants. The whole surface of such plants is covered by a coating impermeable to water (cork, dry scales, etc.).

Another very important peculiarity which enables desert plants to endure a prolonged drought is an increase of the capacity of the cells, or rather of the protoplasm of the cells, to suffer loss of water without permanent injury. We have already seen that many lower plants, e.g. lichens, can endure complete desiccation without losing their vitality. The American plant *Selaginella lepidophylla* (Fig. 34) possesses a similar power of

endurance: this plant is stated to have remained alive in herbaria for eleven years. The higher plants (with the exception of their seeds) are incapable of enduring such complete desiccation, yet the buds and branches of trees, and the vegetative organs of many desert plants, can suffer a considerable loss of water.[1] Amongst xerophytes are not a few plants with thin but hard, almost woody leaves—for instance, species of *Acantholimon* (characteristic of the dry uplands of Armenia), heathers (*Erica*), and numerous plants with heather-like (ericoid) leaves. Such "ericoid" plants, which belong to diverse families, Verbenaceae, Compositae, Thymelaeaceae, etc., are very characteristic of the Cape Province of South Africa. These plants contain comparatively small amounts of water even when in a state of turgor. **Thoday** (1921), who studied the behaviour during drought of the ericoid South African plant *Passerina vulgaris*, found that the turgid leaves contained only 86–89 parts of water per 100 parts of *dry* weight. During wilting (characterized by a rolling of the leaves) the water content fell to 26 per cent of the dry weight. The rolling of the leaves is the result of a decrease in volume of the cells of the mesophyll and of the epidermis; the thickened outer walls of the upper epidermis cannot contract, so the whole leaf folds up with its lower surface inside. Microscopical investigation of the wilting epidermal cells (these cells must be examined in oil or fixed in absolute alcohol and mounted in Canada balsam) showed that they had not only lost their turgor but were actively contracted by the cohesive force of the diminishing cell contents. The contraction may be especially well seen on the vertical walls of the epidermis. These walls are thrown into folds, which disappear at once if the object is moistened with water (Fig. 35).

The abundance of mechanical elements in the leaves and stems of xerophytes of this type distinguishes them from fleshy succulents—which consist almost wholly of parenchymatous tissues—and must be connected with the necessity of

[1 See footnote, p. 243.—ED.]

remaining for long periods in a wilting condition. Herbaceous organs such as the leaves and young stems of common mesophytes, when wilting, lose the mechanical stability due to turgor, and droop like limp rags. In this state they may be torn by gusts of wind which would leave them uninjured when turgid. Moreover, as already pointed out (p. 164), the bending of leaves by wind assists in expelling the moist air from the intercellular spaces, thus accelerating the loss of water from the wilting leaf. The thick, hard cuticle protects the leaves of

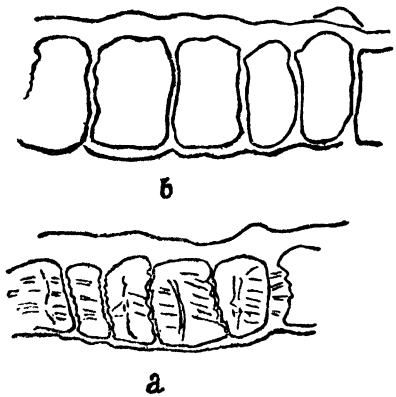

FIG. 35.—Epidermal cells of leaf of *Passerina*: *a*, in a wilted state, and *b*, saturated with water (from Thoday).

sclerophylls from such dangers, and the mechanical fibres which accompany the vascular bundles similarly protect the water-conducting system from deformation.

The relatively rigid cell walls of sclerophylls may also have another very important effect. These walls oppose considerable resistance to the compression caused by the decrease in volume of the cell contents in consequence of loss of water. In this way a considerable tension is set up in the water columns which extend from these cells to the conducting vessels and to the root system. This tension assists the plant to become more rapidly saturated with water when the soil moisture increases at the

beginning of the rainy season or in consequence of the formation of underground dew.

The sclerophyllous type of xerophyte is widely distributed, not only in deserts but also in regions with a more moderate climate, such as the lands bordering on the Mediterranean Sea.[1] In the latter case the evergreen plants, with their thick leathery leaves, are exposed twice a year to conditions which occasion an unfavourable water balance. One of these periods is the dry, hot summer; the other occurs during the comparatively mild winter, when, however, the cooling of the soil causes transpiration to exceed absorption.

The anatomical and physiological peculiarities of the evergreen sclerophyllous plants of the Mediterranean region have been studied in detail by **Bergen** (1904), and especially by **von Guttenberg** (1907, 1927). The leathery character of the leaves is due mainly to the thick walls of both upper and lower epidermis, together with special sclerenchyma cells or strands of cells in the mesophyll. These thickened cells afford a firm support to the mesophyll. For this reason the leaves do not visibly wilt, even when they have lost practically all their water. Neither do they change their shape after the loss of turgor, except for the twisting peculiar to some species. Thus these plants are adapted to two different climatic conditions, to a rainy season and to drought. During the rainy season they transpire water with greater energy than many deciduous trees. During drought they fall into a state of imperceptible wilting, when their stomata close, and only an insignificant cuticular transpiration takes place.

The sclerophyllous type is represented near the coasts of cool seas in Great Britain, Denmark, and North-Western Germany by heather and similar undershrubs. In this case

[1 A very characteristic type of vegetation, known as *maquis* (French) or *macchia* (Italian), is found in temperate regions with long, summer droughts and winter rains. Evergreen, sclerophyllous woody plants are dominant, and bulbous and tuberous plants abundant. In addition to the Mediterranean region, *maquis* occurs in the Cape Province of South Africa, South and West Australia, Central Chili, and California.—ED.]

strong winds are the desiccating agents which provoke the periodic wilting of the leaves. These plants are also met with on peat-mosses, where their xerophytic, or more precisely "xeromorphic", aspect long served to support **Schimper's** hypothesis of the physiological dryness of bog soil. So far as I can judge at the present time such xeromorphy may more correctly be associated with the evergreen habit of these ericaceous plants. **Stocker** (1923) has recently investigated the intensity of transpiration of heather, *Andromeda*, *Ledum*, and other sclerophyllous peat plants. He found that under conditions of a plentiful water supply, the transpiration of these plants is not less than that of ordinary mesophytes. For this reason Stocker suggests that these plants should be excluded from the class of xerophytes. Similar results had been previously obtained with evergreen plants of the Mediterranean region by **Bergen** (1904) and **von Guttenberg** (1917). I have no *a priori* objection to the above suggestion, for the morphological characters of the leaves alone would not entitle a plant to be ranked with the xerophytes, that is, with plants capable of enduring without injury a prolonged period of drought. On the other hand, the mere fact that a plant is capable of a comparatively high rate of transpiration is not a sufficient reason for excluding it from the group of xerophytes. A slow rate of transpiration is characteristic only of succulents of the cactus type, and of plants with continually blocked or deeply sunken stomata, e.g. *Dasylirion* and *Xanthorrhoea*. Xerophytes of other types are, on the contrary, characterized by a high intensity of transpiration.

This proposition—which is still regarded by many authors as a paradox—was definitely put forward by myself in 1916, and investigated in detail in 1917, with the help of my collaborators, **Badrieva and Simonova.** The experiments were carried out near Tiflis, where the climate and vegetation are of a semi-desert character. Wild xerophytes growing on the southern rocky slopes were used, as well as cultivated xerophytes from the open slopes of other parts of the Caucasus, especially

Armenia. For comparison typical mesophytes from the shaded, irrigated parts of the old garden were taken, also certain species belonging to the spring vegetation. The experiments were made with cut leaves dipping into water, and were carried out on clear days, but in the shade, as the leaves wilted too rapidly if exposed to direct insolation. For convenience of comparison the data were referred to a standard humidity deficit of 10 mm., Dalton's formula being used. In addition to the intensity of transpiration, we determined the rapidity with which the water stored in the leaf was expended. This was calculated in percentages of the water content per hour, and was intended as a measure of the rate of change of the water conditions in the leaf. Table XIII, opposite, gives some characteristic results.

From this table it is evident that in general the xerophytes employed possess a higher intensity of transpiration than the mesophytes. The only exceptions were the succulent *Sedum* and the semi-succulents *Zygophyllum* and *Gypsophila*. The transpiration of the two latter, though less than that of the "sun" mesophytes, exceeded that of the "shade" mesophytes. Among the plants with a high intensity of transpiration—between 9 and 14 mg. per sq. cm.—we find a series of apparently well-protected xerophytes, e.g. the snow-white *Helichrysum*, *Verbascum ovalifolium*, and *Stachys Kotschyi*, densely covered with grey hairs, *Glaucium* and *Falcaria* with a bluish deposit of wax on the thick cuticle, and *Caccinia* completely encrusted with lime. These data confirm the suggestion that such means of protection have little significance during normal transpiration, being useful only during wilting.[1]

The figures giving the relative rates of expenditure of water indicate that the accumulation of water in the leaves of the succulents and semi-succulents retards the rate of change. In thin-leaved plants this exchange of water is very rapid, for on the average the water contained in the leaf only suffices for 1½–2 hours' transpiration. *Stachys Kotschyi*, notwithstanding

[1 Cf. text and footnote, p. 262.—ED.

the dense covering of hairs, expends its store of water in less than one hour. It is to be understood that these figures refer

TABLE XIII

Intensity of Transpiration and Rapidity of Expenditure of Water by Xerophytes and Mesophytes (according to Maximov, Badrieva, and Simonova)

Species	Intensity of Transpiration	Rapidity of Expenditure of the Water Store	Character of the Leaves
A. XEROPHYTES			
Sedum maximum	2·8	8	Succulent
Zygophyllum Fabago	4·9	15	Semi-succulent
Gypsophila acutifolia	5·4	20	Hard, fleshy
Caccinia Rauwolfi	8·8	44	Hard, encrusted with lime
Verbascum ovalifolium	8·8	71	Densely hairy
Glaucium luteum	9·2	40	Fleshy, covered with wax
Salvia verticillata	9·9	55	Hard, fleshy
Stachys Kotschyi	12·7	119	Densely hairy
Cladochaeta candidissima (=*Helichrysum candidissimum*)	13·2	40	Densely hairy
Falcaria Rivini (=*F. vulgaris*) ..	13·7	87	Hard, covered with wax
B. MESOPHYTES			
Lamium album	3·6	58	Shade plant
Viola odorata	4·0	58	Shade plant
Vinca major	4·5	45	Shade plant with leathery leaves
Campanula rapunculoides ..	4·8	36	Shade plant
Sisymbrium Loeselii	8·3	62	Sun plants of the spring vegetation
Hirschfeldia adpressa	9·8	40	
Erodium ciconium	9·2	83	

only to conditions under which the water lost by the leaf is replaced by absorption. If the water transpired were not replaced the leaves would wilt, and this would immediately decrease the water expenditure.

The results of these experiments with cut leaves are supported by similar data obtained by me and my co-workers in experiments with potted plants. It may, therefore, be confidently asserted that many xerophytes are characterized by a high intensity of transpiration. Amongst these, in addition to the plants already mentioned, are various species of *Artemisia* (*A. maritima*, *fasciculata*, and *scoparia*), *Haloxylon Ammodendron*, and a series of xerophytic species of *Centaurea*. My co-worker, **Kusmin**, working in the deserts of the Caucasus coast of the Caspian Sea, near Baku, also observed that such xerophytes as *Alhagi camelorum* and *Medicago coerulea*—the only plants remaining green during the summer in the otherwise dried-up desert—possess an intensity of transpiration twice that of the sunflower.

Alexandrov (1924) records some interesting observations on the relative intensities of transpiration of xerophytes and mesophytes. This author selected representatives of three ecological types of plants, namely—of mesophytes, of thin-leaved xerophytes, and of xerophytes of the semi-succulent type with fleshy leaves (*Zygophyllum Fabago*, *Atriplex hortensis*, *Portulaca oleracea*). The experiments were carried out in the hot climate of Tiflis under varying environmental conditions—in the sun and in the shade, in the summer and in the autumn. Under conditions of high tension of the environmental factors, the xerophytes always transpired considerably more than the mesophytes. But in deep shade and in a humid atmosphere the transpiration of mesophytes is sometimes higher than that of xerophytes. Thus the general concept of the higher intensity of transpiration of xerophytes must be somewhat restricted. This restriction, however, does not apply to conditions under which xerophytes, according to the older opinion, need to protect themselves from loss of water—that is, when they are exposed to a dry atmosphere and direct sunlight.

That xerophytes should show such a high intensity of transpiration is not really surprising. As previously mentioned, the enormously developed root system of many xerophytes has

to supply with water only a comparatively insignificant aerial portion of the plant. Under such conditions a high rate of transpiration is not only not dangerous, but is rather an advantage, for an energetic gaseous exchange contributes to a more intense assimilation.[1] Further, xerophytes forming the sparse vegetation of open, strongly insolated habitats, belong to the type of "sun" plants, and the more light such plants obtain (see later, Chapter XI), the higher is their transpiration capacity.

High Osmotic Pressures and their Significance

One more very important physiological peculiarity of xerophytes, which also affects their water relations, must be dealt with: this is the osmotic pressure in their cells. **Zalenski** (1904) was one of the first to call attention to this peculiarity, but his work remained unnoticed, and no further interest was taken in the question until it was made the subject of a special investigation by **Fitting** in 1911. In studying the vegetation of the Sahara, near the oasis of Biskra, he was particularly struck by a member of the family Zygophyllaceae, namely *Peganum Harmala*. Notwithstanding its obvious powers of drought resistance, this plant does not possess any of the peculiarities said to be characteristic of xerophytes. It has no thick cuticle, no hairy covering, no sunken stomata, and its shoots, when cut, wilt rapidly. The desert shrub *Rhus albida* and many other desert plants have a similar character, yet their root systems, though very extensive, do not reach the level of the subsoil water.

These observations would seem to indicate that such plants must possess some special means of obtaining an adequate

[1 There is, of course, no direct connexion between the rate of transpiration and that of carbon assimilation, such as might perhaps be inferred from the text. When the water balance, however, is such as to lead to the stomata being widely open, rapid transpiration would tend to be accompanied by vigorous assimilation. See also the discussion in Chapter X on "The Efficiency of Transpiration", i.e., the ratio of the amount of dry substance formed to the amount of water transpired.—ED.]

water supply from the extremely dry soil of the desert. Fitting is of the opinion that one of the most important peculiarities of these plants is a high osmotic pressure in their cells, and that this renders possible the development of a considerable power of suction. A systematic investigation of the osmotic pressures of desert plants has proved them to be extremely high. For instance, of 46 plants of the rocky desert (one of the driest habitats studied by Fitting), 21 per cent possessed an osmotic pressure equivalent to a 3 gr. mol. solution of nitrate (100 atmospheres) or more, 35 per cent a pressure of more than 1·5 gr. mol. (53 atm.), 32 per cent over 1·0 gr. mol. (37 atm.). Only 11 per cent had pressures not exceeding 0·3 to 0·6 gr. mol., that is, a sap concentration similar to that of ordinary mesophytes. It is important to note that the lowest pressures were observed in annuals, and the highest in perennials.

Fitting sees in the high osmotic pressures of desert plants a twofold significance. In the first place it increases their power of suction, thus enabling the plant to draw the necessary water from very dry soil with a considerable water retaining capacity. Secondly, a high concentration of the cell sap retards transpiration, for the higher the concentration of a solution, the lower the vapour pressure at its surface, and the slower the rate of evaporation. Hence plants with a high osmotic pressure can to some extent dispense with the protective "adaptations" (thick cuticle, sunken stomata, etc.) characteristic of cacti and other xerophytes with a low osmotic pressure.

Fitting thus proved the existence of unexpectedly high osmotic pressures in desert plants. His results aroused great interest and at the same time severe criticism. **Livingston** (1911), from the standpoint of his own investigations on the xerophytes of the Arizona Desert, and from general considerations, was the first to question Fitting's conclusions. Livingston argued that as the water absorbed by the plant must in the first place pass through the cell walls, its entrance is conditioned primarily, not by the osmotic pressure of the cell sap, but by

the absorbing forces of the cell wall, which are more or less equal in all plants. This criticism was supported by the investigations of **Briggs and Shantz** (1912, 1913), who found that all plants possess approximately the same capacity of absorbing water from the soil, in so far as this capacity is indicated by the so-called wilting coefficient. Hence, it was argued, in the absorption by plants of water from a relatively dry soil, differences in the osmotic pressure of the cell sap cannot have any significance. These investigations, as well as those of **Shull** (1916), have been already discussed in Chapter II.

Fitting's second conclusion, namely, that an increase in the concentration of the cell sap must decrease the vapour pressure and with it the rate of evaporation of water, was also disputed by Livingston, who was later supported by **Renner** (1915). For a concentration corresponding to an osmotic pressure of 100 atmospheres, Livingston calculated the retardation of evaporation to be 8 per cent. Renner, by more exact calculations, proved it to be only 7·2 per cent. **Wisser** (1914) also showed, by direct experiment, that the expressed sap of plants with a high osmotic pressure evaporates from a flat dish at the same rate as sap from plants with a low osmotic pressure.

Although Fitting's theoretical conclusions regarding the advantages to xerophytes of high osmotic pressures were seriously disputed, his actual data were confirmed by a series of investigations. Amongst these are: **Hannig** (1912), **Keller** (1913–14, 1918, 1920), **Iljin, Nazarova and Ostrovski** (1915), **Maximov and Lominadze** (1916), **Maximov, Dilanian, and Silikova** (1917), **Blagoveshenski** (1926), and others. All these investigators agree that in general the drier the habitat, especially as regards the amount of water in the soil, the higher are the osmotic pressures of the plants occupying the habitat. But this increased osmotic pressure is actually an inherent peculiarity of the organization of xerophytes. This is shown by the fact that if xerophytes and mesophytes are cultivated under identical conditions, the osmotic

pressures of the former are considerably higher than those of the latter. For instance, on the dry southern slopes of the Tiflis Botanical Garden one may find at the beginning of summer mesophytic plants of the spring vegetation growing together with true xerophytes. By the middle of the summer the mesophytes, unable to endure the drought and heat, have perished, while the xerophytes retain their leaves throughout the whole vegetative period. Together with my co-workers, **Dilanian and Silikova,** I have made determinations of the osmotic pressures in the leaves of both types. Some of the results are given in Table XIV, the osmotic values being expressed in gramme-molecules of KNO_3.

TABLE XIV

Osmotic Values in the Leaves of Xerophytes and Mesophytes (according to Maximov, Dilanian, and Silikova)

Species	Osmotic Values	Species	Osmotic Values
(*a*) MESOPHYTES		(*c*) XEROPHYTES	
Erodium ciconium ..	0·3	*Artemisia maritima* ..	0·5
Papaver strigosum ..	0·3	*Gypsophila acutifolia* ..	0·5
Hirschfeldia adpressa ..	0·3	*Kochia prostrata* ..	0·6
Senecio vernalis ..	0·4	*Centaurea ovina* ..	0·7
		Parietaria judaica ..	0·8
(*b*) SUCCULENTS		*Zygophyllum Fabago* ..	0·8
Sedum maximum ..	0·15	*Dianthus fimbriatus*	
Sedum oppositifolium ..	0·15	(=*D. orientalis*) ..	0·9

Our results are in complete agreement with those of **Fitting.** The lowest osmotic pressures were found in succulents, and the highest in xerophytes with extensive root systems, e.g. *Zygophyllum Fabago* and *Dianthus orientalis.* I am not inclined, however, to admit that a high sap concentration is a direct protection against loss of water, for, as already pointed out, xerophytes are not distinguished by a low intensity of transpiration. It is more probable that these plants, thanks

to their capacity of developing a great power of suction, can absorb water more rapidly, and thus compensate the high rate of expenditure by the actively transpiring foliage. But the chief importance, it seems to me, of the high osmotic pressures found in desert plants is during wilting, when there is a real danger of excessive loss of water.

The significance of high osmotic pressures during wilting is manifold. In the first place, as I pointed out in 1916, a high concentration of the cell sap of xerophytes may be the result of the accumulation of substances which protect the protoplasm from coagulation and desiccation. This suggestion is confirmed, not only by the analogy with freezing (see above, p. 244), but also by the indications obtained by Fitting and others that the high osmotic pressures of many desert plants are caused by the accumulation in the sap of salts, and of organic substances about which little is known at present.

Secondly, a high osmotic pressure of the sap, by causing considerable tension of the cell walls, prevents visible wilting for a long time, even though the water deficit continues to increase. My own investigations, as well as those of **Krasnoselsky-Maximov** (1924), have shown that the more xerophytic plants show signs of wilting only when they have lost 30–40 per cent of their total water content. Delicate shade plants, on the other hand, e.g. the Balsaminaceae, wilt with a loss of 1–2 per cent. This delayed loss of turgor enables the plant to continue the process of carbon assimilation—a question already dealt with in the preceding chapter.

Further, in spite of the apparently conclusive data of **Wisser, Livingston,** and **Renner** regarding the insignificant effect of an increase of concentration on the rate of evaporation, a high osmotic pressure of the sap does considerably retard the desiccation of the plant. This is shown by **Keller's** (1925) experiments with *Salicornia.* Keller noticed that if *Salicornia herbacea* is grown in water cultures with various concentrations of sodium chloride, the intensity of transpiration decreases steadily with the increase of the

concentration of the solution. Moreover—and this is most important in this connexion—the shoots of *Salicornia*, when severed from their roots, showed similar differences during drying. That is, the plants which had been grown in the less concentrated salt solutions lost their water most rapidly. As the plants grown in the more concentrated solutions possessed considerably higher osmotic pressures, Keller attributes to this fact their greater resistance to desiccation.

Finally, another possible significance of a high concentration of the cell sap must not be neglected. Desert soils, in consequence of weathering, coupled with the small amount of leaching out of soluble salts, have always a more or less highly concentrated soil solution. Desert plants must therefore possess much in common with halophytes; these two groups are indeed very similar, though their extreme representatives differ considerably. In both cases the plants have to obtain water from a more or less concentrated soil solution, and if the resulting osmotic resistance to absorption is to be overcome, the osmotic pressure of the plant sap must be increased sufficiently to develop a suction pressure greater than that of the soil solution. It is very possible that this is the most important function of a high osmotic pressure in the cells of many xerophytes.

Are Xerophytes Truly Xerophilous?

In order to understand better the true ecology of xerophytes we must attempt to answer one more question. Are dry conditions really an advantage and moist conditions less advantageous or even injurious to this class of plants? Or have xerophytes been segregated in deserts and other dry habitats where they alone can exist, owing to severe competition with rapidly growing mesophytes in more favourable habitats? In short, are xerophytes actually xerophilous or merely drought resistant?

Observations under natural conditions compel one to doubt the xerophily of xerophytes. For instance, I have myself

observed cacti and other succulents, the whole organization of which leads to the economy of water, flourishing in the Buitenzorg Botanical Garden in West Java, one of the most humid habitats in the world. Again, many xerophytic weeds have spread far beyond the limits of their original dry habitats. For example, *Salsola Kali* was accidentally carried to America, where it has since spread to such an extent in arable land that it has been called "*Salsola pestifera*".[1] Various species of *Atriplex* and *Amaranthus* have become similarly dispersed.

Experimental data, too, agree with these observations. Thus **Spalding** (1904) observed that many desert shrubs develop better with a good water supply than under actual desert conditions. Experiments made by myself and **Alexandrov** (1917) in Tiflis with such xerophytes as *Artemisia fasciculata*, *Centaurea solstitialis*, and *Zygophyllum Fabago*, have shown that if the soil moisture in the experimental pots is increased from 40 per cent to 60 per cent of the water holding capacity, the plant yield is increased $1\frac{1}{2}$–2 times. Parallel experiments with mesophytes (beans, sunflower, corn) showed a similar increase of the yield under the same conditions.

All these data lead to the conclusion that xerophytes are not xerophilous, at least so far as the soil moisture is concerned. Xerophytes develop better with abundant water in the soil, and therefore must be reckoned not as xerophilous but as drought resistant plants.

It is true that an excessive increase of water in the soil (e.g. up to the limits of its water holding capacity), may exert a harmful influence on the roots of many plants, by impeding soil aeration and promoting reduction processes. In ordinary pot cultures this "souring" of the soil is more evident with plants which transpire little, such as many xerophytes, and in particular the succulents. Hence the necessity of avoiding the over-watering of these plants when grown in rooms and

[1 *Salsola Kali* is a widely distributed annual species occurring in Europe, N. and S. Africa, Asia, Australia, and N. and S. America. It is typically a drift-line halophyte of sandy seashores. The American cornfield weed is var. *tragus*, Moq.—ED.]

hot-houses. But there is a great difference, from a physiological point of view, between the necessity for sufficient aeration and preference for a dry soil.

Recent American Work on the Physico-Chemical Properties of Plant Saps[1]

During the last ten years, **J. A. Harris** and his co-workers have carried out extensive investigations of the physico-chemical properties of tissue fluids extracted from plants. Their results showed, in the first place, that different ecological groups are characterized by definite physico-chemical properties of their tissue fluids.

For example, woody plants (trees and shrubs) differ in the physico-chemical properties of their sap from herbaceous plants (annuals and perennials). The sap from leaves of representative woody plants and herbs was investigated for three different types of vegetation, from regions with sharply contrasted climates. These types were—hygrophytic vegetation of the Jamaican montane rain forest; mesophytic vegetation of the northern coast of Long Island, and xerophytic vegetation of the Arizona Desert (**Harris, Gortner, and J. V. Lawrence**, 1921).

The tissue fluids of the leaves of woody plants invariably showed a higher osmotic pressure than those of herbaceous plants. For plants of the Arizona Desert, for instance, the following averages were established: —

	Atmospheres
Trees and shrubs	28·10
Dwarf shrubs and undershrubs	21·45
Perennial herbs	16·35
Winter annuals	14·73

(**Harris, J. V. Lawrence, and Gortner**, 1916).

[1 This section of Chapter IX was written by Professor Maximov for the English edition of his book: it did not appear in the original Russian text.—ED.]

On the average, the osmotic pressure in herbs was 26·47 to 38·63 per cent less than in woody plants. As this general conclusion was based on results obtained from a vast amount of material, grown under the most varied conditions, the authors regard it as expressing a general biological law.

On the other hand, the electrical conductivity of the tissue fluids of woody plants is less than that of herbs. For instance, in Long Island the average specific electrical conductivity ($K + 10^6$) was 10,923 in trees and shrubs, while in herbs it was 14,308.

The authors confirmed the results of other workers that the Cactaceae have a low osmotic pressure (**Harris and J. V. Lawrence,** 1917). In the Jamaican coastal deserts the average osmotic pressure of members of the Cactaceae was the equivalent of 7·52 atmospheres, while that of the neighbouring woody plants reached 42·2 atm. The authors cite these data in order to illustrate the different response of two kinds of organism to similar environmental conditions.

A still lower osmotic pressure was established for typical epiphytes (**Harris,** 1918[b]). In epiphytic Orchidaceae the osmotic pressure varied from 3·32 to 5·06 atm.; in Bromeliaceae, from 4·00 to 5·57 atm. Epiphytes show only a third to a half of the osmotic pressure exhibited by the foliage of the trees on which they dwell.

Mangrove vegetation is characterized by very high osmotic pressures (**Harris and J. V. Lawrence,** 1917[b]). Even in the case of mangrove trees growing in almost pure water, the osmotic pressure was 20–22 atm., while when impregnated with salt, the value reached 44–50 atm.

Hygrophytic, mesophytic, and xerophytic vegetation differ sharply from one another in regard to the osmotic pressure of their sap (**Harris, J. V. Lawrence, and Gortner,** 1916; **Harris and J. V. Lawrence,** 1917). The highest value was found in xerophytes, the lowest in hygrophytes, mesophytes occupying an intermediate position. The following

average osmotic pressures were obtained for herbs and woody plants respectively in different types of vegetation.

	Herbs	Woody Plants
	Atmospheres	Atmospheres
1. Hygrophytes:		
Jamaican montane rain forest ..	8·80	11·44
2. Mesophytes:		
Long Island	10·40	14·40
3. Xerophytes:		
Arizona Desert	15·15	24·97
Jamaican coastal deserts	—	30·05

Within the limits of a given climatic region the physico-chemical properties of the leaf-tissue fluids depend mainly on the water and salt content of the soil. Evidence for this statement is afforded by numerous determinations made by the authors with plants collected from different habitats in the Arizona Desert, and in the Tooele Valley, Utah (**Harris, J. V. Lawrence, and Valentine,** 1924). For instance, at higher altitudes on the Stansbury Mountains in the Tooele Valley, where the soil is sufficiently moist without being saline, woody plants showed a comparatively low osmotic pressure (17·06 atm.), the chlorine content per litre of sap being 0·68 gr. Lower down, in the association of *Artemisia tridentata*, the soil moisture was less and the salt content still rather low. This zone may be regarded as a region where dry-farming is possible. Here the osmotic pressure of woody plants was equivalent to 22 atm., the chlorine content being 2·65 gr. per litre of sap. Still lower, where the association of *Kochia vestita* has established itself, the amount of salt was considerably greater, and the shortage of water during summer more pronounced. Under these conditions dry-farming would be precarious. The woody plants of this habitat showed an osmotic pressure of 27·08 atm., while the chlorine content was 7·58 gr. per litre. Finally, in strongly saline habitats the

osmotic pressure reached on the average 37·87 atm., the chlorine content being 26·45 gr. per litre. During periods of drought both the osmotic pressure and the salt content of plants of such saline localities were extremely high. In the tissues of *Atriplex confertifolia*, for example, an osmotic pressure exceeding 150 atm. was observed, while the chlorine content was 64·4 gr. per litre (**Harris, Gortner, Hoffman, and Valentine,** 1921).

After investigating the differences between the great ecological groups, Harris next studied the physico-chemical properties of nearly related forms of cultivated plants. He and his collaborators investigated in detail two groups of cotton, Egyptian and Upland. The results showed that the varieties of Egyptian cotton differ from those of Upland in their osmotic pressure, their specific electrical conductivity, their chlorine and sulphate contents, and in their hydrogen ion concentration (**Harris, Z. W. Lawrence, W. F. Hoffman, J. V. Lawrence, and Valentine,** 1924; **Harris, J. V. Lawrence, and Z. W. Lawrence,** 1924; **Harris, C. T. Hoffman, and W. F. Hoffman,** 1925; **Harris, W. F. Hoffmann, Sinclair, Johnson, and Evans,** 1926). Thus it was proved that even closely related forms of crop plants may differ in their physico-chemical properties.

It must be noted, however, that even in the same plant the properties of the tissue fluids may differ in different leaves. In trees, leaves taken from the same specimen but at different heights above the ground showed different osmotic pressures (**Harris, Gortner, and J. V. Lawrence,** 1921). In *Betula lutea* Michx., for instance, the following depressions of the freezing point were observed:—

Height, in Feet, of Leaves above the Ground	
66	1·293
52	1·331
39	1·257
25	1·173
11	1·050

In nearly all cases the depression of the freezing point was greater in leaves inserted at a higher level, and the authors therefore hold the view that the osmotic pressure in the leaves of trees increases from a lower level upwards.

Harris also conducted a series of interesting researches on the physico-chemical properties of plant parasites and their hosts. The osmotic pressure of the tissue fluids was investigated in certain tropical Loranthaceae of Jamaica (**Harris and J. V. Lawrence,** 1916), and in desert Loranthaceae in Arizona (**Harris,** 1918[a]). It was found that leafless parasites have lower osmotic pressures than leafy ones, the osmotic pressure of the former (in Jamaica) being 14·2 atm., and that of the latter, 16·2 atm. Further, the osmotic pressure of the leaf-tissue fluids of parasites was, with few exceptions, higher than that of the leaf sap of their hosts. This was observed both in Jamaica and in Arizona. In the case of secondary parasitism the osmotic pressure increased from the host to the primary parasite, and from the primary parasite to the secondary one. For instance, the osmotic pressure of *Cyrilla racemiflora* (host tree) was 14·2 atm.; that of *Dendrophthora gracilis*, a parasite on *Cyrilla*, 15·2 atm.; while *Phthirusa parvifolia*, parasitic on the *Dendrophthora*, had an osmotic pressure of 17·9 atm. The data obtained for *Cuscuta*, however, were of an opposite character. The osmotic pressure in *Cuscuta salina*, a parasite on the extreme halophyte *Spirostachys occidentalis*, was 24·8 atm. to 27·0 atm.; while that of the host plant itself was as high as 38·5 atm. to 44·4 atm. The electrical conductivity and the chlorine content were also lower in *Cuscuta* than in its host (**Harris,** 1924).

The general conclusion to be drawn from the extensive investigations of Harris and his co-workers is that the physico-chemical properties of the tissue fluids of plants depend on (1) the influence of environmental factors and (2) the peculiarities of the respective species. With regard to the second condition, somewhat closely related forms may show marked differences in respect of these properties.

Harris has also elaborated a method of mass determination of the physico-chemical constants of expressed sap, and has drawn up tables which facilitate the correction of cryoscopic data for supercooling as well as the calculation of osmotic pressures (**Harris and Gortner,** 1914; **Harris,** 1915; **J. V. Lawrence and Harris,** 1925; **Harris,** 1925).

CHAPTER X

THE "EFFICIENCY OF TRANSPIRATION"

Transpiration as a test of xerophytism. The quantitative estimation of xerophytism. The "efficiency of transpiration" ("water requirement of plants") and drought resistance. The efficiency of transpiration and environmental conditions—atmospheric humidity; temperature; soil moisture; soil fertilizers; light.

Transpiration as a Test of Xerophytism

An examination of the physiological, anatomical, and morphological peculiarities of xerophytes leads us to the conclusion that the same result, i.e. adaptation to life in a dry habitat, may be attained in diverse ways. Within the group of xerophytes, therefore, several distinct and even contrasted types must be recognized.

Further study of plants of dry habitats in general, and of deserts in particular, has shown that the old definition of xerophytes as "plants of dry habitats exhibiting adaptations for a decrease of transpiration" (**Jost**, "*Vorlesungen über Pflanzenphysiologie*", 3e. Auflage, Jena, 1913) can no longer be accepted. The retention of the same definition in the new edition of this excellent textbook (**Benecke-Jost**, 1924) can only be regarded as a conservative adherence to tradition.

Kamerling (1914) investigated under natural conditions the rate of expenditure of water by various tropical plants of Java and Brazil. This author found that many plants usually regarded as xerophytes transpire daily not less than 100 per cent of their water content. This was the case with many typical xerophytes and maritime plants usually reckoned as xerophytes, e.g. *Eucalyptus*, *Spinifex squarrosus*, *Ipomoea pes-caprae*, *Tibouchina pilosissima*, etc. The thick covering of hairs peculiar to many of these plants did not hinder this loss of water. Kamerling, however, clinging to the traditional view, proposed to confine the term "true xerophytes" to plants expending not more than 2–10 per cent of their water content

daily: all other so-called xerophytes he regarded as "pseudo-xerophytes". If we were to revise the concept of xerophytism in this sense, then, according to Kamerling's data, only epiphytes, many succulents, and certain sclerophyllous trees of moist tropical forests could be classed as true xerophytes. Most of the plants actually growing in dry habitats would have to be referred to the group of pseudo-xerophytes. Apart from a certain crudeness and inexactitude in Kamerling's methods—inevitable under the field conditions of his experiments—I see no reason to doubt the reliability of his results. Granted, then, that these results are correct, his conclusions afford a good example of the absurd lengths to which a desire to uphold the dogma of the economical expenditure of water by "true xerophytes" may be carried.

Kamerling's paper provoked an interesting criticism by **Delf** (1915). **Delf's** own experiments (1912) had previously convinced her of the inadequacy of the traditional belief so far as halophytes are concerned. Her own view is that "xerophilous plants are those which with the help of certain structural modifications can continue to perform their normal vital functions when exposed to climatic conditions involving atmospheric or edaphic drought, or both". This cautious definition shows that Delf had abandoned the idea that a slow rate of expenditure of water is the one criterion by which xerophily may be judged.

Almost simultaneously with Kamerling's paper appeared one by **Bakke** (1914). This paper also will serve to illustrate how deeply rooted is the conviction in the minds of investigators that a close connexion exists between the intensity of transpiration and the degree of xerophytism. Bakke, one of Livingston's co-workers, using the quantitative cobalt chloride method described in Chapter II, determined the *index of transpiring power* of the leaves of a series of plants cultivated on the irrigated lands of the Desert Laboratory at Tucson. This "index" is the ratio of the rate of colour change in standardized cobalt paper placed over moist filter paper to

the rate of change in similar paper applied to the leaf surface. To some extent the *index of foliar transpiring power* (the term is due to **Livingston**) corresponds to Livingston's "relative transpiration".

Bakke regards this "index" as an apparently adequate expression of the degree of xerophytism or of mesophytism. He suggests that plants with an average index of foliar transpiring power below 0·30 should be classed as xerophytes, and above 0·70 as mesophytes. Those between 0·30 and 0·70 form an intermediate group of xero-mesophytes or meso-xerophytes. According to Bakke's determinations, *Viola odorata* (with an average index of 0·37) would be classed with *Panicum* (0·37) and *Sorghum* (0·35). *Rosa "Lamarque"* (0·19) and *Canna indica* (0·13) must be regarded as xerophytes, while the desert plant *Prosopis velutina* (0·61) stands close to the moisture-loving mesophytes. Such conclusions show once again that the intensity of transpiration affords little help towards a solution of the question of the degree of xerophytism of the plant.

Long ago, in my investigations in Tiflis on the physiology of xerophytes (see Chapter IX), I protested against employing the rate of transpiration as a test of xerophytism, pointing out that many xerophytes are characterized not by a low but by a high intensity of transpiration. Further, several Russian authors (**Maximov, Keller, and Zalenski**) have investigated various types of xerophytic vegetation in the south-east—Transcaucasia and Turkestan. These authors came to the general conclusion that such vegetation is exceedingly diverse and that there are no definite anatomical or physiological characteristics common to all desert and semi-desert plants. **Zalenski** (1920) pointed out that the so-called xerophytes fall into several biological groups, and that the intense development of some particular modification in a given xerophyte leads to the omission or weak development of others. For instance, the development of succulence is often accompanied by an absence of a peculiarity characteristic of thin-

leaved xerophytes, i.e. an increase in density of the venation. **Keller** (1924, 1925) is justified when he likens the not infrequent conception of a xerophyte as a combination of the peculiarities of different species, to an attempt to piece together the separate parts of diverse machines, all of which serve the same purpose. Accordingly, in his interesting textbook of general botany, Keller gives detailed descriptions of separate plants belonging to different types of xerophytes, instead of following the traditional method of enumerating the characteristics of a hypothetical xerophytic organization. Similarly, **L. A. Ivanov** (1923), in reviewing the present position of the question of drought resistance, comes to the conclusion that there are no peculiarities common to the group of xerophytes as a whole.

It is only recently that the views of Russian investigators have begun to be noticed in the literature of Western Europe. In the introduction to his extensive summary of the means of estimating the water balance of plants, **Huber** (1924) indicates that the conviction still prevails amongst Western European investigators that xerophytes are distinguished by a low rate of transpiration. "It was only last year",[1] he writes, "that **Maximov** (1923) had the temerity to protest against this use of the transpiration criterion. As a result of his extensive investigations on the vegetation of the Russian steppes, Maximov came to the conclusion that it is not a low rate of transpiration, but the capacity of drought resistance, that is, the ability to endure a considerable loss of water, which is the really characteristic feature of xerophytes" (pp. 2–3).

THE QUANTITATIVE ESTIMATION OF XEROPHYTISM

Huber himself, by a detailed consideration of the water economy (Wasserhaushalt) of the plant, attempted to find some

[1] In consequence of his lack of acquaintance with Russian literature, Huber has mistaken the year. My views, which contradict the current conception, were clearly formulated in the *Journal of the Russian Botanical Society* in 1916, but were only published in Western Europe in 1923.

general principle on which the degree of xerophytism (i.e. of adaptation to dryness of habitat) could be estimated. He rightly insists that such estimates must not be based on a single character, however important—e.g. the intensity of transpiration—but that all peculiarities shared in common must be taken into account. In particular, attention should be directed to any anatomical or physiological characters which facilitate the absorption of water from the soil.

Huber suggests a method of calculating the "water economy" of the plant, thus attempting to express the water relations on a quantitative basis. When functioning normally, the plant must maintain a certain balance between transpiration and absorption, and must be capable of making good any temporary water deficit. As the absorption of water is exclusively a function of the root system, one can assume that it will be proportional (other conditions being equal) to the mass of the roots on the one hand, and to the absorbing power per unit of root-mass on the other. Expressing this in the form of an equation, we have

$$A = mw \cdot \frac{A}{mw},$$

where A is the absorption of water by the root and mw the root-mass. With one and the same root-mass the absorption per unit of mass will depend on the development of the root surface $\left(\frac{flw}{mw}\right)$, as well as on any increase of absorption per unit of surface area $\left(\frac{A}{flw}\right)$ in consequence of an increase of the power of suction. We thus obtain the equation:—

$$A = mw \cdot \frac{flw}{mw} \cdot \frac{A}{flw}.$$

Huber further points out that the absorption of water depends not only on the power of suction of the root (aw) but also on the opposing water retaining capacity of the soil (ac).

Hence the expression $\frac{A}{flw}$ can be replaced by $K(aw - ac)$, where K is a constant.

Analysing in a similar way the elimination of water in the process of transpiration, Huber constructs the corresponding equation:—

$$T = ms \cdot \frac{T}{ms},$$

where T is the transpiration from the shoot and ms the leaf-mass (or the mass of the aerial organs in general). With the same leaf-mass, the transpiration per unit of mass will depend on the development of the shoot surface $\left(\frac{fls}{ms}\right)$ and the transpiration per unit of surface area $\left(\frac{T}{fls}\right)$. From this it is clear that a general reduction of the transpiration of a plant can be brought about either by a decrease of the rate of transpiration per unit area of surface or by a reduction of the transpiring surface itself.

The intensity of transpiration may be compared to that of root absorption, in that it depends not only on the properties of the evaporating surface, but also on environmental conditions—in this case on the atmospheric conditions affecting evaporation. Denoting the transpiration capacity per unit of leaf surface by t and evaporation by E, we obtain the equation:—

$$\frac{T}{fls} = E \cdot \frac{t}{fls}.$$

If we now combine the separate elements concerned in the water balance, we obtain a somewhat formidable equation which, according to Huber, proved serviceable in the analysis of the "water economy" of plants of various ecological types:—

$$\frac{A}{T} = K\frac{mw \cdot \frac{flw}{mw} \cdot \frac{aw - ac}{flw}}{ms \cdot \frac{fls}{ms} \cdot \frac{t}{fls} \cdot E} = K\frac{\frac{mw}{ms} \cdot \frac{flw}{mw} \cdot \frac{aw - ac}{flw}}{\frac{fls}{ms} \cdot \frac{t}{fls} \cdot E}$$

Translated into words, this equation indicates that the plant can the more readily maintain its water balance without deficit: (*a*) the relatively greater—the mass, the surface area, and the sucking power of the roots; and (*b*) the relatively smaller—the water retaining capacity of the soil, the evaporating power of the air, the area of leaf surface, and the evaporating capacity of the leaves. According to Huber himself, a serious defect of this equation is that absorption and transpiration are treated as two independent quantities, whereas in reality they are intimately connected with each other.

Simplifying his complicated equation Huber finally comes to the conclusion that in order to estimate the water economy of an individual plant or an ecological type it is necessary to know at least the following: (1) *For the estimation of absorption*—(*a*) the ratio between the weight of the roots and that of the aerial organs $\left(\frac{mw}{ms}\right)$; (*b*) the absorption of water per unit of weight $\left(\frac{A}{mw}\right)$—in practice, when there is a state of balance with no deficit, the intensity of transpiration per unit of root-weight can be substituted for this ratio; and (*c*) the osmotic pressure. (2) *For the estimation of transpiration*—(*a*) the degree of development of the transpiring surface, and (*b*) the transpiration per unit area of surface. The latter represents, as we have seen, the resultant of the evaporating power of the atmosphere and the transpiration capacity of the plant.

Such are the results obtained by Huber from his analysis of the water balance of the plant. Some of the quantities involved, for instance, osmotic pressure as a measure of the maximum power of suction, and transpiration per unit area of surface, have long been studied. These have been dealt with in the preceding chapters. Others, however, involve comparatively new ideas, and have hitherto been but little investigated. Huber has not only directed attention to these, but has carefully collected the meagre data already published, supplementing them in many cases by his own investigations.

Certain of the quantities dealt with by Huber do not admit of a strictly quantitative treatment. This is true, for instance, of the root-mass, which is proportional to the weight of the root system. The root system does not consist merely of absorbing roots, the greater part (especially as regards weight) in many cases being made up of the conducting tracts and the accumulated reserves. In this respect, the root-masses of annuals and perennials are very different, and cannot be compared so far as the water balance is concerned. It is not surprising, therefore, that data regarding root-mass did not yield very satisfactory results. Huber only succeeded in establishing that in drier, more open habitats, especially when poor in nutrients, the root system, relatively to the sub-aerial organs, is slightly better developed.

Huber attached great importance to the degree of development of the transpiring surface, that is, to the ratio between surface (measured in sq. cm.) and volume (in c.c.) in the sub-aerial organs. The surface area was measured in the usual way by printing the leaves on sensitive paper. To determine the volume of flat leaves Huber simply multiplied the thickness of the leaf by the surface area. The results of his measurements are given in the table (slightly abbreviated) on page 292.

Huber finds that, contrary to the opinion commonly held, the dissection or lobing of leaves does not materially increase the degree of development of the leaf surface, for in thin leaves the cross-sectional area is insignificant. For leaves in general the figure 200 is evidently about the limit of the degree of development of the transpiring surface.

Determinations of the root surface give approximately similar figures. Thus for the roots of oats (omitting the root hairs) the degree of development of the surface is about 200; for the roots of corn, which are thicker, from 70–120. Other cylindrical organs gave the following figures: shoots of *Casuarina*, 100 (i.e. higher than the leaves of most trees); shoots of *Genista radiata*, 40; acicular (needle-shaped) leaves of *Pinus austriaca*, 44 (sun leaves, 39, and shade leaves, 70); acicular sun leaves of the

spruce fir (*Picea excelsa*), 30—shade leaves, 40. The least development of surface is found in the spherical cacti, e.g. in a species of *Echinopsis*, 1·6, and in *Echinocactus ingens* even as low as 0·1; but these are extreme figures. For most leafy plants the degree of surface development varies between 40 and 200, the greatest differences observed being between sun and shade leaves, and between evergreen and deciduous plants.

TABLE XV

The Degree of Development of the Surface Area and the Thickness of Leaves in various Plants (according to Huber)

Species	Degree of Development of the Transpiring Surface	Thickness of Leaf in mm.
Prenanthes purpurea	200	0·10
Chelidonium majus	190	0·10–0·11
Oxalis acetosella	167	0·12
Fagus sylvatica (shade leaves)	153	0·13
Convallaria majalis	125	0·16
Syringa vulgaris	91	0·22
Quercus pedunculata (sun leaves) ..	84	0·21
Betula verrucosa (=*B. alba*)	84	0·21
Quercus ilex	70	0·28
Ruscus aculeatus (cladodes)	60	0·34
Helleborus niger	50	0·40
Ficus elastica	40	0·50
Nerium Oleander	38	0·52
Opuntia sp. (flat stems)	3	7·00

The humidity of the habitat has but an insignificant influence, being completely masked by that of the factors mentioned.

Huber's work need not be further considered in detail here; we shall have occasion to refer to it again when examining the concept of xeromorphic structure. Many of his considerations seem to me both interesting and important: they might, however, have been confirmed more fully and convincingly if he had been acquainted with Russian literature. At present I will deal only with his principal conclusions.

In the first place he contends—and this is in entire agreement with the views that I have consistently maintained—that when investigating the water balance of plants, succulents must not be taken into account. They form a special group which has little in common with other plants. During a considerable part of their life they obtain no water from their environment, their capacity of enduring prolonged drought depending wholly on the amount of their water reserves and the rate at which these reserves are expended. In these plants surface area and transpiration capacity are reduced to a minimum: the degree of osmotic pressure has little significance.

According to Huber, plants devoid of water-storing organs are characterized primarily by high osmotic pressures, for they must be capable of developing a power of suction not inferior to the water retaining capacity of the soil. Moreover, in order to supply its leaves with water, a plant must overcome not only the resistance of the soil, but also the internal resistance to the passage of water. In the case of xerophytes, therefore, the importance of reducing this internal resistance as much as possible is evident. Hence, according to Huber, these plants show a well-developed conducting system. So far as transpiration is concerned, Huber finds that in xerophytes it is not the absolute intensity of transpiration during the period of sufficient water supply which is important, but the decrease of transpiration as the deficiency of water in the soil increases. This decrease commences later in xerophytes than in mesophytes; therefore, at a certain stage in the progressive retardation of the water supply, xerophytes transpire more energetically than mesophytes. But as the wilting point is approached, xerophytes, on account of their thicker cuticle or other protective structures, can reduce their expenditure of water when the stomata close more efficiently than mesophytes.

Huber's main conclusions, as outlined above, were based more on theoretical considerations than on direct experimental data. His view is that the same result, i.e. the capacity for

maintaining the water balance during unfavourable environmental conditions, can be attained by different means: either by an increase of the power of suction, or by a reduction of the transpiring surface, or by a decrease of the transpiring capacity of the leaves. Many of Huber's statements agree closely with views I have expressed, many represent the further development of these views, and to most of them I readily assent. But in one important respect I do not altogether agree with him, namely, in what I regard as his exaggerated estimate of the importance of differences in the power of suction of the root system. These differences have considerable significance in saline soils, where the plants must oppose their power of suction to that of the concentrated soil solution. But they are of no importance in a dry soil, where, as we have seen in Chapter III, the water retaining capacity, after the wilting point is reached, rises at once to several hundred atmospheres, and cannot be overcome by any increase in the power of suction of the plant. Therefore, without altogether denying the significance of the peculiarities mentioned by Huber, I nevertheless continue to hold to my conviction that the chief distinguishing feature of xerophytes is their drought resistance—that is, their capacity of enduring permanent wilting without injury. During periods of prolonged drought no mere peculiarities of the water balance could suffice to ensure such endurance.

The Italian investigator **Catalano** (1920, 1921, 1923, 1924), too, has recently opposed the traditional conception of xerophytes as plants the principal physiological peculiarity of which is the extreme reduction of transpiration.

In one of his most extensive works (1921) **Catalano** attempts to give a rational definition of the concept of xerophily, and to work out a quantitative method by which the degree of xerophytism of different plants can be compared. Catalano points out that a comparison based on any one only of the following relations is inadequate: the intensity of transpiration; the water balance, i.e. the ratio between the absorption

and elimination of water; transpiration during wilting, i.e. under conditions of a cessation of water absorption. He maintains that in order to determine the degree of xerophytism, it is very important to study simultaneously both transpiration and the accumulation of organic substances in the plant (its "organication" according to Pirotta's terminology). These two functions are very closely connected: that is, intense assimilation is usually accompanied by intense transpiration. Conversely, when water is deficient, the plant sinks, as it were, into a peculiar state of lethargy, manifested by a complete cessation of nutrition and growth, and a reduction of transpiration to a minimum.

It would seem, therefore, that neither investigations of the component elements of the water balance, nor even a study of the water balance itself, can give us clear and simple criteria of the degree of xerophytism of a given plant. Thus we cannot hope, by a consideration of some one property or peculiarity, to be able to arrange plants in a linear sequence, according to their degree of adjustment to dry habitats.

THE "EFFICIENCY OF TRANSPIRATION" ("WATER REQUIREMENT OF PLANTS") AND DROUGHT RESISTANCE

We may now consider another series of attempts to find a quantitative expression of the degree of drought resistance of plants. These attempts—due particularly to agronomic investigators—are based on a study of the ratio between the amount of water expended and the dry substance accumulated by the plant during a given interval of time, usually the entire period of vegetation. This ratio, as we have seen in Chapter IV, has been variously termed *the transpiration coefficient*, *the water requirement of plants*, and *the efficiency of transpiration*. The first two of these are usually defined as the amount of water lost (or absorbed) during the growth period per unit of dry substance produced; in the third (**Maximov, 1917**) the ratio

is calculated as the amount of dry substance accumulated per kg. of water transpired. As this relation has often been compared with drought resistance, we may examine it somewhat more in detail, and inquire what it really represents, and how far it is determined by environmental conditions, and how far by the properties of the plant itself.

When once the concept of the transpiration coefficient had been formulated, the question naturally arose as to whether the value of this coefficient is or is not the same for all species of plants. The first experiments in this direction, carried out by **Hellriegel** (1883) under Central European conditions, seemed to point to a similar value in all cases. In nearly all plants investigated (barley, oats, wheat, rye, beans, yellow lupin, peas, red clover, buckwheat, *Brassica Napus*) the coefficient was approximately 1 : 300.

The data given in Hellriegel's classical work have formed for many years one of the foundation-stones of agricultural science. They gave rise to the belief amongst agriculturists that no great variations in the water requirement of different plants are to be expected. Later on, however, with the more detailed study of transpiration, somewhat sharp differences of opinion arose. For instance, **Schröder** (1895) distinguishes, in respect of their water requirement, two groups of cereals. The first group includes wheat, oats, barley, and rye, which require about 350 to 470 gr. of water for the production of 1 gr. of dry substance. The second contains millet, sorghum and corn—these require only 168–196 gr. per 1 gr. of dry substance. That is, the average water requirement of plants of the first group is 2·2 times that of the second. Schröder also found that in the crop plants of the first group—which, as we know, are distinguished by a lower capacity for drought resistance—the average intensity of transpiration was 2·5 times as great as in the second group. Thus there seemed to be some degree of correlation between the water requirement and the intensity of transpiration on the one hand, and the capacity of drought resistance on the other.

Schröder's data were later confirmed and extended by **Kolkunov** (1905), who also found that "the more the plant transpires per unit of dry matter produced, the more it transpires per unit area of leaf surface". At the same time, however, he remarks that "the question of the parallelism between the water requirement and transpiration per unit area still remains unsolved". But with regard to the general connexion between the efficiency and intensity of transpiration on the one hand and drought resistance on the other, Kolkunov concludes quite definitely "that the degree of xeromorphism of a given crop plant corresponds with its rate of transpiration . . . or, in other words, that the degree of adaptation to drought resistance may be expressed in terms of the relative value of its transpiration". Kolkunov traces further a close connexion between the rate of transpiration and the size of the stomata, and, indeed, of the cells in general. He correlates these anatomical and physiological peculiarities of cereals, and concludes that smallness of stomata and of other cells may serve to indicate a high degree of xeromorphism in a plant.

We shall return in Chapter XII to the connexion, suggested by Kolkunov, between drought resistance and the size of cells. This suggestion is not without interest, though its logical implications must be recognized as erroneous: it has indeed met with considerable opposition from and criticism by many investigators (e.g. **Yakushkina and Vavilov**, 1912). We have discussed above the question of a possible relation between the intensity of transpiration and drought resistance, and have come to the conclusion that if such a relation exists, it is in a sense opposite to that suggested by Kolkunov. We may now consider the available data regarding the relation between drought resistance and the efficiency of transpiration.

The most extensive and detailed investigations of the efficiency of transpiration of a large number of plants were carried out by Shantz and his co-workers (**Briggs and**

Shantz, 1914, 1917[b]; Shantz and Piemeisel, 1927) at Akron (Colorado), at one of the experiment stations of the Washington Department of Agriculture. The work was carried out during the years 1911–1917. In the first year 36 species and varieties of plants were investigated, in the second year 44, and in the third 55. The experiments were extended in 1914, 1915, and 1916 to include 68 sets of plants, but in 1917 this number was reduced to 29 sets. At the end of 1917 the experiments were discontinued. The data given in the first two publications refer to 132 sets of 6 pots each, and those in the third publication to an additional 47 sets of 6 pots each. In all, the experiments represent 288 sets of more than 1,800 pots. The plants were grown in large galvanized iron pots, each containing 115 kg. of soil, evaporation from the surface of the soil being prevented by means of closely fitting lids (Fig. 36). Each experiment was repeated six times. In the course of their investigations Briggs and Shantz carefully reviewed the literature relating to the water requirement of plants in a separate publication (Bulletin No. 285, 1913). This review gives most valuable information concerning the question of the efficiency of transpiration. The authors started with the assumption that the determination of the water requirement must be of great interest for agriculture in dry regions, as the plants capable of expending water most productively "must evidently be the best adapted to regions with a limited water supply".

Briggs and Shantz's determinations of the water requirement are summarized in extensive tables in their 1914 and 1917[b] papers, as well as in the 1927 paper. These data, in an abbreviated form and with some slight rearrangement, are reproduced in Table XVI on pages 300–3. The plants are arranged in three groups—A, cereals; B, other crop plants; C, native plants and widely distributed weeds. Group C consists exclusively of xerophytes, for only such plants can successfully develop on the Great Plains of America, the dry climate of which is in many respects similar to that of South-East Russia.

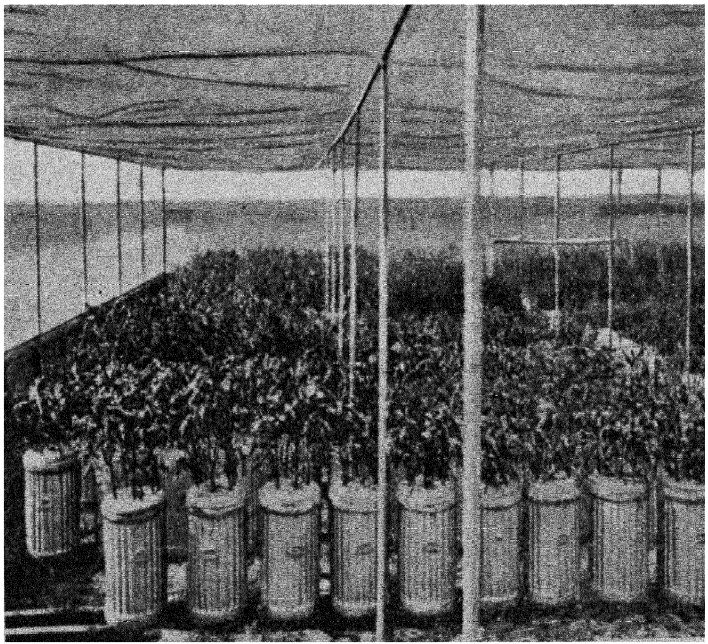

FIG. 36.—A general view of Briggs and Shantz's experiments for determining the water requirement of plants

The values of the transpiration coefficient or water requirement obtained by Briggs and Shantz for cereals entirely agree with the differences found by **Schröder** (1895) between millet, sorghum, and corn on the one hand, and wheat, barley, and oats on the other. The more xerophilous plants of the first group require little more than half the amount of water expended by crops of the more mesophilous second group. Here, however, the parallelism between drought resistance and the efficiency of transpiration ends. We find, for example, that *Agropyron* and *Bromus*—xerophytic plants of the first group —may expend as much as 1,035 and 977 gr. of water per 1 gr. of dry matter produced, while the water required by rice, a swamp plant, is considerably less, only 682 gr. Further, in other crop plants (group B) we find no correlation between the water requirement and drought resistance. If such a correlation exists, we must admit that cabbage (518 gr.) and buckwheat (540 gr.) are amongst the least exacting in respect of their water requirements. On the other hand, sweet clover (731 gr.) and yellow alfalfa (813 gr.), which approach the xerophytes in certain respects and develop well in the driest habitats, are some of the most exacting. Moreover, we should have to recognize a sharp difference in the water balance of such closely allied species as *Cucurbita Pepo* (802 gr.), and *C. maxima*, which expends only 719 gr. of water, or different varieties of potatoes and beans. Finally, in group C, there is a series of common steppe plants and weeds with a high water requirement, and it would be quite incomprehensible how these species can live side by side with others of the same group, with a requirement only a third as great.

Thus the experiments of Shantz and his co-workers did not confirm their original idea of a close connexion between the suitability of a species for cultivation in a dry region—in other words, its drought resistance—and the amount of water expended by it in the production of a unit of dry substance. The authors, however, do not definitely formulate this con-

TABLE XVI

The Water Requirement (and Efficiency of Transpiration) of various Plants[1] *(according to Shantz and L. Piemeisel).*

Plant	Latin Name	Water Requirement	Efficiency of Transpiration
A. CEREALS			
Millet			
Tambov	*Panicum miliaceum*	260	3·85
Black Voronezh	*Panicum miliaceum*	358	3·88
Kursk	*Chaetochloa italica*	274	3·65
German	*Chaetochloa italica*	278	3·60
Turkestan	*Chaetochloa italica*	368	2·72
Sorghum			
Minnesota Amber	*Andropogon Sorghum* var. *vulgaris* ..	274	3·65
Kafir	*Andropogon Sorghum* var. *vulgaris* ..	292	3·42
Kowliang	*Andropogon Sorghum* var. *vulgaris* ..	282	3·55
Milo	*Andropogon Sorghum* var. *vulgaris* ..	311	3·22
Durra	*Andropogon Sorghum* var. *vulgaris* ..	312	3·21
Sudan grass	*Andropogon halepensis* (*sudanensis*) ..	380	2·63
Corn			
Esperanza	*Zea Mays*	229	3·34
Indian Flint	*Zea Mays*	329	3·04
Laguna	*Zea Mays*	369	2·71
China white	*Zea Mays*	375	2·67
Teosinte	*Euchlaena mexicana*	375	2·67

Wheat			
Marquis	*Triticum vulgare*	550	1·82
Turkey	*Triticum vulgare*	455	2·20
Kubanka	*Triticum durum*	491	2·04
Emmer	*Triticum dicoccum*	517	1·93
Barley			
Hannchen	*Hordeum distichon*	523	1·91
White Hull-less	*Hordeum vulgare*	506	1·98
Oats			
Canadian	*Avena sativa*	529	1·89
Swedish select	*Avena sativa*	604	1·66
Sixty-day	*Avena sativa*	594	1·68
Other Gramineae			
Buffalo grass	*Bulbilis dactyloides*	296	3·38
Grama grass	*Bouteloua gracilis*	338	2·96
Rye, spring	*Secale cereale*	634	1·58
Rice, Honduras	*Oryza sativa*	682	1·47
Wheat-grass	*Agropyron desertorum*	678	1·47
Wheat-grass, western	*Agropyron smithii*	1035	0·97
Awnless Brome-grass	*Bromus inermis*	977	1·02
B. Other Crop Plants			
Sugar beet	*Beta vulgaris*	377	2·65
Buckwheat	*Fagopyrum vulgare*	540	1·85

[1 Shantz and his co-workers grew their plants inside a screened enclosure, which reduced the solar radiation to about 80 per cent of its normal value. Control experiments with freely exposed wheat, alfalfa, etc., showed that the enclosure reduced the water requirement about 22 per cent.—Ed.]

TABLE XVI

The Water Requirement (and Efficiency of Transpiration) of various Plants[1] *(according to Shantz and L. Piemeisel).*

Plant	Latin Name	Water Requirement	Efficiency of Transpiration
A. CEREALS			
Millet			
Tambov	*Panicum miliaceum*	260	3·85
Black Voronezh	*Panicum miliaceum*	358	3·88
Kursk	*Chaetochloa italica*	274	3·65
German	*Chaetochloa italica*	278	3·60
Turkestan	*Chaetochloa italica*	368	2·72
Sorghum			
Minnesota Amber	*Andropogon Sorghum* var. *vulgaris*	274	3·65
Kafir	*Andropogon Sorghum* var. *vulgaris*	292	3·42
Kowliang	*Andropogon Sorghum* var. *vulgaris*	282	3·55
Milo	*Andropogon Sorghum* var. *vulgaris*	311	3·22
Durra	*Andropogon Sorghum* var. *vulgaris*	312	3·21
Sudan grass	*Andropogon halepensis* (*sudanensis*)	380	2·63
Corn			
Esperanza	*Zea Mays*	229	3·34
Indian Flint	*Zea Mays*	329	3·04
Laguna	*Zea Mays*	369	2·71
China white	*Zea Mays*	375	2·67
Teosinte	*Euchlaena mexicana*	375	2·67
Wheat			
Marquis	*Triticum vulgare*	550	1·82
Turkey	*Triticum vulgare*	455	2·20
Kubanka	*Triticum durum*	491	2·04
Emmer	*Triticum dicoccum*	517	1·93
Barley			
Hannchen	*Hordeum distichon*	523	1·91
White Hull-less	*Hordeum vulgare*	506	1·98
Oats			
Canadian	*Avena sativa*	529	1·89
Swedish select	*Avena sativa*	604	1·66
Sixty-day	*Avena sativa*	594	1·68
Other Gramineae			
Buffalo grass	*Bulbilis dactyloides*	296	3·38
Grama grass	*Bouteloua gracilis*	338	2·96
Rye, spring	*Secale cereale*	634	1·58
Rice, Honduras	*Oryza sativa*	682	1·47
Wheat-grass	*Agropyron desertorum*	678	1·47
Wheat-grass, western	*Agropyron smithii*	1035	0·97
Awnless Brome-grass	*Bromus inermis*	977	1·02
B. OTHER CROP PLANTS			
Sugar beet	*Beta vulgaris*	377	2·65
Buckwheat	*Fagopyrum vulgare*	540	1·85

[1] Shantz and his co-workers grew their plants inside a screened enclosure, which reduced the solar radiation to about 80 per cent of its normal value. Control experiments with freely exposed wheat, alfalfa, etc., showed that the enclosure reduced the water requirement about 22 per cent.—ED.]

TABLE XVI—*continued*

Plant	Latin Name	Water Requirement	Efficiency of Transpiration
Potato, Irish Cobbler	*Solanum tuberosum*	499	2·00
Potato, McCormick	*Solanum tuberosum*	650	1·54
Cabbage	*Brassica oleracea*	518	1·93
Turnip	*Brassica Rapa*	614	1·63
Rape	*Brassica Napus*	714	1·40
Cotton, Triumph	*Gossypium hirsutum*	568	1·76
Water melon	*Citrullus vulgaris*	577	1·73
Cantaloupe	*Cucumis Melo*	527	1·68
Cucumber	*Cucumis sativus*	686	1·46
Squash	*Cucurbita maxima*	719	1·39
Pumpkin, common	*Cucurbita Pepo*	802	1·25
Cow-pea	*Vigna sinensis*	569	1·76
Chick-pea	*Cicer arietinum*	638	1·57
Bean, navy	*Phaseolus vulgaris*	656	1·52
Clover, sweet	*Melilotus alba*	731	1·37
Peas, garden	*Pisum sativum*	747	1·34
Vetch, hairy	*Vicia villosa*	587	1·70
Bean, horse	*Vicia Faba*	750	1·33
Vetch, purple	*Vicia atropurpurea*	899	1·11
Clover, red	*Trifolium pratense*	759	1·32
Clover, crimson	*Trifolium incarnatum*	606	1·57
Alfalfa, Peruvian	*Medicago sativa*	626	1·60
Alfalfa, Grimm	*Medicago sativa*	835	1·20
Alfalfa, Grimm	*Medicago sativa*	920	1·09
Alfalfa, yellow	*Medicago falcata*	813	1·23
C. NATIVE PLANTS AND WEEDS			
Tumbleweed	*Amaranthus graecizans* (=*A. sylvestris*)	260	3·85
Pigweed	*A. retroflexus*	305	3·28
Purslane	*Portulaca oleracea*	291	3·56
Thistle, Russian	*Salsola pestifer* (=*S. Kali*)	314	3·18
Cocklebur	*Xanthium commune*	415	2·41
Gumweed	*Grindelia squarrosa*	585	1·71
Sage, mountain	*Artemisia frigida*	654	1·53
Sunflower, narrow-leaved	*Helianthus petiolaris*	623	1·60
Sunflower, annuus	*Helianthus annuus*	577	1·73
Lamb's quarters	*Chenopodium album*	658	1·52
Marigold, fetid	*Boebera papposa* (= *Dysodia chrysanthemoides*)	847	1·18
Ragweed, western	*Ambrosia elatior* (= *A. artemisifolia*)	912	1·10
Franseria	*Franseria tenuifolia*	1131	0·88

clusion; indeed, in their 1914 and 1927 papers they refrain from any such generalization.

Notwithstanding the care and accuracy with which the experiments of Briggs and Shantz were carried out, a significant error was introduced, i.e. with the exception of tubers and other storage organs, subterranean parts were in most cases left out of consideration. This would lead to considerable discrepancy in the results, especially in the case of perennials. This source of error was admitted by most other investigators (except Schröder) who have determined the transpiration coefficient.

A less extensive series of investigations with thirty-two species only of crop and wild plants was carried out by **Maximov and Alexandrov** (1917), at the Tiflis Botanic Garden. Our object was similar, i.e. that of establishing some connexion between the efficiency of transpiration and drought resistance. We were particularly interested in the local xerophytes, as the study of these plants, in the hope of discovering the factors conditioning their drought resistance, was one of the chief problems undertaken in the laboratory which I founded in the beginning of 1914.

The experiments continued for three years. A summary of the main results obtained in 1915 and 1916 is given in Table XVII (opposite). The plants are arranged in order of increasing efficiency of transpiration.

An examination of Table XVII shows in the first place that plants with a low efficiency (upper part of table), i.e. not exceeding 1·5 gr. of dry substance per litre of water (water requirement not below 650), appear to be the most typical semi-desert xerophytes. Examples are—*Artemisia* spp., *Zygophyllum Fabago*, *Centaurea ovina*, and *C. solstitialis* (with a covering of gray hairs), *Helichrysum candidissimum* (white and silky), and *Euphorbia*, which usually covers dry slopes facing south, and which can resist the strongest drought. Not less characteristic is the fact that the lower part of the table also contains xerophytes; particularly drought resistant annuals such as *Salsola Kali*, *Amaranthus retroflexus*, *Portulaca oleracea*,

TABLE XVII

Transpiration Coefficient and Efficiency of Transpiration of various Plants (according to Maximov and Alexandrov)

Species	Transpiration Coefficient	Efficiency of Transpiration
In 1915		
Zygophyllum Fabago	741	1·35
Artemisia scoparia	705	1·42
Medicago sativa (England)	664	1·51
Medicago sativa (Turkestan)	641	1·56
Cirsium Acarna	574	1·74
Helianthus annuus	569	1·76
Gossypium hirsutum	462	2·16
Gossypium herbaceum	461	2·17
Wheat (*Poltavka*)	435	2·30
Salsola Kali	273	3·66
Corn (Bessarabian)	260	3·85
Corn (Imeretinian hybr.)	260	3·85
In 1916		
Cladochaeta candidissima (= *Helichrysum candidissimum*)	878	1·14
Brassica Sinapistrum (= *B. arvensis*)	870	1·15
Artemisia fasciculata	800	1·25
Centaurea ovina	767	1·30
Centaurea solstitialis	747	1·34
Artemisia fragrans	747	1·34
Euphorbia virgata	696	1·44
Zygophyllum Fabago	681	1·47
Phaseolus vulgaris	538	1·86
Verbascum ovalifolium	493	2·03
Helianthus annuus	469	2·13
Amaranthus retroflexus	345	2·90
Kochia prostrata	331	3·02
Portulaca oleracea	308	3·25
Panicum italicum (= *Setaria italica*)	302	3·31
Sedum maximum	292	3·42

and the crop plants millet and corn, the only perennials being *Kochia prostrata* and the succulent *Sedum maximum*. All these plants have an efficiency of transpiration exceeding 2·5 gr.,

the transpiration coefficient being less than 400. The remaining plants, which represent the mesophytic vegetation, occupy the middle part of the table, with an efficiency of 1·5 to 2·5 gr., and a transpiration coefficient between 650 and 400. Comparing these determinations with those given above (p. 269) of the intensity of transpiration by plants of different ecological types, we see that the plants which evaporate water most intensely use it less efficiently, the great expenditure of water not being compensated by a corresponding increase of assimilation. In this respect the results of our experiments confirm **Kolkunov's** supposition that there is some relation between the amount of transpiration per unit area of surface and the amount of water absorbed per unit of dry substance formed. It is interesting to note that the majority of xerophytes with a low efficiency of water expenditure possess very extensive root systems, far exceeding in length the sub-aerial portions of the plant. The thought naturally occurs to one that a powerful pump is necessary for the transport of water through these very lengthy root systems, and that energetically transpiring leaves may represent such a pump. On the other hand, members of the group of annual xerophytes with a high efficiency of transpiration are characterized by a relatively large leaf surface, which develops very rapidly (*Amaranthus*, millet, corn, *Salsola Kali*). It is natural to suppose that these plants possess a corresponding intensity of assimilation or—which is not quite the same thing—a pronounced capacity for the energetic accumulation of substance. Between these two groups of xerophytes are plants of a more mesophytic character. These exhibit a lower intensity of transpiration than the xerophytes of the first group, and a lower capacity of accumulating dry substance than the xerophytes of the second group. They therefore occupy an intermediate position as regards their efficiency of transpiration.

This intermediate group, which includes the majority of crop plants, may, so to speak, be invaded by representatives of both of the other more extreme groups.

A careful analysis shows that the plants investigated by **Shantz** can also be divided into three similar groups. Here, too, the majority of crop plants have an efficiency of transpiration between 1·5 and 2·5—that is, a water requirement between 500 and 700. The native steppe plants fall definitely into two groups: (*a*) those with an efficiency of 4–3 gr., and a water requirement of 300–400; and (*b*) with 1·5–1 gr. or 800–1,000. These extreme groups are connected by the sunflower, cocklebur, etc.—plants of a more mesophytic character. The millet cereals in these experiments also approach the second group of xerophytes.

Having thus established the lack of direct proportionality between the efficiency of transpiration and the degree of drought resistance, we cannot go to the opposite extreme and assert that the degree of efficiency affords no indication of the ecological character of a plant. On the contrary, owing to its relative constancy, the magnitude of the efficiency of transpiration affords one of the most satisfactory tests of the ecological status of a plant. It is, indeed, the expression of the correlation between two most important physiological processes—the accumulation of dry substance, and the expenditure of water.

In a short but very suggestive recent paper on drought resistance and soil moisture, **Shantz** (1927) to some extent summarizes his investigations, extending over many years, on the water requirement of plants and their relation to soil water. In this paper he returns to the classification previously suggested by **Kearney and Shantz** (1911). According to this classification, both the cultivated and native plants of the arid and semi-arid regions of North America may be divided into four ecological groups: (1) drought-escaping, (2) drought-evading, (3) drought-enduring, and (4) drought-resisting. The ecological characteristics of the various groups are briefly as follow.

(1) *Drought-escaping plants* grow only under favourable conditions of soil moisture content: by a short and rapid growth

period they ripen their seeds before the soil moisture is exhausted. They show little capacity to resist the desiccation of the soil. These plants form the group of desert ephemerals (see Chapter IX, p. 254). "Any plant which can withstand the extreme atmospheric condition when well supplied with soil moisture, and produce seed in a short period, would probably belong to this group, which includes some of the short-season field crops."

(2) *Drought-evading plants* are those which, either by restricting the amount of growth, or by the efficient and economical use of water, may delay the ultimate exhaustion of the limited supply of soil moisture and thereby evade early desiccation. According to Shantz, from a practical point of view this constitutes by far the most important group. To it belong most of the cereals grown in semi-arid regions, also the native plants which, either by wide spacing or by producing only small plants, conserve the soil moisture. Many of these plants have a low water requirement. Under natural conditions the water requirement may not be important, but in agriculture the quantity of yield is one of the first considerations. The plants included in this group by Shantz correspond to the group of xerophytes indicated by me (p. 305) as having an efficiency of transpiration exceeding (under the conditions of Tiflis) 2·5 gr. To the crop plants of this group belong millet, *Sorghum*, and corn.

(3) Shantz's third group contains the *drought-enduring plants*, largely the desert shrubs. Like drought-evading plants, they make very little growth in one season, and are usually small and widely spaced. When the soil moisture is reduced below the wilting coefficient the leaves wilt or dry *in situ*, or may be entirely shed. The plants, however, remain alive, enduring the drought and making no new growth until water is again available for the roots. For months they may be without any water available for growth, and then rapidly start growth on the addition of water. Most of these plants can endure long dry, hot periods. The characteristic vegetation of North

American deserts and semi-deserts is of the drought-enduring type.

In distinction to the foregoing group (2) drought-enduring plants are by no means always characterized by a low water requirement. On the contrary, to group (3) belong such plants as *Artemisia* and the wild alfalfa, with a water requirement attaining 1,000. Of the plants investigated by myself and Alexandrov, xerophytes with an efficiency of transpiration of less than 1·50 gr. belong to this group; also *Kochia prostrata*, a plant with a high efficiency of transpiration.

(4) Shantz's last group includes the *drought-resisting plants*. These plants resist drought by storing up a supply of water in their fleshy bodies, to be used when none can be obtained from the soil. By means of this stored water they may continue to grow for long periods, often flowering and ripening seeds, and even pushing their roots through the dry soil. The loss of water from plants of this type is always very slow, and the plant temperatures rise unusually high. To this type belong succulents, such as cacti and *Agave*, and many epiphytes. Plants of a non-succulent type, but with large water reservoirs in their stems or in their underground organs, e.g. many trees of the African grasslands, which spring into bloom before the rains, are also included by Shantz in this group.

It will be seen that Shantz's classification of plants growing in regions subject to drought is in many respects similar to that given in the foregoing chapter. But I cannot altogether agree with the inclusion of succulents amongst drought-resisting plants, because, thanks to their great storage and slow expenditure of water, succulents are immune from the potent influence of an internal water deficit. As we have already seen, these plants are lacking in such a characteristic feature of xerophily as high osmotic pressure.

The Efficiency of Transpiration and Environmental Conditions

We may now consider how the magnitude of the efficiency of transpiration depends, not only on the peculiarities of organization of the plant, but also on changes in the environment, and in particular on meteorological conditions and soil moisture.

So far as these external influences are concerned, the effect of the meteorological factors on the water requirement can be more precisely expressed, and therefore more readily studied. All authors who have made determinations of the efficiency of transpiration (or water requirement of plants) extending over many years, have observed that the figures expressing the efficiency fluctuate from year to year. These fluctuations appear to be the result of varying weather conditions. As a rule, in dry years the efficiency of transpiration is lower, that is to say, a larger amount of water is expended unproductively, than in wet years. This is shown by the experiments of **Shantz** and his collaborators, as well as by our own experiments in Tiflis, where the more humid year 1916 yielded higher figures for the efficiency of transpiration than the drier year 1915.

Shantz and Piemeisel (1927) have suggested a method of calculation by means of which water requirement determinations made in different years may be rapidly compared. The average value of the water requirement of a particular crop over the period of years in question is fixed at 100. The yearly values are then expressed as proportions of this average. The values thus obtained are treated as "index numbers", and the expression "points above" or "points below" used to express the *relative water requirement* of the crop for any given year. E.g. Alfalfa, average = 100; year 1911 = 124, i.e. the relative water requirement for 1911 is 24 points above; 1912 = 76, i.e. 24 points below; 1913 = 97, i.e. 3 points below; 1914 = 104, i.e. 4 points above, and so on. The authors claim that

this method of calculation gives a truer value for each year than could be obtained by averaging actual values.

The water requirement of certain crop plants was determined regularly for a series of years by **Tulaikov** (1915, 1922), at the Besenchuk Agricultural Experiment Station in South-East Russia. Table XVIII, which is taken from this author's 1922 work, shows the fluctuations in water requirement during the seven years 1911–1917. Of these 1911 and 1917 were the driest years, and 1913 and 1915 the wettest.

TABLE XVIII

Fluctuations in the Water Requirement during Seven Years at the Besenchuk Experiment Station (according to Tulaikov)

Year	Wheat Beloturka	Wheat Poltavka	Oat Giant	Barley Moravian	Millet Red	Corn
1911	576	628	655	618	443	437
1912	476	444	549	449	301	—
1913	316	339	347	280	256	146
1914	397	388	370	413	228	195
1915	302	316	293	288	198	160
1916	314	323	309	292	162	144
1917	464	467	478	337	280	350
Average	406·5	415·1	430·5	382·2	266·2	239·7

The fluctuations in the water requirement of different plants for the same years (1911–1917) at the Experiment Station at Akron, Colorado, are to be found in Table XXXIII of the above-cited work of **Shantz and Piemeisel** (1927).

Table XIX gives the results of experiments completed during a single year (1917), and carried out simultaneously in different localities, situated in different climatic zones. In order to ensure that the material used should be as uniform as possible, pure line seeds of selected varieties were distributed (from one centre) to the various experiment stations.

TABLE XIX

Water Requirement of Plants grown at various Experiment Stations in 1917 (according to Tulaikov)

Plant	Kostychev	Besenchuk	Saratov	Sumy	Leningrad
Wheat—Beloturka	469	464	349	346	237
Oats	523	478	414	391	292
Barley	508	337	374	—	302
Millet	244	280	219	175	151

These experiments clearly establish the fact that the water requirement increases on passing from west to east, from the moist climate of Leningrad to the dry climate of Saratov, etc. The highest efficiency of transpiration was at Leningrad, the lowest at the Kostychev Experiment Station, the difference between the two approaching 100 per cent.

In these experiments, whether carried out in different years at the same station, or in the same year at different stations, a similar difference is seen between the wheat-oats-barley group of cereals and the millet-corn group to that observed by **Schröder** (see above). The water requirement of the first group is invariably approximately twice that of the second.

The differences between the efficiency of transpiration of plants belonging to one and the same group, e.g. wheat, oats, and barley, and especially of varieties of these plants, appear to be less constant. For example, the efficiency of oats is sometimes higher and sometimes lower than that of barley, and so on. This leads **Tulaikov** to the conclusion that "the transpiration coefficient of plants, which is an expression of their water requirement during the period of growth, is an extremely variable quantity, fluctuating markedly from year to year in different countries, according to the climatic conditions obtaining during the vegetative period".

These fluctuations are generally so large that data obtained for one or two years only, particularly in countries with a

variable climate, are insufficient to denote the water requirement of a given species. The mutual relations of different species in respect of their water requirement may also vary considerably.

The dryness of habitats is due to several factors, each of which can have a different effect on the growth of the plant as well as on its transpiration, and consequently on its efficiency of transpiration. The principal factors are the temperature and humidity of the air and the soil moisture—in other words, the water reserve of the soil. Of factors which particularly influence the accumulation of dry substance, soil manures, which affect mineral and nitrogen nutrition, and light, which influences carbon nutrition, may be mentioned. In order to form a clearer idea respecting the causes of the fluctuation of the efficiency of transpiration in wet and dry years, we may briefly examine the influence of each factor separately. A great deal of valuable and interesting literature bearing on these questions is already available, and has been reviewed in detail by **Briggs and Shantz** (1913[b], II): only work not dealt with in this review need be considered here.

(*a*) *Atmospheric Humidity*

The factor which most clearly manifests its influence is undoubtedly atmospheric humidity. We have already seen that, other conditions being similar, the amount of water lost by the plant is proportional to the moisture deficit. But this deficit does not affect the intensity of assimilation, except indirectly when the plant is wilting, and the loss of water is accompanied by the closing of the stomata, and a decrease in the swelling of the protoplasm and the chloroplasts. Theoretically, therefore, it is to be expected that the efficiency of transpiration will be inversely proportional to the moisture deficit.

Briggs and Shantz's (1917) experiments at Washington, D.C., entirely confirm this supposition. These authors grew

nine kinds of agricultural plants in two plant houses, one kept dry and the other damp, the temperature being maintained as nearly as possible the same in both. The water requirement in the damp house was invariably less than in the dry house, the ratio of damp to dry fluctuating in different cases between 66: 100 and 80: 100 (Table XX).

TABLE XX

The Effect of Differences of Air Moisture on the Water Requirement, 1913 (according to Briggs and Shantz)

Plant	Water Requirement		Plant	Water Requirement	
	Humid Air	Dry Air		Humid Air	Dry Air
Kubanka wheat .	826	1052	*Grimm alfalfa* ..	906	1378
Hannchen barley	758	1037	*Kursk millet* ..	267	386
Spring rye ..	875	1100	*Red Amber sorghum*	223	297
Burt oats ..	760	1043	*Dent corn* ..	210	263
Honduras rice ..	585	743			

Even more pronounced differences were obtained by my co-worker, **E. Lebedintsev** (1927), who cultivated various plants in small glass chambers of half a cubic metre capacity. The atmosphere in one of the chambers was dried with the aid of calcium chloride, that in the other being continually moist. The average relative humidity in the dry chamber was 64 per cent and that in the humid chamber 94 per cent. The sunflower showed in the humid chamber an efficiency of transpiration of 11·3, in the dry chamber of 4·3: the ratio of dry to humid being 0·38. For soya beans the corresponding figures were 6·8 and 3·5: the ratio 0·51. For *Amaranthus retroflexus* 11·1 and 6·1: ratio 0·55. For *Xanthium Strumarium* 8·3 and 3·5: ratio 0·42. For *Phaseolus vulgaris* 9·5 and 5·2: ratio 0·55. Of all the plants investigated the sunflower is seen to be the most sensitive to a lowering of the humidity of the air, for

in the dry chamber its efficiency of transpiration is only about one-third of that in the moist chamber.

The results of these experiments on atmospheric humidity afford a general explanation of the differences in the efficiency of transpiration observed in the same plant in dry and moist years or in dry and moist countries respectively. But these differences, as we have seen above (p. 312), are far from being regular and constant. The key to these irregularities is to be found in the extremely interesting results obtained by **Briggs and Shantz** (1917[b]) in their study of the influence of temperature.

(*b*) *Temperature*

As we have seen, temperature affects transpiration indirectly, as one of the factors determining the moisture deficit. But temperature has also a great influence on the growth of the plant and on the accumulation of dry substance. Each plant, as we know, has its optimal temperature, at which these processes appear to be most energetic, and above or below which the rate of the process is slowed down.[1] In plants of warm climates this optimum is higher than in plants characteristic of cooler regions. In their experiments on the effect of temperature **Briggs and Shantz** used plant-houses with automatically controlled temperatures. In the cool house the temperature was maintained at about 10–13° C., in the warm house at about 27° C. As far as possible, all other factors, including air moisture, were the same in both houses. The table on the following page gives the results of this experiment.

We see from these data that plants of group (*a*) are prejudicially affected by high temperatures, and plants of group (*b*) by low temperatures. The water requirement of the cool-weather crops is, indeed, approximately doubled in the warm house, while that of the hot-weather crops is greatly increased

[1 For a critical examination of the concept of an "optimal" temperature for various physiological processes, see the important paper by **F. F. Blackman** (1905). Cf. also **Stiles** (1925, chap. vii).—ED.]

in the cool house—in the cases of rice and sorghum by four or five times.[1] In my opinion, it is necessary to take these results into account in interpreting the differences in the efficiency of transpiration in different years observed in experiments such as those at the Saratov and Besenchuk Stations. It must be remembered that dry years, particularly in the south-east of Russia, are distinguished not only by great

TABLE XXI

The Influence of Differences of Air Temperature on the Water Requirement, 1913 (according to Briggs and Shantz)

Plant	Cool House	Warm House	Ratio Cool/warm
(*a*) Plants of a cool climate:			
Kubanka wheat	385	826	0·47
Hannchen barley	298	758	0·39
Spring rye	423	875	0·48
Burt oats	403	760	0·53
Grimm alfalfa	429	906	0·47
(*b*) Plants of a hot climate:			
Dent corn	249	210	1·19
Kursk millet	429	267	1·61
Honduras rice	2566	585	4·39
Red Amber sorghum ..	1236	223	5·54

dryness, but also by very high air temperatures. This direct influence of temperature on the efficiency of transpiration and on the development of the plant and the yield in general, has not hitherto been sufficiently taken into consideration. On the other hand, the interesting investigations of **Zalenski** (1921) on stomata showed that "dry fog" and dry winds can be dangerous, especially if accompanied by high air temperatures, which interfere with the normal functioning of the stomata (see pp. 192 and 389).

[1 "North-western Dent, a variety of corn adapted to cool regions, showed little difference in the two houses" (**Briggs and Shantz**, 1917b, p. 12).—ED.]

(*c*) *Soil Moisture*

The influence of soil moisture on the efficiency of transpiration has been less studied than that of atmospheric factors. This is due partly to the more complex nature of the influence itself, and partly to the fact that there are considerable technical difficulties in organizing exact experiments. These difficulties are not always taken into account by investigators, with the consequence that the results obtained lose much of their importance. Soil moisture, as we have already seen, has a great influence on growth, and plants grown in containers with a high water content often have a transpiring surface 5–10 times as great as plants grown in soil with a low water content. The small dimensions of plants grown in dry soil are connected with the resistance offered by the soil to absorption of water by the plant. The result of the small transpiring surface is that the absolute amount of water lost by plants grown in containers with dry soil is very small in comparison with that transpired by plants in containers with damper soil. If now, as has been the case in many experiments, the surface of the soil in the containers is not protected from evaporation, the error due to direct loss of water from the soil (i.e. not transpired through the plant) may become disproportionately large. It is therefore essential in such experiments to use hermetically sealed jars (see Chapter VI).

A source of error considerably more difficult to eliminate is the irregularity in the distribution of moisture in the various soil layers. This irregularity is especially marked in containers with such low water content that the movements of water through the soil are retarded. On account of the small absolute losses of water from these containers, the quantity to be added from time to time is very small, so that only the soil in the immediate neighbourhood of the point of entry of the water is moistened. For this reason the roots of plants growing in containers with dry soil utilize only an insignificant volume of this soil. On the other hand, the actual water content of

this volume is not so low as if the water added became distributed uniformly through the entire volume of soil in the container. The result is that plants in such a dry soil suffer from a deficiency of nutrients as well as of water. In interpreting the results of an experiment of this kind it is often difficult to decide whether moisture or nutrition has been the cause of an observed difference in the transpiration coefficient.[1]

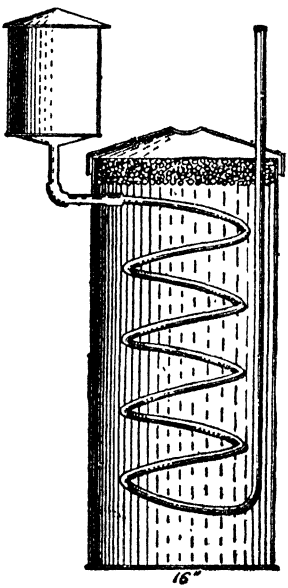

FIG. 37.—Plant container used by Montgomery and Kiesselbach, with an arrangement for the uniform moistening of the soil.

Very detailed and technically excellent water requirement experiments were carried out at the Nebraska Experiment Station by **Montgomery and Kiesselbach** (1912) and **Kiesselbach** (1916). In order to avoid the irregular distribution of soil moisture, and to allow of the normal development of such a large plant as corn, very large containers (40 × 90 cm.), holding nearly 125 kg. of dry soil, with a single plant in each container, were used. Uniformity of irrigation was secured by means of a perforated spiral brass tube buried in the soil of the container (Fig. 37). Evaporation from the soil was minimized by a layer of gravel 3 inches deep, above which was a galvanized-iron lid. Under such favourable conditions for growth, the maize plants were able to develop as freely as under field con-

[1 To obviate this difficulty, **Briggs and Shantz** (1917b, p. 7) adopted the method of growing a small plant in a large mass of soil, to which no water was added during the period of growth. Even so, the soil immediately surrounding the roots may have become more or less desiccated as the experiment proceeded, thus hindering the flow of water towards the roots. See pp. 80–82.—ED.]

ditions. The experiments were carried out with five different degrees of soil saturation, namely, 35, 45, 60, 80, and 100 per cent of the full water holding capacity. For each experiment the amount of available water was calculated, for this alone can convey a true impression of the conditions of water supply to the plant. These calculations were based on the determination of the wilting coefficient of the soil used for the experiment. The unavailable water proved to be 12 per cent of the air-dry soil. Table XXII shows the results of experiments carried out by Montgomery and Kiesselbach in 1910. In order to illustrate the effect of a reduction of soil moisture on the size of the plant, the table includes the average dry weight of the plants (four plants were used for each percentage of soil moisture), the average height and the average amount of water expended by one plant during the entire vegetative period.

TABLE XXII

The Influence of Different Percentages of Soil Moisture on Size and on the Efficiency of Transpiration in Corn (according to Montgomery and Kiesselbach)

Soil Moisture		Available Water in Percentage of Dry Weight	Total Amount of Water Transpired in kg.	Dry Weight of the Crop in gr.	Height of the Stem in cm.	Transpiration Coefficient	Efficiency of Transpiration
Percentage of Water holding Capacity	Percentage of Dry Weight						
35	13·5	1·5	28·2	111	51	253 ± 17	3·95
45	17·3	5·3	68·2	297	75	229 ± 7	4·37
60	23·1	11·1	105·7	443	93	239 ± 10	4·18
80	30·8	18·8	127·1	484	101	262 ± 7	3·82
100	38·5	26·5	108·1	372	100	290 ± 4	3·45

These experiments confirm the data of other authors regarding the progressive increase—up to a certain point—of the efficiency of transpiration with the decrease of soil moisture.[1]

[1 But see discussion in **Briggs and Shantz** (1913b, II).—ED.]

In this case the limit appears to be 45 per cent of the full water holding capacity of the soil, which corresponds to 5 per cent of available water. With a further decrease of soil moisture to a point where the available water was only 1·5 per cent, the water was spent less efficiently, as the plant suffered considerably in development. This is indicated by a marked decrease in dry weight and in height, and by a less uniform development of plants in different containers, as shown by a considerable increase of the probable error (the figures of probable error are given by **Briggs and Shantz**, 1913[b], II).

The decrease of yield with the decrease of soil moisture shows that the parallel increase of the efficiency of transpiration does not, in any case, compensate for the decrease of the total water expended.

From the foregoing it would seem clear that a high efficiency of transpiration by no means implies that the plant-body in general is well developed. The lessening output of water with decreased soil moisture is correlated with reduced assimilation and development of the plant. It is only with a decrease of soil moisture from 100 per cent to 80 per cent that the accumulation of dry substance increases simultaneously with the efficiency of transpiration. This indicates that an excessively high soil moisture is unfavourable to the development of the plant.

(*d*) *Soil Fertilizers*

In addition to soil moisture, the degree of fertility of the soil has a considerable effect on the efficiency of transpiration. In the first place, fertilizers influence the accumulation of dry substance. Many experiments have shown that, especially with poor soils, manuring increases considerably the efficiency of transpiration. This is evidently due to the fact that with a sufficient supply of mineral salts assimilation increases without a corresponding increase of transpiration. Further, indications are not wanting that manuring of the soil directly diminishes the intensity of transpiration, while in the absence of manures

transpiration increases (**Burgerstein**, 1876, 1878; **Reed**, 1910). These statements, however, require confirmation. As an example of the effect of manuring on the water requirement some experiments on corn by **Montgomery and Kiesselbach** (1912) may be cited (Table XXIII).

TABLE XXIII

The Influence of Conditions of Mineral Nutrition on the Water Requirement of Corn (according to Montgomery and Kiesselbach)

Soil	Average Dry Weight, in gr.		Water Requirement	
	Without Manure	With Manure	Without Manure	With Manure
Infertile	113	376	550 ± 16	350 ± 8
Intermediate	184	414	479 ± 11	341 ± 4
Fertile	270	473	392 ± 6	347 ± 6

We see that without the addition of manures the water requirement on a poor soil is considerably higher than on a fertile one, and that the effect of adding a full quantity of manure is very strongly marked with the poor soil, but only slight with the fertile soil. From this it is clear that in experiments on the efficiency of transpiration the nature of the soil must be taken into account. In order to obtain reliable comparative results it is necessary to use the same soil throughout a given series of experiments, or else to add such manures as will neutralize any effects due to differences of soil fertility.

(*e*) *Light*

Of the remaining factors that influence the efficiency of transpiration, the effect of light must be mentioned. Light affects transpiration and assimilation in the same direction, the effect being an accelerating one in both cases.

If the degree of acceleration were the same for both processes, the ratio between transpiration and assimilation would remain constant. But the influence of light on these two processes is not the same; therefore with varying light conditions the water requirement also changes. Up to the present, however, we have no very precise experiments, at least so far as determinations of the actual light intensities used (or the amount cut off by the screens employed) are concerned. Using screens of different textures, **Hellriegel** (1883) found the following mean changes in the water requirement of barley: in full light, 349; under a coarse screen, 483; under a medium screen, 519; under a close screen, 576.

The yield of dry substance decreased rapidly with the decrease of light, the corresponding averages in Hellriegel's experiments being 42·7 gr. (full light), 13·8 (coarse screen), 11·3 (medium screen), and 7·1 (close screen). It is therefore evident that even the coarsest screen markedly depressed the assimilation, in consequence of which the water requirement considerably increased.

In regions where clear weather prevails, and light is abundant, other results might well be obtained. Shade plants in particular would show an increase rather than a decrease in the efficiency of transpiration. Up to the present, however, we have no exact experiments in this direction, although they would undoubtedly be of considerable interest.

The study of the efficiency of transpiration can thus give us a great deal of very valuable information regarding the water balance, as well as the assimilation of the plant. But to obtain this it is indispensable not to limit oneself to an examination of the ratio between the yield of dry substance and the expenditure of water (which ratio is the efficiency of transpiration). The absolute values of the dry substance accumulated and of the water lost must also be kept continually in view. Some authors have attempted to express the drought resistance of the plant in terms of the value of the

efficiency of transpiration, and even to make this value a basis for the selection of drought resistant varieties of crop plants. The relation between transpiration and assimilation, however, is more complicated than this, and such attempts to simplify the relation are unjustified. As **Tulaikov** (1922) has rightly observed, the average values of the water requirement of plants are markedly divergent only in the case of strongly contrasted groups, as, for example, cereals of the wheat and millet groups respectively. Within the limits of these groups, and especially within the limits of the same species, the water requirement is very similar, but its approximate value may change from year to year. He is therefore of opinion that "the attempt to select a variety or race of any given species (wheat, barley, oats, etc.) that under all conditions of growth would be characterized by a strongly marked capacity to develop with a small amount of water, can hardly be successful".

Kiesselbach (1916) came to a similar conclusion in regard to the question of the selective value of the water requirement in plant breeding. Although he found that this coefficient fluctuated, in different varieties of corn, between 230 and 296, he was obliged to acknowledge that the varieties regarded as particularly drought resistant have a coefficient practically coincident with the average value for all the eleven varieties investigated.

Richardson's (1923) attempt to establish a definite correlation between drought resistance and the transpiration coefficient was also unsuccessful. This author carried out an extensive series of experiments with different plants at two experiment stations in Victoria (Australia). He found that different varieties of wheat differ very little in their water requirement, especially when this is calculated on the total dry weight. More pronounced differences were observed when the amount of water expended is referred to the weight of the grain. The absolute values of the transpiration coefficient obtained by Richardson were nearer to those found in Central Europe than to the values obtained in such dry regions as

South-East Russia and the Great Plains of North America. Over four years the average coefficients were as follow: for peas 344, barley 350, wheat 380, oats 390, mustard 414, rye 421, vetch 593, alfalfa 790. Simultaneously Richardson studied the influence of atmospheric and soil conditions—temperature, air and soil moisture, manures, etc.—on the values of the transpiration coefficient. His results were similar to those of other investigators.

CHAPTER XI

THE RELATIONS BETWEEN WATER AND LEAF STRUCTURE

Drought resistance and xeromorphic structure. The concept of xerophytism. Anatomical differences in leaves inserted at different levels on the stem. Physiological differences in leaves at different levels on the stem. Influence of water supply on leaf structure. Influence of light on leaf structure. Transpiration of "sun" and "shade" leaves. Influence of environmental moisture on the structure and water relations of plants: (*a*) atmospheric moisture; (*b*) soil moisture.

Drought Resistance and Xeromorphic Structure

The attempt to establish a direct connexion between drought resistance and either the intensity or the efficiency of transpiration has proved, as we have seen, a failure. The problem of drought resistance has turned out to be a very complicated one. The recognition, with more intensive study, of a great diversity of types of xerophytes, has rendered ambiguous the meaning of the term "xeromorphic structure", which until recently seemed so precise. Many xerophytes, and amongst them such common ones as *Artemisia* or *Peganum*, have proved not to be xeromorphic in the sense in which this term is used by the majority of investigators, i.e. possessing anatomical characters which secure a minimal transpiration. Many "xeromorphic" plants, such as evergreen trees and certain marsh plants, are peculiar to humid habitats and have but little capacity for drought resistance. It therefore becomes necessary to reconsider the concept of xerophytism.

The Concept of Xerophytism

Kamerling (1914), as mentioned above, distinguishes between "true xerophytes", with a low rate, and "pseudo-xerophytes", with a high rate of transpiration. **Montfort** (1918) goes still further, and suggests the following classes: (1) xeromorphic xerophytes, (2) non-xeromorphic xerophytes,

(3) hygromorphic xerophytes, (4) xeromorphic hygrophytes, (5) non-hygromorphic hygrophytes, and (6) hygromorphic hygrophytes. By xerophytes and hygrophytes he means plants growing in dry and damp habitats respectively. The terms xeromorphic and hygromorphic imply the presence or absence of characters tending to prevent an excessive loss of water. The very intricacy of this terminology seems to me indicative of an erroneous point of view, and to suggest that xeromorphy, or—which is really the same—a drought resistant structure, must needs involve a restriction of transpiration. As if plants had no other means of adjusting their water balance—for instance, by an increased water supply or by their capacity of enduring wilting!

The concept of a xerophytic or drought resistant structure can only acquire real significance when our preconceived ideas concerning the restriction of transpiration are laid aside, and the subject approached anew in an unbiased manner. What is required is to study side by side (*a*) the actual modifications of structure found in plants under conditions of a deficient water supply and high evaporation, and (*b*) the physiological peculiarities resulting from these structural modifications.

According to the well-known theorem of **Le Chatelier**, every change in the direction of an intensification of the environmental conditions influencing a body or a system of bodies, augments the resistance of the latter to a further increase of this influence. In Chapter IV, in discussing the influence of soil moisture on transpiration, we met with an instance of such an increase of resistance. In what follows I shall adopt the standpoint that such changes in plant structure as are induced by the intensification of those external factors which tend to increased loss of water actually augment the resistance of the plant to the effect of a further intensification of these factors. In other words, the effect of these factors is to increase the drought resistance of the plant. From this point of view the structural changes occurring in response to

dryness of habitat are changes in the direction of greater xeromorphy.[1]

The unbiased attitude referred to above was adopted by **Zalenski** (1904) in his remarkable quantitative-anatomical investigation of different leaves of the same plant. This investigation might well have become a turning-point in the history of the question, had it not been published in the Russian language only, and in a not readily procurable edition. For these reasons it remained unknown to a wide circle of non-Russian investigators, who subsequently (**Yapp**, 1912; **Heuser**, 1915; **Rippel**, 1919; **Rübel**, 1920) rediscovered the laws previously formulated by Zalenski.

It is necessary, therefore, prior to a further consideration of the question of drought resistance, to give a somewhat detailed account of Zalenski's results and conclusions. The starting-point of Zalenski's work was an observation made by him in 1901, that the network of veins in the leaves of plants growing in dry, open habitats is far better developed than in plants growing in woodland shade or, in general, under conditions of low evaporation.[2] This observation was directly opposed to the prevailing conviction that plants of dry soil were well protected against excessive evaporation, and therefore had no need of a rapid water supply. Conversely, it was supposed that in plants of damp soil adaptations for the increase of transpiration were to be expected. The fact that Zalenski's observations ran counter to the generally accepted view may possibly account for their having escaped notice,

[1 Practically the same point of view is to be found in **Kohl's** well-known *Die Transpiration der Pflanzen* (1886). On p. 95 he points out that dryness of air and other external conditions induce structural changes which tend to counteract the effect of these conditions on the transpiration of the plant—"die Transpirationsbedingungen bringen mit anderen Worten ihr eigenes Correctiv hervor". Kohl himself was no teleologist. —ED.]

[2 **Kohl** (1886, p. 115) had previously pointed out that the number and size of the conducting elements of the xylem of stems are closely correlated with the amount of transpiration from the leaves, and therefore with habitat and leaf size. The greater the transpiration the better developed the xylem.—ED.]

though they were published in a journal of such wide circulation as the *Berichte der Deutschen Botanischen Gesellschaft* (1902).

Anatomical Differences in Leaves Inserted at Different Levels on the Stem

When measuring the venation, Zalenski found that this was developed unequally in different parts of the same leaf, and in different leaves on the same individual plant. His first problem, therefore, was to ascertain the rules which govern the variations in the total length of the veins per unit area of leaf surface in relation to the height of insertion of the leaf on the stem. An exact quantitative measurement of the length of the veins in a considerable number of species showed that the higher the point of attachment of the leaf to the stem, the stronger the relative development of its venation, and conversely, the lower the leaf, the more feeble the development of the veins. This difference between the total length of the vascular bundles per unit area of leaf surface in the upper and lower leaves respectively of the same plant may be considerable. For example, in *Glyceria spectabilis* (= *G. aquatica*) the difference between the first and the seventh leaf (numbering the leaves from below upwards) was 98 per cent; in *Knautia arvensis*, between the first and the fifth leaf, 88 per cent; in *Cichorium Intybus*, between the first and the third leaf, 67 per cent, and so on. Further, the rate of increase in density of the venation (on ascending the stem) was greater in plants of exposed than in those of more sheltered habitats. On the other hand, in plants growing in deep shade, the upper and lower leaves sometimes showed no difference whatever in this respect. This difference in the density of the venation is illustrated in Figs. 38 and 39, reproduced from one of the photomicrographs in Zalenski's book. Fig. 38 shows the venation of a lower leaf of *Nicotiana rustica*, and Fig. 39 that of a leaf of the same plant, inserted 43 cm. above the soil.

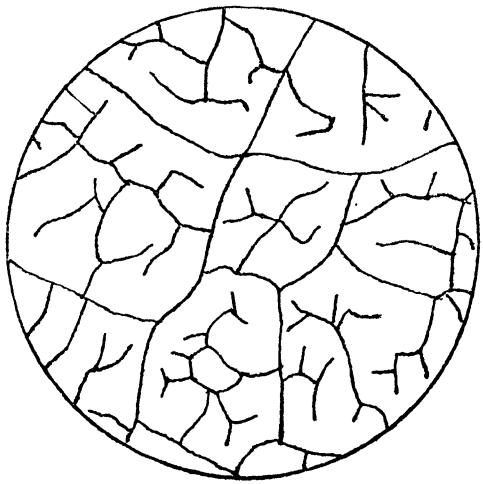

FIG. 38.—Venation of a lower leaf of *Nicotiana rustica* (after Zalenski).

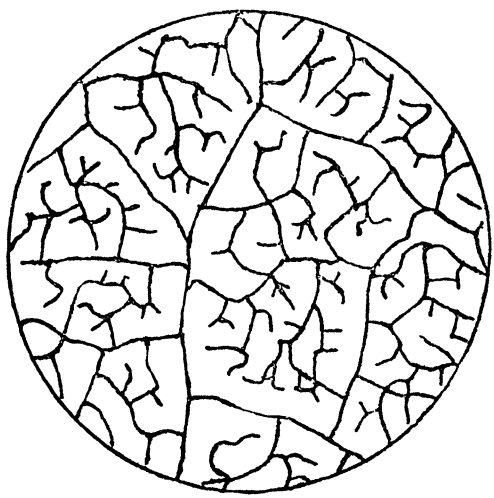

FIG. 39.—Venation of an upper leaf of *Nicotiana rustica* (after Zalenski).

In his search for the causes of such an unequal development of the venation, Zalenski undertook a detailed study of the other anatomical elements composing the leaf. The presence of a denser network of veins in the upper leaves might be the result of one of two causes: either it might be due to the smaller size of the mesophyll cells occupying the spaces between the veins, the quantitative relations between the number of leaf cells and the length of the veins being more or less the same per unit area of surface in all the leaves; or, on the other hand, the veins of the upper leaves might branch and anastomose more freely, the dimensions of the cells remaining the same. In the second case the numbers of cells enclosed in the meshes of the network of veins would be less in the upper than in the lower leaves.

In order to answer this question, Zalenski made a series of exact and minute measurements of the epidermal and mesophyll cells in different leaves of the same plant.

These measurements showed that the first alternative was in accordance with the actual facts. In fully developed leaves of a given shoot, the mesophyll cells were invariably smaller, the higher the point of insertion of the leaf and the greater its distance from the root system. The same rule applied also to the dimensions of the guard cells of the stomata, the epidermal cells, the hairs, and in fact to the cells of all the tissues of which the leaf is composed. As a result, the number of stomata per unit area of surface increased with the height of the leaf above the soil.

Further investigations of the mesophyll showed that in some cases the differences in anatomical structure of different leaves of the same plant were not only quantitative but also qualitative. In some plants palisade tissue may be absent from the lower leaves, but typically developed in the upper leaves of the same shoot. In other cases, the lower leaves are dorsiventral in structure, with palisade tissue on the upper and spongy mesophyll on the lower side, while the upper leaves have an isobilateral structure, with

palisade tissue adjacent both to the lower and to the upper epidermis.

Side by side with the variations in the dimensions of the cells, there are corresponding differences in the intercellular spaces. These become progressively smaller with increasing height of insertion of the leaf on the shoot.

Zalenski summarizes the results of his measurements of the various anatomical elements composing the leaf as follows. In comparison with the state of affairs in the lower leaves, the higher the leaf is inserted on a given shoot—

(1) the greater the total length of the vascular bundles (including the finest branches) per unit area of leaf surface;

(2) the smaller the dimensions of both the upper and the lower epidermal cells;

(3) the smaller the unicellular or multicellular hairs (if any);

(4) the smaller the stomata on both the upper and the lower sides of the leaf;

(5) the greater the number of stomata per unit area of leaf surface;

(6) the greater the number of hairs (if any) per unit area of leaf surface;

(7) the thicker the outer wall of both upper and lower epidermal cells;

(8) the less sinuous the lateral walls of the epidermal cells;

(9) the better developed the coating of wax (bloom), if any;

(10) the smaller the dimensions of all kinds of mesophyll cells;

(11) the more typical the development of palisade parenchyma;

(12) the less typical the development of spongy parenchyma;

(13) the weaker the development of the system of intercellular spaces;

(14) on the whole the stronger the development of mechanical tissues.

As an example, the variations of the different anatomical elements in a specimen of *Dactylis glomerata*, 64 cm. high,

gathered by Zalenski on September 4, 1902, on the outskirts of a wood, may be given (Table XXIV).

TABLE XXIV

Variations in the Anatomical Elements of Leaves of Different Tiers in Dactylis glomerata (according to Zalenski)

Tier of leaf	1st	3rd	5th	6th	7th
Height of insertion (in cm.).. ..	0	10·2	25·2	37·0	51·0
Length of leaf (cm.)	7·1	10·3	18·5	18·0	13·2
Breadth of leaf (cm.)	0·3	0·35	0·54	0·52	0·45
Length of vascular bundles (in mm. per sq. cm. of leaf surface) ..	371	511	557	625	626
Mean diameter of cells of upper epidermis (mm.)	0·0418	0·0294	0·0272	0·0217	0·0189
Number of stomata in field of view (upper side) ..	34	42	61	80	64
Length of stoma (mm.)	0·0434	0·0415	0·0403	0·0356	0·0384

In this instance the only deviation from the rules given above is in the number and size of the stomata of the uppermost leaf. In an overwhelming majority of cases, however, such deviations are not observed.

The result of Zalenski's measurements and observations is to establish the general rule that the anatomical structure of the individual leaves of one and the same shoot is, so to speak, a function of their distance from the root system. This rule may justly be called "Zalenski's law".

Zalenski further compared these variations in anatomical structure of the lower and upper leaves of the same shoot, with the structural peculiarities found in plants of damper and drier habitats respectively. We have already seen that this

author noticed very early in his work that the vascular network is denser in plants of dry habitats, as it is in the upper leaves of a shoot. Zalenski, therefore, concluded that the upper leaves of a shoot, as compared with the lower leaves, possess a more xerophytic or (more precisely) a more xeromorphic structure. This view is supported by the fact that the upper leaves have thicker outer epidermal walls, a thicker cuticle, a greater development of hairs, and so on.

Zalenski's work, as already mentioned, remained unknown to workers in other countries, and until comparatively recently no other account had been published of any systematic investigation of the structural differences of leaves at different levels on the same shoot. Only in **Sorauer** (1878) are indications to be found that in barley the upper leaves have more numerous vascular bundles per mm. of breadth than the lower ones, and that the structure of the epidermis differs in different leaves. Strictly speaking, **Yapp** (1912), in a detailed study of the structure of the marsh plant *Spiraea Ulmaria*, was the first to obtain data fully in accordance with those of Zalenski.

Yapp paid particular attention to the stomata in relation to the heights of insertion of successive leaves on the stem. On proceeding from the lower to the upper leaves, the stomata (as well as the ordinary epidermal cells) rapidly, and on the whole regularly, decreased in size and increased in numbers per unit area. He obtained the following very interesting figures when investigating a complete consecutive series of twenty-one mature leaves from a flowering shoot of *Spiraea*.[1]

[1 The dense pubescence of the stomatal surface of the majority of leaves of the type form of *S. Ulmaria* renders accurate counting of stomata impossible. For this series of stomatal counts, therefore, the nearly glabrous var. *denudata* was used. The lower, glabrous leaves of the type, however, show a similar rise in the numbers of stomata in successive leaves. Consecutive leaflets of tall radical leaves also obey the same rule of increasing numbers of stomata with increasing height of insertion on the leaf axis. The laws governing the distribution of hairs on the leaves and leaflets of *S. Ulmaria*—also a function of the distance of the part concerned from the root system, in other words, from the water supply—are given in **Yapp** (1912).—ED.]

The figures represent the numbers of stomata per sq. mm. of leaf surface: 393 (1st or lowest leaf), 303, 313, 322, 313, 352, 482, 440, 543, 678, 807, 776, 856, 945, 934, 928, 1,095, 1,188, 1,293, 1,083, 1,090 (21st or highest leaf).

With regard to other anatomical features, e.g. the dimensions of mesophyll cells, the degree of development of intercellular spaces, the size of the epidermal cells and the sinuosity of their lateral walls, the thickness of cuticle and the frequency and length of hairs, Yapp rediscovered practically the same rules as those formulated by Zalenski eight years previously.

TABLE XXV

Size of certain Anatomical Elements (in Micr.) in Leaves at Different Levels in Spiraea Ulmaria (according to Yapp)

Tier of leaf	Depth of Epidermal Cells		Size of Palisade Cells	
	Upper	Lower	Length	Diameter
2nd (from bottom)	22·0	15·5	30·0	15·5
18th* or 22nd†	15·5*	8·0*	19·0†	9·5†

On the whole, Yapp comes to the same conclusion as Zalenski, though independently of him, namely, that the upper leaves of a plant are more xeromorphic in structure than the lower ones. Yapp is inclined to attribute the observed differences of structure in part to differences of turgor in the cells of the lower and upper leaves, respectively, during development.[1] The upper, more xeromorphic leaves develop during the summer, and in a drier stratum of air (and therefore under conditions inducing greater transpiration) than the lower, less xeromorphic spring leaves. Yapp suggests, further, that the supply of water to the developing upper leaves may be diminished owing to "a partial deflexion of the water current into the continually increasing number of mature leaves".

[1 This suggestion is supported by the results of some as yet unpublished researches by **Yapp and Mason**; see footnote, p. 344.—ED.]

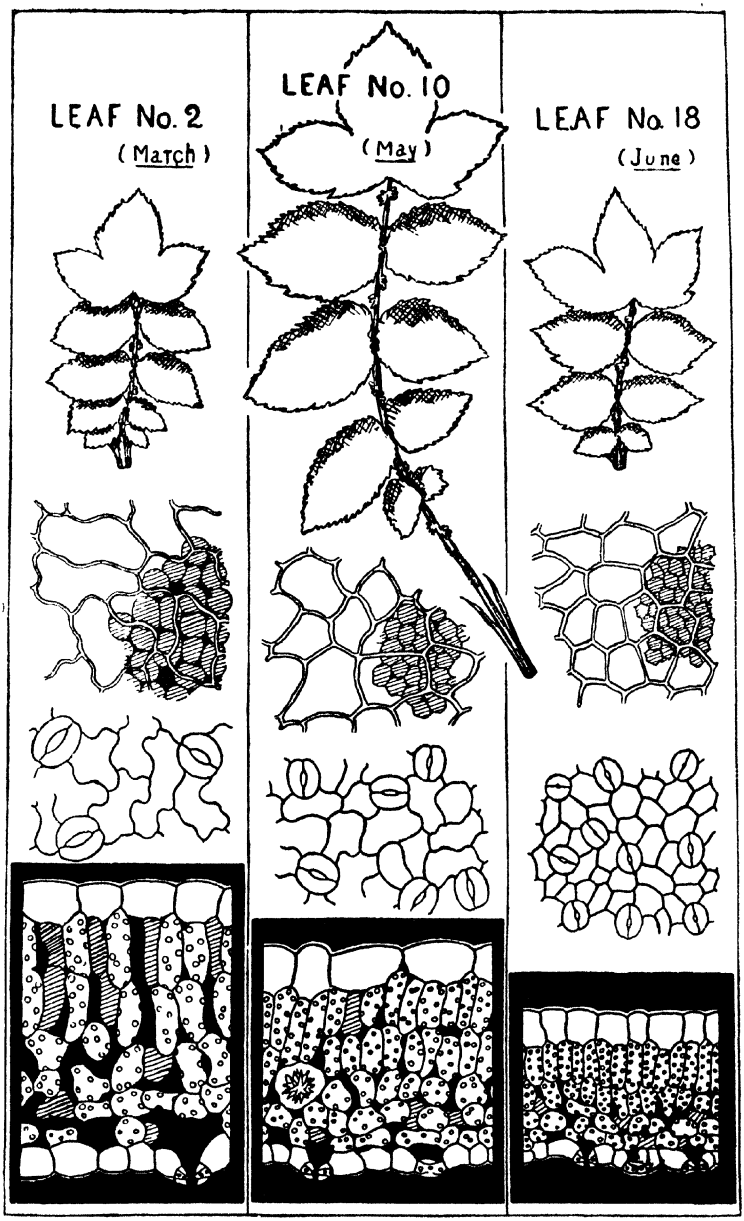

FIG. 40.—Three leaves from one flowering shoot of *Spiraea Ulmaria*. Under each leaf are shown (from above downwards): the upper epidermis with palisade cells and intercellular spaces showing through it from below; the lower epidermis with stomata, and a cross-section of the leaf lamina (from Yapp).

Zalenski, too, believes that the fundamental cause of the greater xeromorphy of the upper leaves may be the impeded supply of water to the latter, owing to water being intercepted by the lower leaves. But to us the facts themselves are more important than their interpretation. I have pleasure in reproducing one of the drawings from **Yapp's** paper (Fig. 40); this will serve as an excellent illustration both of this author's own work and of Zalenski's law, which has been enunciated above.

Subsequently Zalenski's results were further confirmed by the detailed work of **Heuser** (1915), who studied the relation between the structure of the leaves of wheat and their positions on the culm; also by **Rippel** (1919), in an investigation of the influence of soil moisture on the structure of the leaves of white mustard. We shall refer to these two works later.

Physiological Differences in Leaves at Different Levels on the Stem

The marked anatomical differences between the leaves of different tiers imply very important physiological differences. We have already learned from the work of Mme. **Krasnoselsky-Maximov** (1917) that there is an unequal distribution of water in the leaves of a plant, the water content being invariably greater in the lower leaves. This inequality is particularly marked in plants with somewhat fleshy leaves, such as *Zygophyllum*. In one experiment, during the period of maximum saturation (in the morning), the following results were obtained—the figures represent the water content in percentages of the *dry weights* of the leaves. In the uppermost leaves (of *Zygophyllum*), 362 per cent; four tiers lower, 377; six tiers lower, 443; seven tiers lower, 490; and eight tiers lower, 549 per cent. These data were subsequently confirmed by **Maximov and Krasnoselsky-Maximov** (1924). In the sunflower, during the period of maximum saturation, the figures obtained were: 7th tier (counting from below), 462 per

cent; 11th tier, 396; 14th tier, 365; and 16th tier, 357 per cent. In *Atriplex hortensis*, 2nd tier, 1,167 per cent; 3rd tier, 1,017; 4th tier, 862; 5th tier, 793; 6th tier, 698; 7th tier, 580; and in the 8th or uppermost tier, 537 per cent.[1] These very marked differences in the leaves at different levels on the same shoot show the necessity of very careful selection when variations in the water content of leaves are being investigated.

But though richer in water under normal conditions, the lower leaves readily give up much of this water to the upper leaves during wilting. A water deficit is thus established much sooner in the lower than in the upper leaves, especially in the early stages of wilting. In one of our experiments with *Atriplex*, in the first 24 hours of wilting the upper leaves lost only 13 per cent of their water content, and were still turgid: meanwhile the lower leaves had already lost 37–39 per cent, and were

[1 The above account of the distribution of water in leaves may be supplemented by a brief summary of some of the results (not yet published) obtained by **Yapp and Mason**, when investigating the effect on mature leaf structure of the degree of turgor during development (see also footnote, p. 344).

The following figures (which are percentages of the *fresh weights*) give the averages of many determinations of the water content of leaves inserted at different levels on the stems of plants growing in open beds, with freely exposed shoots. *Helianthus annuus:* 1st leaf (the lowest), 88·98 per cent; 2nd leaf, 87·69; 3rd, 87·19; 4th, 85·78; 5th, 84·97; partly expanded leaves, 83·81; unexpanded leaves just separated from terminal bud, 84·88; small leaves tightly enclosing bud, 85·80; terminal bud, including minute leaf rudiments and the actual stem apex, 86·14 per cent. *Vicia Faba:* 1st leaf, 89·21 per cent; 2nd, 88·56; 3rd, 87·63; 4th, 86·93; 5th, 86·63; 6th, 86·21; 7th, 86·03; 8th, 85·89; 9th, 85·54; partly expanded, 84·93; unexpanded, but separated from bud, 84·73; enclosing bud, 85·30; terminal bud, 85·88 per cent. Under normal conditions, so long as the oldest leaves have not passed their period of maximal functional activity, and new leaves are still being developed from the terminal bud: (1) The maximal water content is practically invariably in the lowest foliage leaf (in *Helianthus* in the cotyledons). (2) The water content of successive leaves steadily diminishes with decreasing age and increasing height on the stem (as found by Mme. Krasnoselsky-Maximov), till the minimum is reached in certain young, immature leaves. In *Helianthus* the minimum is usually in leaves which have reached approximately one-third to two-thirds of their full expansion, but in *Vicia* at a somewhat earlier stage, while the leaflets are still folded together (cf. footnote, p. 344). (3) The still younger leaves of the apical region show a steady *increase* in water content, rising to a secondary maximum in the apical bud. The only previous record of this secondary maximum in the youngest leaves was made by **von**

distinctly flaccid. Towards evening, other samples were taken from another specimen of *Atriplex*, which had begun to wilt at the same time as the first specimen, and was now in a completely wilted condition. By this time the lower leaves had lost 42–48 per cent of their water, while the uppermost leaves had lost much more than previously, namely 24 per cent. In the sunflower this more rapid loss of water by the lower leaves may ultimately bring about a reversed distribution of water in the leaves, and after prolonged wilting the upper leaves may contain as much or even more water than the lower leaves.

Similar results were obtained by Mme. **O. Alexandrov** (1925).

What is the cause of this greater loss of water by the lower leaves? Is it the internal translocation of water in the direction of leaves with greater powers of suction (see Chapter VIII),

Hoehnel (1878), whose data on this subject seem to have escaped the notice of most subsequent investigators.

It was further found that: (*a*) the average water content of the leaves of a plant decreases with its height and age; (*b*) as the oldest leaves die and the youngest approach maturity, the water content curve becomes less steep, and the positions of the maximum and minimum less definite; (*c*) other things being equal, young stems, petioles, midribs, and in general organs with a low ratio of surface to volume, have a considerably higher water content than organs (e.g. leaf lamina) with a high surface : volume ratio; (*d*) very young stems show, like leaves, decreasing water content with increasing height, but this gradient—as regards the basal regions—is soon reversed owing to secondary growth in thickness.

The explanation of these differences in the water content in various parts of the plant may be looked for, partly in factors affecting the water balance, and partly in structural and other factors which affect the relative amount of dry substance. As is brought out in the text, the water balance, especially during certain hours of the day, tends to be less favourable in the upper than in the lower parts of the plant. This, together with structural differences, such as the thinner leaves, with more numerous cell walls per unit volume, of the upper parts, and the vacuolation of the cells—increasing with age from above downwards—may go far to explain the general decrease of water content with increasing height above the soil. The effect of thick cell walls in reducing the relative water content is particularly well seen in the basal portions of the stem, where secondary thickening has taken place. The secondary rise to the apex (in the absence of vacuolation) may be attributed largely to lower transpiration owing to the less exposed positions of the youngest leaves. In the terminal bud itself these leaves practically become part of a stem-like organ, with a low surface : volume ratio.—ED.]

or simply the more intense transpiration of the lower leaves? The question of the rate of transpiration from leaves of different tiers thus becomes of considerable interest. According to the current view, the upper leaves being more xeromorphic than the lower should be better protected against loss of water, and should therefore show a less intense transpiration. From the opposite standpoint, however, developed in my investigations (**Maximov**, 1916, 1917, 1923), the upper leaves represent, as it were, a more powerful pump, and should therefore transpire more intensely than the lower.

Zalenski himself had planned and carried out some experiments on the transpiration of different leaves of the same plant. No results, however, were published for many years, so ultimately this work was undertaken by my colleague, **W. Alexandrov** (1922), at the Tiflis laboratory. In view of the importance of the problem, Alexandrov employed various methods of determining the intensity of transpiration. In the first place he experimented with leaves still attached to the stem of the plant, using the method of sucking air through a vessel containing the leaf (**Freeman**, 1908; see above, Chapter VI). These experiments were performed chiefly with sunflowers grown in beds, the containers with the leaves being protected by a white screen from the direct rays of the sun. Potted plants were also used, in which case the experiments were conducted in a light room. The results showed that under these conditions the upper leaves transpired much more vigorously than the lower ones. For example, in one experiment in the open, a sunflower leaf of the 10th tier transpired in one hour, 189 mg. per sq. dm. of surface; a leaf of the 18th tier, 245 mg.; and one of the 24th tier, 339 mg. An indoor experiment showed still more marked differences: a leaf of the 17th tier transpired 133 mg.; one of the 20th tier, 143; one of the 23rd tier, 490; and one of the 28th tier, 514 mg.

The results obtained by this first method were checked by weighing detached leaves with their petioles dipping into water. The object of this variation of the experiment was to equalize

the water supply, as it seemed possible that in the intact plant the unenclosed leaves might deflect water from those in the containers. The results of experiments with detached leaves, however, confirmed those obtained by the suction method. In one experiment, for instance, a leaf of the 7th tier transpired in one hour 130 mg. per sq. dm. of surface; a leaf of the 8th, 160; of the 9th, 320; of the 17th, 420; of the 18th, 760; and of the 20th, 540. Only the immature topmost leaf showed a certain, though insignificant, departure from the general rule.

Finally, in order to place the reliability of the results beyond question, they were tested by yet another method. Certain leaves of an intact, potted sunflower were enclosed in tinfoil —transpiration being thus prevented—while the remaining free leaves were allowed to transpire freely. By wrapping and unwrapping in turn the leaves of the upper and lower zones respectively, it was possible to compare the intensity of transpiration of the two sets of leaves without detaching any of them, and at the same time to employ that most satisfactory of all methods, the weighing of intact, rooted plants. In each experiment three leaves of a certain zone were left uncovered. The results entirely confirmed those of the previous experiments. In one instance the intensity of transpiration of the lower leaves was 310 mg., and that of the upper, 713; in another the figures were 480 and 670; in a third, 271 and 621. Experiments with *Atriplex* and *Ricinus communis*, in which various methods were again employed, confirmed the results of the experiments with the sunflower.

It was only after **Alexandrov's** experiments, carried out in 1916–18, were already completed, that **Zalenski** (1923) published a note on the results of some of his experiments on the same subject. He, too, found that the upper leaves of plants transpire considerably more water per unit area of surface than the lower leaves on the same shoots.

To complete our survey of the physiological peculiarities of the leaves of the upper as compared with those of the lower tiers, two further points must be mentioned. The first is that

the osmotic pressure is always considerably greater in the cells of the upper than in those of the lower leaves. This was first observed in succulents by **Pringsheim** (1906), who accounted for the internal translocation of water from lower to upper leaves during wilting, by differences of osmotic pressure. Subsequently, **Zalenski** (1911), when dealing with other peculiarities of the upper leaves of shoots, pointed out differences also of osmotic pressure. Finally, **Iljin and Soboleva** (1917) have shown that higher osmotic pressures, which are characteristic of leaves more distant from the root system, are found also in the distal portions of the leaf lamina (most remote from the water supplying petiole) as compared with the basal or proximal portions. Thus high osmotic pressures, which, as we have already seen, distinguish more xerophilous from less xerophilous plants, are also characteristic of those leaves, and even parts of leaves, which are most distant from the water supply.

The second point is that the intensity of carbon assimilation is, as proved by **Alexandrov** (1923), considerably greater in the upper than in the lower leaves. This physiological difference is correlated, at least in part, with differences of anatomical structure. This question, however, lies outside the scope of the present work.

We are now in a position to sum up the peculiarities by which the upper, more xeromorphic leaves are distinguished from the lower, less xeromorphic ones. From the anatomical point of view, the most important of these are: a denser network of veins, a more strongly developed palisade and less developed spongy mesophyll, the smaller dimensions of all anatomical elements, a greater number of stomata per unit area, and a thicker cuticle. The chief physiological peculiarities are: a higher osmotic pressure, greater suction pressure, more intense transpiration, more rapid supply of water to the transpiring cells, and a greater intensity of carbon assimilation. There now arise the questions of the causes of these wide differences between different leaves on the same plant and

even on the same shoot, and of the possibility of modifying the structure and properties of leaves by experimental interference.

Influence of Water Supply on Leaf Structure

The earliest observations and experiments in this direction were again due to **Zalenski** (1904). From the outset of his investigations he noticed that the differences of structure between the upper and lower leaves were the greater the drier the habitat. Conversely, in specimens gathered from deeply shaded and humid habitats, e.g. deciduous woodland, these differences tended to disappear entirely. From this he drew the conclusion that the differences of structure are in some way connected with increased loss of water. But the differential drying effect of different strata of the external atmosphere on the upper and lower leaves respectively is not in itself sufficient to account for the observed anatomical differences. Zalenski himself attributes far greater importance to the deflexion of water by the fully developed and transpiring leaves from the still growing tip (see pp. 334–6). To test this hypothesis he removed the already expanded leaves from several specimens of *Coleus*. The structure of the upper leaves which developed subsequently resembled that of the lower leaves in a looser network of veins, reduced number of stomata per unit area, and increased size of cells.

In this connexion it is interesting to note that "pollarding" of trees results in the production of leaves resembling lower rather than upper leaves in structure. On the other hand, the first leaves which expand after the transplanting of trees are smaller and more xeromorphic in structure than they would normally be. In the first case the developing leaves receive an increased, and in the second case a decreased, water supply.

More recently the connexion between the water supply of the leaf and its structure was traced in detail by **W. Alexandrov** and his collaborators, **O. Alexandrov and A. Timofeev**

(1921). These authors selected two rapidly growing species—one a tendril climber, *Bryonia dioica*; the other a twiner, *Ipomoea purpurea*. By removing all lateral buds, these plants were induced to grow to a length of 8 m., so that any changes in the number and size of the various anatomical elements could be readily followed. The most convincing results were obtained with the heliophilous plant *Ipomoea*. To modify the water supply, in one experiment all the expanded leaves of a particular plant were cut off on three successive occasions: on June 11th up to the 50th tier; on August 29th from the 51st to the 65th tier; and on September 25th from the 66th to the 80th tier. Within the limits of each of these three series of leaves, the anatomical elements changed in strict accordance with Zalenski's law, namely the size of the cells diminished, the number of stomata per unit area increased, and so on. On each removal of a series of leaves there was observed a more or less complete return to the original less xeromorphic structure, the leaves developed still later exhibiting a gradient of structure in conformity with Zalenski's law. It is, however, of interest to note that the first leaves to develop after the removal of those at a lower level were more xeromorphic in structure than those which followed them at a somewhat higher level. The leaves which developed immediately after cutting off the lower leaves had of course originated in buds with a restricted water supply, while the later leaves arose after the removal of the mature leaves which, *ex hypothesi*, were the cause of this restriction.[1] In *Bryonia*, on the first leaves developed after cutting, stomata of various sizes were noticed. The smaller of these stomata had probably already been formed before the lower leaves were cut off, while the larger ones must have developed under more favourable conditions of water supply.

Such is the profound influence exercised by the conditions of water supply on the structure of the leaf. A restricted water

[1 The results of these experiments are almost exactly parallel to some previously obtained by Yapp (1912, pp. 847–8) with *Spiraea Ulmaria*. In this case, however, the production or inhibition of hairs was the chief feature investigated.—ED.]

supply causes a more xeromorphic structure, while an increase in the supply, brought about by the removal of the lower leaves, leads to a more hygromorphic structure.

The structure of the leaf is deeply influenced, however, not only by the water supply, but also by the conditions of transpiration.[1] In this connexion it must be borne in mind that the upper and lower leaves of ordinary herbaceous plants develop under very different environmental conditions, a fact on which **Yapp** (1912) lays some stress. The upper leaves are more exposed to sunshine and to the drying effects of winds. But this difference of external conditions, as shown by the experimental removal of leaves, is of secondary importance as compared with the deflexion of the water current due to transpiration from the already expanded leaves. Hence in

[1 In the last analysis the influence on leaf structure of environmental moisture—irrespective of whether this affects the water supply or transpiration conditions—must be due to its effect on the water relations in the still immature cells of the developing leaves. Of these relations the degree, the duration, and, perhaps, the incidence of turgor are probably of prime importance. In this connexion two questions arise: First, at what stage or stages of development are the modifications induced by differences of turgor impressed on the leaf? Secondly, is the influence of the water factor a purely mechanical one, or is it, in any degree, of what may be termed a stimulatory nature? **Yapp and Mason** (see footnote, p. 337) have endeavoured to obtain light on these questions by determining the water content of leaves under various conditions and at different stages of development, special attention being paid to the apical region of the plant. These authors found that: (1) the *minimal water content* occurs, not in the youngest leaves, but in leaves which have already begun to expand (see footnote, p. 337). In such leaves cuticular transpiration is probably at its maximum and stomatal control slight or wanting. (2) Combining the results of all experiments with normally exposed, vigorous plants growing in open soil, the *greatest range of water content* (i.e. the difference between the absolute maximum and minimum) is found at the same stage of development as the minimal water content. E.g. *Helianthus:* 1st leaf (lowest), average water content, 88·98 per cent (of the *fresh* weight), range 2·98 per cent; 4th leaf, average 85·78, range 2·46; partly expanded leaves, average 83·81, range 7·19; just separated from bud, average 84·88, range 4·29; leaves enclosing terminal bud, average 85·80 per cent, range 3·51 per cent. In *Helianthus*, then, the lowest average and the greatest range are found in leaves which have reached about one-third to two-thirds of their full expansion: in *Vicia*, both occur in leaves just separated from the terminal bud. Although the absolute water content of an organ is not a sufficient criterion of the degree of turgor of its cells, these results indicate greater fluctuations of turgor in the leaves in question than in either the

studying the influence of external conditions it is more convenient to use leaves of different specimens, grown under different conditions, or in diverse natural habitats.

We may now proceed to examine the experimental and anatomical material at our disposal concerning the question of the influence of transpiration conditions on the structure and physiological peculiarities of plants, and especially of leaves.

We have seen that the intensity of transpiration depends mainly on two factors—the intensity of light and the moisture of the air, or, more precisely, the saturation deficit. Other factors such as temperature, air currents, etc., which are closely associated with the two mentioned above, are but of secondary importance. We shall therefore confine our attention to these

leaves still in the bud, or older, more mature leaves. (3) Although the average minimum and the greatest range of water content occur at a slightly earlier stage in *Vicia* than in *Helianthus*, there is evidence even in *Vicia* of a relatively low turgor in the unfolding leaves. In four sets of experiments normally grown shoots were enclosed about two days before the experiment in damp bell-jars, exposed plants being used as controls. On an average the leaves in damp air contained 2·13 per cent more water than the controls, but this increment was distributed unequally amongst the different leaves. The following figures give the average increases in water content in still, humid air as compared with ordinary air; the figures in brackets are the ranges observed in the experiments: 1st leaf (lowest), 1·74 per cent (2·91 per cent); 2nd leaf, 1·69 (3·11); 3rd leaf, 2·05 (3·04); 4th leaf, 2·40 (3·89); partly expanded leaves, 2·86 (5·30); separated from bud, 1·53 (4·33); terminal bud, 1·52 per cent (3·44 per cent). These figures show that under conditions tending to restore the water balance, the greatest increment of water (and therefore the greatest increase of turgor) occurs in the partly expanded leaves. The same fact is also indicated by the tendency, found in plants either grown or placed under conditions favouring high water content, for the position of the minimum to shift somewhat nearer the apex of the plant. (4) In simultaneous experiments with plants of various ages (raised from seeds sown at intervals of a week), the water content of unfolding leaves, *at the same stage of development*, on the whole decreases with the height of the plant. E.g. the following figures give the water content of leaves just separated from the terminal bud in five sets of vigorous, growing plants of *Vicia*: plants 20 cm. high, 85·66 per cent; 28 cm., 85·80; 43 cm., 85·25; 48 cm., 84·31; 66 cm., 84·16 per cent. Similar results were obtained with *Helianthus*. In these experiments unfolding leaves at the same stage of development, but at different levels on their respective stems, were compared. The results prove that during what is probably a critical stage of development the upper leaves contain less water than the lower—in other words, their cells

two chief factors, and especially light, the influence of which has been more thoroughly investigated.

Influence of Light on Leaf Structure

The anatomical differences between "sun" and "shade" individuals of the same species, and even between "sun" and "shade" leaves of the same individual, were first studied in detail by **Stahl** in his well-known 1883 paper. Stahl's observations were subsequently extended by **Pick** (1882), **Dufour** (1887), **Surož** (1892), **Nordhausen** (1903, 1912), **Hesselman** (1904), **Rosé** (1913), and others. One of the most

are less turgid. Under average conditions in nature, the differences may well be greater than those recorded here, for the lower leaves normally develop at a more humid season of the year than the upper.

So far as the first of the two questions propounded above is concerned, these results render it probable that the water factor influences leaf structure mainly during the actual expansion of the leaf—that is, at a comparatively late stage of development. It is while the leaf is enlarging after leaving the bud that the turgor of the still plastic cells is lowest and the fluctuations of turgor greatest. Any marked water deficit due either to external causes such as dryness of soil or atmosphere, or to internal causes such as resistance to flow or the amount of transpiring surface developed (both of which affect the upper more than the lower leaves), would produce its maximal effect at this stage. The critical stage of development, then, is probably the stage of cell enlargement. As regards the second question, it would seem that the water factor affects mature structure to a great extent mechanically, by influencing the degree of expansion of the individual cells, and therefore indirectly the thickness of their walls (cf. **Yapp**, 1912; also p. 374 of this book). Hence the smaller size of the cells, the denser network of veins and the more numerous stomata per unit area, in the upper leaves and in leaves developed under dry conditions. It may further be suggested that the epidermis, as the first tissue to be exposed, and to suffer loss of water by cuticular transpiration, is very probably the first leaf tissue to have the size of its cells limited in this way. Thus the epidermis, particularly perhaps in the case of a dry atmosphere, may play an active part in determining the final structure of the leaf. But in certain cases the water factor would appear to influence the form of cells and not merely their size. This phenomenon may be of a more complex nature. For example, the production of such elongated cells as epidermal and root hairs and palisade cells is in many cases accentuated by dry conditions. **Yapp** (1912, pp. 842–50) has suggested that in these cases reduced turgor may act as a stimulus, to which the cells respond, when turgor is again restored, by increased growth in length. As we have seen, the intermittent turgor here postulated is undoubtedly of frequent occurrence in developing leaves. Cf. this footnote, p. 344.—Ed.]

striking differences between "sun" and "shade" leaves is the prevalence of palisade mesophyll in the former and of spongy mesophyll in the latter. In other words, the mesophyll cells of sun leaves show a tendency to elongate in a direction perpendicular to the surface of the leaf. Correlated with this is the greater thickness of sun leaves. In sun leaves, too, the cells fit together more closely, the intercellular spaces being in consequence less voluminous. The number of stomata per unit area is greater, the conducting and mechanical tissues are more strongly developed and the cells of the epidermis have thicker walls. It is of interest to note that, according to **Nordhausen** (1903), these differences are not the result of the direct influence of light on the unfolding leaves but, at least in the case of trees and shrubs, are predetermined by the conditions of illumination (and transpiration) under which the buds were formed during the previous year. Nordhausen found that buds formed under shade conditions, if exposed to light in the following spring, develop leaves with a shade structure. Conversely, buds formed in strong light produce leaves of the sun type when subsequently transferred to shade.[1]

[1 **Nordhausen** (1903, p. 40) interprets his results as indicating that the ultimate size, thickness, and structure of the leaves formed during his experiments were to a large extent determined in the leaf rudiments while still enclosed in the bud. He postulates an *indirect* action of the environmental factors—in other words, he supposes that these factors exercise a delayed or after-effect on leaf structure. In other cases, however, notably in herbaceous plants, there is no doubt that the effect is *direct*. In my own experience, particularly as regards the effect of the water content of developing leaves (one of the most potent of factors), the mature structure of the individual leaf is largely determined at a relatively late stage, when the leaf is expanding after leaving the bud. There is little reason to suppose this to be otherwise even in the trees and shrubs with which Nordhausen worked. It should be borne in mind that in woody plants the unfolding shoots of the current year are separated from the absorbing parts of the root system by the perennial axes. The structure of these axes, including the conducting tissues of both stems and roots, has been influenced by the environmental conditions of the previous year or years. The water supply to the developing leaves of woody plants must therefore be affected by the structure of the xylem of these pre-existing axes to an extent which does not obtain in ordinary herbs. Hence, it appears to me, the true explanation of Nordhausen's results may well be looked for in the predetermined structure of the perennating portions of the plant, rather than in a delayed

These differences between sun and shade leaves have long been regarded as indications of the greater xeromorphy of sun plants. Several authors, including **Areschoug** (1882 and 1906), have even been inclined to regard the palisade tissue, with its closely fitting cells and intercellular spaces reduced to a minimum, as an adaptation for reducing transpiration, which is greatly intensified by direct insolation. This view seemed to receive confirmation from the observation of **von Hoehnel** (1879), that, other conditions being equal, shade leaves transpire more than sun leaves.

Transpiration of "Sun" and "Shade" Leaves

When, however, the question of the comparative transpiration of sun and shade leaves was submitted to the test of experiment (**Géneau de Lamarlière**, 1892), it was found that the intensity of transpiration of sun leaves was not less but considerably greater than that of shade leaves. Géneau de Lamarlière carried out his work under the direction of Bonnier in the famous "Laboratoire de Biologie végétale" at Fontainebleau, near Paris, from which have issued so many valuable researches on the influence of environment on the organization of plants. Géneau's work is remarkable for the painstaking thoughtfulness with which his experiments were conducted. He investigated all the main vital functions of both sun and shade leaves —assimilation, respiration, and transpiration. From the results obtained Géneau concluded that all these processes are carried on much more vigorously in sun than in shade leaves, at all events when calculated per unit area of leaf surface.

The intensity of transpiration, in particular, was investigated with the utmost care by no fewer than six different methods: (1) Sun and shade leaves of the same species were cut and immediately weighed; then laid side by side (without

effect (presumably of a stimulatory nature) of the environment on the leaf rudiments, while these are being laid down in the bud. The matter would repay further investigation from this point of view. See footnote, p. 346.—Ed.]

water) on white paper in the shade, and allowed to wilt. The leaves were again weighed after one and two hours. (2) The amounts of water absorbed by cut sun and shade shoots, fixed in potometers with graduated tubes, were determined, the respective leaf areas being ascertained at the end of the experiment. (3) The cut ends of leafy shoots were inserted into tubes of water and the joints sealed. The mounted shoots were weighed when set up and again after a few hours. (4) Still attached leafy twigs were covered by containers with tubes of calcium chloride and the water transpired calculated from the increase in weight of these tubes. (5) In this case Boussingault's method was employed. Entire sun and shade plants, grown in glass pots (the surface of the soil being sealed with a layer of mercury), were placed under two separate bell-jars, and a current of air (dried by sulphuric acid) drawn through the apparatus by means of an aspirator. Half of the stream of dry air was passed through each bell-jar and then through a calcium chloride tube. The water transpired was absorbed by the calcium chloride, the increase in weight of the two tubes enabling the transpiration from the sun and shade plants respectively to be calculated. Fig. 41 shows Géneau's somewhat complicated apparatus, which may be regarded as the prototype of what has been called (not altogether justifiably) "Freeman's method" (see Chapter IV). (6) The last, and, according to Géneau himself, perhaps the best method, was the weighing of entire rooted plants grown in watertight vessels. In order to prevent evaporation from the soil, the latter was covered with glass plates, luted to the vessels, with a single opening for the stem of the plant.

Géneau obtained consistent results by all six methods, i.e. other conditions being equal, the intensity of transpiration of leaves developed in the sun is greater than that of leaves developed in the shade. The following are the results of a few experiments. Method (1): sun and shade leaves of oak transpired during one hour, respectively, 170 and 110 mg. per sq. dm. Method (2): sun and shade leaves of beech, 240 and

110 mg. Method (3): *Ampelopsis hederacea*, 200 and 100 mg. Method (4): sun and shade leaves of yew (in 24 hours), 2,660 and 950 mg. Method (5): white lupin, 900 and 320 mg.

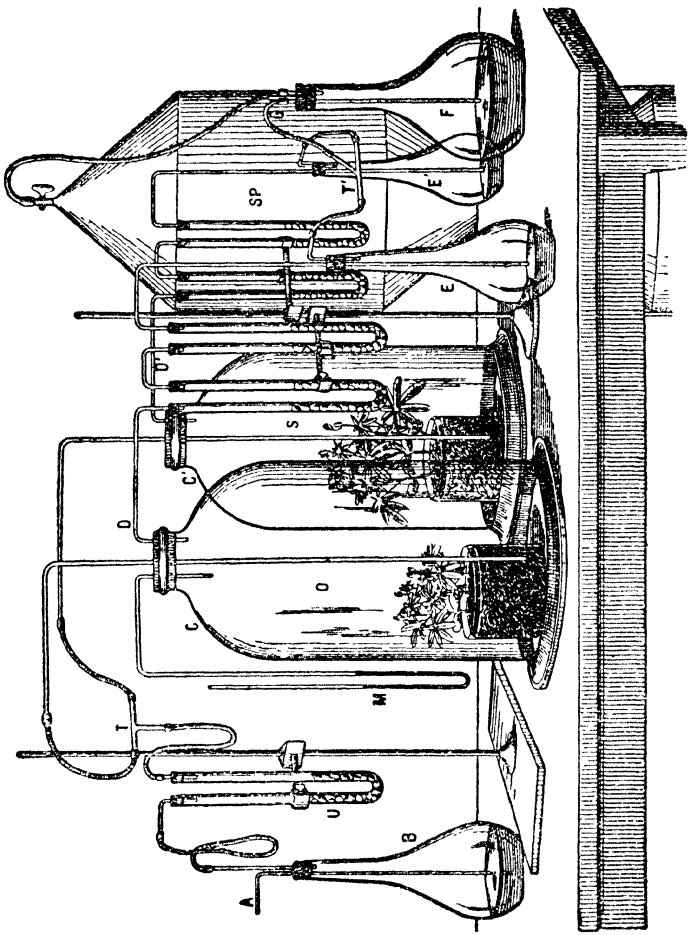

FIG. 41.—Apparatus used by Géneau de Lamarlière for the determination of the relative transpiration of "sun" and "shade" leaves.

Method (6): also lupin, 5,900 and 2,600 mg. In the last two cases the duration of the experiments is not specified. In all the experiments the difference between the transpiration of sun and shade leaves was very considerable, the sun leaves

not infrequently transpiring from two to three times as much per unit area as shade leaves.

Géneau's data, which were sharply opposed to the then prevalent, and still widely spread opinion that xeromorphic structure must necessarily lead to a restriction of transpiration, were received with considerable scepticism. In Part I of his well-known Monograph on Transpiration (1904, p. 57), **Burgerstein** wrote: "Dieser Befund von Géneau ist überraschend; denn es lässt sich a priori annehmen, und die Ergebnisse der Hoehnel'schen Versuche haben es gezeigt, dass Schattenblätter infolge der schwächeren Verdickung und Kutikularisierung der Epidermisaussenwände sowie infolge der grösseren Ausbildung der Interzellularen unter gleiche äussere Transpirationsbedingungen wie Sonnenblätter gebracht, grössere Transpirationswerte ergeben als letztere."

Notwithstanding Burgerstein's sceptical attitude, the data obtained by actual experiment at length prevailed against *a priori* opinions. Géneau's results were fully confirmed later by a whole series of investigations (e.g. **Hesselman**, 1904; **Sampson and Allen**, 1909; **Stocker**, 1923; **Kokhanovsky**, 1926). Only the recent detailed work of Frl. **Dietrich** (1926) need be discussed here.

The aim of Frl. Dietrich's work, which was carried out in Fitting's laboratory, was twofold. First, to ascertain in what degree and in which direction the transpiration of sun species (heliophilous plants) differs from that of shade species (heliophobous plants). Secondly, to investigate the differences between the transpiration of sun and shade specimens of the same species. From the results it was hoped to determine the extent to which the differences between sun and shade species are the result of the direct influence of environmental conditions. Fourteen species of shade plants were investigated, but only six sun species, as it was chiefly the behaviour of shade plants which was taken into consideration.

Determinations of the rate of transpiration *per unit of leaf surface* showed that it is always notably higher in heliophilous

than in heliophobous plants. This was the case whether the experiments were carried out in the shade or in the sun, and whether sun or shade specimens were used in the experiments. But if individuals of the same species, grown under different conditions, were taken, the results were more complicated. Specimens grown in the shade transpire more under shade conditions than do sun specimens. But when transferred to sun conditions, sun specimens transpire more than shade specimens. This is due to the fact that when both kinds of individuals are transferred from shade to sun conditions, the intensity of transpiration of the sun specimens is increased to a greater extent than that of the shade specimens.

Dietrich also determined the rate of transpiration *per unit of fresh weight*. On this basis she found that under shade conditions the rates of transpiration of sun and shade species are nearly the same, though in some shade plants the rate is even higher than in sun plants. But under sun conditions the rate of transpiration of sun plants is always higher than that of shade plants.

Dietrich's investigations, then, have not confirmed **Schimper's** (1898) view that shade plants possess peculiar adaptations for increasing transpiration. On the contrary, they fully agree with my results (1916, 1923) and with those of **Stocker** (1923) and **Keller** (1925), according to which the intensity of transpiration of shade plants is lower than that of sun plants. This physiological feature has thus been shown to be a fixed genetic character of heliophilous and heliophobous species, as well as one induced directly by the environmental conditions in sun and shade individuals of the same species.

The greater loss of water from sun plants naturally implies an increased demand for water from the root system. **Maximov and Lebedintsev** (1923) have shown that the root system meets this increased demand by a stronger development, though of course light cannot exercise a direct influence on underground roots. The action of light manifests itself not only in the greater vigour of the roots of sun as compared

with those of shade plants, but also in the fact that an intensified growth of the root system takes place when the plant is transferred from shade to light. At the same time there is an increased development of conducting elements in the axial organs of the plant. For example, in one experiment with beans, the dry weight of the roots per sq. cm. of transpiring surface was only 0·34 mg. in shade individuals, but 2·39 mg. in sun plants. Shade plants transferred to the light a fortnight previously, already showed 1·10 mg. per sq. cm. of leaf surface.

Comparing these data with the relative lengths of the vascular bundles per unit area, we see that the cells of the mesophyll are under far less favourable conditions as regards water supply in shade than in sun plants. Mlle. Lebedintsev has shown that in sun leaves of the bean the length of the veins is 2 to 2·5 times as great per unit area as in shade leaves. Thus, in one experiment, the lowest leaf of a sun individual had 683 mm. of veins per sq. cm. of surface, that of a shade plant 515 mm.; the second leaves (from below), 929 and 555; the third, 1,143 and 611; the fourth, 1,254 and 548. It is interesting to note that the density of the network increases markedly in the upward direction in sun plants, but remains almost stationary in shade individuals. Therefore the translocation as well as the absorption of water in shade plants must be considerably impeded. This accounts for the fact—which Burgerstein regarded as paradoxical—that the thin and tender leaves of shade plants transpire less water than the "better protected" leaves of sun plants. It is the deficient water supply rather than intense transpiration that explains the readiness with which shade plants wilt.[1] This insufficient water supply produces what **Zalenski**, in one of his

[1 It should, however, be borne in mind that the deficiency of water referred to is experienced by shade plants mainly when they are experimentally transferred to more strongly insolated conditions. So long as they remain in the habitat in which they developed, the roots and conducting system of shade plants are no doubt just as adequate to supply their needs as are those of sun plants.—ED.]

latest publications (1920), has termed "internal physiological dryness".

Huber (1924[c]), in his survey of the water relations of plants, paid much attention to the water supply of sun and shade plants. Pointing out that for heliophilous plants, which live under conditions of intense water loss, the capacity of transferring water rapidly to the evaporating cells is of great importance, Huber calculated the conductivity of the xylem in sun and shade branches of the oak, and compared this with the amount of water transpired. He obtained the following interesting results. The intensity of transpiration per sq. dm. per hour in a sun branch was 75·7 mg., and in a shade branch about a third less, i.e. 45·9 mg. On the other hand, the cross-sectional area of the conducting elements (the "conducting area" of Huber) per sq. dm. of leaf surface in the shade shoot was half that in the sun shoot, i.e. 0·20 and 0·42 sq. mm. Therefore the respective amounts of water crossing 1 sq. cm. of "conducting area" in one hour must be 18·0 c.c. in the sun branch and 22·5 c.c. in the shade branch. In other words, in spite of the feebler transpiration of the shade shoot, the rate of flow of water in its vessels must be greater, and in consequence the resistance to flow also greater, than in the sun shoot. No wonder, then, that with increased need of water, e.g. in direct insolation, shade leaves wilt more readily than sun leaves, in spite of a lower absolute water loss.

Similar results were obtained somewhat earlier by **Rübel** (1920). For sunflowers grown in the sun he found an average transpiration capacity of 0·77, and for shade specimens 0·49. The average "conducting area" for sun individuals was 0·174 sq. mm. per sq. dm. of leaf surface, and for those grown in shade only 0·095. Rübel, too, found that in regard to the amount of water passing unit cross-sectional area of xylem in unit time, the advantage lies with the sun plants—in the ratio of 100:116.

I have dealt with the peculiarities of sun and shade plants in considerable detail, because light conditions are so closely

connected with the water relations of the plant. An arid climate is almost invariably characterized by a large preponderance of clear days, and consequently by intense insolation. Moreover, the almost complete absence of trees, together with the sparseness of the vegetation, permits the scorching rays of the sun to penetrate even to the lower leaves of the plants. Xerophytes are therefore simultaneously heliophytes, as **V. L. Komarov** puts it, and no doubt many features of their organization depend on the light conditions under which they have to live and develop. It may be said without exaggeration that in steppes, deserts, and semi-desert regions, the only living shade plants to be found are those dwelling in deep clefts of the rocks.

There is nothing inherently improbable in the suggestion that certain features commonly found in xerophytes, and hitherto regarded as paradoxical by many authors, e.g. a high intensity of transpiration or a great development of the root system, are really heliophilous rather than xerophilous characters. It is still difficult, if not impossible, to draw a hard and fast line between the two, for under natural conditions intense light is almost invariably associated with dryness. Even under experimental conditions, the influence of these two factors cannot always be successfully separated.

The exact quantitative correlation between light intensity and the anatomical structure of the leaf can be ascertained only by the use of artificial illumination, as natural daylight is too variable to be measured accurately. The introduction into laboratories of electric lamps of sufficient power to ensure adequate carbon assimilation and to permit of the growing of plants under artificial illumination (**Harvey**, 1922; **Maximov**, 1925) opens wide possibilities. One such preliminary experiment was conducted by myself in January 1925, in a greenhouse at the Leningrad Botanic Garden. Bean plants were grown at different distances from an electric lamp of 2,000 candles. Fig. 42 shows the structure of the leaves of two of the plants, one of which (A1) was grown at a distance of

1 metre, and the other (A2) at 3 metres from the lamp. The differences in structure are very marked. In the more

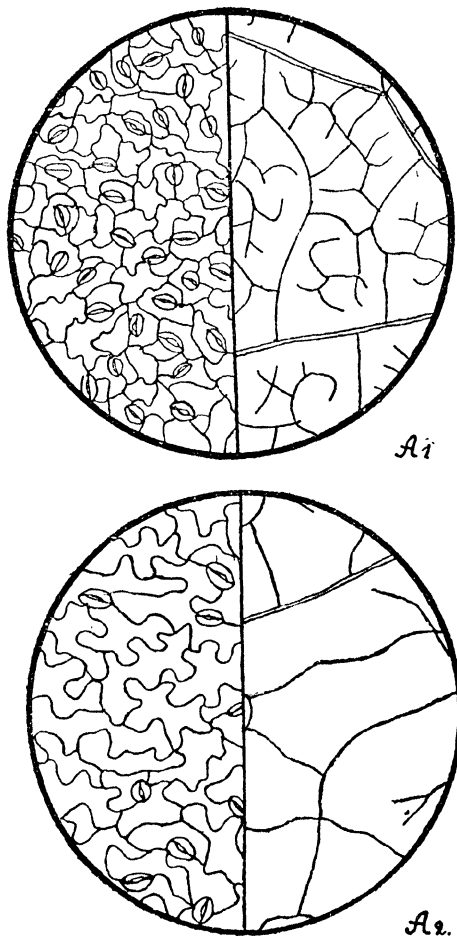

FIG. 42.—Structure of the leaves of two specimens of bean, grown under electric light. *A*2 was grown at three times the distance of *A*1 from the source of light. In both cases, the *left* half of the circle shows the lower epidermis, the *right* half the network of veins.

strongly illuminated specimen the number of stomata per unit area is about four times as great, the dimensions of the epidermal

cells only a third to a quarter as large, and the network of nerves considerably denser than in the less well-lighted plant.

Keller and Leisle (1922; see also **Keller**, 1925) have made an interesting attempt to compare—anatomically and physiologically—plants of very different ecological types, but systematically closely related. From each of the two genera, *Asperula* and *Galium*, they selected a couple of species, one of which was a typical steppe plant and the other a shade plant of the forest. Of the genus *Asperula*, the steppe species chosen was *A. glauca* (= *A. galioides*), with glaucous, narrow, needle-shaped, and rather thick leaves with slightly recurved margins and strongly developed palisade tissue—in brief, a typical xerophyte of the open steppe and of semi-arid regions. The second species was *A. odorata*, characteristic of humid, deeply shaded spots in deciduous woodland. This species has comparatively broad, thin leaves, with a single layer of poorly developed palisade, consisting of short, loosely arranged cells. The relation between the two species of *Galium*—*G. verum* and *G. Cruciata*—is similar, though the differences between them are less pronounced than those between the species of *Asperula*. The results of the experiments are shown in the table on page 358. The figures for the steppe species of each pair are taken as 100 in each case, so that relative magnitudes only are indicated.

Keller (1928, not yet published), in a recent paper presented to the third conference of Russian botanists, gave an account of some new and interesting work on the relation between the length of the veins per unit area and the intensity of transpiration. He investigated a large number of genera, each genus being represented by several species, systematically closely related, but ecologically different. In all cases the species peculiar to more open and sunny habitats possessed a considerably greater length of veins per unit area and a greater intensity of transpiration. Moreover, this increase in transpiration was in nearly all cases directly proportional to the increase of the density of venation. This law of the dependence of transpiration on the length of the veins, formulated by

Keller, is in my opinion a striking illustration of the fact that the rate of transpiration depends to a great extent on the conditions of the supply of water to the mesophyll. The investigations of Mlle. **Lebedintsev** (1927; see below, p. 361), however, show that this law cannot be applied to plants grown under pronounced differences of air moisture.

Similar results were obtained by **Cribbs** (1919, 1921) when investigating (by the cobalt paper method) the "index of foliar transpiring power" of the American lime (*Tilia americana*).

TABLE XXVI

Comparison of the Anatomical Structure and Intensity of Transpiration of Steppe and Forest Species of "Asperula" and "Galium" (according to B. Keller and Leisle)

Species	Habitat	Length of Network of Veins	Number of Stomata	Intensity of Transpiration		
		Per Unit Area		I	II	III
Asperula glauca (=*A. galioides*)	steppe	100	100	100	100	100
A. odorata ..	forest	30	14	31	46	56
Galium verum ..	steppe	100	100	100	100	100
G. Cruciata ..	forest	38	21	33	46	53

Cribbs selected a series of dune habitats in which this species occurs, varying from very dry dunes, where the trees are fully exposed, to the shady depths of dune forest. The 1919 paper contains photographs of the habitats in which the experiments were performed. Cribbs found that transpiration increased with increasing dryness of the habitat—the latter being determined by means of Livingston's atmometers. The results of the experiments show the following gradation: habitat **A**, the most shaded, evaporation 12·5 c.c., index 0·15; habitat **C**, less shaded, evaporation 22, index 0·28; habitat **E**, entirely open (top of dune), evaporation 30 c.c., index 0·55. Cribbs comes to the conclusion that the more humid the habitat, the more

mesophytic is the structure of the leaf of the lime-tree and the lower its transpiration. Conversely, the drier the habitat, the smaller and more leathery the leaves, and the higher their transpiration.

It must be noted, however, that if xerophytes are simultaneously heliophytes, it cannot be said that mesophytes, or even hygrophytes, are necessarily sciophytes (shade plants). Many hygrophytes are at the same time heliophytes; buckwheat, for instance, can endure neither dryness of the soil nor shade. The sunflower, again, may be looked upon as a pronounced example of a heliophilous mesophyte, while the cotton plant, a true "child of the sun", requires abundant irrigation. A detailed experimental investigation of the peculiarities of plants of this kind, in which they could be compared with true xerophytes on the one hand and shade-loving mesophytes on the other, is desirable. This would perhaps enable us more definitely to distinguish between the effects of light and dryness on a plant. Hitherto such a clear separation has not been attained. This may possibly account for the fact that many of the results of investigations on the influence of environmental moisture on the structure and physiology of plants have been uncertain and contradictory.

Influence of Environmental Moisture on the Structure and Water Relations of Plants

As regards environmental moisture, we must distinguish between the humidity of the soil and that of the air. In nature both factors may act together, as in damp forests or in other humid climates. But they may also be sharply demarcated, as in the river valleys of steppe and desert regions and under conditions of artificial irrigation. We may therefore consider separately the available experimental data on the influence of air and soil moisture respectively on plants. This separate treatment is the more necessary as these two factors induce by no means identical structural and physiological changes in the plant.

(*a*) *Atmospheric Moisture*

The most complete and detailed work on the influence of atmospheric moisture on plants is that of **Eberhardt** (1903), which we may take as the basis of our statement. Eberhardt cultivated his plants under bell-jars, the air in which was kept either moist or dry by means of vessels containing either water or sulphuric acid. Both potted plants and plants growing in the open soil were used, in both cases evaporation from the soil into the bell-jars being prevented by plates of glass on which the jars rested, all joints being carefully sealed. In addition, "normal" specimens were grown under bell-jars raised above the glass plates by wooden wedges, in order to allow free circulation of air. Thus the conditions of light and temperature were uniform in all the bell-jars, the only variable factor being the humidity of the air. Eberhardt carried on his experiments for three years, using a great variety of plants —lupin, beans (*Phaseolus* and *Vicia Faba*), castor oil, *Fuchsia*, lilac, willow, poplar, the xerophyte *Zygophyllum Fabago*, and many others.

In general, damp air had much the same effect as shade on the form and structure of the plants, while the influence of dry air was very similar to that of strong light. Thus in dry air—as contrasted with humid air—the internodes were shorter, the leaves smaller but thicker, the root system better developed, the xylem vessels more numerous and their walls thicker, the number of vascular bundles in the petiole greater (in spite of the smaller size of the leaf). The cells of the epidermis, cortex, pith, etc., were smaller, the number of stomata per unit area greater, the cuticle thicker, the palisade tissue better developed, and so on. On the whole, a dry atmosphere promotes the differentiation of the tissues, while humid air to a considerable extent checks this differentiation. Increased humidity also retards the formation of cork, as well as flowering and fruiting. Structurally, the "normal" specimens, developed in moderately moist air, occupied an intermediate

position between the plants grown in a dry and a damp atmosphere respectively.

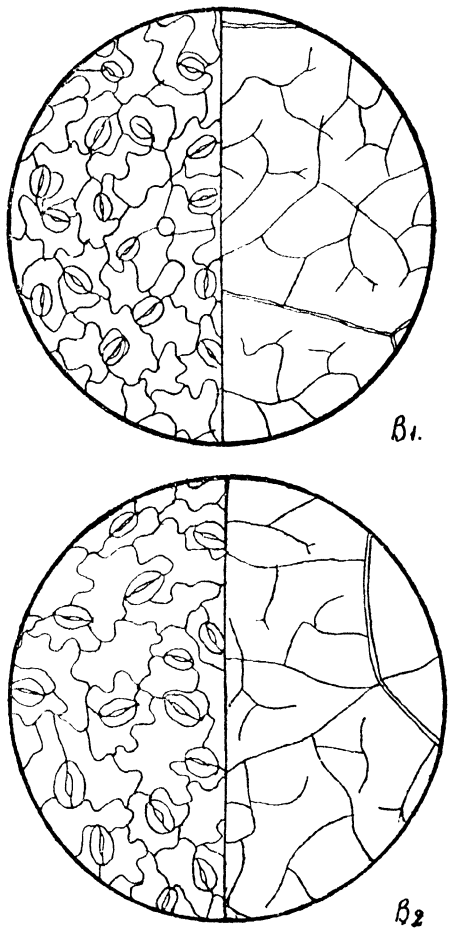

FIG. 43.—Influence of air moisture on the structure of bean leaves. *B* 1, a leaf of a plant grown in a drier; *B* 2, in a moister atmosphere. *Left*, lower epidermis; *right*, veins (after Lebedintsev).

Similar results have been obtained by my co-worker, Mlle. **E. Lebedintsev,** in an investigation not yet completed. Growing plants in glass cases, with different degrees of atmospheric

moisture, she observed that in specimens grown in a drier atmosphere the length of the veins per unit area was greater and the stomata more numerous. Fig. 43 shows the leaf structure of two bean plants: the upper leaf (B1) was grown in a drier atmosphere (average relative humidity 64 per cent), while the lower leaf (B2) was grown in a moister atmosphere (average relative humidity 92 per cent). In the first plant (drier air) the length of the veins was greater by 20 per cent and the number of stomata greater by 24 per cent than in the second (moister air).

It must be pointed out, however, that the relation between air moisture and plant structure is not altogether a simple one. According to the investigations of Lebedintsev, an approach to complete saturation of the air induces changes of leaf structure in the reverse direction to those usually brought about by increasing humidity. The development of the mesophyll is retarded, while the number of stomata per unit area and the density of the network of veins are increased, the increase sometimes reaching 100–120 per cent. These observations of Mlle. Lebedintsev throw some light on the contradictory statements met with regarding the influence of atmospheric moisture on the structure of leaves. For instance, in older works it is frequently stated that the number of stomata increases in moist air, though **Eberhardt's** careful investigations show the exact opposite. The explanation of this contradiction is probably that the earlier authors worked with a completely saturated atmosphere, while Eberhardt used more moderate degrees of humidity.

Under natural conditions, however, an atmosphere continually at or near the saturation point is a rare phenomenon. From this it may be supposed that the relations established by Eberhardt are those most frequently realized in nature.

These structural modifications, brought about by differences of atmospheric moisture, must have an effect on the water relations of the plants concerned. Yet, strange as it may appear,

this question has hitherto been to a great extent neglected, and still requires careful investigation. The only exact experiment hitherto published is one by **Kiesselbach** (1916), in which corn was grown both in an ordinary and in a humid greenhouse. Subsequently he determined the intensity of transpiration in plants grown under these different conditions; for this purpose, however, the plants were subjected to similar conditions. Practically no difference in the intensity of transpiration was recorded for the two sets of plants, the reason for which may have been the comparatively small difference of humidity in the two greenhouses. The experiments of Mlle. **Lebedintsev**, however, indicate that the problem is more complex than Kiesselbach's results would suggest. She actually found a higher transpiration capacity in plants grown in a moist atmosphere than in those developed under drier conditions, though the latter possess a denser network of veins and more numerous stomata. The explanation of her results must probably be sought in the fact that moist air checks the development of cuticle, and consequently creates conditions favourable to an increase of cuticular transpiration. The close connexion between the thickness of the cuticle and its permeability was recently pointed out by **Rudolph** (1925). This author, however, in his interesting paper, only determined the relation between the thickness of the cuticle and the rate of penetration of poisonous substances (mostly sulphuric acid) into the leaf, inducing the browning and death of the chlorenchyma. Rudolph did not carry out any direct determinations of cuticular transpiration itself, and it was only on such indirect evidence that he considered it to be more or less proportional to the permeability of the cuticle.

Such direct determinations have recently been carried out in my laboratory by **Agamov** (1927). Agamov investigated the cuticular transpiration of both wilted leaves with already closed stomata, and leaves with artificially sealed stomata. In the latter case he used leaves bearing stomata

only on one side. The experiments showed that cuticular transpiration is in reality directly dependent on the permeability of the cuticle, as determined by Rudolph's method. This dependence, however, is complete only in leaves with sealed stomata. In wilted leaves the stomata are never absolutely hermetically closed: hence transpiration through the cuticle is always more or less increased by stomatal transpiration.

(*b*) *Soil Moisture*

The influence of soil moisture on the structure and physiological peculiarities of plants must now be considered. Leaving out of account the earlier researches on this subject, we may pass to the more recent work of **Heuser** (1915) on the wheat plant, and of **Rippel** (1919) on white mustard (*Sinapis alba*).

Heuser studied the anatomical structure of wheat leaves in relation both to the height of insertion of the leaf on the stem and to the influence of environmental conditions. In the course of this work he too rediscovered the rules established twelve years earlier by Zalenski. With regard to the influence of soil moisture on leaf structure, Heuser found that with additional moisture the length and width of the leaf increased, but the thickness remained the same. The dimensions of the individual cells also increased. This involves an increase in the size of the stomata, but a reduction of their number per unit area. Abundant soil moisture also results in a less compact venation, though in general the number of vascular bundles in the leaf increases with the greater size of the leaf blade (due to moisture). Heuser was unable to establish any correlation between the number of stomata per unit area and the needs of the plant for water.

Rippel's researches (1919), like those of Heuser, were carried out almost exclusively on a single species, in this case white mustard. In his work, which was very detailed, Rippel adopted the statistical method of studying variation, hitherto rarely applied to investigations in physiological anatomy.

Rippel first determined the length of the vascular bundles per unit area of leaf surface. In dry cultures this was considerably greater than in moist cultures. Table XXVII shows the importance of comparing, in this respect, leaves inserted at various heights on the stem.

TABLE XXVII

Length of Veins in cm. per sq. cm. of Leaf Surface in Mustard Plants Grown in Moist and in Dry Soil (according to Rippel)

Tier of leaf	Dry Culture	Moist Culture	Difference
1	63·7 ± 3·40	54·7 ± 0·68	9·0 ± 3·47
2	70·7 ± 2·97	57·7 ± 1·53	13·0 ± 3·34
3	79·2 ± 2·49	62·7 ± 1·57	16·5 ± 2·94
4	90·1 ± 4·28	61·9 ± 1·81	28·2 ± 4·65
5	100·3 ± 9·91	76·0 ± 6·0	24·3 ± 11·59
Average ..	86·8 ± 3·96	67·3 ± 3·98	19·5 ± 5·62

We see from the above data that the difference between dry and moist cultures becomes more pronounced as we proceed from the lower to the upper leaves. In other words, the increase in density of the venation, normally found in plants as the successive leaves are unfolded, is more rapid and intense in dry- than in moist-soil cultures. Rippel's data, indeed, strongly support **Zalenski's** suggestion that such differences are due to a diminished water supply to leaves still being formed in the bud.[1]

The other anatomical elements of dry- as compared with moist-soil cultures showed differences similar to those found in upper as compared with lower leaves of the same shoot. The dimensions of the epidermal and palisade cells were smaller, the stomata more numerous, the lateral walls of the epidermal cells less sinuous, and the leaves thinner. Rippel succeeded in finding one essential difference between the effect

[1 Evidence is adduced in footnote, p. 346, that leaf structure is chiefly influenced by the water supply at a relatively late stage of development, rather than in the bud itself.—ED.]

of dry soil and that of dry air, i.e. plants grown in a dry soil develop considerably less mechanical tissue than those in damp soil.[1] Dry air, on the other hand, as shown by the researches of **Lothelier** (1893) on spiny plants, induces a considerable increase of mechanical tissue.

Some authors are inclined to attribute the dwarfed habit of plants developed under conditions of water shortage to decreased nutrition due to a lower intensity of transpiration. **Rippel**, however, points out that this is incorrect. In his experiments, the total ash- and nitrogen-content of dry-soil plants was greater than in damp-soil cultures. This agrees with the fact long ago noticed by Hellriegel, that plants developed on drier ground are usually of a more intense green colour.

A comprehensive investigation of the differences in transpiration of plants grown under the influence of different degrees of soil moisture was carried out by my pupil, Mlle. **Frey** (1923), in the Tiflis Laboratory during 1916, 1917, and 1919.

Plants were grown in soils containing respectively 60–70 per cent and 35–40 per cent of their total moisture capacity. The higher degree of humidity may conventionally be termed optimal, the lower, minimal, as in the arid climate of Tiflis plants developing with as low a water content of the soil as 40 per cent are dwarfed. For example, the leaf surface of the thorn-apple (*Datura*), grown under optimal conditions of soil moisture, was 753 sq. cm., and under minimal conditions, 154 sq. cm.; for the sunflower the corresponding figures were 2,023 and 157; for maize, 9,192 and 2,962; beans (*Phaseolus*), 1,539 and 496; *Atriplex hortensis*, 2,219 and 952; and for *Zygophyllum Fabago*, 1,370 and 231. Thus, one of the most important features of xeromorphy—a general reduction of the leaf surface—is induced by deficiency of soil moisture.

In the majority of cases, however, this restriction of the leaf

[1] In Rippel's dry-soil cultures there was a reduction both of collenchyma, and especially of lignified mechanical tissues: on the other hand there was an increase of the woody water-conducting elements.—ED.]

surface was accompanied, not by a decrease but by an increase of the intensity of transpiration; less frequently it remained unchanged. For instance, if the intensity of transpiration of plants grown in the drier soil (the soil moisture during the actual experiment being at the optimal level) is taken as 100, plants grown under optimal conditions of soil moisture yield the following figures: thorn-apple, 59; maize 41; beans, 51.[1] Only the more xerophilous species showed a higher transpiration capacity in the individuals grown in moist soil, e.g. *Atriplex*, 112, and *Zygophyllum Fabago*, 209. In most cases, then, plants grown under conditions of inadequate soil moisture, combined with dry atmosphere, did not develop characteristics tending to reduce the intensity of transpiration. The differences of leaf structure, so far as thickness of the leaves and the number of stomata per unit area are concerned, were too slight to account for the observed differences of transpiration capacity.

Frey's work, carried out as it was under the peculiar summer conditions of Tiflis, with the meteorological factors—insolation, dryness of the atmosphere, etc.—in a high state of tension, is very interesting on account of the failure to detect any general tendency to reduce the loss of water in plants of dry soil. Such restriction was shown only by the most xerophilous plants. But it is possible that the direct effect of soil moisture was somewhat obscured by the intense dryness of the atmosphere. It therefore seemed desirable to repeat the experiments under conditions of reduced transpiration.

Such experiments were conducted in 1925 by my co-worker, Mme. **Kokin** (1926), in Leningrad. These experiments have distinctly shown that a decrease of soil moisture induces changes of leaf structure in the direction of increased xero-

[1 On the other hand, Mlle. **Frey** found that the intensity of transpiration of plants of humid soil exceeded that of dry-soil plants when the transpiration was determined under the same conditions of soil moisture as those in which the plants respectively had been grown. Owing to differences of leaf area, the absolute transpiration of dry-soil plants was considerably less than that of plants of humid soil.—ED.]

morphy. The number of stomata and the length of the veins per unit area of leaf surface are increased, and the cell dimensions diminished. Fig. 44 illustrates the leaf structure

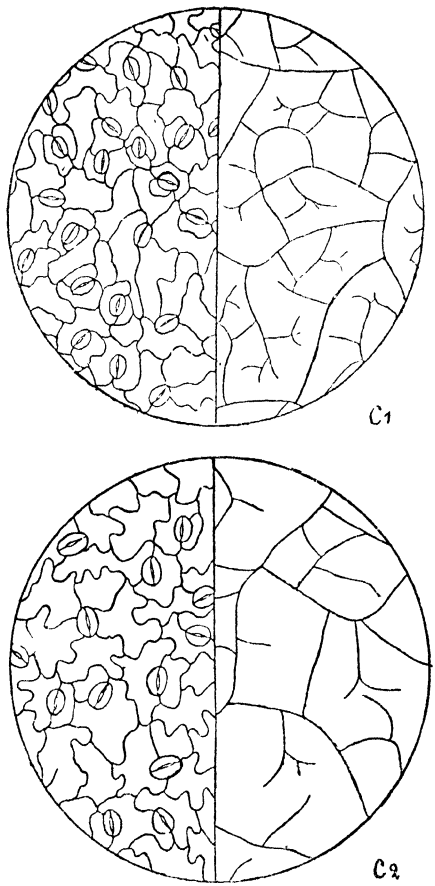

FIG. 44.—Influence of soil moisture on the structure of bean leaves. *C*1, leaf of a plant grown in a drier; *C*2, in a moister soil. *Left*, lower epidermis; *right*, veins (after Kokin).

of two specimens of bean (*Phaseolus*). One of these (C1) was grown in a soil containing 30 per cent of its total water holding capacity (only 7 per cent of water being available for the plant);

the other (C2) in soil with 60 per cent of water (the amount of available water reaching 20 per cent).

It must be noted that in practice it is scarcely possible to draw a hard and fast line between the respective effects of soil moisture and air moisture, for these two factors are closely connected with one another. Increased transpiration induces increased absorption, which in turn leads to increased desiccation of the soil immediately surrounding the roots. Owing to this fact, as we have already seen, plants exposed to conditions of intense transpiration may enter on a state of permanent wilting, even in a relatively humid soil. For example, a soil moisture of 40 per cent of the total water capacity allows of a fair development of plants in the relatively humid climate of Central Europe. The same degree of soil moisture in the climate of Tiflis, however, would prove almost minimal and produce but a dwarfed growth, while 25 per cent, the driest soil employed by **Rippel**, would be inhibitory. The combined effect of different degrees of air and soil moisture deserves most careful investigation. At present we only have the somewhat obsolete data of **Kohl** (1886), who experimented with the effect of moist and dry soil and moist and dry air on *Tropaeolum majus*. Under conditions of moist soil and moist air, he obtained leaves with a thin cuticle, tangentially elongated epidermal cells and a complete absence of collenchyma. In moist soil, combined with a dry atmosphere, the cuticle was thick, the epidermal cells radially elongated, with thickened outer walls, and the collenchyma well developed. The effect on structure of dry soil and moist air was somewhat similar to the first named (moist air and moist soil), but the total leaf area was considerably reduced and the cells of the epidermis, though thin-walled, were almost cubical in shape. Finally, under conditions of dry soil and dry air the thickness of the cuticle and the radial elongation of the epidermal cells were most pronounced. These results, which have found their way into most textbooks, require confirmation and extension. It may well be that a detailed investigation, carried out with all

the precautions suggested by Rippel, would throw light on many of the contradictions hitherto associated with the question of the effect of environmental moisture on the structure and the water relations of plants.

In the investigations discussed above, the influence of soil moisture was studied by growing plants in pots in which the required degree of soil moisture was maintained by adding daily the amount of water lost, as determined by weight. But the problem may be approached in another way. In the case of dry cultures, instead of keeping the soil moisture at a constant low level, the soil may from time to time be allowed to dry out, until the plant begins to wilt, when water—to the so-called optimum—is again added. At my suggestion, **Tumanov** (1927) used this method in his experiments. He cultivated two series of sunflowers in pots. One series was carefully kept under conditions of optimal moisture, by watering the plants both morning and evening. The second series was periodically subjected to permanent wilting, after which the plants were once more well watered. As a result, the plants subjected to periodic wilting showed signs of suffering from water deficit, and produced a lower yield. At the same time they displayed a number of interesting anatomical and physiological peculiarities.

As regards anatomical structure, the periodically wilted plants were distinguished by marked xeromorphy. The number of stomata per unit area was greater by 35 per cent than in the moist series, the network of veins denser by 24 per cent, and the length of a single stoma less by 16 per cent. In conformity with these changes of anatomical structure, the plants subjected to wilting showed a greater intensity of transpiration and assimilation. A few days after watering, when the depressing influence of wilting was passing away, the intensity of transpiration of the dry cultures exceeded that of the control plants by 30 per cent or even by 72 per cent. The increase in the intensity of accumulation of dry substance, ascertained both directly by the half-leaf method, and in-

directly on the basis of increased efficiency of transpiration, was still greater. Fig. 45 shows the structure of the middle leaves

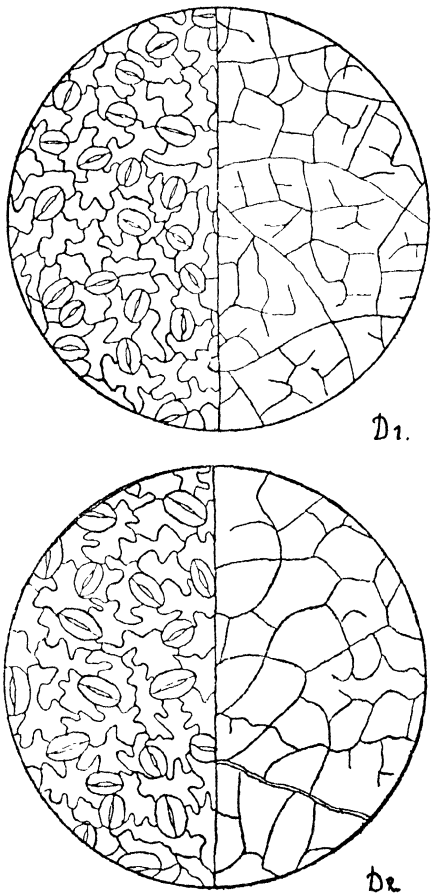

FIG. 45.—Influence of periodic wilting on the structure of sunflower leaves. *D*1, leaf of plant repeatedly subjected to wilting; *D*2, leaf of plant continually supplied with water. *Left*, lower epidermis; *right*, veins (after Tumanov).

of two sunflower plants, one of which (D1) was subjected to permanent wilting thirteen times during development. The other (D2) was regularly watered both morning and evening.

The greater xeromorphy of the wilted plant is distinctly marked.

We may now sum up the general results obtained by **Tumanov** on the effect of permanent wilting; by **Zalenski, Yapp, Rippel, Alexandrov,** etc., in regard to the structure of leaves inserted at different heights on the same stem; and by many other investigators respecting the differences between sun and shade leaves, and between leaves of plants developed under different conditions of soil and air moisture. These investigations, conducted from various points of view, justify the statement that *all influences which result in a greatly increased loss of water by the plant, or a restricted supply of water to the developing leaves, lead to essentially similar changes of leaf structure.* These structural changes, which may be termed "xeromorphic", tend to facilitate the water supply and simultaneously to increase the gaseous exchanges. By virtue of this, xeromorphic plants are distinguished not by a lower but by a higher rate of such processes as transpiration and assimilation.[1]

[1 **Salisbury** (1927) has recently made a very interesting study of the causes and ecological significance of stomatal frequency. His results confirm and considerably extend certain of the investigations dealt with in this chapter. In general, Salisbury finds a more or less close correlation between the number of stomata per unit area of leaf surface and the degree of humidity of the environment. High stomatal frequencies are associated with xerophytic, and low frequencies with hygrophytic conditions. Further, just as the stomatal frequency increases with the height of the leaf on the plant (cf. **Zalenski, Yapp,** and others), so too the frequency augments with the tallness of the species. Particular attention was paid to woodland plants. The author found that the potentiality for developing a high stomatal frequency on the whole increases from the interior of the wood outwards and from the ground flora upwards. Thus the mean height of the stratum formed by the *herbaceous shade flora* was 0·23 m.; the mean stomatal frequency for plants of this stratum being 92 per sq. mm. The *marginal flora* had a mean height of 0·61 m., with a mean stomatal frequency of 167. The *shrub stratum*—height 2·4 m., stomatal frequency 199; and the *tree stratum*—height 13·0 m., stomatal frequency 224. With the exception of tall, exposed plants such as *Typha angustifolia*, aquatic plants have relatively low stomatal frequencies, but mud forms of e.g. *Alisma plantago* have considerably higher frequencies than the water forms. Experimental evidence was obtained that the high frequencies of "sun" as compared with "shade" leaves of the same species are to be attributed to differences of humidity rather than illumination. In individual leaves the frequency

This conclusion is diametrically opposed to the traditional conception of xerophytes as plants which reduce the activity of all their vital functions, and especially transpiration, in order to conserve the store of water which they have accumulated with great difficulty. I have therefore thought it necessary to substantiate my point of view—hitherto regarded by the majority of botanists as a kind of heresy—somewhat fully. This explains the detailed treatment adopted in the present chapter.

generally increases from the base to the apex of the lamina and from the midrib to the leaf margin.

In order to express the numerical relations between stomata and ordinary epidermal cells, **Salisbury** introduces the concept of the *stomatal index*. This is given by the formula $I = \frac{S}{E+S} \times 100$, where I is the stomatal index, S the number of stomata per unit area, and E the number of epidermal cells in the same unit area. For a given species, the stomatal indices of leaves grown under different conditions are far more constant than the stomatal frequencies. This indicates that differences in stomatal frequency are due rather to differences in the size of the cells (i.e. to the spacing of the stomata), than to differences in the ratio of stomata to epidermal cells. The author comes to the provisional conclusion that a low index is characteristic of aquatics, but that plants of drier habitats are distinguished by higher indices.—ED.]

*

CHAPTER XII

DROUGHT RESISTANCE IN PLANTS

The essentials of a xerophytic organization. The selection of drought resistant varieties of crop plants. Cell size and drought resistance. Different kinds of drought and drought resistance: (*a*) atmospheric drought; (*b*) soil drought. The basis of drought resistance. Susceptibility to drought at various stages of development. Analysis of the problem of drought resistance.

The Essentials of a Xerophytic Organization

Anatomical and physiological investigations of leaves attached at different heights on the stem, and the study of the effect of light and humidity on the structure and vital processes of the plant, have (as we have already seen in Chapter XI) completely modified our ideas respecting the essential features of a xerophytic organization. Leaving out of account the highly peculiar and specialized succulent type, we may regard the following peculiarities as characteristic of xerophytes. Anatomically, there is a decrease in the size of all cells (including the stomata), a thickening of the cell walls, a strong development of palisade mesophyll, a denser network of veins, and an increase in the number of stomata per unit area. Physiologically, there is an increase in the intensity of transpiration[1] and assimilation, in osmotic pressure, and in the capacity to endure wilting.

Of the essential factors inducing a xeromorphic structure must be mentioned solar radiation, and a water deficit in the leaves leading to the deflexion of water from the embryonic tissues. This shortage of water does not permit of the normal development of the cells during the so-called "stretching growth", or period of cell enlargement.[2] The cell walls, therefore, cease to expand comparatively early, and proceed to become thicker. The result is the production of smaller cells with thicker walls. This decrease in cell size leads to other structural

[1 Cf. text and footnote, p. 383.—Ed.]

[2 For definite evidence in favour of this view, see footnote, p. 346.—Ed.]

peculiarities, e.g. a denser network of veins (for the number of cells occupying the spaces between the veins, as shown by Zalenski, is more or less constant), smaller leaves, and so on. Intense radiation induces the cells of the chlorenchyma to grow perpendicularly to the leaf surface, thereby converting potential spongy mesophyll into palisade tissue.[1] This results in an increase of assimilative capacity. At the same time, the increased number of stomata allows of more rapid transpiration per unit area. Finally, intense insolation combined with deficiency of water leads to higher osmotic pressures, which in turn are apparently related in some way to an increased power of resistance of the protoplasm to injury during wilting. Such may be accepted as a working hypothesis regarding the xerophytism induced in plants by the direct influence of external conditions. This hypothesis might perhaps be elaborated further, or even modified, but so far as I am aware, it is entirely in accordance with established facts.

THE SELECTION OF DROUGHT RESISTANT VARIETIES OF CROP PLANTS

This point of view suggests what is probably the most promising line of approach in the selection of drought resistant varieties of crop plants. We must avoid the earlier method of attempting to select varieties on account of their possession of peculiarities reminiscent of various kinds of xerophytes—the latter often having nothing in common with the species in question. It would be useless to endeavour to breed, for example, succulent forms of wheat or corn, or to attempt to obtain varieties with a thick covering of hairs or wax. The most fruitful method is to study the modifications induced in the given species by cultivation under dry conditions, and then to select those varieties which structurally most nearly approach the forms experimentally produced under the influence of drought. The credit for the adoption of this principle must be

[1 But cf. an alternative suggestion at the end of footnote on p. 346.—ED.]

given to **Kolkunov**, though apparently he did not clearly recognize, or at any rate enunciate, the principle itself. Kolkunov's investigations, which were planned on broad lines and carried on persistently for twenty years, deserve the most careful consideration.

Though disagreeing with many of Kolkunov's statements, and, indeed, with the theoretical explanation of his results put forward by this author, I nevertheless regard his work as of great importance. Its value lies especially in the application of the results of studies on the physiological peculiarities of the plant to the problem of drought resistance. It is therefore necessary to give a summary of the principal contributions of this investigator.

At the outset Kolkunov based his investigations on the assumption that as a plant growing under arid conditions can only draw upon the limited supply of water in the soil, the less water it expends, the better it will thrive. His first problem, therefore, was to determine the structural peculiarities which affect the rate of transpiration. Assuming that this rate depends on the degree of xeromorphy, Kolkunov entitled this part of his work, "an anatomical and physiological investigation of xerophily in crop plants". Cereals were investigated in 1905 and sugar-beets in 1907.

Other physiological questions arose in connexion with the anatomical structure of drought resistant plants, such as the dependence of assimilation on structure, the significance of the transpiration current in the process of ripening of the grain, and so on. These questions, however, were not studied by Kolkunov till later, as his initial problem involved a great deal of work and time.

Cell Size and Drought Resistance

Kolkunov (1905) began his researches by a detailed anatomical and physiological analysis of different kinds of wheat and other crop plants. In the first place he found that different

varieties of the same species differ neither in the presence or absence of nor in the arrangement of particular tissues, but only in the size of their anatomical elements. The size of these elements fluctuates about a mean value characteristic of the given variety. Only the larger systematic units, such as wheat or millet, differ one from another anatomically, e.g. the different varieties of millet are all characterized by a special parenchymatous tissue surrounding the vascular bundles.

In his anatomical work Kolkunov paid particular attention to the length of the stomata, assuming that the size of the stomata must determine the amount of transpiration, and that the rate of transpiration must serve as a measure of drought resistance. The results of his measurements and experiments appeared to him to confirm this view. He selected, for instance, a series of spring wheats of different varieties, with different powers of drought resistance, and accurately measured the length of their stomata. With four wheats of Western origin he obtained the following measurements: in Bordeaux, 95·8 microns; Chiddam, 94·2; Elsassian, 94·0, and Heine, 85·8. In four Eastern wheats the lengths of the stomata were: in Turkestan irrigated, 80·6 microns; Kubanka, 74·0; Ulka, 68·2; and Turkestan mountain wheat, 64·4 microns. Judging from these figures, the less drought resistant Western wheats have considerably larger stomata than the more resistant Eastern varieties.

An extensive series of experiments with cut leaves appeared to show that the rate of transpiration per unit area of leaf surface is to a considerable degree determined by the size of the stomata. Kolkunov compared, for instance, the transpiration of *Echinochloa Crus-galli*, belonging to the millet group, with that of three varieties of wheat—Ulka, Kubanka, and Elsassian. Taking both the transpiration and stomatal length in *Echinochloa* as 1·00, he obtained the following ratios. For the intensity of transpiration, 1·00:1·70:2·00:2·27, and for the lengths of the stomata, 1·00:1·75:1·92:2·34—that

is, the rates of transpiration in the different cereals were strictly proportional to the respective lengths of their stomata.

From such data Kolkunov concluded that he had found a solution to his first problem, i.e. to ascertain which structural peculiarities affect the rate of transpiration, and thereby determine the drought resistance of the cereals in question. He formulated his conclusions in the following terms: a decrease of transpiration in cereal crop plants is mainly brought about by a decrease of their anatomical coefficients, the most convenient criterion of which is the relative length of the stomata.

Kolkunov's second paper (1907) dealt with various kinds of beet, which were selected on account of their great practical importance in agriculture. Beet, moreover, is a suitable subject for the investigation of certain purely physiological questions which, however, are also important from the agricultural point of view. These are the relation of the degree of xerophytism to the assimilation of nitrates and the accumulation of food reserves.

In the first place Kolkunov measured the anatomical elements of various species and varieties of beets. He found that the wild beets had the largest cells, table-beets and forage-beets had somewhat smaller cells, while the smallest cells were found in the Kleinvanzleben and Vilmorin's sugar-beets. The dimensions of the root cells were proportional to those of the leaf cells. He also discovered that cell size, or more precisely, the tendency under certain definite conditions to form cells of a definite size, is a strictly inherited character. This renders it possible to select from any variety of beet or other plant more or less xeromorphic pure lines, which may be distinguished by the size of their cells.

Kolkunov's belief regarding the xerophytism of plants with small cells was based on determinations of the intensity of transpiration, forms with small cells transpiring less than those with large cells. But these results are inconsistent with the data given in Chapter XI regarding the relative intensity of transpiration of upper and lower leaves, sun and shade leaves,

and so on. This discrepancy, together with the doubtful reliability of Kolkunov's methods, make it difficult to accept the correlation between cell size and transpiration which this author claims to have established. Later on, however, Kolkunov adopted a method which seems to be more reliable, as it is not based on preconceived ideas. For several years he visited, during early autumn, localities in which the beet crops had suffered from drought, and selected in the field damaged plants on the one hand, and well-developed specimens on the other. On investigating these plants anatomically, he found that the finest roots were those of plants with the smallest cells.

Entirely different results were obtained with beet grown under favourable conditions. In this case the plants with the largest cells had also the largest roots. Table XXVIII gives the results of experiments with beet grown in the grounds of the Polytechnic Institute of Kiev during the dry year of 1905 and the wet year of 1906.

TABLE XXVIII

Correlation between Cell Size and Root Development of Beet Grown under Dry and Humid Conditions respectively (according to Kolkunov)

Group	Diameter of the Parenchymatous Cells in Microns	Average Weight of Root in gr.	
		Dry Year, 1905	Humid Year, 1906
I	8–11	271·7	—
II	11–14	172·7	64·3
III	14–17	67·0	139·2
IV	more than 17	33·3	207·6

These data are entirely convincing: in humid years the size of the roots is directly proportional, and in dry years inversely proportional to the size of the cells. Kolkunov supposes that under favourable conditions, with a sufficient water supply, the specimens with large cells assimilate rapidly and accumu-

late a large amount of reserve material. Under dry conditions, however, such specimens transpire so energetically that they suffer from deficiency of water. In consequence the accumulation of organic material is retarded to such an extent that the large-celled plants actually develop less—instead of more—luxuriantly than those with smaller cells.

Kolkunov's researches with corn (1910) confirmed these experimental results. In humid years the best yields were obtained from varieties with large cells—Liming, Hogue's Yellow Dent, Reid's Yellow Dent, and others, and smaller yields from varieties with small cells—Cinquantino, Bessarabka, North-Western, Carantino. These results, so far as yield is concerned, were reversed in dry years. Another very interesting fact emerged from these investigations, i.e. the existence of a correlation between the dimensions of the cells and the length of the growth period. The varieties with smaller cells mature earlier than those with larger cells. The absolute sizes of the plants agree with these differences in the time of maturation. Varieties which ripen late attain, as is well known, a larger size. Early varieties, on the other hand, comparatively soon transfer their activities from increasing their leaf area to the formation of flowers and fruits: consequently there is less time for the accumulation of the food necessary for the production of large plants. As early maturation enables the plant to escape the drought of summer (as in the case of desert ephemerals), the relation between cell size and drought resistance may prove to be merely incidental.

Kolkunov's very interesting and important, though perhaps somewhat one-sided, investigations met with severe criticism. He was often accused, for instance, of using material which was insufficiently pure from a genetic point of view. **Yakushkina and Vavilov** (1912), for example, at the Plant Breeding Station of the Agricultural Institute of Moscow, investigated seventeen pure lines selected from different varieties of oats. These authors confirmed **Kolkunov's** statement regarding the inheritance of cell dimensions. On the other hand, they could

find no connexion, in any of the plants investigated, between the size of the cells and such physiological peculiarities as the length of the growth period, the intensity of tillering and resistance to fungal attack. Neither did they discover any correlation between cell size and the yield of the crop. They did not investigate the capacity for drought resistance of their varieties, as such investigations were impracticable in the humid climate of Moscow. No precise anatomical correlations were observed between the size of stomata, their number per unit area and the dimensions of the leaf.

In the following year (1913), however, **Kolkunov** replied to the criticisms of **Yakushkina and Vavilov**. Having subjected their data to careful analysis, he concluded that in reality they confirmed rather than contradicted his theory. In view, however, of their justifiable criticism respecting the lack of genetic purity of the material used in his experiments, **Kolkunov** decided to test his results by using pure lines of one and the same variety of wheat (1925). After a lengthy search he succeeded in selecting from material supplied by the Besenchuk Experiment Station four lines of Beloturka wheat, which could be more or less sharply distinguished by the size of their stomata. Two of these (Nos. 132 and 155) had larger cells than the other two (Nos. 73 and 189). The absolute dimensions of the cells varied somewhat from year to year, but the relative sizes remained more or less constant. Thus in the year 1914 the lengths of the stomata of the four strains respectively were 60·5, 59·8, 56·4, and 54·3 microns; in the year 1916, 60·5, 59·8, 56·1, and 54·1; and in the year 1921, 63·1, 61·3, 58·7, and 58·0. This material gave him the pure strains of different degrees of xeromorphy which he required. Experiments with these pure lines of wheat were begun in 1915.

Kolkunov carried out his experiments with different degrees of soil moisture. He found that with abundant water the best yields were obtained from wheats with the larger stomata, under dry conditions from those with smaller stomata, while

with average conditions the wheat with stomata of an intermediate length gave the best result. This is clearly seen in Table XXIX, which gives the results of **Kolkunov's** 1917 experiments. In each case the maximal yield is printed in heavier type.

TABLE XXIX

The Yield of Different Pure Lines of Beloturka Wheat under Different Conditions of Soil Moisture (according to Kolkunov)

No. of Line	30 per cent of Moisture		60 per cent of Moisture		75 per cent of Moisture	
	Entire Yield	Yield of Grain	Entire Yield	Yield of Grain	Entire Yield	Yield of Grain
132	19·5	5·7	27·9	9·7	**43·0**	**19·0**
155	22·8	8·2	33·0	13·0	32·0	14·0
73	26·3	8·6	**46·1**	**19·7**	28·8	11·3
189	**31·3**	**11·2**	33·7	12·5	22·9	6·5

From these results the author concludes that, in strains of plants characterized by cells of different sizes, for each particular size there is a certain optimal combination of external conditions under which the plant gives its maximal yield. In Kolkunov's opinion this explains why very complicated correlations are obtained when experiments are performed in different years and under different growth conditions. It might also explain why, when his experiments were repeated at certain other experiment stations, results differing from his own were obtained.

In order to explain the correlation between the size of cells, drought resistance, and yield, Kolkunov puts forward the following hypothesis. **Brown and Escombe** (1900) found that gaseous diffusion through a perforated membrane is proportional, not to the area, but to the diameter of the openings. From this "diameter law" Kolkunov calculates that the exchange of gases between the leaf and the atmosphere—that is, the intensity of assimilation and of transpiration—is propor-

tional to the length of the stomata. But this proportionality is only observed while the plant has a sufficient amount of water; a decrease in the water content is accompanied by reduced assimilation. From this it is clear that plants with larger stomata, and therefore a greater rate of transpiration, must be the first to suffer from lack of water and to diminish their assimilation. Plants, on the other hand, with smaller stomata, and slower gaseous exchange, may, under conditions of drought, accumulate as much or even more dry substance than the former. Hence, for each complex of climatic conditions there is an optimal size of the stomata. Under moist conditions the large-celled varieties, and under dry conditions the small-celled varieties, are the best developed.

From the discussions in previous chapters it will be obvious that Kolkunov's hypothesis cannot withstand even the most superficial criticism, and that he has entirely failed to grasp the significance of Brown and Escombe's work. If a leaf had but a single stoma, or if the number of stomata per unit area were constant, then indeed the rates of diffusion of carbon dioxide and water vapour would be determined by the linear dimensions of the stomata. But we know that this is not so, for a decrease in the size of the stomata is generally (though not always) accompanied by an increase in the number per unit area, and as **Yapp's** investigations (1912) have shown, under these conditions the diffusion capacity of the leaf increases rather than diminishes.[1] Small-celled leaves, then, such as those of the upper, more insolated part of a shoot,

[1] Yapp's calculations were made from a lower and an upper leaf of *Spiraea Ulmaria*. The lower leaf (2nd) had 303 stomata per sq. mm., with an average pore area (for a single stoma) of 0·0000136 sq. mm., and the upper (18th) 1,188 stomata, with a pore area of 0·00000136 sq. mm. The transpiration capacity per unit area of the two leaves was calculated to be in the ratio—lower: upper = 21·2 : 25·4. Similarly, **Salisbury** (1927) has estimated that the diffusion capacity of the fully open stomatal pores of leaves of *Scilla nutans*, grown in dry and moist air respectively, is greater (per unit area) in the more xeromorphic leaves with smaller but more numerous stomata. Both these calculations agree with Professor Maximov's conclusions regarding the greater intensity of transpiration in xerophytes. —ED.]

exhibit more rapid gaseous exchanges than the large-celled leaves of the lower parts of the same plant (see Chapter XI, **Zalenski, Alexandrov, Géneau de Lamarlière, Dietrich,** and others). There is therefore no reason to expect large-celled races of plants to show a higher intensity of transpiration and assimilation than those with smaller cells. Further, Kolkunov himself does not adduce any incontestable experimental evidence in support of his view.

Kolkunov's hypothesis, then, was founded on the entirely erroneous assumption that the rate of gaseous exchange increases with the length of the stomata. In consequence, the hypothesis itself, by which he attempts to explain the connexion between drought resistance and the small size of the stomata, must be rejected. This, however, in my opinion, does not involve a denial of the connexion itself, for such a correlation does undoubtedly exist. But its explanation is not to be sought in a simultaneous decrease of the intensity of transpiration and of the size of the stomata. Rather is increased drought resistance to be regarded as one aspect of a general increase of the power of enduring injurious conditions; such an increase usually accompanies a reduction in size of the cells of the plant. Zalenski and Kolkunov himself have already shown that when such a reduction in size occurs, it affects all tissues of the plant simultaneously.[1] Thus small stomata are found associated with small epidermal and mesophyll cells in the leaf, and even with small parenchymatous cells in the root.

The reduction in cell size can be directly correlated—independently of differences in the intensity of gaseous exchange—with an increase of resistance to various unfavourable external factors. Spores, many of which have great powers of endurance, are generally very small. It is true that as yet we do not know the cause of the greater endurance of small cells.

[1 This general statement does not of course affect the fact that considerable differences in the size of the cells of corresponding tissues are commonly found in different parts of the same plant, when these parts (e.g. leaves at different levels on the stem) are developed under different external or internal conditions. See Chapter XI.—ED.]

Does the size of the cell as such play any important part, or is it the protoplasm which, on becoming more resistant, prevents further increase in size of the cells? Or, finally, are both the size of the cell and the resistance of the protoplasm conditioned by some other cause, such as the accumulation of dissolved substances in the cell with a consequent increase of osmotic pressure? In this connexion it may be significant that (at all events when other conditions are the same) the osmotic pressure is usually higher in small-celled than in large-celled organisms. The interesting researches of **G. A. Levitsky and N. E. Kusmina** (1923) support the idea that the small size of the cells of resistant varieties is due to the presence of some growth-inhibiting factor. They discovered that the embryonic cells in certain varieties of beet are uniform in size, whereas in the adult organs the dimensions of the cells are distinctly different. In any case, there appears to be a definite correlation between cell size and the power of resisting unfavourable environmental conditions. Great credit is due to Kolkunov for being the first to realize this correlation and to establish its existence in different plants. That he interpreted the facts erroneously must not be allowed to detract from the value of his observations.

Such are the results obtained by **Kolkunov** and by other authors inspired by his ideas. Their work, which extended over a period of many years, was devoted to the investigation of the anatomical and physiological peculiarities of drought resistant plants. The problem proved far more complicated than Kolkunov had expected at the beginning of his investigations. At that time he imagined that its solution lay in the mere selection of species or races with a low intensity or a high efficiency of transpiration.

Different Kinds of Drought and Drought Resistance

The complexity of the problem is increased by the fact that drought itself is by no means a simple phenomenon. It is, indeed, necessary to distinguish different kinds of drought and

drought resistance, just as on analysis we have already recognized different types of xerophytic organization. The various kinds of drought may have the same effect on the growing organism, or they may act independently, and produce very different results.

(*a*) *Atmospheric Drought*

In the first place we must distinguish between atmospheric drought and soil drought. It was long since observed that a hot, dry wind can produce rapid wilting or even desiccation of the plant, even with feeble insolation and a relatively high degree of soil moisture. This has been clearly proved in the case of plants grown in containers with an optimal water content of the soil.

This wilting of the plant under conditions of abundant water supply to the root system may be due to one of two causes: either to an inadequately developed root system, or to an inability to conduct water with sufficient rapidity to the leaves. In order, therefore, to withstand the effect of drying winds, a plant must possess a highly developed root system, ample water conducting tissue and small or deeply dissected leaves.

Typical plants of this kind are the steppe wormwood (*Artemisia fragrans*) and various desert or semi-desert species of Umbelliferae, the leaves of which are composed mainly of branching veins thinly covered with a layer of parenchyma.

The strongly dissected leaves of many xerophytes appeared to be an enigma, so long as the dogma of their low consumption of water was accepted. In order to bring about the required reduction of the transpiring surface, it was supposed that large, massive leaves, such as those of *Agave* and *Sempervivum*, were necessary. But the question assumed another aspect when the fact was established that many xerophytes have a high rate of transpiration. Such rapid transpiration necessitates an abundant water supply, a well-developed conducting system, and, what is equally important, a short and easy path along

which water can travel from the veins to the evaporating cells of the mesophyll of the leaf.

The greatest difficulty encountered by water in its passage through the plant is in passing from one parenchymatous cell to another. It is significant, therefore, that xerophytes which are habitually exposed to very dry air show a weak development of mesophyll. Moreover, the mesophyll cells are more or less directly connected with the large parenchymatous cells sheathing the veins: these cells appear to aid in the distribution of water to the mesophyll. The replacement of normal leaves by flattened assimilating petioles (phyllodes), or even shoots (cladodes), is common amongst xerophytes, e.g. in the Mediterranean flora and the Australian Acacias. In these cases I am inclined to regard the reduction of the distance between the water-conducting veins and the evaporating cells of the mesophyll (see above) as the important principle involved, rather than a mere decrease of the area of the transpiring surface. The above-mentioned parenchymatous sheaths surrounding the veins (**Alexandrov**, 1924) are very frequent in xerophytes, and must be regarded as one of the "adaptations" of these plants. From the point of view of the importance of rapid water conduction in the case of atmospheric drought, some observations by **Yapp** (1912) are extremely interesting. He observed that when wilting leaves are exposed to the drying effect of a strong wind the desiccation of the mesophyll does not proceed uniformly over the whole lamina. The first portions of the lamina to suffer under these conditions are the margins (or apices of linear leaves) and very frequently the thin parenchymatous areas between the main veins (Fig. 46). In other words, the first parts to dry out are those most remote from the water supply. In severe cases desiccation may proceed until only the tissue immediately surrounding the larger veins remains living and green, thus producing what is practically a deeply dissected leaf.[1]

[1 **Schröder** (1909) observed a somewhat similar localization of withering in leaves as a consequence of severe wilting —ED.]

The investigations of **Žoltkewich** (1913) indicate the great significance of the conducting system in the determination of

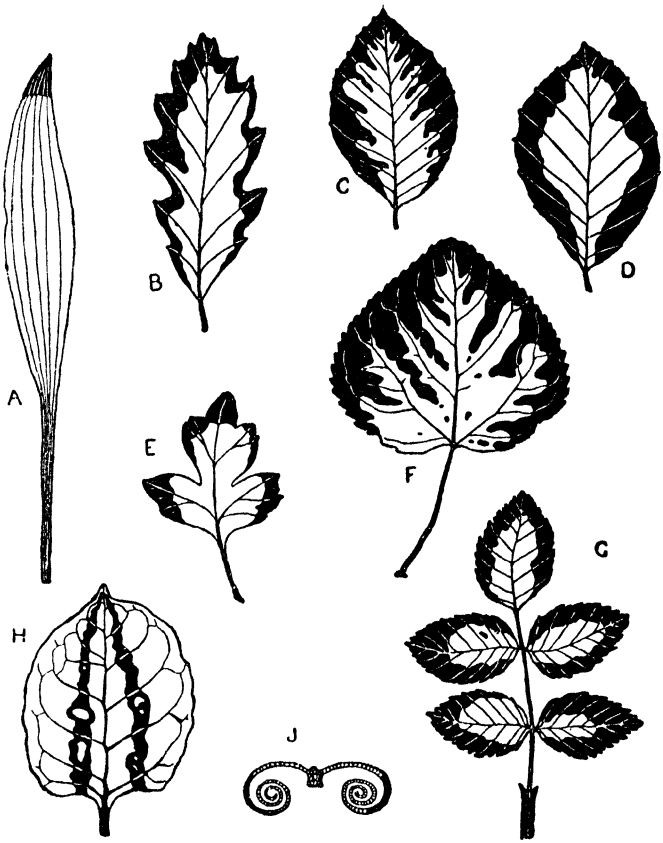

FIG. 46.—Desiccation of portions of the leaf lamina by drying winds. *A*, *Plantago lanceolata; B*, *Quercus Robur; C* and *D*, beech; *E*, hawthorn; *F*, poplar; *G*, rose; *H*, *Polygonum cuspidatum; J*, ditto, section through unfolding leaf, showing that the longitudinal withered bands were marginal at the time of injury. The desiccated portions are shown in black (from Yapp).

drought resistance. This author found that the drought resistant alfalfa possesses a much better developed conducting system in the stem than the less resistant clover. In alfalfa the xylem

is arranged in a compact, rather broad ring, while in the clover the greater part of the transverse section of the stem is occupied by the pith, surrounding which is a circle of poorly developed groups of xylem. The respective water conducting capacities of the two stems agreed with their anatomical structure, that of alfalfa being about 4 to 4·5 times that of the clover. Unfortunately Žoltkewich did not investigate the density of the venation in the leaves of the two plants. This high conducting capacity of the stem of alfalfa is correlated with its extremely large root system, and also with its greater intensity of transpiration, as compared with the clover, facts which were also noticed by Žoltkewich.

The recent investigations of **Zalenski** (1921) on the physiological action of "dry fog"[1] on plants yielded extremely important information regarding the influence of atmospheric drought on plants and the varying powers of endurance of different species. These experiments have shown that the "fog" acts on plants mainly by reason of the high temperature and the accompanying great dryness of the air, the dust particles as such producing no appreciable result. The high temperature has a very peculiar effect, bringing about the hydrolysis of starch in the guard cells of the stomata. This causes a great increase of osmotic pressure, in consequence of which the stomata open widely, even in cases where they had already closed owing to wilting. There is no doubt that this opening of the stomata in a dry, hot atmosphere very rapidly leads to the complete desiccation of the plant. The results of these experiments, in which the stomata are, so to speak, forcibly opened, afford perhaps the most convincing evidence available of the protective effect of wilting.

Zalenski's experiments showed, further, that the rapidity of opening of the stomata, under the influence of a high temperature, more or less depends on the capacity of drought

[1 Professor Maximov informs me that the "dry fog" of S.E. Russia is a dense haze brought by winds blowing from the deserts of Central Asia. The air is charged with minute particles of dust. The "fog" is thus comparable to the Italian *sirocco*.—ED.]

resistance of the plant. The stomata of less drought resistant plants, such as oats and wheat, open much earlier than do those of more resistant plants, e.g. millet and corn (see Table XXX).

TABLE XXX

The Rate of Stomatal Opening in Different Plants under the Influence of a High Temperature (39° C.). *The letter "O" Indicates Open and the letter "Z" Closed Stomata (according to Zalenski)*

	Duration (in hours) of Exposure to High Temperature				
	4	8	11	22	31
Oats	O	O	O	O	O
Poltavka wheat ..	O	O	O	O	O
Beloturka wheat ..	Z	Z	O	O	O
Elisseev rye ..	Z	Z	Z	O	O
Barley	Z	Z	Z	Z	O
Corn	Z	Z	Z	O	O
Millet	Z	Z	Z	Z	Z

The results of these laboratory experiments on the influence of high temperature on stomatal opening were confirmed by the investigations of **Zalenski and Doroshenko** (1923), carried out under field conditions at the Saratov Experiment Station during the very dry years 1920–1921. These authors observed that on very hot days, with a temperature of 35–37° C., many crop plants as well as wild species had widely opened stomata, the plants themselves being either strongly wilted or even in a state of complete desiccation. On the other hand, species that retained their freshness even on the hottest days (e.g. millet, corn, lilac, and wild vine) had tightly closed stomata. Plants with a stomatal apparatus particularly sensitive to heat under laboratory conditions showed a similar sensitivity in the field when exposed to the intense heat of summer.

These investigations of **Zalenski and Doroshenko** are extremely valuable. They throw light on the internal factors

determining drought resistance, and indicate that at least one cause of the high resistance of such plants as millet and corn must be the peculiarities of the stomatal mechanism.

It must not be forgotten, however, that we are here dealing not so much with the resistance of the plant to water loss in general, as with the particular case of the ability of the stomatal apparatus to withstand the effect of high temperatures. High temperature is one only of the factors occasioning atmospheric drought, so that plants that can endure prolonged heating may be termed thermophilous rather than xerophilous. This side of the question of drought resistance deserves more attention than it has generally received. It is possible that the capacity of withstanding heat may explain such cases as that observed by Zalenski of the marked endurance exhibited by the wild vine (*Ampelopsis quinquefolia*)—a semi-shade plant, in no way xeromorphic, but a native of a warm climate. It may also explain the high capacity of enduring atmospheric drought shown by cucurbitaceous plants such as melons, water melons, and pumpkins.

(*b*) *Soil Drought*

As mentioned above, we must distinguish between soil drought and atmospheric drought. The soil may be said to be in a condition of drought when it entirely ceases to provide the plant with water, or else provides it in quantities insufficient to replace the water lost by transpiration, even though the intensity of transpiration itself is not high. In either case the plant wilts, and, which is typical of soil drought, the wilting is permanent. On the other hand, wilting due to atmospheric drought is usually temporary.

We have already examined in detail the phenomena of wilting in Chapter VIII. It is therefore unnecessary here to do more than recall the fact that permanent wilting, accompanied by injury to, or death of, the root hairs, has more severe consequences than temporary wilting. In general, then,

soil drought is more injurious to the plant than atmospheric drought.

The most disastrous of all is a combination of both kinds of drought, such as may occur during dry, hot weather, when the soil has lost all the water available to the plant. For plants the struggle against soil drought is much more difficult than that against atmospheric drought. In the latter case a strong development of the root system and conducting elements may suffice to replace the water lost by transpiration. In the case of soil drought, however, these means are not sufficient. It was long supposed that plants might succeed in their struggle against soil drought by improving their water-absorbing apparatus. Xerophilous plants, for example, were supposed to be more capable than others of utilizing the soil water, thus leaving in the soil a smaller amount of unavailable water. This hypothesis, however, must be abandoned, for **Briggs and Shantz** (1912) have established beyond doubt (see Chapter II), that the amount of unavailable water in the soil depends only on the nature of the soil, and is practically the same for all species grown in the same kind of soil.

The principal means of overcoming the effects of soil drought, then, are (1) a reduction of the rate of water loss after the commencement of wilting; (2) the accumulation of water reserves, and—most important of all—(3) an increase of the capacity of enduring without serious injury the state of permanent wilting. The first is secured by the production of a thicker cuticle or deposit of wax; by diminishing the absorption of solar radiation by means of a screen of light-reflecting hairs, or by other peculiarities mentioned in Chapter IX. The succulents afford the most striking example of the second means, i.e. the accumulation of stores of water. Such plants can endure without injury the cutting off of their external water supply for many weeks or even months. To a smaller extent water is also stored by many plants which are by no means of a succulent nature. Such water stores are especially frequent in roots or other underground organs

(e.g. the cultivated potato), the aerial organs often showing no traces of succulence. In many of these plants the amount of water stored may at first sight appear insignificant, as compared with the high intensity of transpiration. But the significance of these reserves becomes clearer if we estimate their importance in terms of the rate of transpiration of wilting, rather than of normally transpiring plants.

The most efficient means, however, of overcoming the injurious effects of soil drought is a high capacity to endure permanent wilting. This is most pronounced in plants which are able to withstand complete desiccation. Such are certain lower plants, e.g. lichens and mosses, and a few highly organized plants, for example, *Selaginella lepidophylla* (see p. 263) or the epiphytic fern *Polypodium polypodioides*, recently investigated by **Pessin** (1924).[1] The great majority of higher plants, and in particular agricultural crop plants, are much less resistant in this respect, and perish long before they attain an air-dry condition.

THE BASIS OF DROUGHT RESISTANCE

The comparative resistance of different groups and species, and more particularly of different races of crop plants, to the loss of water has not as yet been investigated. The reasons for this are, first, that hitherto the cause of drought resistance has been sought in the morphological and anatomical peculiarities of the plant, and secondly, the considerable experimental difficulties inherent in such studies.

Long ago I expressed the opinion that the basis of drought resistance is the capacity of enduring wilting. This view is supported by certain data, of a preliminary nature, obtained by my assistant, **Tumanov** (1927). He investigated the respective capacities of enduring wilting of eight varieties of spring wheat, sharply contrasted as regards drought resistance. The plants were grown in large flower-pots, and at first were

[1 See also footnote, p. 243.—ED.]

allowed to develop in the open, with a sufficient supply of soil moisture. When the plants began to stalk, that is to say, when they had reached the period of their development when they are, as we shall see later, particularly susceptible to drought, the pots were transferred to a greenhouse and left unwatered for two weeks. At the end of this period the soil in the pots was dry and the plants in a state of permanent wilting; many of them indeed had perished. The soil was then again watered, when the surviving plants recovered. After some days a record was made of the plants that had died and of those that had recovered. The results of these experiments are given in Table XXXI.

TABLE XXXI

Endurance of Permanent Wilting of Different Varieties of Spring Wheat (according to Tumanov)

Name of Variety	Number of Pure Line	The Number of Plants		Percentage of Survivals
		Used in the Experiment	Which Survived	
Ferrugineum rossicum ..	Tulun 120/32	33	31	94
Ferrugineum rossicum ..	Tulun 81/14	10	9	90
Caesium	Omsk 111	11	9	82
Lutescens	"Marquis"	35	8	77
Ferrugineum rossicum ..	Tulun 916/4	18	9	50
Pseudohostianum ..	"Prelude" 330/16	35	17	49
Ferrugineum rossicum ..	Tulun 324	19	8	42
Anglicum	Pusa 4	34	8	23

The table shows that the percentage of survivals varied considerably, from 94 per cent (in Tulun No. 120/32) to 23 per cent (in the Indian irrigated wheat, Pusa 4). In general the varieties investigated fall into two groups—the drought resistant varieties with an endurance not lower than about 80 per cent, and the less resistant strains with an endurance not higher than 50 per cent. This division entirely agrees with

the characteristics exhibited by the same varieties and lines during field experiments.

These preliminary experiments of **Tumanov**, however, do not justify us in drawing the conclusion that drought resistance experiments with potted plants can entirely take the place of more complicated and difficult investigations under field conditions. Nevertheless, Tumanov's results appear to me clearly to indicate that the capacity of enduring prolonged wilting is one of the most important of the characters the sum total of which determines drought resistance in plants. If this is so, the internal physico-chemical properties of the protoplasm would appear to play the principal rôle in drought resistance, rather than the more superficial morphological or anatomical peculiarities of the plant.

The centre of interest of the problem of drought resistance is, in fact, tending to be transferred to the specific properties of the protoplasm of different plants. The problem thus falls within the purview of colloid chemistry, together with other phenomena depending on the stability of the protoplasm, such as the power of resistance to frost, to injury by salts or poisons, and even to attacks by plant or animal parasites. This opens an extremely interesting and important field of research. At present, however, this field is practically virgin ground, and as such lies outside the real scope of this book. I shall therefore limit myself here to a reference to certain recent works, particularly by American investigators (**Harvey**, 1918; **Rosa**, 1921; **Newton**, 1924), in which the authors attempt to explain the endurance of frost by plants. This explanation is based on the phenomenon of "hardening", and the changes in the colloids of the cell accompanying this process (see Chapter VIII). The interesting work of **MacDougal** (1920) on the water relations of living plant tissues, particularly as affected by the biocolloids of the plant cell, may also be mentioned.

Tumanov's recent (1927) researches on the sunflower, carried out in my laboratory, have shown that repeated wilting

results in a "hardening" process analogous to that observed at low temperatures. Tumanov found that a single permanent wilting strongly decreased the yield (to 40 per cent) of dry matter, at the same time checking the development of the assimilating surface. Subsequent wilting of a similar character caused no significant injury to the plant.

Up to the present we have no conception of the actual modifications undergone by the colloid substances of the protoplasm in connexion with such "hardening" against drought. Moreover, it is not yet clear to what extent the data concerning "hardening" agree with the recent investigations of Iljin mentioned in Chapter VIII.

The results of Tumanov's experiments show that further wilting induces in plants a more xeromorphic structure. This, as we have already seen, leads to a greater intensity of assimilation, which in turn gradually neutralizes the unfavourable consequences of the initial wilting, in spite of subsequent exposures to soil drought. We thus arrive at a somewhat paradoxical conclusion, i.e. that drought during the early stages of development may be actually beneficial.

Susceptibility to Drought at Various Stages of Development

We may now consider another set of phenomena that also appears to be of great importance in the study of the drought resistance of plants, and in the comparison of different varieties one with another. This is the changes in the capacity of enduring water loss, and drought in general, that plants undergo during their development.

We have already seen that ripe seeds possess the greatest power of resisting water loss. Such seeds are not only capable of enduring practically complete desiccation but even require it for the process of maturation. It is indeed in an air-dry condition that they preserve their vitality. This resistance to injury due to desiccation continues also during the earliest

stages of germination. It is a well-known fact that seedlings two or three days old (particularly those of cereals) can be again dried without losing their vitality. As development proceeds, toleration towards drying rapidly lessens, and seedlings that have unfolded their first leaves are very susceptible to water loss.

Even during the later stages of development the resistance of plants to water loss, and therefore to wilting—which determines their power of enduring soil drought—does not remain constant, but undergoes considerable fluctuations, which again are particularly marked in cereals. These fluctuations were long ago observed by several workers, especially **Brounov** (1899, 1912), who studied the question in detail, and applied the term "critical period" to those stages of development at which the plant appeared to be particularly susceptible to the action of any meteorological factor—in this case deficiency of water. For cereals such a critical period in respect of soil moisture is that which precedes the "heading" of the crop; that is, the period of rapid growth in length of the internodes, leading to the emergence of the ear from the tube formed by the leaf sheaths.

In the first instance the existence of these critical periods in the development of the plant was established by a comparison of the yield and of the march of the meteorological factors (and especially of soil moisture) in different years. It was found that if during the critical period the water supply was sufficient, the yield was high; if it was deficient, the yield was low. These results were fully confirmed later by experiments in which the plants were grown in suitable containers (**Pullmann**, 1905).

Finally, at my suggestion the question of the critical periods of cereals was re-investigated by **Moliboga** (1927). Moliboga cultivated his plants in containers in the usual way, and at definite stages of development (the actual stage being different in different cases) watering was discontinued. The plants were thus exposed, at some period or other of their existence, to permanent wilting, after which the optimal soil moisture was

again restored by watering. The results showed that the effect of the same degree of wilting varied according to the stage of development of the plant. The consequences of wilting at the time of tillering were transient, and had practically no effect on subsequent development or on the yield. On the other hand, wilting during the period when the stems are rapidly growing in length and the flowers are developing, results in a considerable decrease in both the height of the plants and the yield. Finally, wilting at a still later stage, when flowering is over, has only an insignificant effect on the plant.

From the physiological point of view, this unequal susceptibility of plants to soil drought at different periods of development may be readily explained. It is during the period of maximal growth in length that the plant requires most water for the expansion of its tissues. A deficiency of water at this period leads to a sharp decrease in size of the cells, and to the deflexion of nutrients from the developing flowers by the energetically transpiring leaves.

From the agricultural point of view the study of the critical periods and an exact determination of the times at which they occur are of great importance. This would render it possible to evaluate the climate of a country from the point of view of its suitability for the cultivation of particular crops, and to predict from the usual time of occurrence of drought the probable yield. It is not surprising, therefore, that the study of the critical periods, initiated in Russia especially by **Pullmann, Brounov** (1912), **Hauer** (1908, 1915), and other workers connected with the Board of Agricultural Meteorology has recently attracted the attention of Western European investigators, e.g. **Azzi** (1922), **Beauverie** (1922), and others.

The study of critical periods again emphasizes the importance of exercising great care in estimating the drought resistance of plants. Reliable estimates cannot be made merely from data indicating that in certain years, under such and such climatic conditions, particular species or varieties proved capable of resisting drought to a greater or less extent. Some plants, with

an earlier critical period, may suffer most from a spring drought; others, with a later period, may be more sensitive to summer drought. Hitherto, however, few investigations have been made in this direction, and it is very desirable that more attention should be paid to this question, in selecting drought resistant varieties.

Analysis of the Problem of Drought Resistance

We may now return to the question of the drought resistance of crop plants. Literally, drought resistance means the capacity of plants to endure drought and to recover readily after permanent wilting, with the minimum of damage to the plant itself and to the yield produced. We must, however, bear in mind that the expression "drought resistance" is by no means always used exactly in this sense. Frequently all plants suitable for cultivation in dry countries are referred to as drought resistant, just as plants that grow in arid regions are usually termed xerophytes. But we have seen that, in order to avoid misunderstanding, the ephemerals, which complete their life-cycle during some six to eight of the more humid weeks of the year, must be excluded from the true xerophytes, and may be termed "drought-escaping" plants (**Shantz**, 1927). Similarly, we must also exclude from the drought resistant plants proper those crop plants which have a short vegetative period, and also winter crops which ripen early, and thus succeed in completing their development before the beginning of the summer drought. These plants may have great significance for agriculture in dry regions, and undoubtedly the physiological peculiarities which permit them to accelerate their development merit the most careful study. But from such plants we can gain no insight into the nature of drought resistance itself, or into the actual reasons why drought resistant plants can often endure long periods of extreme dryness of both soil and air. The plants referred to above may be even less useful in this respect than those of

the irrigated regions of Turkestan or Egypt, which have been investigated by some authors. A careful analysis of the phenomenon is the first condition of success in attacking the problem of drought resistance. The most important initial step must be to select from the miscellaneous group of plants capable of growing in dry regions those which can really endure—and do not merely escape or evade—severe drought. In my opinion, it is only when we have thus decided which plants are truly drought resistant that we can attack with any prospect of success the problem of determining which are the peculiarities of organization that actually confer on plants the faculty of enduring intense drought. Failing such a preliminary investigation, productive physiological work on the causes and factors involved in drought resistance would seem to be impossible.

The plant breeder, however, who wishes to select species or races of agricultural plants suitable for cultivation in dry regions, has many options open to him. But he must be clear in his own mind as to which he means to adopt. He can, for instance, select early ripening varieties, which mature before, and so escape, the dry period. Or he can choose forms which expend their water economically, and therefore find the winter supply of soil moisture sufficient for their complete development—of grain as well as straw. But though plants of both these classes may be of great value as agricultural crops in areas with a small rainfall, they cannot be regarded as truly drought resistant. Such plants are liable to succumb if the summer drought sets in earlier than usual, or if the winter reserves of soil water are rapidly exhausted. But one may also endeavour to select plants with an organization which will enable them successfully to withstand severe soil and atmospheric drought. From what we already know of these anatomical peculiarities, we may suppose that they will be those which characterize a xerophilous structure (see Chapter XI), namely, other things being equal, small cells, a dense network of veins, numerous (but small) stomata per unit area, a relatively great

development of the root system, and so on. Physiologically these peculiarities are for the most part associated with intense assimilation, intense transpiration, reduced growth in height, high osmotic pressure, etc. But these relatively easily observable peculiarities appear of secondary importance as compared with the capacity to endure without injury an intense loss of water—one of the most important properties of true drought resistant plants. This property is connected with the capacity of the protoplasm to endure considerable fluctuations in its degree of swelling, without the loss of vital activity and without the appearance of irreversible coagulation. This capacity of enduring water loss may completely mask the significance of the other anatomical and physiological peculiarities, and thus mystify investigators who endeavour to find a strict correlation between drought resistance and these external peculiarities. Such forms alone are really drought resistant, and we may consider that the anatomical and physiological peculiarities of these plants are in some way connected with protection from drought.

BIBLIOGRAPHY

NOTE.—Russian names are spelt according to the system advocated in the *Slavonic Review*. But in order to avoid confusion in cases where a different spelling was employed in the original work cited, the alternative form is given in brackets.

Agamov, S., (1927). Ueber die cuticulare Transpiration. *Bull. Jard. Bot. de Leningrad*, **26**, 576–594. (Russian, with German abstract.)

Ahrns, W., (1924). Weitere Untersuchungen über die Abhängigkeit der gegenseitigen Mangenverhältnisse der Kohlenhydrate im Laubblatt vom Wassergehalt. *Bot. Archiv.*, **5**, 234–259.

Alexandrov, O., (1925). Sur les oscillations des quantités d'eau enmagasinées dans les feuilles. *Jour. Soc. Bot. de Russie*, **8**, 143–156. (Russian, with French abstract.)

Alexandrov, W., (1920). Ueber die Productivität der Transpiration. *Trav. Jard. Bot. de Tiflis*, sér. II, livr. **2**, 1–56. (Russian, with German abstract.)

(1922). Le régime d'eau de la feuillage d'une mésophyte. *Moniteur Jard. Bot. de Tiflis*, sér. II, livr. **1**, 57–72. (Russian, with French abstract.)

(1923[a]). La photosynthèse de différentes feuilles sur une tige de la même plante. *Scientific Papers of the Applied Section of the Tiflis Bot. Gard.*, **3**, 45–54. (Russian, with French abstract.)

(1923[b]). Ueber die Zusammenziehung der Blattfläche der kräutigen Pflanzen. *Bull. Univ. Tiflis*, **3**, 262–275. (Russian, with German abstract.)

(1924[a]). Sur l'intensité de la transpiration de quelques plantes herbacées. *Scientific Papers of the Applied Section of the Tiflis Bot. Gard.*, **4**, 1–28. (Russian, with French abstract.)

(1924[b]). Sur une cause vraisemblable de la productivité grande de la transpiration de quelques plantes herbacées. *Jour. d'agron. scient.*, **1**, 663–671. (Russian.)

(1925). A brief record of the phenomena occurring during the wilting of plants. *Bull. of Agric. Res. Inst. of Don and North Caucasus*, 4–5. (Russian, with English abstract.)

Alexandrov, W., Alexandrov, O., and Timofeev, A., (1921). Die Wasserversorgung der Blätter und ihre Struktur. *Scientific Papers of the Applied Section of the Tiflis Bot. Gard.*, **2**, 85–106. (Russian, with German abstract.)

Aloi, A., (1891). Relazioni esistenti tra la traspirazione delle piante terrestri ed il movimento delle cellule stomatiche. *Malpighia*, **5**, 419–426.

Arends, J., (1925). Ueber den Einfluss chemischer Agenzien auf Stärkegehalt und osmotischen Wert der Spaltöffnungsschliesszellen. *Archiv. f. wiss. Bot.*, **1**, 84–115.

Areschoug, F. W. C., (1882). Der Einfluss des Klimas auf die Organisation der Pflanzen, insbesondere auf die anatomische Struktur der Blattorgane. *Engler's Bot. Jahrb.*, **2**, 511–526.

(1906). Ueber die Bedeutung des Palisadenparenchyms für die Transpiration der Blätter. *Flora*, **96**, 329–336.

Atkins, W. G., (1916). Some recent researches in plant physiology. —London.

Azzi, G., (1922[a]). The problem of agricultural ecology. *Geografiske Annaler*, 137–146.

(1922[b]). Il clima del grano in Italia. *Nuovi Annali del Ministero per Agricoltura*, **2**, 453–625.

Bachmann, F., (1922). Studien über Dickenänderungen von Laubblättern. *Jahrb. f. wiss. Bot.*, **61**, 372–429.

Bakke, A. L., (1914). Studies on the transpiring power of plants as indicated by the method of standardized hygrometric paper. *Jour. Ecol.*, **2**, 145–173.

Balls, W. L., (1912). The stomatograph. *Proc. Roy. Soc. London*, **85B**, 33–41.

(1919). The cotton plant in Egypt.—London.

Baranov (Baranow), **P. A.,** (1925). Essai de caractéristique comparative-anatomique des xérophytes et mésophytes des montagnes. *Bull. Univ. Asie Centr., Taschkent*, **8**, 1–39. (Russian, with French abstract.)

Barger, G., (1904). A microscopical method of determining molecular weights. *Chem. Soc. Trans.*, **85**, 286–324.

Bartholomew, E. T. (1926). Internal decline of lemons. III. Water deficit in lemon fruits caused by excessive leaf evaporation. *Amer. Jour. Bot.*, **13**, 102–117.

Bayliss, W. M., (1918). Principles of general physiology.—London.

Beauverie, J., (1922). Sur la "période critique" du blé. *Compt. Rend.*, **175**, 632–635.

Benecke-Jost, (1924). Pflanzenphysiologie. IV. Aufl.—Jena.

Bergen, J. Y., (1904). Transpiration of sun leaves and shade leaves of *Olea europaea* and other broad-leaved evergreens. *Bot. Gaz.*, **38**, 285–296.

Bergman, H. F., (1920). The relation of aeration to the growth and activity of roots and its influence on the ecesis of plants in swamps. *Ann. Bot.*, **34**, 13–33.

Berkeley, Earl of, and Hartley, E. G. J., (1906). On the osmotic pressures of some concentrated aqueous solutions. *Phil. Trans. Roy. Soc. London*, **206A**, 481–507.

Bernbeck, O., (1907). Der Wind als pflanzenpathologischer Factor. —Dissert., Bonn.

(1924). Wind und Pflanze. *Flora*, **117**, 293–300.

Blackman, F. F. (1895). Experimental researches on vegetable assimilation and respiration. No. II. On the paths of gaseous exchange between aerial leaves and the atmosphere. *Phil. Trans. Roy. Soc. London,* **186B,** 503–562.

(1904). Residual vitality. *New Phyt.,* **3,** 33–39.

(1905). Optima and limiting factors. *Ann. Bot.,* **19,** 281–295.

Blackman, V. H., (1914). The wilting coefficient of the soil. *Jour. Ecol.,* **2,** 43–50.

(1921). Osmotic pressure, root pressure and exudation. *New Phyt.,* **20,** 106–115.

Blackman, V. H., and Knight, R. C., (1917). A method of controlling the rate of air movement in transpiration experiments. *Ann. Bot.,* **31,** 217–220.

Blagoveshenski (Blagowestshensky), **A. W.,** (1924). The botanical station of the University of Central Asia in the summer of 1924. *Bull. Univ. Asie Centr., Taschkent,* **7,** 8–14. (Russian, with English abstract.)

(1926). Der osmotische Wert bei den Gebirgspflanzen Mittelasiens. *Jahrb. f. wiss. Bot.,* **65,** 279–313.

Bode, H. R., (1923). Beiträge zur Dynamik der Wasserbewegung in den Gefässpflanzen. *Jahrb. f. wiss. Bot.,* **62,** 92–127.

Bogdanov, S., (1893). Ueber das Verhalten der keimenden Samen zum Wasser im allgemeinen, und speziell zur Bodenfeuchtigkeit. *Landw. Versuchs-Stat.,* **42,** 311–366.

Bonnier, G., (1890). Influence des hautes altitudes sur les fonctions des végétaux. *Compt. Rend.,* **111,** 377–380.

Bonnier, G. et Mangin, L., (1884). Recherches surl a respiration et transpiration des champignons. *Ann. Sci. Nat., Bot.,* 6e sér., **17,** 210–315.

Bose, J. C., (1923). Physiology of the ascent of sap.—London.

Bottazzi, F., (1908). Osmotischer Druck und elektrische Leitfähigkeit der Flüssigkeiten der einzelligen pflanzlichen und tierischen Organismen. *Ergeb. d. Physiol.,* **7,** 161–402.

Briggs, L. J., and McCall, A., (1904). An artificial root for inducing capillary movement of soil mixture. *Science,* N.S., **20,** 566–569.

Briggs, L. J., and McLane, J. W., (1907). The moisture equivalent of soils. *U.S. Dept. of Agric. Bur. of Soils Bull.,* **45.**

(1910). Moisture equivalent determinations and their application. *Proc. Amer. Soc. of Agronomy,* **2,** 138–147.

Briggs, L. J., and Shantz, H. L., (1911). The wax seal method for determining the lower limit of available soil moisture. *Bot. Gaz.,* **51,** 210–219.

(1912a). The wilting coefficient and its indirect determination. *Bot. Gaz.,* **53,** 20–37.

Briggs, L. J., and Shantz, H. L.—*continued.*

(1912[b]). The relative wilting coefficients for different plants. *Bot. Gaz.*, **53**, 229–235.

(1913[a]). Die relativen Welkungskoeffizienten verschiedener Pflanzen. *Flora*, **105**, 224–240.

(1913[b]). The water requirement of plants. I. Investigations in the Great Plains in 1910 and 1911. II. A review of the literature. *U.S. Dept. of Agric. Bur. of Plant Ind. Bull.*, **284**, 1–48; **285**, 1–96.

(1914). Relative water requirement of plants. *Jour. Agric. Res.*, **3**, 1–63.

(1915). An automatic transpiration scale of large capacity for use with freely exposed plants. *Jour. Agric. Res.*, **5**, 117–132.

(1916). Hourly transpiration rate on clear days as determined by cyclic environmental factors. *Jour. Agric. Res.*, **5**, 583–649.

(1917[a]). Comparison of the hourly evaporation rate of atmometers and free water surfaces with transpiration rate of *Medicago sativa*. *Jour. Agric. Res.*, **9**, 277–292.

(1917[b]). The water requirement of plants as influenced by environment. *Proc. Second Pan-Amer. Scientific Congress.*

Brilliant, A. W., (1924). La teneur en eau dans les feuilles et l'énergie assimilatrice. *Compt. Rend.*, **178**, 2122–2124.

Bristol, B. M., (1916). On the remarkable retention of vitality of moss protonema. *New Phyt.*, **15**, 137–143.

Brounov (Brounoff), **P. J.**, (1899). On the dependence of crop yield on sun spots and on meteorological factors.—*Bur. of Agric. Meteorology, St. Petersburg.* (Russian.)

(1912). Les cultures agricoles et le temps.—St. Petersburg.

Brown, A. J., (1907). On the existence of a semipermeable membrane enclosing the seeds of some of the Gramineae. *Ann. Bot.*, **21**, 79–87.

Brown, H. T., and Escombe, F., (1900). Static diffusion of gases and liquids in relation to the assimilation of carbon and translocation in plants. *Phil. Trans. Roy. Soc. London*, **193B**, 223–291.

(1905). Researches on some of the physiological processes of green leaves, with special reference to the interchange of energy between the leaf and its surroundings. *Proc. Roy. Soc. London*, **76B**, 29–111.

Brown, M. A., (1910). The influence of air currents on transpiration. *Proc. Iowa Acad. Sc.*, **17**.

Burgerstein, A., (1876). Untersuchungen über die Beziehungen der Nährstoffe zur Transpiration der Pflanzen. *Sitzungsber. d. K. Akad. d. Wiss. Wien*, Abt. 1, **73**, 190–244.

Burgerstein, A.—*continued.*

(1878). Untersuchungen über die Beziehung der Nährstoffe zur Transpiration der Pflanzen. II. *Sitzungsber. d. K. Akad. Wiss. Wien,* Abt. 1, **78,** 607–637.

(1897). Ueber die Transpirationsgrösse von Pflanzen feuchter Tropengebiete. *Ber. deut. Bot. Ges.,* **15,** 154–165.

(1904). Die Transpiration der Pflanzen. Eine physiologische Monographie.—Jena.

(1920[a]). Die Transpiration der Pflanzen. II. Teil (Erganzungsband).—Jena.

(1920[b]). Aenderungen der Spaltöffnungsweite unter dem Einfluss verschiedener Bedingungen. *Verhandl. zool.-bot. Ges. Wien,* **70,** 113–131.

(1925). Die Transpiration der Pflanzen. III. Teil (2 Erganzungsband).—Jena.

Buscaglioni, L., e Pollacci, G., (1901–1902). Ulteriori ricerche sull' applicazione delle pellicole di collodio allo studio di alcuni processi fisiologici delle piante ed in particular modo della traspirazione vegetale. *Atti. R. Inst. Bot. Pavia,* **2,** ser. 7.

Caldwell, J. S., (1913). The relation of environmental conditions to the phenomenon of permanent wilting in plants. *Physiol. Res.,* **1,** 1–56.

Cannon, W. A., (1905). A new method of measuring the transpiration of plants in place. *Bull. Torrey Bot. Club,* **32,** 515–529.

(1911). The root habits of desert plants. *Carnegie Inst. Washington Publ.,* **131,** 1–96.

(1917). Root growth of *Prosopis* and *Opuntia* under conditions of a small oxygen supply in the soil. *Year Book Carnegie Inst. Washington,* **16,** 82–83.

(1919). Reactions of roots of species with dissimilar habitats to different amounts of carbon dioxide in the soil. *Year Book Carnegie Inst. Washington,* **18,** 92–94.

Cannon, W. A., and Free, E. E., (1920). Root adaptation to deficient soil aeration. *Year Book Carnegie Inst. Washington,* **19,** 62.

Carey, A. E., and Oliver, F. W., (1918). Tidal lands.—London.

Catalano, G., (1920). Xerophilia e traspirazione. *Boll. d. Soc. di Sc. Natur. ed Econom. Palermo.*

(1921). Determinazione razionale della xerofilia. *Boll. R. Orto bot. Palermo,* **2,** fasc. 2, 171–221.

(1923). Percentuale limite di umidità del suolo per la organicazione delle xeròfile. *Boll. d. Soc. di Sc. Natur. ed Econom. Palermo.* **5.**

(1924). Sulla organicazione delle xeròfile. *Atti d. Soc. Agron. Italiana,* Anni IV–V, **3.**

Church, A. H., (1919). Thalassiophyta and the subaerial transmigration.—Oxford.

Clapp, G. L., (1908). A quantitative study of transpiration. *Bot. Gaz.*, **55**, 254–267.

Clements, F. E., (1907). Plant physiology and ecology.—New York.

(1921). Aeration and air content. The rôle of oxygen in root activity. *Carnegie Inst. Washington Publ.*, **315**, 1–183.

Comes, O., (1880). La luce e la traspirazione delle piante. *Atti della R. Accad dei Lincei, Roma,* Seria 3, **7**, Separate, 36 pp.

Cribbs, J. E., (1919). Ecology of *Tilia americana.* Comparative studies of the foliar transpiring power. I. *Bot. Gaz.*, **68**, 262–286.

(1921). Ecology of *Tilia americana.* II. *Bot. Gaz.*, **71**, 289–313.

Crocker, W., (1924). Discussions of the work at the Boyce Thompson Institute and its application. *Trans. Illum. Eng. Soc.*, **19**, 998–999.

Crump, W. B., (1913[a]). Notes on water content and the wilting point. *Jour. Ecol.*, **1**, 96–100.

(1913[b]). The coefficient of humidity: a new method of expressing the soil moisture. *New Phyt.*, **12**, 125–147.

Dachnowski, A., (1908). The toxic property of bog water and bog soil. *Bot. Gaz.*, **46**, 130–143.

(1909). Bog toxins and their effect upon soils. *Bot. Gaz.*, **47**, 389–405.

(1910). Physiologically arid habitats and drought resistance in plants. *Bot. Gaz.*, **49**, 325–339.

(1914). The effects of acid and alkaline solutions upon the water relation and the metabolism of plants. *Amer. Jour. Bot.*, **1**, 412–439.

Darwin, F., (1898). Observations on stomata. *Phil. Trans. Roy. Soc. London,* **190B**, 531–621.

(1914[a]). On a method of studying transpiration. *Proc. Roy. Soc. London,* **87B**, 269–280.

(1914[b]). The effect of light on the transpiration of leaves. *Proc. Roy. Soc. London,* **87B**, 281–299.

(1916). On the relation between transpiration and stomatal aperture. *Phil. Trans. Roy. Soc. London,* **207B**, 413–437.

Darwin, F., and Pertz, D. F. M., (1911). On a new method of estimating the aperture of stomata. *Proc. Roy. Soc. London,* **84B**, 136–154.

Dehérain, P., (1869). Sur l'évaporation de l'eau et la décomposition de l'acide carbonique par les feuilles des végétaux. *Ann. Sci. Nat., Bot.*, 5[e] sér., **17**, 381–384.

Delf, M., (1911). Transpiration and behaviour of stomata in halophytes. *Ann. Bot.*, **25**, 483–505.

Delf, M.—*continued.*
(1912). Transpiration in succulent plants. *Ann. Bot.*, **26**, 409–441.
(1915). The meaning of xerophily. *Jour. Ecol.*, **3**, 110–121.
(1916). Studies of protoplasmic permeability by measurement of rate of shrinkage of turgid tissues.—1. The influence of temperature on the permeability of protoplasm to water. *Ann. Bot.*, **30**, 283–310.

Dietrich, M., (1926). Die Transpiration der Schatten- und Sonnenpflanzen in ihren Beziehungen zum Standort. *Jahrb. f. wiss. Bot.*, **65**, 98–194.

Dixon, H. H., (1910). Transpiration and the ascent of sap. *Progressus Rei Bot.*, **3**, 1–66.
(1912). A thermoelectric method of cryoscopy. *Notes from the Bot. School of Trinity Coll., Dublin*, **2**, 121–134.
(1914). Transpiration and the ascent of sap in plants.—London.
(1924). The transpiration stream.—London.

Doyarenko, A. G., (1909). A short manual for pot experiments with crop plants.—Moscow. (Russian.)

Dufour, L., (1887). Influence de la lumière sur la forme et la structure des feuilles. *Ann. Sci. Nat., Bot.*, 7e sér., **5**, 311–413.

Eberdt, O., (1889). Die Transpiration der Pflanzen und ihre Abhängigkeit von äusseren Bedingungen.—Marburg.

Eberhardt, P. H., (1903). Influence de l'air sec et de l'air humide sur la forme et sur la structure des végétaux. *Ann. Sci. Nat., Bot.*, 8e sér., **18**, 61–152.

Edelstein, V. J., (1902). Zur Kenntniss der Hydatoden an den Blättern der Holzgewächse. *Bull. Acad. Sci. St. Petersburg*, **17**, 59–64.

von Faber, F. C., (1915). Physiologische Fragmente aus einem tropischen Urwald. *Jahrb. f. wiss. Bot.*, **56**, 197–220.

Famintsin (Famintzin), **A. S.**, (1883). The exchange of substance and the transformation of energy in plants.—St. Petersburg. (Russian.)

Farmer, J. B., (1918). On the quantitative differences in the water conductivity of the wood in trees and shrubs. Part II. The deciduous plants. *Proc. Roy. Soc. London*, **90B**, 232–250.

Findlay, A., (1913). Osmotic pressure.—London.

Fischer, M., (1910). Œdema. A study of the physiology and the pathology of water absorption by the living organism. —New York.

Fittbogen, J., (1873). Untersuchungen über das für eine normale Produktion der Haferpflanze notwendige Minimum von Bodenfeuchtigkeit, etc. *Landw. Jahrb.*, **2**, 353–371.

Fitting, H., (1911). Die Wasserversorgung und die osmotischen Druckverhältnisse der Wüstenpflanzen. *Zeitschr. f. Bot.*, **3**, 209–275.

Flood, M. G., (1919). Exudation of water by *Colocasia antiquorum*. *Proc. Roy. Dublin Soc.*, N.S., **15**, No. 36, 506–512.

Freeman, G. F., (1908). A method for the quantitative determination of transpiration in plants. *Bot. Gaz.*, **46**, 118–129.

Frey, Lucy, (1923). The influence of soil moisture on the transpiring power of plants. *Trav. Soc. Natur. de Petrograd.*, **33**, 173–210. (Russian, with English abstract.)

Gain, E., (1895[a]). Action de l'eau du sol sur la végétation. *Rev. Gén. Bot.*, **7**, 15–26, 71–84, 123–138.

(1895[b]). Recherches sur le rôle physiologique de l'eau dans la végétation. *Ann. Sci. Nat., Bot.*, 7[e] sér., **20**, 63–223.

Ganong, W. F., (1905). New precision appliances for use in plant physiology. II. *Bot. Gaz.*, **39**, 145–152.

(1908). A laboratory course of plant physiology. Ed. 2.—New York.

Gante, T., (1916). Ueber den osmotischen Druck einiger einheimischer Xerophyten und Beobachtungen über das Verhalten ihrer Stomata.—Dissert., Jena.

Gardiner, W., (1883–84). On the physiological significance of water glands and nectaries. *Proc. Cambridge Phil. Soc.*, **5**, 35–50.

Gates, F. C., (1914). Winter as a factor in xerophily of certain evergreen ericads. *Bot. Gaz.*, **57**, 445–489.

Gavrilov (Gavriloff), **L. G.,** (1924). L'influence de la temperature sur l'absorption de l'eau par les racines des plantes supérieurs. *Bull. Jard. Bot. de Petrograd*, **22**, 20–34. (Russian, with French abstract.)

Géneau de Lamarlière, (1892). Recherches physiologiques sur les feuilles développées à l'ombre et au soleil. *Rev. Gén. Bot.*, **4**, 481–496, 529–544.

Giltay, E., (1900). Nochmals über Transpiration in den Tropen und in Mitteleuropa. *Beih. Bot. Centralbl.*, **9**, 112–118.

Goebel, K., (1891). Pflanzenbiologische Schilderungen. IV. Die Vegetation der Venezolanischen Paramos.—Jena.

Gradmann, H., (1923). Windschutzeinrichtungen an den Spaltöffnungen der Pflanzen. *Jahrb. f. wiss. Bot.*, **62**, 449–527.

Grafe, V., (1920[a]). Die physikalisch-chemische Analyse der Pflanzenzelle. *Handb. der biol. Arbeitsmethoden*, Abt. XI, Teil 2, **1**, 1–28.

(1920[b]). Messung der Gas- und Wasserbewegung im Pflanzenorganismus. *Handb. d. biol. Arbeitsmethoden*, Abt. XI, Teil 2, **1**, 105–186.

Gray, J., and Peirce, G. J., (1919). The influence of light upon the action of stomata and its relation to the transpiration of certain crops. *Amer. Jour. Bot.*, **6**, 131–155.

Gregory, E., (1886). Comparative anatomy of the filz-like hair covering of leaf organs.—Dissert., Zürich.

von Guttenberg, H., (1907). Anatomisch-physiologische Untersuchungen über das immergrüne Laubblatt der Mediterranflora. *Engler's Bot. Jahrb.*, **38**, 383–444.

(1917). Ueber die Ursachen des Dickenwachstums der Bäume. *Oesterr. Vierteljahrschr. Forstw. N.F.*, **35**, 1–5.

(1927). Studien über das Verhalten des immer Laubblattes der Mediterranflora zu verschiedenen Jahreszeiten. *Planta*, **4**, 727–779.

Haberlandt, F., (1877). Das Austrocknen abgeschnittener und benetzter, sowie abgeschnittener und nicht benezter grüner Blätter und Pflanzenteile. *Wiss.-prakt. Unters. auf. d. Gebiete d. Pflanzenbaues*, **2**, 130.

Haberlandt, G., (1892). Anatomisch-physiologische Untersuchungen über das tropische Laubblatt. *Sitzungsber. d. K. Akad. d. Wiss. Wien*, Abt. 1, **101**, 785–816.

(1894). Ueber Bau und Funktion der Hydatoden. *Ber. deut. Bot. Ges.*, **12**, 367–378.

(1894–95). Anatomisch-physiologische Untersuchungen über das tropische Laubblatt. II. Ueber wassersezern. und absorbierende Organe. *Sitzungsber. d. K. Akad. d. Wiss. Wien*, Abt. 1, **103**, 489–538; **104**, 55–116.

Halket, A. C., (1913). On various methods for determining osmotic pressures. *New Phyt.*, **12**, 164–176.

Hannig, E., (1912). Untersuchungen über die Verteilung des osmotischen Drucks in der Pflanze in Hinsicht auf die Wasserleitung. *Ber. deut. Bot. Ges.*, **30**, 194–204.

Harris, J. A., (1915). An extension to 5·99° of tables to determine the osmotic pressure of expressed vegetable saps from the depression of the freezing-point. *Amer. Jour. Bot.*, **2**, 418–419.

(1918[a]). On the osmotic concentration of the tissue fluids of desert Loranthaceae. *Mem. Torrey Bot. Club.*, **17**, 307–315.

(1918[b]). On the osmotic concentration of the tissue fluids of phanerogamic epiphytes. *Amer. Jour. Bot.*, **5**, 490–506.

(1924). The tissue fluids of *Cuscuta*. *Bull. Torrey Bot. Club*, **51**, 127–131.

(1925). A table to facilitate correction for undercooling in cryoscopic work. *Amer. Jour. Bot.*, **12**, 499–501.

Harris, J. A., and Gortner, R. A., (1914). Note on the calculation of the osmotic pressure of expressed vegetable saps from the depression of the freezing-point, with a table

Harris, J. A., and Gortner, R. A.—*continued.*
for the values of P for $\Delta = 0{\cdot}001°$ to $\Delta = 2{\cdot}999°$. *Amer. Jour. Bot.*, **1**, 75–78.

Harris, J. A., Gortner, R. A., and Lawrence, J. V., (1921). The osmotic concentration and electrical conductivity of the tissue fluids of ligneous and herbaceous plants. *Jour. Phys. Chem.*, **25**, 122–146.

Harris, J. A., Gortner, R. A., Hoffmann, W. F., and Valentine, A. T., (1921). Maximum values of osmotic concentration in plant tissue fluids. *Proc. Soc. Exper. Biol. and Med.*, **18**, 106–109.

Harris, J. A., Gortner, R. A., Hoffmann, W. F., Lawrence, J. V., and Valentine, A. T., (1924). The osmotic concentration, specific electrical conductivity, and chloride content of the tissue fluids of the indicator plants of Tooele Valley, Utah. *Jour. Agric. Res.*, **27**, No. 12, 893–924.

Harris, J. A., Hoffmann, C. T., and Hoffmann, W. F., (1925). Sulphate content of the leaf tissue fluids of Egyptian and Upland cotton. *Jour. Agric. Res.*, **31**, No. 7, 653–661.

Harris, J. A., Hoffmann, W. F., Sinclair, W. B., Johnson, A. H., and Evans, R. D., (1925). The leaf tissue fluids of Egyptian cotton. *Jour. Agric. Res.*, **31**, No. 11, 1027–1033.

Harris, J. A., and Lawrence, J. V., (1916). On the osmotic pressure of the tissue fluids of Jamaican Loranthaceae parasitic on various hosts. *Amer. Jour. Bot.*, **3**, 438–455.

(1917[a]). Cryoscopic determination of tissue fluids of plants of Jamaican coastal deserts. *Bot. Gaz.*, **64**, No. 4, 285–305.

(1917[b]). The osmotic concentration of the sap of the leaves of mangrove trees. *Biol. Bull.*, **27**, No. 3, 202–211.

(1917[c]). The osmotic concentration of the tissue fluids of Jamaican montane rain forest vegetation. *Amer. Jour. Bot.*, **4**, 268–298.

Harris, J. A., and Lawrence, J. V., with the co-operation of **Gortner, R. A.**, (1916). The cryoscopic constants of expressed vegetable saps, as related to local environmental conditions in the Arizona deserts. *Physiol. Res.*, **2**, 1–49.

Harris, J. A., Lawrence, J. V., and Lawrence, Z. W., (1924). The chloride content of the leaf tissue fluids of Egyptian and Upland cotton. *Jour. Agric. Res.*, **28**, No. 7, 695–703.

Harris, J. A., Lawrence, Z. W., Hoffmann, W. F., Lawrence, J. V., and Valentine, A. T., (1924). The tissue fluids of Egyptian and Upland cottons and their F hybrid. *Jour. Agric. Res.*, **27**, No. 5, 267–327.

Harvey, R. B., (1918). Hardening process of plants and developments from frost injury. *Jour. Agric. Res.*, **15**, 83–112.

(1922). Growth of plants in artificial light. *Bot. Gaz.*, **74**, 447–451.

Hasselbring, H., (1914[a]). Relation between the transpiration stream and the absorption of salts. *Bot. Gaz.*, **57**, 72–73.

(1914[b]). The effect of shading on transpiration and assimilation of the tobacco plant in Cuba. *Bot. Gaz.*, **57**, 257–286.

Hauer, W. K., (1908). Influence of meteorological conditions on the growth of oats in the Chernozem region. *Ann. Agro-meteorol.*, **4**, 1–269. (Russian.)

(1915). On the problems and methods of agro-meteorology. *Ann. Agro-meteorol.*, **14**, 1–39. (Russian.)

Hawkins, L. A., (1910). The porous clay cup for the automatic watering of plants. *Plant World*, **13**, 220–227.

Hayoz, C., (1922). Beiträge zur Kenntnis der Saugkraft des Efeublattes.—Dissert., Freiburg in d. Schweiz.

Hedgcock, G., (1902). The relation of the water content of the soil to certain plants, principally mesophytes. *Bot. Survey of Nebraska, VI, Studies in the Vegetation of the State II*, 5–79.

Hellriegel, F., (1883). Beiträge zu den Naturwiss. Grundlagen des Ackerbaus.—Braunschweig.

Henslow, G., (1887). A contribution to the study of the relative effects of different parts of the solar spectrum on the transpiration of plants. *Jour. Linn. Soc.*, **22**, 81–98.

Hess, Eugen, (1910). Ueber die Wuchsformen der Alpinen Geröllpflanzen. *Beih. Bot. Centralbl.*, **27**, Abt. II, 1–170.

Hesselman, H., (1904). Zur Kenntnis des Pflanzenlebens schwedischer Laubwiesen. *Beih. Bot. Centralbl.*, **17**, 311–460.

Heuser, W., (1915). Untersuchungen über den anatomischen Bau des Weizenblattes je nach der Höhe seines Standortes am Halme und unter dem Einfluss äusserer Bedingungen. *Kühn-Archiv.*, **6**, 391.

Hill, T. G., and Hanley, J. A., (1914). The structure and water content of shingle beaches. *Jour. Ecol.*, **2**, 21–38.

Höfler, K., (1920). Ein Schema für die osmotische Leistung der Pflanzenzellen. *Ber. deut. Bot. Ges.*, **38**, 288–298.

von Hoehnel, F., (1878). Ueber den Gang des Wassergehaltes und der Transpiration bei der Entwickelung des Blattes. *Wollny's Forsch. a. d. Gebiet der Agric.-Phys.*, **1**, 299–327.

(1879). Ueber die Transpirationsgrösse der forstlichen Holzgewächse, etc. *Mitteil. a. d. forstl. Versuchswesen Oesterreichs*, **2**.

Holle, H., (1915). Untersuchungen über Welken, Vertrocknen und Wiederstraffwerden. *Flora*, **108**, 73–126.

Holtermann, C., (1907). Der Einfluss des Klimas auf den Bau der Pflanzengewebe.—Leipzig.

Horn, T., (1922). Das gegenseitige Mengenverhältnis der Kohlenhydrate im Laubblatt in seiner Abhäng. vom Wassergehalt. *Bot. Archiv.*, **3,** 137–173.

Huber, B., (1923[a]). Transpiration in verschiedener Stammhöhe. 1. *Sequoia gigantea. Zeitschr. f. Bot.*, **15,** 465–501.

(1923[b]). Theoretische Betrachtungen zur Kohäsionstheorie der Wasserbewegung in der Pflanze. *Biol. Centralbl.*, **43,** 30–49.

(1923[c]). Beiträge zur Kenntnis der Wasserbewegung in der Pflanze. I. *Ber. deut. Bot. Ges.*, **41,** 242–245.

(1924[a]). Eine einfache Methode zur Messung der Verdunstungskraft am Standort. *Ber. deut. Bot. Ges.*, **42,** 19–25.

(1924[b]). Beiträge zur Kenntnis der Wasserbewegung in der Pflanze. II. Die Strömungsgeschwindigkeit und die Grösse der Widerstände in den Leitbahnen. *Ber. deut. Bot. Ges.*, **42,** 27–32.

(1924[c]). Die Beurteilung des Wasserhaushaltes der Pflanzen. Ein Beitrag zur vergleichenden Physiologie. *Jahrb. f. wiss. Bot.*, **64,** 1–120.

Iljin, V. (W.) **S.,** (1911). Transpirationsgang bei den getauchten Pflanzen. *Trav. Soc. Nat. St. Petersburg,* **42,** 361–414. (Russian, with German abstract.)

(1914[a]). Die Regulierung der Spaltöffnungen im Zusammenhang mit der Veränderung des osmotischen Druckes. *Beih. Bot. Centralbl.*, Abt. 1, **32,** 15–35.

(1914[b]). Die Probleme des vergleichenden Studiums der Pflanzentranspiration. *Beih. Bot. Centralbl.*, Abt. 1, **32,** 36–65.

(1916). The relation of transpiration to assimilation in steppe plants. *Jour. Ecol.*, **4,** 65–82.

(1922[a]). Wirkung der Kationen von Salzen auf den Zerfall und die Bildung von Stärke in der Pflanze. *Bioch. Zeitschr.*, **132,** 492–510.

(1922[b]). Synthese und Hydrolyse von Stärke unter dem Einfluss der Anionen von Salzen in Pflanzen. *Bioch. Zeitschr.*, **132,** 511–525.

(1922). Physiologischer Pflanzenschutz gegen schädliche Wirkung von Salzen. *Bioch. Zeitschr.*, **132,** 525–542.

(1922[d]). Ueber den Einfluss des Welkens der Pflanzen auf die Regulierung der Spaltöffnungen. *Jahrb. f. wiss. Bot.*, **61,** 670–697.

(1923[a]). L'influence de la sécheresse sur la régulation des stomates et sur l'accroissement des plantes. *Preslia, Vestnik Česko-slovenska Botan. Spolenčnosti,* **2,** 43–55.

Iljin, V. S.—*continued.*

(1923[b]). Einfluss des Welkens auf die Atmung der Pflanzen. *Flora,* **116,** 379–403.

(1927). Ueber die Austrocknungsfähigkeit des lebenden Protoplasmas der vegetativen Pflanzenzellen. *Jahrb. f. wiss. Bot.,* **66,** 947–964.

Iljin, V. (W.) **S., and Alexeyev** (Alexejev), **A.,** (1917). L'influence de l'humidité sur la marche de l'assimilation de carbone chez les graminées des steppes. *Trav. Soc. Nat. Petrograd,* **56,** 49–64. (Russian, with French abstract.)

Iljin, V. (W.) **S., Nazarov** (Nasarova), **P., and Ostrovski** (Ostrovskaja), **M.,** (1915). Osmotic pressure in plants in relation to soil moisture. *Bull. Acad. Sci. Petrograd,* 749–768. (Russian.)

Iljin, V. (W.) **S., Ostrovski, M. K., and Becker, M. G.,** (1917). Les limites de la pression osmotique et le xérophytisme. *Trav. Soc. Nat. Petrograd,* **56,** 103–117. (Russian, with French abstract.)

Iljin, V. (W.) **S., and Sabinin** (Sabinina), **M. A.,** (1917). Sur la marche de la fermeture des stomates et de son influence sur l'assimilation de carbone. *Trav. Soc. Nat. Petrograd,* **56,** 69–101. (Russian, with French abstract.)

Iljin, V. (W.) **S., and Soboleva, O. J.,** (1917). Sur la distribution de la pression osmotique dans la lamelle foliaire. *Trav. Soc. Nat. Petrograd,* **56,** 103–116. (Russian, with French abstract.)

Irmscher, E., (1911). Ueber die Resistenz der Laubmoose gegen Austrocknen und Kälte. *Jahrb. f. wiss. Bot.,* **50,** 387–449.

Ivanov, L. A., (1913). Plant physiology.—St. Petersburg. (Russian.)

(1916). On the transpiration of trees. Separate from *Russ. Forestry Jour.*

(1923). The present state of the question of drought resistance. *Bull. Appl. Bot. and Plant Breeding,* **13,** 3–32. (Russian, with English abstract.)

(1924). Ueber die Transpiration der Holzgewächse im Winter. I. u. II. *Ber. deut. Bot. Ges.,* **42,** 44–49, 210–218.

Ivanov, L. A., and Thielman, M., (1923). Ueber den Einfluss des Lichtes verschiedener Wellenlänge auf die Transpiration der Pflanzen. *Flora,* **116,** 295–311.

Jeffreys, H., (1918). Some problems of evaporation. *Phil. Mag.,* **35,** 270–280.

Jones, W. Neilson, (1914). A self-recording porometer and potometer. *New Phyt.,* **13,** 353–364.

Jørgensen, I., and Stiles, W., (1915–17). Carbon assimilation. A review of recent work. *New Phyt.,* **14–16.**

Jost, L., (1907). Lectures on plant physiology. Authorized English translation by R. J. Harvey Gibson.—Oxford.

(1913). Vorlesungen über Pflanzenphysiologie. 3e. Aufl.—Jena.

Junk, E., (1925). Tabulae biologicae. Herausgegeben von C. Oppenheimer und L. Pincussen.—Berlin.

Kamerling, Z., (1913). Kleine Notizen. *Ber. deut. Bot. Ges.,* **31,** 483–493.

(1914). Welche Pflanzen sollen wir "Xerophyten" nennen? *Flora,* **106,** 433–454.

Kanitz, A., (1915). Temperatur und Lebensvorgänge.—Berlin.

Kaznov, P. V., (1918). On the length of the veins of leaves. *Mém. Inst. Agronom. Voronezh,* **3,** 55–72. (Russian, with English abstract.)

Kearney, T. H., and Shantz, H. L., (1911). The water economy of dry-land crops. *Year Book U.S. Dept. Agric.,* **10,** 351–362.

Keller, B., (1913–14). On the osmotic pressure of the cell sap of plants in relation to the properties of the soil. *Pochvovedenije* (*La pédologie*), **15,** 41–70; **16,** 11–32. (Russian.)

(1918). Quelques données sur la force osmotique du suc cellulaire en rapport avec le caractère des habitats. *Mém. Inst. Agronom. Voronezh,* **2,** 27–45. (Russian, with French abstract.)

(1920). Sur la pression osmotique de suc cellulaire des plantes de differents lieux d'habitation. *Jour. Soc. Bot. de Russie.,* **5,** 84–90.

(1923). Die Pflanzenwelt der russischen Steppen, Halbwüsten und Wüsten.—Voronezh. (Russian, with German abstract.)

(1923–24). General botany. Parts I and II.—Voronezh. (Russian.)

(1925). Halophyten- und Xerophyten-Studien. *Jour. Ecol.,* **13,** 224–261.

Keller, B., and Leisle, E. T., (1922). The plant as a living machine. *Bull. Voronezh Exper. Station,* 1–16.

Kerner von Marilaun, A., (1893). Pflanzenleben.—Vienna.

Kerner von Marilaun, A., and Oliver, F. W., (1895). The natural history of plants. English edition.—London.

Kiesselbach, T., (1916). Transpiration as a factor in crop production. *Agric. Exper. Stn. of Nebraska, Res. Bull.,* **6.**

Kihlmann, A. O., (1890). Pflanzenbiologische Studien aus Russisch-Lappland. *Acta Soc. pro Fauna et Flora Fennica,* **4,** 107–371.

Kiselëv (Kisselew), **N.,** (1925). Veränderung der Durchlässigkeit des Protoplasma der Schliesszellen im Zusammenhange mit stomatären Bewegungen. *Beih. Bot. Centralbl.,* Abt. 1, **41,** 287–308.

Knight, R. C., (1915). A convenient modification of the porometer. *New Phyt.*, **14**, 212–216.

(1916). On the use of the porometer in stomatal investigation. *Ann. Bot.*, **30**, 57–76.

(1917[a]). The interrelations of stomatal aperture, leaf water content, and transpiration rate. *Ann. Bot.*, **31**, 221–240.

(1917[b]). Relative transpiration as a measure of the intrinsic transpiring power of the plant. *Ann. Bot.*, **31**, 351–361.

(1919). Transpiration. *Sci. Prog.*, **13**, 561–566.

(1922). Further observations on the transpiration, stomata, leaf water content, and wilting of plants. *Ann. Bot.*, **36**, 361–383.

(1924). The response of plants in soil and water culture to aeration of the roots. *Ann. Bot.*, **38**, 305–325.

Kochanovsky, L., (1926). Some investigations on the transpiration of plants under the conditions of a sub-alpine zone. *Journ. Soc. Bot. Russ.*, **9**, 239–250. (Russian, with English abstract.)

Kohl, F. G., (1886). Die Transpiration der Pflanzen und ihre Einwirkung auf die Ausbildung pflanzlicher Gewebe.—Braunschweig.

Kokin (Kokina), **S.,** (1925). Ueber den Einfluss der Bodenfeuchtigkeit auf die Geschwindigkeit der Wasseraufnahme durch die Wurzeln. *Bull. Jard. Bot. de Leningrad*, **24**, 1–17. (Russian, with German abstract.)

(1926). Zur Frage über den Einfluss der Bodenfeuchtigkeit auf Pflanzen. *Bull. Jard. Bot. de Leningrad*, **26**, 1–19. (Russian, with German abstract.)

Kolkunov (Kolkunow), **W.,** (1905). Contributions to the problem of breeding drought resistant crop plants. I. Anatomical and physiological investigations of the degree of xerophily of certain cereals. *Mém. Polytech. Inst. Kiev*, **5**, No. 4. (Russian.)

(1907). II. Anatomical and physiological investigations of certain races of sugar beet. *Ibid.*, **7**, No. 1. (Russian.)

(1910). The results of the study of some varieties of corn from the point of view of physiological anatomy. *Chosiastvo*, **5**, 1541–1554, 1591–1598. (Russian.)

(1913). Zur Frage über die Wechselbeziehungen zwischen den anatomischen Koefficienten und den physiologischen Eigenschaften der Pflanzen. *Russ. Jour. f. experim. Landw.*, **14**, 321–340. (Russian, with German abstract.)

(1925). Einige Ergebnisse der Untersuchungen über Dürrewiderstandsfähigkeit bei Kulturpflanzen. *Zeitschr. Pflanzenzücht*, **10**, 297–310.

Kolkwitz, R., (1901). Ueber die Atmung ruhender Samen. *Ber. deut. Bot. Ges.*, **19**, 285–288.

Konstantinov, P. N., (1925). On the transpiration and drought resistance of plants. *Jour. Agronom. Scient.*, **2**, 405–414. (Russian.)

Kossovich (Kossowitsh), **P. S.,** (1892). Durch welche Organe nehmen die Leguminosen den freien Stickstoff auf. *Bot. Zeit.*, **50**, 697–702.

(1916). A textbook of soil science. Ed. 2.—St. Petersburg. (Russian.)

Kozarov (Kosaroff), **P.,** (1897). Einfluss verschiedener äusserer Factoren auf die Wasseraufnähme der Pflanzen.—Dissert., Leipzig.

Krasnoselsky-Maximov (Krasnosselsky-Maximow), **T. A.,** (1917). Daily variations in the water content of leaves. *Trav. Jard. Bot. de Tiflis*, **19**, 1–22. (Russian.)

(1925). Untersuchungen über Elastizität der Zellmembran. *Ber. deut. Bot. Ges.*, **43**, 527–537.

Krebs, W., (1894). Die Erhaltung der Mansfelder Seen.—Leipzig.

Kümmler, A., (1922). Ueber die Funktion der Spaltöffnungen weissbunter Blätter. *Jahrb. f. wiss. Bot.*, **61**, 610–670.

Laidlaw, C. G. P., and Knight, R. C., (1916). A description of a recording porometer and a note on stomatal behaviour during wilting. *Ann. Bot.*, **30**, 47–56.

Landolt-Bernstein, (1912). Physikalisch-chemische Tabellen.—Leipzig.

Lawrence, J. V., and Harris, J. A., (1925). A practical method for the determination of the chloride content of plant tissue fluids. *Ecol.*, **6**, No. 4, 391–396.

Leather, J. W., (1910). Water requirements of crops in India. *Mem. Dept. Agric. India*, **1**, No. 8, 133–184; No. 10, 205–281.

Lebedev, A. T., (1913). The significance of water vapour in the régime of soil and subsoil water.—St. Petersburg. (Russian.)

Lebedintsev (Lebedincev), **E.,** (1927). Physiologische und anatomische Besonderheiten der in trockener und feuchter Luft gezogenen Pflanzen. *Ber. deut. Bot. Ges.*, **45**, 83–96.

Leclerc du Sablon, M., (1913). Sur les causes du dégagement et de la rétention du vapeur d'eau chez les plantes. *Rev. Gén. Bot.*, **25**, 49–83; 104–122.

Leitgeb, H., (1886). Beiträge zur Physiologie der Spaltöffnungsapparate. *Mitteil. Bot. Inst. Graz*, **1**, 123–184.

Lepëshkin (Lepeschkin), **W. W.,** (1902). Ueber die Bedeutung der wasserabsondernden Organe für die Pflanzen. *Flora*, **90**, 42–60.

(1906). Zur Kenntniss des Mechanismus der aktiven Wasserausscheidung durch die Pflanzen. *Beih. Bot. Centralbl.*, Abt. 1, **19**, 409–452.

Lepëshkin, W. W.—*continued.*
(1909). Zur Kenntniss des Mechanismus der photonastischen Variationsbewegungen und der Einwirkung des Beleuchtungswechsels auf die Plasmamembran. *Beih. Bot. Centralbl.*, Abt. 1, **24**, 308–356.
(1925). Lehrbuch der Pflanzenphysiologie.—Berlin.

Levitski, G. A., and Kusmin (Kuzmina), **N.**, (1923). Zur Frage über die Ursachen der erblichen Verschiedenheiten in der Zellgrösse bei den Pflanzen nach Untersuchungen an *Beta vulgaris*. *Bull. Plant Breeding and Seed Dept. of Sugar Trust*, **6**, 84–91. (Russian, with German abstract.)

Levitski (Levitzki), **St.**, (1918). A propos de la résistibilité du blé vis-à-vis l'aridité. *Russ. Jour. f. experim. Landw.*, **19**, 83–92. (Russian, with French abstract.)

Lidforss, B., (1906). Die wintergrüne Flora. *Lunds Univ. Arskr.* N. F. Afd. 2, **2**, No. 13, 1-78.

Linsbauer, K., (1916). Beiträge zur Kenntniss der Spaltöffnungsbewegungen. *Flora*, **109**, 100–143.

Livingston, B. E., (1904). Physical properties of bog water. *Bot. Gaz.*, **37**, 383–385.
(1905). Physiological properties of bog water. *Bot. Gaz.*, **39**, 348–355.
(1906). The relation of desert plants to soil moisture and to evaporation. *Carnegie Inst. Washington Publ.*, **50**, 1–77.
(1907). Relative transpiration in Cacti. *Plant World*, **10**, 110–114.
(1908). A method for controlling plant moisture. *Plant World*, **11**, 39–40.
(1911[a]). The relation of the osmotic pressure of the cell sap in plants to arid habitats. *Plant World*, **14**, 153–164.
(1911[b]). Light intensity and transpiration. *Bot. Gaz.*, **52**, 417–438.
(1915). Atmometry and the porous cup atmometer. *Plant World*, **18**, 21–30, 51–74, 95–111, 143–149.
(1917). A quarter century of growth in plant physiology. *Plant World*, **20**, 1–15.

Livingston, B. E., and Brown, W. H., (1912). Relation of the daily march of transpiration to variations in the water content of foliage leaves. *Bot. Gaz.*, **53**, 309–339.

Livingston, B. E., and Free, E., (1917). The effect of deficient soil oxygen on the roots of higher plants. *Johns Hopkins Univ. Circ.*, **293**, 182–185.

Livingston, B. E., and Hawkins, L. A., (1915). The water relation between plant and soil. *Carnegie Inst. Washington Publ.*, **204**, 1–48

Livingston, B. E., and Hopping, A., (1915). Permanent standardization of cobalt chloride paper for use in measuring the transpiring power of plant surfaces. *Year Book Carnegie Inst. Washington,* **13,** 86.

Livingston, B. E., and Kôketsu, R., (1920). The water supplying power of the soil as related to the wilting of plants. *Soil Science,* **9,** 469–485.

Livingston, B. E., and Shreve, Edith, (1916). Improvements in the method for determining the transpiring power of the plant by hygrometric paper. *Plant World,* **19,** 287–309.

Livingston, B. E., and Thone, F., (1920). A simplified non-absorbing mounting for porous porcelain atmometers. *Science,* **52,** 85–87.

Lloyd, F. E., (1908). The physiology of stomata. *Carnegie Inst. Washington Publ.,* **82,** 1–142.

(1912). The relation of transpiration and stomatal movement to the water content of the leaves in *Fouquieria splendens. Plant World,* **15,** 1–4.

(1913). Leaf water and stomatal movement in *Gossypium* and a method of direct visual observation of stomata *in situ. Bull. Torrey Bot. Club.,* **40,** 1–26.

(1920). Environmental changes and their effect upon boll shedding in cotton. *Ann. N. Y. Acad. Sc.,* **29,** 1–131.

Loftfield, J. V., (1921). The behaviour of stomata. *Carnegie Inst. Washington Publ.,* **314,** 1–104.

Lothelier, M. A., (1893). Recherches sur les plantes à piquants. *Rev. Gén. Bot.,* **5,** 480–513.

Lubimenko, W. N., (1924). Biology of Plants.—Leningrad. (Russian.)

Lundegårdh, H., (1911). Ueber die Permeabilität der Wurzelspitzen von *Vicia Faba* unter verschiedenen äusseren Bedingungen. *K. Svenska Vetenskapsakad. Handlingar,* **47,** No. 3, 1–254.

Lundström, A., (1899). Anpassung der Pflanzen an Regen und Tau.—Upsala.

MacDougal, D. T., (1912). The water balance of desert plants. *Ann. Bot.,* **26,** 71–93.

(1920). Hydration and growth. *Carnegie Inst. Washington Publ.,* **297,** 1–176.

(1921). Growth in trees. *Carnegie Inst. Washington Publ.,* **307,** 1–41.

(1925). Absorption and exudation pressures of sap in plants. *Proc. Amer. Phil. Soc.,* **64,** No. 2, 102–130.

MacDougal, D. T., and Spalding, E. S., (1910). The water balance of succulent plants. *Carnegie Inst. Washington Publ.* **141,** 1–77.

McLean, R. C., (1919). Studies in the ecology of tropical rain forest. *Jour. Ecol.*, **7**, 5–54, 121–172.

Marloth, R., (1908). Das Kapland. *Wissensch. Ergebnisse der deutschen Tiefsee-Expedition "Waldivia."* **2,** Teil 3.—Jena.

Mason, T. G., (1922). The physiological humidity of the soil and its direct determination. *West Ind. Bull.*, **19,** No. 2, 137–154.

Maximov (Maximow), **N. A.,** (1912). Chemische Schutzmittel der Pflanzen gegen Erfrieren. *Ber. deut. Bot. Ges.*, **30,** 52–65, 293–305, 504–516.

(1914). Experimentelle und kritische Untersuchungen über das Gefrieren und Erfrieren der Pflanzen. *Jahrb. f. wiss. Bot.*, **53,** 327–420.

(1916). Recherches sur la transpiration des plantes xérophytes comparées à celles des mésophytes. *Jour. Soc. Bot. de Russ.*, **1,** 56–75. (Russian, with French abstract.)

(1917). Contributions to the question of the daily march and regulation of transpiration. *Trav. Jard. Bot. de Tiflis.*, **19,** 23–108. (Russian.)

(1923). Physiologische-ökologische Untersuchungen über die Dürreresistenz der Xerophyten. *Jahrb. f. wiss. Bot.*, **62,** 128–144.

(1925). Pflanzenkultur bei elektrischem Licht und ihre Anwendung bei Samenprüfung und Pflanzenzüchtung. *Biol. Centralbl.*, **45,** 627–639.

Maximov (Maximow), **N. A., and Alexandrov** (Alexandrow), **V.** (W.), (1917). The water requirement and drought resistance of plants. *Trav. Jard. Bot. de Tiflis.*, **19,** 139–194. (Russian.)

Maximov, (Maximow), **N. A., Badrieva, L. G., and Simonova, W. A.,** (1917). The intensity of transpiration of plants of different ecological types. *Ibid.*, 109–138. (Russian.)

Maximov (Maximow), **N. A., Dilanian, A., and Silikova, A.,** (1917). Osmotic pressure in the leaves of xerophytes and mesophytes in the surroundings of Tiflis. *Ibid.*, 195–205. (Russian.)

Maximov (Maximow), **N. A., and Krasnoselsky-Maximov, T. A.,** (1924). Wilting of plants in its connexion with drought resistance. *Jour. Ecol.*, **12,** 95–110.

Maximov (Maximow), **N. A., and Lebedintsev, E.,** (1923). Ueber den Einfluss von Beleuchtungsverhältnissen auf die Entwickelung des Wurzelsystems. *Ber. deut. Bot. Ges.*, **41,** 292–297.

Maximov (Maximow), **N. A., and Lominadze, T.,** (1916). Contributions à l'étude de la pression osmotique chez les plantes. *Jour. Soc. Bot. de Russ.*, **1,** 166–178. (Russian, with French abstract.)

Maximchuk (Maximtschuk), **L. P.**, (1923). Zur Frage über den Zusammenhang zwischen der Transpiration und Zellengrösse. *Arbeiten des wissenschaftlichen Selections-Institutes zu Kiev*, **1**, 21–35. (Russian, with German abstract.)

Mayer, A., et Plantefol, L., (1924). Equilibre des constituants cellulaires et intensité des oxydations de la cellule. Imbibition et oxydation. *Compt. Rend.*, **178**, 1385–1388.

Meschayev (Meschaieff), **W.**, (1882). Ueber die Anpassungen zum Aufrechthalten der Pflanzen und die Wasserversorgung bei der Transpiration. *Bull. Soc. Nat. de Moscow*, **57**, 299–322. (German.)

Mez, C., (1904). Physiologische Bromeliaceenstudien. *Jahrb. f. wiss. Bot.*, **40**, 157–229.

Miller, E. C., and Saunders, A. R., (1923). Some observations on the temperature of the leaves of crop plants. *Jour. Agric. Res.*, **26**, 15–45.

Mina, J., and Butovski (Butowski), **A.**, (1923). Wasserbilanz in den Blättern einiger Kulturpflanzen. *Arbeiten des wissenschaftlichen Selections-Inst. zu Kiev*, **1**, 7–20. (Russian, with German abstract.)

von Minden, M., (1899). Beiträge zur anatomischen und physiologischen Kenntnis wassersezernierender Organe. *Bibliotheca Botanica*, **9**, Heft 46, 1–76.

Mitscherlich, E. A., (1921). Das Wirkungsgesetz der Wachstumsfactoren. *Landw. Jahrb.*, **56**, 71–92.

Modestov (Modestow), **A. P.**, (1915). The root system of herbaceous plants. I.—Moscow. (Russian.)

(1916). Longueur des racines dans les conditions du développement naturel. *Receuil d'articles scient. dedié au Prof. C. Timiriazev*, 325–356.—Moscow. (Russian, with French abstract.)

von Mohl, H., (1846). Ueber das Vermögen der lebenden Pflanze die Verdunstung des Zellsaftes zu beschränken. *Bot. Zeit.*, **5**, 321–324.

Moliboga, A., (1927). The influence of desiccation of the soil at different stages of vegetation on the growth and yield of cereals. *Bull. Appl. Bot. and Plant Breeding*, **17**, 183–202. (Russian, with English abstract.)

Molisch, H., (1912). Das Offen- und Geschlossensein der Spaltöffnungen, veranschaulicht durch eine neue Methode (Infiltrationsmethode). *Zeitschr. f. Bot.*, **4**, 106–122.

(1921). Ueber den Einfluss der Transpiration auf das Verschwinden der Stärke in den Blättern. *Ber. deut. Bot. Ges.*, **39**, 339–344.

Montfort, C., (1918). Die Xeromorphie der Hochmoorpflanzen als Voraussetzung der "physiologischen Trockenheit der Hochmoore". *Zeitschr. f. Bot.*, **10**, 347–357.

(1920). Physiologische Grundlegung einer Guttationsmethode zur relativen Prüfung der Wasseraufnahme. *Jahrb. f. wiss. Bot.*, **59**, 467–524.

(1921). Die aktive Wurzelsaugung aus Hochmoorwasser im Laboratorium und am Standort und die Frage seiner Giftwirkung. *Jahrb. f. wiss. Bot.*, **60**, 184–256.

(1922). Die Wasserbilanz in Nahrlösung, Salzlösung, und Hochmoorwasser. *Zeitschr. f. Bot.*, **14**, 98–172.

Montgomery, E. G., and Kiesselbach, T. A., (1912). Studies in the water requirement of corn. *Nebraska Agric. Exper. Stn. Bull.*, **128.**

Morse, H. N., (1914). The osmotic pressure of aqueous solutions. *Carnegie Inst. Washington Publ.*, **198**, 1–222.

Muenscher, W. C., (1915). A study of the relation of transpiration to the size and number of stomata. *Amer. Jour. Bot.*, **2**, 487–504.

(1922). The effect of transpiration on the absorption of salts by plants. *Amer. Jour. Bot.*, **9**, 311–329.

Nathansohn, A., (1912). Allgemeine Botanik.—Leipzig.

Neger, F. W., (1912). Spaltöffnungsschluss und künstliche Turgorsteigerung. *Ber. deut. Bot. Ges.*, **30**, 179–194.

(1913). Biologie der Pflanzen auf experimenteller Grundlage (Bionomie).—Stuttgart.

Neger, F. W., und Lacon, G., (1914). Studien über den Einfluss der Abgasen auf die Lebensfunktionen der Bäume. *Mitteil. aus d. sächsisch. Forstl. Vers. Anst. Tharandt*, **1**, 177–233.

Nestler, A., (1896). Untersuchungen über die Ausschiedung von Wassertropfen an den Blättern. *Sitzungsber. d. K. Akad. d. Wiss. Wien*, Abt. 1, **105**, 521.

Newton, R., (1922). A comparative study of winter wheat varieties, with especial reference to winter-killing. *Jour. Agric. Sci.*, **12**, 1–19.

(1924). The nature and practical measurement of frost resistance in winter wheat. *Univ. of Alberta Res. Bull.*, **1**, 1–53.

Nicolič, M., (1925). Beiträge zur Physiologie der Spaltöffnungsbewegung. *Beih. Bot. Centralbl.*, Abt. 1, **41**, 309–346.

Nordhausen, M., (1903). Ueber Sonnen- und Schattenblätter. I. *Ber. deut. Bot. Ges.*, **21**, 27–45.

(1912). Ueber Sonnen- und Schattenblätter. II. *Ber. deut. Bot. Ges.*, **30**, 483–503.

(1916). Ueber die Saugkraft transpirierender Sprosse. *Ber. deut. Bot. Ges.*, **34**, 619–639.

Nordhausen, M.—*continued.*

(1917). Zur Kenntnis der Saugkraft und der Wasserversorgung transpirierender Sprosse. *Jahrb. f. wiss. Bot.*, **58**, 295–335.

(1921). Weitere Beiträge zum Saftsteigeproblem. *Jahrb. f. wiss. Bot.*, **60**, 307–354.

Olsson-Seffer, P., (1909). Hydrodynamic factors influencing plant life on sandy sea shores. *New Phyt.*, **8**, 37–51.

Pessin, L., (1924). A physiological and anatomical study of the leaves of *Polypodium polypodioides*. *Amer. Jour. Bot.*, **11**, 370–381.

Pfeffer, W., (1877). Osmotische Untersuchungen.—Leipzig.

(1897). Pflanzenphysiologie. 2 Aufl.—Leipzig.

(1900–1903). The physiology of plants. English translation of Ed. 2.—Oxford.

Pfeiffer, T., (1918). Der Vegetationsversuch.—Berlin.

Pfeiffer, T., Blanck, E., und Flügel, M., (1912). Wasser und Licht als Vegetationsfactoren und ihre Beziehungen zum Gesetz vom Minimum. *Landw. Vers.-Stat.*, **81**, 169–236.

Pfeiffer, T., Blanck, E., und Friske, K., (1913). Der Einfluss verschiedener Vegetationsfactoren, namentlich des Wassers, auf die Erziehung von Maximalerträgen in Vegetationsgefässen. *Landw. Vers.-Stat.*, **82**, 237–298.

Piche, A., (1872). Note sur l'atmismomètre, instrument destinée à mesurer l'évaporation. *Bull. Assoc. Sci. France*, **10**, 166–167.

Pick, H., (1882). Ueber den Einfluss des Lichtes auf die Gestalt und Orientierung der Zellen des Assimilationsgewebes. *Bot. Centralbl.*, **11**, 400–438.

Pool, R. G., (1923). Xerophytism and comparative leaf anatomy in relation to transpiration power. *Bot. Gaz.*, **76**, 221–240.

Priestley, J. H., (1920). The mechanism of root pressure. *New Phyt.*, **19**, 189–200.

(1922). Further observations upon the mechanism of root pressure. *New Phyt.*, **21**, 41–48.

Priestley, J. H., and Armstead, Dorothy, (1922). The physiological relation of the surrounding tissue to the xylem and its contents. *New Phyt.*, **21**, 62–80.

Priestley, J. H., and North, Edith, (1922). The structure of the endodermis in relation to its function. *New Phyt.*, **21**, 113–138.

Priestley, J. H., and Tupper-Carey, R. M., (1922). The water relations of the plant growing point. *New Phyt.*, **21**, 210–230.

Pringsheim, E., (1906). Wasserbewegung und Turgorregulation in welkenden Pflanzen. *Jahrb. f. wiss. Bot.*, **43**, 89–144.

Pulling, H. E., and Livingston, B. E., (1915). The water supplying power of the soil as indicated by osmometers. *Carnegie Inst. Washington Publ.*, **204**, 49–84.

Pullmann, J. A., (1905). The influence of soil moisture on the yield of oats. *St. Petersburg, Board of Agric. Meteorology*, 1–20. (Russian.)

Ramenski, L. G., (1915). On the methods of studying vegetation in relation to climate.—St. Petersburg, 1–31. (Russian.)

Reed, H. S., (1910). The effect of certain chemical agents upon the transpiration and growth of wheat seedlings. *Bot. Gaz.*, **49**, 81–109.

Reinitzer, F., (1881). Ueber die physiologische Bedeutung der Transpiration. *Sitzungsber. d. K. Akad. d. Wiss. Wien*, Abt. 1, **83**, 11.

Renner, O., (1910). Beiträge zur Physik der Transpiration. *Flora*, **100**, 451–547.

(1911). Experimentelle Beiträge zur Kenntnis der Wasserbewegung. *Flora*, **103**, 171–247.

(1912). Versuche zur Mechanik der Wasserbewegung. 1. Der Druck in den Leitungsbahnen von Freilandspflanzen; 2. Ueber Wurzeltätigkeit. *Ber. deut. Bot. Ges.*, **30**, 576–580, 642–648.

(1915[a]). Theoretisches und experimentelles zur Kohäsionstheorie der Wasserbewegung. *Jahrb. f. wiss. Bot.*, **56** (*Pfeffersfestschrift*), 617–667.

(1915[b]). Die Wasserversorgung der Pflanzen. *Handwörterb. d. Naturwiss.*, **10**, 538–557.

Richardson, A. E. V., (1923). The water requirements of farm crops. Factors influencing the transpiration ratio of cereal and fodder crops in Australia. *Jour. Dept. Agr. of Victoria*, April–July, 1923.

Ricôme, H., (1903). Influence du chlorure de sodium sur la transpiration et l'absorption de l'eau chez les végétaux. *Compt. Rend.*, **137**, 141–143.

Riede, W., (1921). Untersuchungen über Wasserpflanzen. *Flora*, **114**, 1–118.

Rigg, G. R., (1913). The effect of some Puget Sound bog waters on the root hairs of *Tradescantia*. *Bot. Gaz.*, **55**, 314–326.

(1916[a]). Decay and soil toxins. *Bot. Gaz.*, **61**, 295–310.

(1916[b]). The toxicity of bog water. *Amer. Jour. Bot.*, **3**, 436–437.

Rippel, A., (1919). Der Einfluss der Bodentrockenheit auf den anatomischen Bau der Pflanzen, insbesondere von *Sinapis alba*, etc. *Beih. Bot. Centralbl.*, Abt. 1, **36**, 187–260.

(1925). Wachstumsgesetze bei höheren und niederen Pflanzen. —Freising-München.

Rosa, J. R., (1921). Investigations on the hardening process in vegetable plants. *Columbia Agric. Exp. Stn. Res. Bull.*, **48.**

Rosé, E., (1913). Energie assimilatrice chez les plantes cultivées sous différents éclairements. *Ann. Sci. Nat., Bot.*, 9e sér., **17,** 1–110.

Rotmistrov, W. G., (1910). The root system of annual crop plants. —Odessa. (Russian.)

Rübel, E., (1920). Experimentelle Untersuchungen über die Beziehungen zwischen Wasserleitungsbahn und Transpirationsverhältnissen bei *Helianthus annuus. Beih. Bot. Centralbl.*, Abt. 1, **37,** 1–61.

(1922). Geobotanische Untersuchungsmethoden.—Berlin.

Rudolph, K., (1925). Epidermis und epidermale Transpiration. *Bot. Archiv.*, **9,** 49–94.

de Rufz de Lavison, J., (1910). Du mode de pénétration de quelques sels dans la plante vivante. Rôle de l'endoderme. *Rev. Gén. Bot.*, **22,** 225–227.

Ruhland, W., (1915). Untersuchungen über die Hautdrüsen der Plumbaginaceen. *Jahrb. f. wiss. Bot.*, **55,** 409–498.

Rybin, V. (W.) **A.,** (1923). Ueber den Einfluss von Mineralsauren auf die absorptive Tätigkeit des Wurzelsystems. *Trav. Soc. Nat. de Petrograd,* **53,** 149–172. (Russian, with German abstract.)

van Rysselberghe, F., (1901). Influence de la température sur la perméabilité du protoplasme vivant pour l'eau et les substances dissoutes. *Rec. Inst. Bot. de Bruxelles,* **5,** 209–249.

Rywosch, S., (1925). Ueber die Beziehungen zwischen der Zahl der Spaltöffnungen und dem Bau des Blattes. *Ber. deut. Bot. Ges.*, **43,** 67–76.

Sabinin, D. A., (1921). Sur l'influence de la réaction du milieu sur la perméabilité du protoplasme. *Jour. Soc. Bot. de Russie,* **6,** 23–31. (Russian, with French abstract.)

(1923). The methods of determining the osmotic suction pressure of the root system. *Bull. Inst. Recher. Biol. Univ. de Perm,* **2,** livr. 5, 195–206. (Russian.)

(1925). On the root system as an osmotic apparatus. *Bull. Inst. Recher. Biol. Univ. de Perm,* **4,** suppl. 2, 1–136. (Russian, with English abstract.)

Sachs, J., (1858). Ueber eine Methode die Quantitäten der vegetabilischen Wärme zu bestimmen. *Sitzungsber. d. K. Akad. d. Wiss. Wien,* Abt. 1, **26,** 159.

(1859). Bericht über die physiologische Tätigkeit an der Versuchstation in Tharandt. *Landw. Versuchst.*, **1,** 203–240.

(1860). Beiträge zur Lehre von der Transpiration der Gewächse. *Bot. Zeit.*, **18,** 121–126.

Salisbury, E. J., (1927). On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. *Phil. Trans. Roy. Soc. London,* **216B,** 1–65.

Sampson, A., and Allen, L., (1909). Influence of physical factors on transpiration. *Minnesota Bot. Stud.,* ser. IV, **1,** 33–59.

Sauvageau, C., (1890). Observations sur la structure des feuilles des plantes aquatiques. *Jour. de Bot.* Separate.

(1891). Sur les feuilles de quelques Monocotyledones aquatiques. *Ann. Sci. Nat., Bot.,* 7e ser., **13,** 103–295.

Schander, R., und Schaffnit, E., (1919). Untersuchungen über das Auswintern des Getreides. *Landw. Jahrb.,* **52,** 1–66.

Schimper, A. F., (1889). Die epiphytische Vegetation Americas. *Bot. Mitt. aus den Tropen,* Heft 2.

(1898). Pflanzengeographie auf physiologischer Grundlage.—Jena.

(1903). Plant geography upon a physiological basis. English edition.—Oxford.

Schlösing, T., (1869). Végétation comparée du tabac sous cloche et à l'air libre. *Ann. Sci. Nat., Bot.,* 5e sér., **10,** 366–369.

Schröder, D., (1909). Ueber den Verlauf des Welkens und die Lebenszähigkeit der Laubblätter.—Dissert., Göttingen, 1–110.

Schröder, G., (1886). Ueber die Austrocknungsfähigkeit der Pflanzen. *Unters. Bot. Inst. Tübingen,* **2,** 1–51.

Schröder, H., (1911). Ueber die selektiv-permeable Hülle des Weizenkorns. *Flora,* **102,** 186–208.

Schröder, M., (1895). The transpiration of various crop plants. *Agric. and Forestry,* 320–336. (Russian.)

Schröter, C., (1908). Das Pflanzenleben der Alpen.—Zürich.

(1922). Das Pflanzenleben der Alpen. 2 Aufl.—Zürich.

Schwendener, S., (1881). Ueber Bau und Mechanik der Spaltöffnungen. *Monatsber. Preuss. Akad. der Wiss.,* 833–867.

(1899). Gesammelte botanische Mitteilungen.—Berlin.

v. Seelhorst, C., (1911). Die Bedeutung des Wassers im Leben der Kulturpflanzen. *Jour. f. Landw.,* **59,** 259–291.

Shantz, H. L., (1927). Drought resistance and soil moisture. *Ecology,* **8,** 145–157.

Shantz, H. L., and Piemeisel, L. N., (1927). The water requirement of plants at Akron, Colorado. *Jour. Agric. Res.,* **34,** 1093–1190.

Shantz, H. L., and Piemeisel, R. L., (1924). Indicator significance of the natural vegetation of the south-western desert region. *Jour. Agric. Res.,* **28,** 721–801.

Shive, J. W., and Livingston, B. E., (1914). The relation of atmospheric evaporating power to soil moisture content at permanent wilting in plants. *Plant World,* **17,** 81–121.

Shreve, E., (1914). The daily march of transpiration in a desert perennial. *Carnegie Inst. Washington Publ.,* **194,** 1–64.

(1916). An analysis of the causes of variations in the transpiring power of Cacti. *Physiol. Res.,* **2,** 73–127.

(1923). Seasonal changes in the water relations of desert plants. *Ecology,* **4,** 266–292.

(1924). Factors governing seasonal changes in transpiration of *Encelia farinosa. Bot. Gaz.,* **77,** 432–439.

Shreve, F., (1914). The direct effect of rainfall on hygrophilous vegetation. *Jour. Ecol.,* **2,** 82–98.

Shull, C. A., (1913). Semipermeability of seed coats. *Bot. Gaz.,* **56,** 169–199.

(1916). Measurement of the surface forces in soils. *Bot. Gaz.,* **62,** 1–31.

Sierp, H., und Noack, K., (1921). Studien über die Physik der Transpiration. *Jahrb. f. wiss. Bot.,* **60,** 459–498.

Sorauer, P., (1878). Ueber den Einfluss der Luftfeuchtigkeit. *Bot. Zeit.,* **36,** 1–13, 17–25.

(1880). Studien über Verdunstung. *Forsch. a. d. Gebiet der Agrikulturphysik v. Wollny,* **3,** 351–490.

Spalding, V. M., (1904). Biological relations of certain desert shrubs. I. The creosote bush (*Covillea*) in its relation to water supply. *Bot. Gaz.,* **38,** 122–138.

Spanjer, O., (1898). Untersuchungen über die Wasserapparate der Gefässpflanzen. *Bot. Zeit.,* **56,** 35–81.

Sresnevski (Sresnevsky), **B. J.,** (1905). On evaporation from the surface of the human body and from plants. *Proc. 2nd Climat. and Hydrolog. Congress, St. Petersburg,* **1,** 311–333. (Russian.)
On humidity.—St. Petersburg, 1–73. (Russian.)

Stahl, E., (1883). Ueber den Einfluss des sonnigen oder schattigen Standortes auf die Ausbildung der Laubblätter. *Jenaische Zeitschr. f. Naturw.,* **16,** 1–39.

(1894). Einige Versuche uber Transpiration und Assimilation. *Bot. Zeit.,* **52,** 117–146.

(1919). Zur Physiologie und Biologie der Exkrete. *Flora,* **113,** 1–132.

Stålfelt, M. G., (1916). Ueber die Wirkungsweise der Infiltrationsmethode von Molisch und einige Versuche mit derselben. *Svensk. Bot. Tidskrift,* **10,** 37-46.

(1924). Tallens och granens kolsyreassimilation och dess ecologiska betingelser (Untersuchungen zur Oekologie der Kohlensäureassimilation der Nadelbäume). *Meddel. från Stat. Skogsförsöksanstalt,* **21,** No. 5, 181–258.

Stefan, J., (1881). Versuche über die Verdampfung. *Sitzungsber. d. K. Akad. d. Wiss. Wien,* Abt. II, **85,** 943.

Stein, Emmy, (1912). Bemerkungen zu der Arbeit von Molisch "Das Offen- und Geschlossensein der Spaltöffnungen veranschaulicht durch eine neue Methode". *Ber. deut. Bot. Ges.,* **30,** 66–68.

(1913). Ueber Schwankungen stomätarer Oeffnungsweite.—Dissert., Jena.

Steinberger, A. L., (1922). Regulation des osmotischen Wertes in den Schliesszellen. *Biol. Centralbl.* **42,** 405–419.

Stiles, W., (1924[a]). Permeability. *New Phyt.* Reprint, No. 13.—London.

(1924[b]). Evaporation in wind. *Ann. Bot.,* **38,** 299–304.

(1925). Photosynthesis.—London.

Stiles, W., and Jørgensen, I., (1917). Studies in Permeability. V. The swelling of plant tissue in water and its relation to temperature and various dissolved substances. *Ann. Bot.,* **31,** 415–434.

Stocker, O., (1923). Die Transpiration und Wasserökologie nordwestdeutscher Heide- und Moorpflanzen am Standort. *Zeitschr. f. Bot.,* **12,** 1–41.

(1924[a]). Oekologisch-pflanzengeographische Untersuchungen an Heide-, Moor-, und Salzpflanzen. *Die Naturwiss.,* **12,** 637–646.

(1924[b]). Beiträge zum Halophytenproblem. I. Oekologische Untersuchungen an Strand- und Dünenpflanzen des Darss (Vorpommern). *Zeitschr. f. Bot.,* **16,** 289–330.

(1925). Beiträge zum Halophytenproblem. II. Standort und Transpiration der Nordseehalophyten. *Zeitschr. f. Bot.,* **17,** 1–24.

Strugger, S., und Weber, F., (1926). Zur Physiologie der Stomatanebenzellen. *Ber. deut. Bot. Ges.,* **44,** 272–278.

Surož, J. N., (1892). The influence of light on the structure of leaves. *Trav. Soc. Natur. St. Petersburg,* **22,** 18–45. (Russian.)

Szymkiewietz, D., (1924). Etudes climatologiques. IV. Sur le rôle écologique des vents. *Acta. Soc. Bot. Poloniae,* **2,** No. 2, 1–22.

Thoday, D., (1909). A critical examination of Sachs's method for using increase of dry weight as a measure of carbon dioxide assimilation in leaves. *Proc. Roy. Soc. London,* **82B,** 421–476.

(1918). On turgescence and the absorption of water by the cells of plants. *New Phyt.,* **17,** 108–113.

(1921). On the behaviour during drought of leaves of two Cape species of *Passerina,* with some notes on their anatomy. *Ann. Bot.,* **35,** 585–601.

Thoday D.—*continued.*

(1922). On the organization of growth and differentiation in the stem of the sunflower. *Ann. Bot.*, **36**, 489–510.

Thomas, N., and Ferguson, A., (1917[a]). On evaporation from a circular water surface. *Phil. Mag.*, **34**, 308–321.

(1917[b]). On the reduction of transpiration observations. *Ann. Bot.*, **31**, 241–255.

Van Tieghem, Ph., (1886). Transpiration et chlorovaporization. *Bull. Soc. Bot. de France*, **33**, 152–155.

Timiriazev (Timiriazeff), **K. A.**, (1896). The struggle of the plant against drought.—Moscow. (Russian.)

Trabert, W., (1896). Neuere Beobachtungen über die Verdampfungsgeschwindigkeit. *Meteorol. Zeitschr.*, **31**, 261–263.

Transeau, E., (1905–1906). The bogs and bog flora of the Huron River valley. *Bot. Gaz.*, **40**, 351–375; **41**, 17–42.

Trelease, S. F., and Livingston, B. E., (1916). The daily march of transpiring power as indicated by porometer and by standardized hygrometric paper. *Jour. Ecol.*, **4**, 1–14.

Tröndle, A., (1910). Der Einfluss des Lichtes auf die Permeabilität der Plasmahaut. *Jahrb. f. wiss. Bot.*, **48**, 171–282.

Tschirch, A., (1881). Ueber einige Beziehungen des anatomischen Baues der Assimilationsorgäne zu Klima und Standort mit spezieller Berücksichtigung des Spaltöffnungsapparates. *Linnaea*, **43**, 139–252.

Tulaikov, N. M., (1915). Coefficients de transpiration des plantes cultivées. *Jour. russ. de l'agric. exper.*, **16**, 36–76. (Russian, with French abstract.)

(1916). Rôle de pression osmotique de la solution de sol dans la culture du blé "bélotourka". *Jour. russ. de l'agric. exper.*, **17**, 122–164. (Russian, with French abstract.)

(1922). Das Wasserbedürfniss der Pflanzen nach den Ergebnissen der Vegetationsversuche. *Ber. Landw. Landes-Vers. stat. zu Saratov*, **3**, Lief. 1/2, 21–36; Lief. 3/4, 1–14. (Russian, with German abstract.)

(1925). The utilization of water by plants under field and greenhouse conditions. *Soil Sci.*, **21**, 75–91.

Tumanov, J. J., (1927). Ungenügende Wasserversorgung und das Welken der Pflanzen als Mittel zur Erhöhung ihrer Dürreresistenz. *Planta (Arch. f. wiss. Bot.)*, **3**, 391–480.

Ule, W., (1891). Zur Beurteilung der Evaporationskraft eines Klimas. *Meteorolog. Zeitschr.*, **26**, 91–96.

Unger, F., (1861). Beiträge zur Anatomie und Physiologie der Pflanzen. XI und XII. Neue Untersuchungen über die Transpiration der Gewächse. *Sitzungsber. d. K. Akad. d. Wiss. Wien.*, Abt. 1, **44**, 81–127, 327–368.

Ursprung, A., (1913). Ueber die Bedeutung der Kohäsion für das Saftsteigen. *Ber. deut. Bot. Ges.*, **31**, 401–402.

(1915[a]). Ueber die Blasenbildung in Tonometern. *Ber. deut. Bot. Ges.*, **33**, 140–153.

(1915[b]). Ueber die Kohäsion des Wassers im Farnannulus. *Ber. deut. Bot. Ges.*, **33**, 153–163.

(1923). Zur Kenntniss der Saugkraft. VII. Eine neue vereinfachte Methode zur Messung der Saugkraft. *Ber. deut. Bot. Ges.*, **41**, 338–343.

(1925). Einige Resultate der neuesten Saugkraft-messungen. *Flora (Goebel's Festschrift)*, **118-119**, 566–599.

(1926). Ueber die gegenseitigen Beziehungen der osmotischen Zustandsgrössen. *Planta*, **2**, 640–660.

Ursprung, A., und Blum, G., (1916[a]). Zur Methode der Saugkraft-messung. *Ber. deut. Bot. Ges.*, **34**, 525–539.

(1916[b]). Zur Kenntniss der Saugkraft. I. *Ber. deut. Bot. Ges.*, **34**, 539–554.

(1918[a]). Zur Kenntniss der Saugkraft. II. *Ber. deut. Bot. Ges.*, **36**, 577–599.

(1918[b]). Besprechung unserer bisherigen Saugkraft-messungen. *Ber. deut. Bot. Ges.*, **36**, 599–618.

(1919). Zur Kenntniss der Saugkraft. III. *Hedera Helix*. Abgeschnittenes Blatt. *Ber. deut. Bot. Ges.*, **37**, 453–462.

(1920). Dürfen wir Ausdrücke osmotischer Wert, osmotischer Druck, Turgordruck, Saugkraft synonym gebrauchen? *Biol. Centralbl.*, **40**, 193–216.

(1921[a]). Zur Kenntniss der Saugkraft. IV. Die Absorptionszone der Wurzel. Der Endodermissprung. *Ber. deut. Bot. Ges.*, **39**, 70–79.

(1921[b]). Zur Kenntniss der Saugkraft. V. Eine Methode zur Bestimmung des Widerstandes, den der Boden der Wasserabsorption durch die Wurzel entgegensetzt. *Ber. deut. Bot. Ges.*, **39**, 139–148.

(1924). Eine Methode zur Messung des Wand- und Turgordruckes der Zelle nebst Anwendungen. *Jahrb. f. wiss. Bot.*, **63**, 1–110.

Ursprung, A., and Hayoz, C., (1922). Zur Kenntniss der Saugkraft. VI. Weitere Beiträge zur Saugkraft des normalen und abgeschnittenen Hederablattes. *Ber. deut. Bot. Ges.*, **40**, 368–373.

Vesque, J., (1876). De l'absorption de l'eau par les racines dans ses rapports avec la transpiration. *Ann. Sci. Nat., Bot.*, 6[e] sér., **4**, 89–137.

(1878). De l'influence de la température du sol sur l'absorption de l'eau par les racines. *Ann. Sci. Nat., Bot.*, 6[e] sér., **6**, 169–209.

Vikhlyaev (Vichliaev), **J.**, (1908). Die kritische Periode in der Entwicklung des Hafers. *Russ. Jour. f. exper. Landw.*, **9**, 257–271. (Russian, with German abstract.)

Volkens, G., (1887). Die Flora der ägyptisch-arabischen Wüste auf Grundlage anatomisch-physiologischer Forschungen.—Berlin.

de Vries, H., (1874). Ueber das Welken abgeschnittener Sprosse. *Arbeit. d Bot. Inst. Wurzburg*, **3**, 287–301.

(1884). Eine Methode zur Analyse der Turgorkraft. *Jahrb. f. wiss. Bot.*, **14**, 427–601.

Walter, H., (1923). Protoplasma- und Membranquellung bei Plasmolyse. *Jahrb. f. wiss. Bot.*, **62**, 145–213.

(1924). Plasmaquellung und Wachstum. *Zeitschr. f. Bot.*, **16**, 353–417.

(1925). Der Wasserhaushalt der Pflanze in quantitativer Betrachtung.—Freising-München.

(1925–26). Die Verdunstung von Wasser in bewegter Luft und ihre Abhängigkeit von der Grosse der Oberflache. *Zeitschr. f. Bot.*, **18**, 1–47.

(1926). Die Anpassungen der Pflanzen an Wassermangel. Das Xerophytenproblem in Kausal-physiologischer Betrachtung.—Freising-München.

Warming, E., (1909). Œcology of plants.—Oxford.

Warming, E., und Graebner, P., (1918). Lehrbuch der ökologischen Pflanzengeographie.—Berlin.

Weaver, J. E., (1919). The ecological relations of roots. *Carnegie Inst. Washington Publ.*, **286**, 1–128.

(1920). Root development in the grassland formation. A correlation of the root systems of native vegetation and crop plants. *Carnegie Inst. Washington Publ.*, **292**, 1–151.

Weaver, J. E., Jean, F. C., and Crist, J. W., (1922). Development and activities of roots of crop plants. *Carnegie Inst. Washington Publ.*, **316**, 1–115.

Weber, F., (1916). Ueber eine einfache Methode zur Veranschaulichung des Oeffnungszustandes der Spaltöffnungen. *Ber. deut. Bot. Ges.*, **34**, 174–183.

(1923). Zur Physiologie der Spaltöffnungsbewegung. *Oesterr. Bot. Zeitschr.*, **72**, 43–57.

Weber, F., und Hohenegger, H., (1923). Reversible Viscositätserhöhung des Protoplasmas durch Kälte. *Ber. deut. Bot. Ges.*, **41**, 198–205.

Weinrowsky, P., (1899). Untersuchungen über die Scheitelöffnungen bei Wasserpflanzen. *Fünfstücks Beiträge z. wiss. Bot.*, **3**, 205.

Wetzel, K., (1924). Die Wasseraufnahme der höheren Pflanzen gemassigter Klimate durch oberirdische Organe. *Flora*, **117**, 221–269.

Widtsoe, J. A., (1912). The production of dry matter with different quantities of irrigation water. *Utah Agr. St. Bull.*, **116**, 64.

Wiesner, J., (1877). Untersuchungen über den Einfluss des Lichtes und der strahlenden Wärme auf die Transpiration der Pflanzen. *Sitzungsber. d. K. Akad. d. Wiss. Wien*, Abt. 1, **74**, 477.

(1882). Studien über das Welken von Blüten und Laubsprossen. *Sitzungsber. d. K. Akad. d. Wiss. Wien*, Abt. 1, **86**, 209–265.

(1887). Grundversuche über den Einfluss der Luftbewegung auf die Transpiration der Pflanzen. *Sitzungsber. d. K. Akad. d. Wiss. Wien*, Abt. 1, **96**, 182.

(1889). Der Absteigende Wasserstrom und dessen physiologische Bedeutung. *Bot. Zeit.*, **47**, 1–24.

(1905). Ueber korrelative Transpiration, mit Hauptrucksicht auf Anisophyllie und Phototrophie. *Sitzungsber. d. K. Akad. d. Wiss. Wien*, Abt. 1, **114**, 477–496.

Wiggans, R. G., (1921). Osmotic concentration of the guard cells. *Amer. Jour. Bot.*, **8**, 30–40.

Wilms, J., (1899). Einfluss des Wassergehaltes und Nährstoffreichtums des Bodens auf die Lebensfähigkeit und Ausbildung der Kartoffelpflanze. *Jour. f. Landw.*, **47**, 251–292.

Wisser, K., (1914). Ueber den angeblichen chemischen Transpirationsschutz der Pflanzen.—Dissert., Kiel.

Wollny, E., (1898). Untersuchungen über die Verdunstung und das Productionsvermögen der Kulturpflanzen bei verschiedenem Feuchtigkeitsgehalte der Luft. *Forsch. auf d. Gebiet. d. Agric. Physik*, **20**, 528.

Wotchal, E. Ph., (1897). The movement of water in the plant.—Moscow.—(Russian.)

Yakushkina (Jakushkina), **O., and Vavilov, N.,** (1912). Anatomische Untersuchungen einiger Rassen des Hafers im Zusammenhange mit der Frage über Beziehungen zwischen physiologischen Eigenschaften und anatomischen Koefficienten. *Russ. Jour. Exper. Landw.*, **13**, 830–861. (Russian, with German abstract.)

Yapp, R. H., (1909). On stratification in the vegetation of a marsh and its relations to evaporation and temperature. *Ann. Bot.*, **23**, 275–319.

(1912). *Spiraea Ulmaria* and its bearing on the problem of xeromorphy in marsh plants. *Ann. Bot.*, **26**, 815–870.

(1925). The inter-relations of plants in vegetation, and the concept of "association". *Festschrift Carl Schröter*, 684–706.—Zürich.

Zalenski (Zalensky), **V.** (W.), (1902). Ueber die Ausbildung der Nervation bei verschiedenen Pflanzen. *Ber. deut. Bot Ges.*, **20**, 433–440.

(1904). Materials for the study of the quantitative anatomy of different leaves of the same plant. *Mém. Polytech. Inst. Kiev.*, **4**, 1–203. (Russian.)

(1911). The osmotic pressure and the transpiration of different leaves of the same plant. *Compt. Rend. Soc. Natur. de Kiev.*, 50–52. (Russian.)

(1918). On the methods of determining osmotic pressure in leaves. *Bull. Agric. Exper. Stn. Saratov*, **1**, No. 2, 1–10. (Russian.)

(1920). The indications of xerophily in plants. *Proc. 3rd Russ. Plant Breeding Congress, Saratov*, 38–40. (Russian.)

(1921). Ueber die physiologische Wirkung des Höhenrauches auf die Pflanzen. 1. Mitt. *Bull. Agric. Exper. Stn. Saratov*, **3**, Nos. 1–2, pp. 1–21. (Russian, with German abstract.)

(1923). Transpiration from the upper and lower leaves of plants. Separate from *Bull. Univ. Saratov*, 1–4. (Russian.)

Zalenski (Zalensky), **V.** (W.), **and Doroshenko, A.**, (1923). Ueber die physiol. Wirkung des Höhenrauches auf die Pflanzen. 2 Mitt. *Bull. Agric. Exper. Stn. Saratov.*, **4**, 7–21, (Russian.)

Žemčuznikov (Žemčužnikov), **E. A.**, (1919). On the methods of studying transpiration. *Proc. Soc. Natur. Rostov-Don*, **4**, 1–6. (Russian.)

(1923–24). The question of stomatal regulation of transpiration. *Bull. Agric. Res. Inst. Don and North Caucasus, Rostov-Don.* I. No. 148, 1–13: II, No. 163, 1–34. (Russian, with English Abstract.)

Zöbl, A., und Mikosch, C., (1892). Die Funktion der Grannen der Gerstenähre. *Sitzungsber. d. K. Akad. d. Wiss. Wien*, Abt. 1, **110**, 1033–1060.

Žoltkewich (Sholtkewitsch), **W.**, (1913). Zur Frage über die Ursachen der verschiedenen Widerstandsfähigkeit von Klee und Luzerne gegen Dürre. *Russ. Jour. Exper. Landw.*, **14**, 166–180. (Russian, with German abstract.)

INDEX

NOTE.—In cases where several pages are cited, the more important ones are printed in heavy type.

A

Absolute alcohol as fixative for stomata, **178**, 183

Absorption, by root—in moist sawdust, 50–51; in soil, 35, **60–82**, 288–290; in solutions, 50–54; in water, 47–59: in shade plants, 353: influence of environment on, 83–98: of water—by cell, **35–47**, 84–85; by leaves, 95–98; from bog soils, 88–91: relation of, to transpiration, **80–82**, 125, 130, 214, 215

Accumulation of dry substance, effect of environmental conditions on, **306, 313**

Acidity of soil, influence of on root absorption, 87–88

Active root suction, 55, **57–59**

Adaptation to dry-land conditions, 25

Aeration of soil, 91–92

Agamov, on cuticular transpiration, 363–364

Air movements, influence of on transpiration, 161–164

Alexandrov, O., on water content of leaves, 338

Alexandrov, W., on—anatomy of leaves, 387; assimilation, 341; intensity of transpiration, 339–340; leaf area, 128, **227**; transpiration of xerophytes and mesophytes, 270. See also **Maximov and Alexandrov**

Alexandrov, W., Alexandrov, O., and Timofeev, on water supply and structure of leaves, **342 343**, 372, 384

Algae, drought resistance of, 243

Allen, see **Sampson and Allen**

Aloi, 157

Alpine plants, transpiration of, 169–170

Anabiosis of—desert plants during dry season, **258–259**, 263; lower plants, 25

Anatomy of plant, influence of environment on, 359–373

Anatomy of leaves, 327–336; dependence of, on various factors, **328–336, 344–373**; effect of, on wilting of plants, 259–267; of light and shade plants, 346–359; of prairie and forest plants, 357–358

Annulus of fern sporangium, suction pressure of, 238

Area of leaf, **127–128, 227, 291–292**; variation of during daytime, 227

Areschoug, on anatomy of leaves, 348

Artificial illumination, experiments with, 157, **355–356**

Assimilation in—leaves at different heights on stem, 341; xeromorphic plants, 372

Assmann psychrometer, 111, 146, 162

Atkins, on exudation pressure, 52

Atmometer, **140, 154**, 163, 199, 205, 208; Bellani's, 143, Livingston and Thone's, 144–145; Piche's, **140, 141**, 146, 206: calibration of, 144–145; defects and advantages of, **140, 143–144, 146–147**; precautions in use of, 144

Atmosphere, "evaporating power of", 80

Atmospheric drought, 386–391

Atmospheric humidity, influence of, on—anatomy of plants, **360–364, 369**; evaporation, 135–137; transpiration, 156, **157–161**, 165, 166, 201; water requirement, 313–315

Auto-irrigator, Livingston's, 80–82

Autumnal shedding of leaves, causes of, 86

Azzi, on critical periods in plant development, 398

B

Bachmann, on—diffusion of gases, 175; porometer, 184; water deficit, 226–227
Badrieva, see **Maximov, Badrieva and Simonova**
Bakke, 112; on transpiration of xerophytes, 285–286
Balance for transpiration experiments, 116, 123
Balancing method for determining wilting coefficient, 65
Balls, on—transpiration, 121; porometer, 181
Bartholomew, on translocation of water in lemon plants, 239
Beauverie, on critical periods in plant development, 398
Bellani atmometer, 143
Benecke-Jost, 8; on xerophytes, 284
Bergen, on sclerophyllous plants, 267
Bergman, on poisonous effect of carbon dioxide on roots, 91–92
Bernbeck, on—assimilation, 242; transpiration, 164
" Bilanzquotient", 220
Blackman, F. F., 26; on—assimilation, 240; influence of temperature on absorption, 84; optimal temperature, 315
Blackman, V. H., on—exudation, 49; osmotic pressure, 39
Blackman, V. H., and Knight, on transpiration, 163
Blagoveshenski, on osmotic pressures of xerophytes, 273
Blum, see **Ursprung und Blum**
Bogdanov, on absorption of soil water, 70
Bog soils, absorption of water from, 88–91; "physiological dryness" of, **88–89,** 130; toxic effect of, on roots, 89
Bog xerophytes, 88–91
Bonnier, on transpiration at high altitudes, 169
Bose, on transpiration, 165–166
Boussingault's method of estimating transpiration, 349
Briggs and McLane, on moisture equivalent of soil, 68
Briggs and Shantz, on—daily march of transpiration, **148–153,** 154, 156; efficiency of transpiration, **297–300,** 304; relative transpiration, 205–206; transpiration, 147, 204, **205–206,** 208; transpiration balances, 116, **123;** water requirement, **131,** 392; water requirement and environment, 105, **313–320;** "wax seal" method, **64,** 117; wilting, **64–70,** 79, 80; wilting coefficient, 77, 78, **273**
Brilliant, on assimilation, 241–242
Bristol, on drought resistance of moss protonemata, 25
Bromeliaceae, osmotic pressure of, 279
Brounov, on critical periods in plant development, 397, 398
Brown, H. T., and Escombe, on—assimilation, 240; diffusion of gases, **172–176,** 183, 382; energy relations of leaf, 103
Brown, W. H., see **Livingston and Brown**
Burettes, use of as potometers, 198
Burgerstein, 97; on—effect of acids on absorption and transpiration, 87; self-recording balances, 123; stomatal movements, **191,** 199; transpiration, 8, 124, **126,** 147, **351;** and fertilizers, 321; of succulents, 251
Butovski, see **Mina and Butovski**

C

Cactaceae, osmotic pressure of, 279; " drought-resisting " characteristics of, 309; transpiration of, 252–253
Caldwell, on—permanent wilting, 62, **232–233,** 246; wilting, **69–70,** 80, 234
Cannon, on—cacti, 253; effect on roots of oxygen deficit, 92; transpiration, 109–110; xerophytes, 250

Carbon dioxide, toxic effect of on roots, 91–92
Carey and Oliver, on concentration of soil solution, 95
Casparian strip, 35, **36**
Catalano, on xerophytes, 294–295
Cell, behaviour of during wilting, **234–238**, **243–248**; cause of death by wilting, **236**, 247–248; equation for saturation of, 38; growth of, dependence on swelling of protoplasm, 45–47; size of, correlated with—accumulation of food, 379–380; distance from root, **330–332**, **334–336**; drought resistance, 297, **375–385**; root development, 378–379; transpiration, 378–379 · suction pressure of, 78, **236–238**
Cell size, hereditary, 378–385
Cell wall, elasticity of, **37**, 38; permeability of, 36–38; pressure of, see "wall pressure"
Cereals, stomatal movements in, 187–188
Cesalpino's theory of root absorption, 35
Chlorine content of tissue fluids, 280–281
Chlorovaporization, 165
Church, 25
Cladodes in xerophytes, 387
Clements, on—effect on roots of oxygen deficit, 92; transpiration, 120
Cobalt chloride method of estimating transpiration, 111–114
Coefficient of temperature, 84
Coefficient of transpiration, 105, **130–131**, 132, **295–324**
Cohesion theory of wilting, 228–238
Colloids of plant cell, changes in, 395: suction pressure (= imbibition pressure) of, 39, **43–44**
Comes, on transpiration, 166
Competition for water between parts of a plant, 240
Concentration of cell sap of xerophytes, 271–276
Concentration of soil solution, influence of on water supply, **92–95**
Condensation method of determining transpiration, 107–111
Conducting system, importance of in drought resistance, 386–389
Correlative transpiration, 240
Cotton, effect of wilting on yield of, 239
Cribbs, on transpiration of *Tilia* on dunes, 358
Critical period, 397–399
Crocker, on artificial sunlight, 157
Crump, 69
Cuticle, of xerophytes, 262; permeability of, 363
Cuticular transpiration, **133**, 134, 194, **363–364**

D

Dachnowski, on—effect of acids on absorption and transpiration, 87; soil toxins, 89
Dalton, Law of evaporation, **135–136**, **159–161**, 201
Darwin, F., hygroscopes, 179, 191: on—stomata, **179–183**, 191, 194; transpiration and light, **166–167**, 169; transpiration and relative humidity, 158
Darwin and Pertz, porometer, 179–184
Death from desiccation, 26, **243–248**
De Candolle's "spongiole theory", 35
Dehérain, 107
Delf, on—concentration of soil solution, 95; temperature coefficient of absorption, 84–85; xerophytes, 285
Desert ephemerals, 254–255
Desert plants, anabiosis of, during dry season, **258–259**, 263; analogy with xerophytes, 276; drought endurance of, 250; osmotic pressure of, 94, **271–276**; rate of transpiration of, 250; relative transpiration of, 200; stomatal movements of, 187; water content of, **222–226**, 263, 264; water supply of, 98

Desiccation of plant tissues, 25–26, **243–248**; analogy with freezing, 244–245; prevention of, 246–247
Dew, underground, **98**, 266
"Diameter law" of Brown and Escombe, **172–176**, 183, 382
Dietrich, on transpiration of sun and shade leaves, **351–352**, 383
Diffusion capacity of stomata, **196–198**, 383
Diffusion—of gases, 171–176; Brown and Escombe's law for, 172; —of solutes, effect of temperature on, 84;—of water vapour, **134–139**, **161**, 201
Dilanian, see **Maximov, Dilanian and Silikova**
Dixon, on regulation of transpiration, 11, **212**
Doroshenko, see **Zalenski and Doroshenko**
Drought, atmospheric, 386–391; beneficial effect of, 396; comparison of with freezing, 244–248; soil, 391–393
"Drought-enduring" plants, 258–259, **308–309**
"Drought-escaping" plants, 255, **307–308**
"Drought-evading" plants, 308
Drought resistance, 30–31, 131, **374–401**; and xeromorphic structure, **325–327**, 333: of—cereals and crop plants, 296; Cucurbitaceae, 391; leaves of higher plants, 243; lower plants, 25–26, **243**, **244**; seeds, 26, 243, 244, **396**; xerophytes, 287 relation of —to efficiency of transpiration, **304–309**, 322–324; to intensity of transpiration, 377–385; to size of cells, 297, **376–385**
"Drought-resisting" plants, 309
Drought resistant varieties of crop plants, selection of, 375–383, **398–401**
"Dry fog", 192, 316, **389**
Dryness, atmospheric, influence on plant structure, 357–359; internal physiological, 354; physiological, 94, 130
Dufour, on anatomy of leaves, 346

E

Eberdt, on—stomatal movements, 178; transpiration, 123, **124–125**; transpiration and wind, 164
Eberhardt, on anatomy and atmospheric moisture, **360**, 362
Economy of transpiration, 129
Efficiency of transpiration, see also "Transpiration coefficient" and "Water requirement"; 116, **131–132**, **295–324**; effect of environmental conditions on, 310–322; fluctuation of, in different years, 311; of—cereals, 300–301; other crop plants, 301–303; Russian xerophytes, 304–306; weeds, 303: relation of, to drought resistance, 304–309
Electrical conductivity of tissue fluids, **279**, 281
Enzyme action in guard cells of stoma, **177**, 189
Ephemerals, 254–255
Epiphytes, "drought-resisting",309; resemblance of, to succulents, 253; water absorption by, 95
Equilibrium method of determining suction pressure, 41–43
Escombe, see **Brown, H. T., and Escombe**
Evans, see **Harris and collaborators**
Evaporating power of the atmosphere, 80
Evaporation, 146; contrasted with transpiration, **133–139**, 147, **205–208**; Dalton's formula for, **135–136**, **159–161**; effect of meteorological factors on, 159–169; measurement of, 139–148; physical laws of, 135–139; Stefan's formula for, **136–137**, 183; Thomas and Ferguson's formula for, 136, **137**
Evaporimeter, 149, 155, 156, 162, 205; defects and advantages of, **140**, 146, **147**; Piche's, 140; Wild's, 139
Exudation pressure of root, see "Root pressure"

F

von Faber, on stomata, 186
Famintsin, 121
Farmer, on root pressure, 59, 86
Ferguson, see **Thomas and Ferguson**
Fern sporangium, see "Annulus"
Fertilizers, influence of, on efficiency of transpiration, 320–321
Fischer, on effect of acids on absorption, 88
Fitting, on—cacti, 254; desert plants, 257; osmotic pressure of desert plants, 94, **271–274**
Fog "dry", see "dry fog"
Free, see **Livingston and Free**
Freeman, on transpiration, **109**, 339, 349
Freezing of plant tissues, 244–248; analogy with desiccation, 244–248; prevention of, by chemical solutions, 246–247
Frey, on transpiration, 366–367
Frost resistance of plants, **244–248**, 395
Fungi, drought resistance of, 243

G

Gain, on—abnormal development of plants in saturated atmosphere, 104; unavailable water, 64
Ganong, on transpiration, 117
Géneau de Lamarlière, on—transpiration, 108; transpiration of sun and shade leaves, **348–351**, 383
Germination of seeds, 396–397; effect of water on, 70
Goebel, on temperature of bog soil, 89
Gortner, see **Harris and collaborators**
Gradmann, on stomata, 176
Graebner, see **Warming and Graebner**
Grafe, on—self-recording balances, 123; suction pressure, 42
Growth, dependence of on saturation of cell, 45–47
Gray and Peirce, on stomatal movements, 178
Guard cells, enzyme reaction in, **177**, 189; osmotic pressure in, 177; permeability of, 177; starch content of, **176**, 190; turgor of, 177
Guettard, experiments on transpiration, 107
Guttation, 58, 186, 219, 228; method of studying water absorption, **89–91**, 93
von Guttenberg, on sclerophyllous plants, 267

H

Haberlandt, F., 97
Haberlandt, G., on absorption of mineral salts, 105
Hairs, distribution of, 333
Hales, on absorption by aerial organs, 96
Halophytes, 93–95; analogy of with desert plants, 276
Hanley, see **Hill and Hanley**
Hannig, on osmotic pressures—in roots, 78; of xerophytes, 273
"Hardening" against—frost, **244–248**, 396; drought, 395–396
Harris and collaborators, on physical chemistry of plant saps, 278–283
Hartig, on water content of Birch, 86
Harvey, experiments with artificial illumination, 355; on frost resistance, 395
Hasselbring, on absorption of mineral salts, 105
Hauer, on critical periods in plant development, 398
Hawkins, see **Livingston and Hawkins**
"Hebelpachymeter", 227
Hedgcock, on unavailable water, 63
Heliophilous plants, see "sun plants"
Heliophobous plants, see "shade plants"
Hellriegel, 366; on—atmospheric humidity and transpiration, 157; efficiency of transpiration, and

light, 322; transpiration coefficient, 296
Henslow, on transpiration, 166
Hess, on root competition, 256
Hesselman, on—anatomy of leaves, 346; transpiration, 351
Heterobaric leaves, 182
Heuser, on anatomy of leaves, 327, 336, **364**
Hill and Hanley, on underground dew, 98
von Hoehnel, 133; on—anatomy of leaves, 337; transpiration of sun and shade leaves, 348
Hoffman, C. T., see **Harris and collaborators**
Hoffman, W. F., see **Harris and collaborators**
Hohenegger, see **Weber and Hohenegger**
Holle, on cell shrinkage during wilting, 235
Holtermann, on—harmfulness of transpiration, 102; xerophytes, 250
Homobaric leaves, 182
Hopping, see **Livingston and Hopping**
Horn hygroscope, **179**, 191
Houdaille, on evaporation, 162
Huber, 9: on—psychrometer, 146; relative transpiration, 208–209; transpiration, **105, 122,** 130; water economy of plant, 287–294; water supply of sun and shade plants, 354; xerophytes, 287–294
Humidity, atmospheric, influence on —intensity of transpiration, 313–315; leaf structure, **360–364,** 369; transpiration, 134, 156, **157–161,** 165, 166, 201
Hydrogen, effect of on roots, 91
Hydrogen ion concentration of tissue fluids, 281
Hygrometer, 160
Hygrometric method of determining transpiration, 110
Hygrophytes, **249,** 326; osmotic pressure of, 279–280
Hygroscope, horn, **179,** 191; *Yucca,* 179
Hygroscopic coefficient of the soil, 68

I

Iljin, on—absorption, 97; assimilation, 241; cell shrinkage during wilting, **236,** 246; chemistry of stomatal movements, 193; frost resistance, **246–247,** 396; osmotic pressure in stomatal guard cells, 177; respiration of barley, 45; stomatal movements, 191; transpiration, 120, 195; porometer, 183
Iljin, Nazarov and Ostrovski, on osmotic pressure of xerophytes, 273
Iljin and Sabinin, on stomatal movements, 187
Iljin and Soboleva, on osmotic pressure in leaves, 341
Imbibition pressure of colloids, see "suction pressure"
Incipient drying, **201–202,** 204, 228, 230
Incipient wilting, 232–233
Index of foliar transpiring power, **113, 285–286, 358**
Injection method of investigating condition of stomata, 184–186
Intensity of transpiration, 121, **126–128,** 130, 138, 289, 366–367; of—leaves, 339–340; sun and shade leaves, 348–359; xerophytes and mesophytes, **268–271, 357–358:** relation of to drought resistance, **357–359, 377–385**
Internal physiological dryness, 354
Ivanov, on—transpiration, 122; as turgor regulator, 104; terminology, **126, 129, 131;** of xerophytes, 287
Ivanov and Thielman, on transpiration and light, **167–168,** 169

J

Jeffreys, on evaporation, 136
Johnson, see **Harris and collaborators**
Jones, W. Neilson, porometer, 181
Jørgensen, see **Stiles and Jørgensen**
Jost, on xerophytes, 284

K

Kamerling, on—desert plants, 252; stomata, 185; transpiration of xerophytes, 284–285, 325
Kanitz, on temperature coefficient of absorption, 84
Kearney and Shantz, on classification of plants in relation to soil moisture, 307–309
Keller, on—desert ephemerals, 254; length of venation, and transpiration, 357–358; osmotic pressure of xerophytes, 273, **275–276**; transpiration of sun and shade plants, 352; xerophytes, 250, 255, **257–258**, 286, **287**
Keller and Leisle, on comparison of steppe and forest plants, 357–358
Kelvin, on vapour pressure, 159–160
Kerner von Marilaun, 250
Kiesselbach, on — efficiency of transpiration and environment, 318, 323; evaporation, 162; transpiration of corn, 27–28, **116, 363**. See also **Montgomery and Kiesselbach**
Kihlmann, on temperature of bog soil, 89
Kiselëv, on osmotic pressure of stomatal guard cells, 177
Knight, on porometers, 181–182; relative transpiration, 206–208; water content, 226; wilting, 229. See also **Blackman, V. H., and Knight, Laidlaw and Knight.**
Kochanovsky, on transpiration—at high altitudes, 169–170; of sun and shade leaves, 351
Kohl, on—atmospheric moisture and anatomy, 369; stomatal movements, 178; transpiration, 123, **124, 327**
Kôketsu, see **Livingston and Kôketsu**
Kokin, on—anatomy and soil moisture, 367–368; regulation of transpiration, 214–215
Kolkunov, on drought resistance and cell size, **297, 376–385**; water requirement, 306
Kolkwitz, on respiration of barley, 44
Komarov, on xerophytes, 355
Kosovich, on—poisonous effect of carbon dioxide, 92; water retaining capacity of soil, 60
Kozarov, on—absorption, 84; effect of oxygen deficit on roots, 91
Krasnoselsky-Maximov, on—cell shrinkage during wilting, 235; stomatal movements, 192; translocation of water in plants, 239; water content of leaves, 204, **223–226**, 336; wilting, 230. See also **Maximov and Krasnoselsky-Maximov**
Krebs, on evaporation, 146
Krutizky, on transpiration, 121
Kümmler, on stomata, 189
Kusmin, 270. See also **Levitski and Kusmin**

L

Lacon, see **Neger and Lacon**
Laidlaw and Knight, on porometers, 181, **191**
Lambrecht's polymeter, 110
Larmor, on effect of viscosity on diffusion of gases, 183
Lawrence, J. V., see **Harris and collaborators**
Lawrence, Z. W., see **Harris and collaborators**
Leaves, absorption of water by, 95–98; anatomy of, dependence on various factors, **328–336, 344–373**; area of, **127–128, 227, 291–292**; assimilation in, 341; intensity of transpiration of, 339–340; osmotic pressure in, 341; shrinkage of during wilting, 128; "sun" and "shade", differences between, 346–358; temperature of, 103–104; thickness of, 291–292; transpiration capacity of, 383; water content of, 201, 204, 206, 207, 214, 215, **336–338, 344–348**; xerophytic, 386–387
Lebedev, on underground dew, 98

Lebedintsev, on—atmospheric humidity and anatomy, 358, **361–363**; water requirement and atmospheric humidity, 314. See also **Maximov and Lebedintsev**
Le Chatelier's theorem, 326
Leclerc du Sablon, on transpiration and—atmospheric humidity, 157; light, 167
Leisle, see **Keller and Leisle**
Leitgeb, on stomata, 186
Lemon fruits, effect of wilting on, 239
Lepëshkin, on—permeability and light, 167; turgor pressure, 39
Levitski and Kusmin, on size of cells, 385
Lichens, drought resistance of, 243, 244, 393
Lidforss, on frost resistance, 245
Light, influence of—on plant anatomy, 344–359; on efficiency of transpiration, 321–322; on stomatal movements, 189–190; on transpiration, **164–169**, 177
Linsbauer, on stomatal movements, 190
Livingston, atmometers, **140–145**, 162; auto-irrigator, 80: on—bog soil, 89; index of foliar transpiring power, 286; investigation of transpiration, 126, 169; osmometers, 73–74; osmotic pressure of xerophytes, **272–273**, 275; plasmolysis during wilting, 234; relative transpiration, **129**, **207–209**, 286; transpiration of cacti, 252 See also **Pulling and Livingston, Shive and Livingston, Trelease and Livingston**
Livingston and Brown, W. H., on—incipient drying, 201; relative transpiration, 199–200; water content of leaves, **222–223**, **226**
Livingston and Free, on effect of oxygen deficit on roots, 91
Livingston and Hawkins, auto-irrigator, 80–82: on—water relations between plant and soil, 80–82; water supplying power of soil, 74
Livingston and Hopping, 112
Livingston and Kôketsu, on—osmometers, 75; soil points, 75
Livingston and Shreve, E., improvement of cobalt chloride method of estimating transpiration, 112–113
Livingston and Thone, atmometer, 144, 145
Lloyd, on—intensity of transpiration, 176; stomatal movements, **176**, 178, 183, **187**; stomatal regulation of transpiration, **196–199**, 212–214; transpiration, 120; wilting, 239
Loftfield, on—regulation of transpiration, 198, **212–214**; stomatal movements, 179, **187–188**, **190**, **192**, **212–214**
Lominadze, see **Maximov and Lominadze**
Lothelier, on anatomy of spiny plants, 366
Lubimenko, 250
Lundegardh, on effect of acids on absorption, 88
Lundström, on absorption of water by leaves, 95
Lute, for transpiration experiments, 117

M

Macchia (maquis), 266
MacDougal, on water relations of living tissues, 395
MacDougal and Spalding, on—transpiration of cacti, 253; xerophytes, 250
McLane, see **Briggs and McLane**
McLean, on absorption of mineral salts, 105
Mangroves, osmotic pressure of, 279
Marloth, on xerophytes, 250
Mason, see **Yapp and Mason**
Masure, 157
Maximov, container for transpiration experiments, 118; experiments with artificial sunlight, 157, **355–356**: on—daily march of transpiration, 148, **153–156**; efficiency of transpiration, 295;

freezing of plants, **244–245**, 248; regulation of transpiration, 204, **211–212**; stomatal movements, 187; transpiration of xerophytes and mesophytes, 286; water content of leaves, 339; wilting, 233–234
Maximov and Alexandrov, on—efficiency of transpiration, 304–307; xerophily of xerophytes, 277
Maximov, Badrieva and Simonova, on transpiration of xerophytes, 267–269
Maximov, Dilanian and Silikova, on osmotic pressure of xerophytes, 273–275
Maximov and Krasnoselsky-Maximov, on—assimilation, 241, 275; water content of leaves, 204, **225**, **336–337**; wilting, 229, 238
Maximov and Lebedintsev, on—development of root system, 352–353; sun and shade plants, 352–353
Maximov and Lominadze, on osmotic pressure of xerophytes, 273
Maximchuk, on daily march of transpiration, 148
Meschayev, on translocation of water in plant, 239
Mesophytes, 249, 359; intensity of transpiration of, **268–271**, 286; osmotic pressure of, **273–274**, **279–280**; relative wilting coefficient of, 67; stomatal movements of, 188
Meso-xerophytes, 286
Mez, on leaf scales of Bromeliaceae, 96
Micro-organisms, growth of, 45–46
Miller and Saunders, on effect of sunlight on leaf temperature, 103–104
Mina and Butovski, on water content, 226
Mist, "dry", see "Dry fog"
Modestov, on length of root system, **28**, 115
von Mohl, on—evaporation, 134; stomatal movements, 176
Moisture, atmospheric, influence of on leaf structure, 360–364
Moisture, soil, influence of on—efficiency of transpiration, 317–320; leaf structure, 364–371
Moisture equivalent of the soil, 68
Moliboga, on critical periods in plant development, 397–398
Molisch, injection method, 184–185; on stomata, 186–187, **190**, 191
Montfort, on—bog soil, 88, **89–91**; classification of xerophytes, 325–326; concentration of soil solution, 93; terminology for water relations of plants, 220
Montgomery and Kiesselbach, on efficiency of transpiration and environment, **318–319**, 321
Mosses, drought resistance of, 243, 244, 393
Movement of water in plant, 238–242
Muenscher, on—ash content of plants, 105; stomatal regulation of transpiration, 202–203

N

Nathansohn, on xerophytes, 250
Nazarov, see **Iljin, Nazarov and Ostrovski**
Neger, on—homobaric and heterobaric leaves, 182; stomata, 182; xerophytes, 250
Neger and Lacon, on transpiration terminology, 129
Newton, on frost resistance, 245, 395
Nicolić, on stomatal movements, 177
Nitrogen, effect of on roots, 91
Non-stomatal regulation of transpiration, **200–212**, 215, **253**
Nordhausen, on anatomy of leaves, 346, **347–348**
North, see **Priestley and North**

O

Oliver, see **Carey and Oliver**
Olsson-Seffer, on underground dew, 98

Ombrophilous plants, see "shade plants"
Optimal temperature, 315
Orchidaceae, osmotic pressure of, 279
Organic substances, accumulation of—correlated with cell size, 379–380; in the plant, 295
"Organication" of plant, 295
Osmometers, 36, **73–77**, 84
Osmotic pressure, in leaves, 341; of —Cactaceae, 279; desert plants, 94, **271–276**; guard cells of stoma, 177; halophytes, 94; hygrophytes, 279–280; mangroves, 279; mesophytes, **273–274**, **279–280**; parasites and hosts, 282–283; root cells, **50**, **54**, 63; small-celled plants, 385; solutions, 39; succulents, **274**, 341; tissue fluids, 278–283; xerophytes, **271–276**, **278–280**, 293
Ostrovski, see **Iljin, Nazarov and Ostrovski**

P

Paraffin, use of in microscopic work, **40**, 42, 43
Parasites, physico-chemical properties of sap, 282–283
Passive root suction, 55, **57–59**
Peat, absorption of water from, 88–91
Peirce, see **Gray and Peirce**
Permanent wilting, **62**, **64–65**, 70, **231–238**, **240–248**, 259, 391; test for, 232
Permeability of—cell wall, 36–38; cuticle, 363; protoplasm, 36, **37**, **167–168**, 177
Pertz, see **Darwin and Pertz**
Pessin, on resistance to soil drought, 393
Petrolatum, 64
Pfeffer, on root pressure, 53; transpiration balance, 115
Phyllodes in xerophytes, 387
Physico-chemical properties of sap of—different ecological types, 278–282; plant parasites and hosts, 282–283
Physiological dryness — internal, 354; of bog soil, 130; of saline soil, 94
Piche, evaporimeter (atmometer), **140**, **141**, 146
Pick, on anatomy of leaves, 346
Piemeisel, L. N., see **Shantz and Piemeisel, L. N.**
Piemeisel, R. L., see **Shantz and Piemeisel, R. L.**
Pirotta, 295
Planimeter, 127
Plasmolysis—analogy of with wilting 234–236; during wilting, 246–247
Plasmolytic method of determining —suction pressure, 40–41; wall pressure, 41
Poiseuille's Law of flow of liquid through tube, 184
"Pollarding", effect of on leaves, 342
Polymeter, 110
Porometer, Balls's, 181; Darwin's, 179–184; Jones's, 181; Knight's, **181–182**, 206; Laidlaw and Knight's, 181
Porous porcelain cup for transpiration experiments, 118–119
Potometer, **47–48**, 83, 84, **123–125**, 158, **198**, 206, 213; defects of experiments with, 221; Vesque's, **48**, **55–57**
Pots for transpiration experiments, 118–119
Priestley, on exudation pressure, 52–53
Priestley and North, on Casparian strip, 35
Pringsheim, on—osmotic pressure in succulent leaves, 341; translocation of water in succulents, 239
Protoplasm, composition of, 43; death of on drying, 243–248; drought resistance of, **395–396**, **401**; injury to during wilting, **236**, **246–248**; semi-permeability of, 36, **37**, **167–168**, **177**; swelling of, 44
Pseudo-xerophytes, 285, 325
Psychrometer, Assmann, 111, **146**, **162**

Pulling and Livingston, Osmometer, 74
Pullmann, on critical periods in plant development, **397**, 398

R

Radiation (solar), influence of on transpiration, **150–152**, **156**, 164, **165–169**
Radio-atmometer, Livingston's, 143
Ramenski, on evaporation, 162
Recovery after wilting, 243
Reed, on transpiration and fertilizers, 321
Regulation of transpiration—non-stomatal, **200–212**, 215, **253**; stomatal, **194–199**, 200, 206, **212–215**
Reinitzer, on harmfulness of transpiration, 102
Relative transpiration, 113, **129**, **199–200**, **206–209**, 286; of desert plants, 200
Relative water requirement, 310; see also "Transpiration coefficient" and "Efficiency of transpiration"
Relative wilting coefficient, 66–71
Renner, on—concentration of soil solution, 93; evaporation from free surface, 136; osmotic pressure of xerophytes, 273; root suction, 55; stomata, 176; stomatal regulation of transpiration, 197; transpiration, 125; xerophytes, 250
Reynolds Green, 35
Richardson, on transpiration coefficient and drought resistance, 323–324
Ricôme, on concentration of soil solution, 93
Rigg, on bog soil, 89
Rippel, on anatomy of leaves, 327, 336, **364–366**, 372
Root, absorption of water by, 47–82; development of dependence on cell size, 378–379; exudation pressure of, see "root pressure"; mass of, 291; osmotic pressure of cells of, **50**, **54**, 63; suction pressure of, **49–59**, **61–63**, **71–73**, 92, **93–94**
Root hair, 61
Root pressure, **49**, 59, 86, **102–103**; determination of, 49–51
Root regulation of transpiration, 211–215
Root suction, active and passive, **55**, **57–59**; resistance of soil to, 71–82
Root system, influence of light on development of, 352–353; length of, 28–29
Rosa, on frost resistance, 245, 395
Rosé, on anatomy of leaves, 346
Rotmistrov, on length of root system, **28**, 115
Rübel, on—atmometers, 143, 144; transpiration, **112**, 130, 327; transpiration of sun and shade plants, 354
Rudolph, on permeability of cuticle, 363
Rybin, on—concentration of soil solution, 93; effect of electrolytes on absorption, 87–88

S

Sabinin, formula for exudation pressure, 53–54; on—concentration of soil solution, 94; effect of acids on exudation, 88. See also **Iljin and Sabinin**
Sachs, 35; on—effect of temperature on absorption, **83**, 86; root absorption, 58, **61**, 64; water relations of soils, 62–63
Salisbury, on—diffusion capacity of stomata, 383; stomatal frequency, 372–373
Salt, effect of on growth of plants, 92–95; use of in controlling weeds, 92
Salt marsh plants, structure of, 94–95
Sampson and Allen, on—effect of acids on absorption and transpiration, 87; transpiration at high altitudes, 169; transpiration of sun and shade leaves, 351

Sand dunes, water supply of, 98
Saturation deficit of atmosphere, influence on transpiration, 134–135
"Saugkraft", 38
Saunders, see **Miller and Saunders**
de Saussure, hygrometer, 160; on wilting, 91
Schaffnit, see **Schander und Schaffnit**
Schander und Schaffnit, on freezing of plants, 244
Schimper, on—importance of water to plant, 26; leaf scales of Bromeliaceae, 96; physiological dryness of bog soils, 88, 89; saline soils, 94; transpiration of shade plants, 352; tropophytes, 86, xerophytes, 250
Schlösing, on abnormal development of plants in saturated atmosphere, **104** 157
Schröder, D., on—drought resistance, **243–244**, 246; localization of withering, 387
Schröder, G., on drought resistance of lower plants, 243
Schröder, M., on water requirement of cereals, 296, 299
Schröter, on physiological dryness of bog soil, 89
Schwendener, on—harmfulness of transpiration, 102; stomatal movements, 176, **195**
Seed coat, permeability of, 75–78
Seed osmometers, 76
Seeds, drought resistance of, 243, 244, **396–397**; germination of, **70, 396–397**
Seedlings, drought resistance of, 397
Semi-desert plants, midday water deficit of, 224
Semi-subterranean xerophytes, 255–258
"Shade" leaves, structure of, 346–348; transpiration of, 348–359; wilting of, 240
Shade (ombrophilous) plants, transpiration of, 351–359; wilting of, 229–230
Shakespear, G. A., 135
Shantz, on—classification of plants in relation to soil moisture, 399; desert plants, 255, 259; efficiency of transpiration, 297–298, 307. See also **Briggs and Shantz, Kearney and Shantz**
Shantz and Piemeisel, L. N., on—efficiency of transpiration, 298, **300–303**; relative water requirement, 310–311
Shantz and Piemeisel, R. L., on xerophytes, 254, 258
Shingle beach, vegetation of, 256; water supply of, 98
Shive and Livingston, criticism of Briggs and Shantz's wilting experiments, 69
Shreve, on—desert plants, 259; transpiration, 202; transpiration of cacti, 252 See also **Livingston and Shreve**
Shull, on—measurement of surface forces in soils, 75–78; water retaining capacity of soil, **75–78**, 273
Silikova, see **Maximov, Dilanian and Silikova**
Simonova, see **Maximov, Badrieva and Simonova**
Sinclair, see **Harris and collaborators**
Soboleva, see **Iljin and Soboleva**
Soil, acidity of, 87–88; hygroscopic coefficient of, 68; moisture equivalent of, 68; of bogs, **88–91**, 130; oxygen content of, 91–92; resistance of to root suction, 71–82; "souring" of, 277; temperature of, influence on absorption, 83–87; translocation of water in, 78–82; unavailable water of, **62–66**, 392; ventilation of, 91–92; water content of, **77**, 222; water deficit of, 81–82; water relations of, 62–63; water retaining capacity of, **60**, 68, **75–78**, 288–289; water supplying power of, 74: wilting coefficient of—for different plants, 66–68; for different soils, 66
Soil—drought, 391–393; moisture, influence of on efficiency of transpiration, 317–320; "points",

75; solution, acidity of, 87–88; concentration of, 92–95; toxins, 89–90
Sorauer, on—anatomy of leaves, 333; transpiration, **119,** 157
"Souring" of soil, 277
Spalding, on xerophytes, 277. See also **MacDougal and Spalding**
Specific transpiration, 129
"Spongiole theory" of root absorption, 35
Spores, drought resistance of, 384
Sresnevski, on transpiration and humidity, **159–161, 201–202**
Stahl, cobalt chloride method of estimating transpiration, 111–114; on—anatomy of leaves, 346; stomata, 186; transpiration and absorption, 86
Stålfelt, on stomata, 185
Static diffusion of gases, 172
Stefan, on evaporation, **136, 137,** 172, 183
Stein, on stomata, 185
Steinberger, on osmotic pressure of stomatal guard cells, 177
Steppe plants, water supply of, 98
Stiles, on—evaporation, 137; optimal temperature, 315; permeability of protoplasm, 8, 37, 41; suction pressure, 39; temperature coefficient of absorption, 84
Stiles and Jørgensen, on—suction pressure, 42; temperature coefficient of absorption, 84–85
Stocker, on—concentration of soil solution, 95; transpiration—of peat plants, 130; of sun and shade leaves, 351, 352
Stomata, condition of, under different environmental conditions, 186–193; diffusion capacity of, 196, **197,** 198, **383;** diffusion of gases through, **171–176,** 382–384; effect of "dry fog" on, 389; fixation of by absolute alcohol, **178–179,** 183; frequency of in woodland and other plants, 372; function of, 171–172; movements of, see "stomatal movements"; number per unit area of leaf, 330–336; of—different varieties of wheat, **377, 381–384;** xerophytes, 260–261: opening of at high temperatures, 389–391; "play" of, 177; size of, **330–336, 377–385;** sunken, 176, **260–261**
Stomatal index, 373
Stomatal movements, 174; chemistry of, 177, **193;** daily march of, **186–189, 208;** during wilting, 190–191: effect on, of—light, 177, **189–190;** temperature, **192–193, 389–393:** measurement of, 178–186; mechanics of, 176–178: of—cereals, 187–188; desert plants, 187; mesophytes, 188: regulation of transpiration by, **194–199,** 200, 206, **212–215**
Stomatal transpiration, 133–134
Structure of leaf, dependence of on water supply, 386–388
Strugger and Weber, on starch content of stomatal guard cells, 176–177
Succulents, 251–254; "drought-resisting" characteristics of, 309; osmotic pressure of, **274,** 341; prevalence of in deserts, 251; resemblance of to epiphytes, 253; transpiration of, **251,** 267; water balance of, 293
Suction force, 38
Suction pressure, **38–59;** during wilting, 236–238; methods of determining, 40–43: of—annulus cells of fern sporangium, 238; cell, 78, **236–238;** colloids, **39, 43–44;** root, **49–59, 61–63, 71–73,** 92, **93–94**
Sulphate content of tissue fluids, 281
"Sun" leaves, structure of, 346–348; transpiration of, 348–359; water content of, 240
Sun (heliophilous) plants, transpiration of, 229, **351–359;** wilting of, 228
Sunlight—artificial, 157, **355–356;** influence of on leaf temperature, 103–104
Surož, on anatomy of leaves, 346

Swelling of protoplasm, 241; measurement of, 44; of micro-organisms, 45–46
"Syndeticon", 182–183
Szymkiewitz, on evaporation and transpiration, 163

T

Temperature, coefficient of, 84: effect of, on—diffusion of salts, 84; root absorption, 83–87. high, effect of on—stomata, **192–193, 389–391**; water requirement, 315–316: of soil, 83–87; of wilted and turgid leaves, 104; reduction of by transpiration, 103–104
Thermophilous plants, 391
Thielman, see **Ivanov and Thielman**
Thoday, on—cell shrinkage during wilting, 235; drought resistance of—*Myrothamnus*, 243; *Passerina*, 235, **264, 265**: measurement of leaf area, **128, 227**; suction pressure, 39, **53**; turgor pressure, 39; water content, 27
Thomas and Ferguson, on—calibration of atmometers, 145; evaporation from free surface, 136, **137**, 138
Thomson, see **Kelvin**
Thone, see **Livingston and Thone**
Van Tieghem, on transpiration, 165
Timiriazev, on harmfulness of transpiration, 102
Timofeev, see **Alexandrov, W., Alexandrov, O., and Timofeev**
Tissue fluids, physico-chemical properties of, 278–283
Trabert, on accuracy of evaporimeters, 146
Translocation of water—in soil, 78–82; in shade plants, 353
Transient wilting, 228–238; test for, 232
Transpiration—and development of xylem, 327; capacity, 383; coefficient of, 105, **130–131**, 132, **295–324**; contrasted with evaporation, **133–139**, 147, 208; correlative, 240; cuticular and stomatal, **133–134, 194, 363–364**; daily march of, **148–170**, 209–210; dependence of, on—absorption, **80–82**, 125, 214, 215; cell size, 378–379; density of venation, 357–358: effect of meteorological factors on, 27–28, 120–122, **147–170**; efficiency of, **131**, 132, **295–309**: effect of environmental conditions on, 310–322; relation of, to drought resistance, **304–309**, 322–324: harmful consequences of, **101–102, 104**; inevitability of, 101–102: intensity of, 121, **126–128**, 130, 138, 289, **357–358**, 366–367; relation of to drought resistance, **357–359, 377–385**: influence on, of—air movements, 161–164; atmospheric humidity, 156, **157–160**; light, **164–169**, 177; solar radiation, **150–152, 156, 164–169**: non-stomatal regulation of, **200–212**, 215, **253**; of—alpine plants, 169–170; leaves at different heights on stem, 339–340; sun and shade leaves, 348–359; xeromorphic plants, 372; xerophytes and mesophytes, 268–271: physiological results of, 101–106: quantitative study of, 106–126;—gravimetric, 107–123; volumetric, 123–126: regulation of, 194–215; relative, 113, 129, **199–200, 206–209**, 286; root regulation of, 211–212; specific, 129; stomatal regulation of, 194–215; terminology, 126–132; useful functions of, 102–106
Transpiration coefficient, see also "Efficiency of transpiration" and "Water requirement"; of Russian xerophytes, 304–306
"Transpirationsvermogen", 208
Trelease and Livingstone, 112
Tröndle, on permeability and light, 167
Tropophytes, seasonal changes in, 86

True xerophytes, **255–259**, 285, 325
Tulaikov, on—transpiration terminology, 131; water requirement, **311–312**, **323**
Tumanov, on—anatomy and atmospheric moisture, 370–372; assimilation, 241; drought resistance, 245; "hardening" against drought, 395–396; permanent wilting of wheat, 393–395
Turgor, 39; in leaves of different ages, **337–338**, **344–346**; modifications induced by differences in, 344–346
Turgor pressure, 39

U

"Uberbilanz", 220
Ule, psychrometer, 146
Unavailable water in soil, **62–66**, 392
Underground dew, **98**, 266
Unger, on transpiration, 157, **160**, 194
"Unterbilanz", 220
Ursprung, on suction pressure, 78, **42–43**, 96
Ursprung und Blum, on—concentration of soil solution, 94; resistance of soil to root suction, **71–73**, **78**; suction pressure, 38–42;—of root, **49–52**, 94;—during wilting, 236–237

V

Valentine, see **Harris and collaborators**
Vascular system, development of in leaves, **328–333**, **353–361**, **364–366**, **368–371**
Vavilov, see **Yakushkina and Vavilov**
Vesque, on absorption, **55–57**, 84, 221; potometers, **48**, **55–57**, 124
Volkens, on—absorption by leaves, 95; desert ephemerals, 254; harmfulness of transpiration, 102; xerophytes, 250
de Vries, 58

W

Wall pressure, 38, **39**; plasmolytic method of determining, 41
Walter, 8, 9; on—conditions of growth of cells, 241; evaporation and transpiration, 137–139; growth of micro-organisms, 45–46; stomatal regulation of transpiration, 214; suction pressure, 43, **45**; transpiration terminology, 130; xerophytes, 250
Warming, on—importance of water to plant, 26; succulents, 251
Warming and Graebner, on xerophytes, 250
"Wasserhaushalt", 287
Water, absorption of—by root, 35, **47–82**; cell, **35–47**, 84–85; aerial organs, 95–98: accumulation of, by xerophytes, **251–254**, **262–263**; competition for, between parts of plant, 240; importance of to plant, 26–31; influence of on structure of leaves, 342–348; movement of in plant, 238–242; unavailable, **62–66**, 392
Water balance of plants, 28–31, **219–228**; calculation of, 288–295
Water capacity of soils, 62–63
Water conducting capacity, 389
Water content—and stomatal movements, 199; diurnal fluctuations of, 204, **222–228**: of—deciduous trees, 86; desert plants, **222–226**, **263–264**; leaves, 201, **204**, 206, **207**, 214, 215; leaves at different levels on stem, **336–338**, **344–348**; leaves during wilting, 215; plant, **26–31**, 129; soil, **77**, 222
Water cultures, peculiarities of plants grown in, 57
Water deficit, effect of on—assimilating capacity of leaf, 240–242; stomata, 190–192: in plants at midday, 222–228; of soil, 81–82; of tropophytes in autumn, 85–86
Water economy of plants, 287–295
Water relations of—plant cell, 43–45; soils, 62–63

Water requirement of plants, see also "Efficiency of transpiration" and "Transpiration coefficient"; 105, **132, 295–324**; effect of environmental conditions on, 310–324: of —cereals, 296, **299, 300–301**; other crop plants, 296, **299, 301–303**; weeds, 299, 303: relative, 310
Water retaining capacity of—soil, **60**, 68, **75–78**, 288–289; dry peat, 91
Water supplying power of soil, 74
Wax seal method of Briggs and Shantz, 64, 117
Weaver, on—cohesiveness of protoplasm, 85; length of root system, **28–29**, 115; root systems of xerophytes, **255, 256**
Weber, on chemistry of stomatal movements, 193. See also **Strugger and Weber**
Weber and Hohenegger, on protoplasm, 85
Wetzel, on absorption by aerial organs, 96–97
Wiesner, 97; heat theory of transpiration, **166**, 168, 169; on—correlative transpiration, 240; daily march of transpiration, 157; transpiration and light, **165**
Wiggans, on osmotic pressure of stomatal guard cells, 177
Wild evaporimeter, 139
Wilting, analogy of with plasmolysis, 234–236; as regulator of transpiration, 210–212; causes of, 386–396; cohesion theory of, 228–238; effect of, on—carbon nutrition, 240–242; crop yield, 30, **239**; leaf area, 128; protoplasm, 234–238; stomata, 190–191; structure of plant, 30: incipient, 232–233; of shade plants, **229, 353**; permanent, **62, 64–65**, 70, **231–238, 240–248**, 259, 391; endurance of, 393–398; stomatal movements during, 190–191; transient, 228–238; water content during, 215
Wilting coefficient of soil, **65–71**, 79;—for different plants, 66–68; —for different soils, 66
Wilting point, determination of, 65
Wind, effect of on—assimilation, 242; stomata, 164, 192; transpiration, 156, **161–164**, 208, 386–387
Wisser, on osmotic pressure of xerophytes, 273
Wollny, on abnormal development of plants in saturated atmosphere, **104**, 157

X

Xero-mesophytes, 286
Xeromorphic plants, characteristics of, 372
Xeromorphic structure, and drought resistance, **325–327, 333**; of—leaves, 341–342; peat plants, 88; salt marsh plants, 94; upper leaves of shoot, 333
Xeromorphy, factors determining, 374–375; of periodically wilted plants, 370–372; of shade plants, 348
Xerophytes, 249-283; adaptability of to mesophytic conditions, 276–277; anatomy of, 259–267; bog, 88–91; cell size of, 374–375; characteristics of, 374; conducting system of, 293, **386–389**; drought resistance of, 287; heliophily of, 354–355; intensity of transpiration of, **267–271, 284–287**; leaves of, 386–391; osmotic pressure of, **271–276, 278–280**, 293; pseudo-, 285, 325; semi-subterranean, 255–258; succulent, 250–254; true, **255–259**, 285, 325; xerophily of, 276–278
Xerophytism, degree of, 287–295

Y

Yakushkina and Vavilov, on—cell size, 380–381; drought resistance, 297
Yapp, on—anatomy of leaves, 327, **333–336**, 343, 372; evaporation, 162, **164**; shingle beach vegeta-

tion, 256; stomata, 172, **333–336**, 383; withering of leaves, 387–388
Yapp and Mason, 226, 334; on—water content of leaves, **337–338**, **344–346**
Yucca hygroscope, 179

Z

Zalenski, Law of leaf structure, **332**, 343; on—anatomy of leaves, **327–336**, 365, 372, 384; "dry fog", 192, 316, **389**; high temperature and stomatal movements, **192–193**, **389–390**; osmotic pressure of xerophytes, 271; transpiration, 339, 340; water supply and leaf structure, **342**, 353; xerophytes, 286
Zalenski and Doroshenko, on high temperature and stomatal movements, 390–391
Žemčužnikov, experiments on transpiration, **118**, 120, 121; on—daily march of transpiration, 148; stomatal regulation of transpiration, 214
Žoltkewich, on drought resistance, 388–389

Practical Plant Ecology

By A. G. TANSLEY, F.R.S.

Cr. 8vo. *Second Impression* *7s. 6d.*

The study of vegetation (known as plant ecology) is on the whole a modern study, and hitherto there has been no British practical handbook on the subject.

The present work, by the first President of the British Ecological Society and editor of the Society's *Journal of Ecology*, aims at providing beginners, whether amateurs, school teachers, or university students, with a guide to the field study of vegetation.

Elements of Plant Biology

By A. G. TANSLEY, F.R.S.

La. Cr. 8vo. *Illustrated. Fourth Impression* *10s. 6d.*

"This excellent handbook differs from the ordinary textbooks with similar titles in that it has far closer touch with general biology. . . . The treatment throughout is eminently clear and the suggestions for . . . practical work . . . excellent."—*School Guardian.*

An Introduction to the Study of Ore Deposits

By F. H. HATCH, O.B.E., PH.D., M.I.C.E.,

Past-President Inst. Mining and Metallurgy; Adviser on Metalliferous Mining to the Mines Department

Demy 8vo. *Illustrated* *7s. 6d.*

A short treatise on the origin of ore deposits, suitable for students and practising mining engineers. It gives first a historical summary of the theories of ore genesis, and then of the views held by leading mining geologists to-day, illustrated by typical examples from the most important deposits now being worked.

Textbook of Petrology

VOL. I. THE PETROLOGY OF THE IGNEOUS ROCKS

By F. H. HATCH, PH.D., F.G.S., AND R. H. RASTALL, M.A., F.G.S.

Cr. 8vo. *Illustrated. Eighth Edition* *15s.*

Containing a summary of the modern theories of Petrogenesis, a description of the rock-forming minerals, and a synopsis of the chief types of igneous rocks and their distribution as illustrated by the British Isles.

VOL. II. THE PETROLOGY OF THE SEDIMENTARY ROCKS

By F. H. HATCH, PH.D., F.G.S.

Cr. 8vo. *Illustrated. Second Edition* *12s. 6d.*

Containing a description of the sediments and their metamorphic derivatives, similar in scope to Vol. I Textbook.

Health, Disease, and Integration

By Dr. H. P. NEWSHOLME

Demy 8vo. 12*s.* 6*d.*

This study of the basic factors underlying the maintenance of health and the production of disease is based on an intimate analysis of a series of cases of encephalitis lethargica. The writer is led to formulate a broader view than that commonly held at present of the origins of this disease. This broader interpretation of the phenomena of the disease he applies to those of a number of infectious and constitutional diseases. The principles of integration, and of the disintegration constituting disease, are traced more deeply towards their foundations in the psyche. After discussing habit-formation in relation on the one hand to points of lessened physical and mental resistance, and on the other to the respective spheres of influence of heredity and environment, the writer analyses some of the factors concerned in the loss of integration leading to mental defect and to mental disease. His book closes with an application of the principles of integration, as outlined by him, to certain social and spiritual problems, from the point of view of a wider Preventive Medicine which seeks to deal with all the agencies militating against health in its most comprehensive sense.

Fundamentals of Objective Psychology

By JOHN FREDERICK DASHIEL

Professor of Psychology, University of North Carolina

Sm. Demy 8vo. 16*s.*

There is arising nowadays a scepticism as to the validity of introspection as a basis for the science of psychology; even the most extreme subjectivists have recognized as the explanatory foundation of their science facts and speculations based upon neural physiology. This book, then, is a survey of the psychological field from an objective point of view and aims at demonstrating the soundness of Behaviourism as a basis for scientifically attacking the many different problems of human nature. Its chapter headings include :—The General Characteristics of Behaviour, The Analysis of Behaviour; The Effectors, The Receptors, The Connecting System; Motivation; Learning, Perceiving, Social Behaviour, Language Habits, Thinking, Personality, etc.

Hypnosis and Self-Hypnosis

By BERNARD HOLLANDER, M.D.

Cr. 8vo. 6*s.*

Dr. Hollander's new book is the result of thirty years' experience of experimental hypnosis and hypnotic treatment. He shows that it is not sleep which is needed for hypnosis, but a peculiar state of self-abstraction in which the senses become curiously exalted and acute, a state induced by bringing into prominence the sub-conscious mind. In this state the mind will perform amazing feats, and spontaneous and lasting cures may be effected. Detailed and authenticated evidence is given of these and other phenomena, a study of which does much to eludicate the mysteries of Thought-transference, Clairvoyance, Premonitions, etc. The book will interest medical and psychological experts, while in style and language the general reader has been considered.

All prices are net.

GEORGE ALLEN & UNWIN LTD
LONDON: 40 MUSEUM STREET, W.C.1
CAPE TOWN: 73 ST. GEORGE'S STREET
SYDNEY, N.S.W.: WYNYARD SQUARE
AUCKLAND, N.Z.: 41 ALBERT STREET
WELLINGTON, N.Z.: 4 WILLIS STREET
TORONTO: 77 WELLINGTON STREET, WEST