THE BOOK WAS DRENCHED

UNIVERSAL
LIBRARY
OU_166693
UNIVERSAL
LIBRARY

OSMANIA UNIVERSITY LIBRARY

Call No. 633/W62C Accession No. 2710/

Author Whyte, R.O.

Title Crop production & environment

1946

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

CROP PRODUCTION AND ENVIRONMENT

BY G. V. JACKS AND R. O. WHYTE (*in collaboration*)

*

The Rape of the Earth

*

BY R. O. WHYTE, AUTHOR OR JOINT AUTHOR OF THE FOLLOWING PUBLICATIONS OF THE IMPERIAL AGRICULTURAL BUREAUX:

Vernalization or Lysenko's method for the pre-treatment of seed
(with P. S. Hudson)

Grassland and forage crops in Thuringia, Czechoslovakia and Hungary
Erosion and soil conservation
(with G. V. Jacks)

Research on grassland, forage crops and the conservation of vegetation in the United States of America

Alternate husbandry
(with G. V. Jacks, J. E. Nichols, E. L. Taylor, A. W. Ashby and W. J. Thomas)

Imperata cylindrica. Taxonomy, distribution, economic significance and control
(with C. E. Hubbard, D. Brown and A. P. Gray)

OTHER PUBLICATIONS

The history of research on vernalization (*Chronica Botanica*)

The provision of animal fodder in Agriculture and animal husbandry in the British Colonial Empire

The fodder resources of Palestine
(in preparation)

The fodder resources of Cyprus
(in preparation)

EDITOR OF

Proceedings of the Fourth International Grassland Congress

Production of grass seed
(I.A.B.)

Production of seed of herbage and forage legumes
(I.A.B.)

The control of weeds, by cultural, chemical and biological means
(I.A.B.)

The provision of animal fodder in tropical and sub-tropical countries
(I.A.B.)

CROP PRODUCTION AND ENVIRONMENT

by

R. O. WHYTE

FABER AND FABER LIMITED
24 Russell Square
London

First published in Mcmxlvi
by Faber and Faber Limited
24 Russell Square London W.C.1
Printed in Great Britain by
Latimer Trend & Co Ltd Plymouth
All rights reserved

CONTENTS

	Preface	*page* 9
I.	Introduction	11
II.	Growth and Development	21
III.	Growth and Development (*cont.*)	33
IV.	Temperature of Environment	61
V.	Development Before Seed Dormancy	90
VI.	Light in Relation to Development	102
VII.	Darkness and Development	128
VIII.	Phasic Development	140
IX.	Location of Response to Environmental Factors	149
X.	Hormones, Growth and Reproduction	158
XI.	Hormones and Photoperiodism	167
XII.	Relationships of Developmental Physiology	177
XIII.	Resistance to Adverse Environment	192
XIV.	Crop Production and Geographical Distribution	209
XV.	Breeding and Analyses of Environmental Requirements	231
XVI.	Manipulation of Developmental Physiology of Crops	245
XVII.	Developmental Physiology of Economic Crops	257
XVIII.	Developmental Physiology of Economic Crops (*cont.*)	275
XIX.	Developmental Physiology of Economic Crops (*cont.*)	298
XX.	Tropical and Subtropical Crops	326
	Bibliography	337
	Glossary	356
	Index of Authors' Names	359
	Index of Plant Genera and Species	364
	Index of Subjects	368

ILLUSTRATIONS

PLATES

1. Apices dissected from grasses and cereals *facing page* 56
2. Longitudinal median sections of onion seedlings *after page* 56
3. Longitudinal median sections of onion seedlings *after page* 56
4. Dissection of vegetative shoot of a dicotyledon (privet) *facing page* 57
5. Some of the earlier equipment of Garner and Allard at Arlington, Virginia, for their studies on photoperiodism 68
6. Equipment for control of temperature and photoperiod of individual leaf blades 69
7. Effect of night temperature on growth of tomatoes 76
8. Kok-saghyz seedlings after 29 days in growth chambers under conditions indicated 77
9. Seedlings from four successive sowings of barley grown in 16-hour photoperiods and different temperatures 112
10. The effects of photoperiod may be localized 113
11. Pyrethrum produces flowers only when grown where photoperiods are long 128
12. Effect of various wavebands of supplementary radiation on photoperiodic response 129
13. Effect of intermittent irradiation on photoperiodic response 136
14. Effect of photoperiod on microsporogenesis in Biloxi soybean *after page* 136
15. Effect of photoperiod on microsporogenesis in Biloxi soybean *after page* 136
16. Light for an hour in the middle of the dark period delays the blooming of chrysanthemums *facing page* 137
17. Inhibiting influence of leaves on photoperiodic response of Nobel spinach 144

18. After grafting of a leaf of Agate soybean on to a Biloxi plant, the latter has been induced to flower *facing page* 145
19. Technique of grafting 160
20. Vernalization of cereals 161
21. The use of cereals in Canada to produce herbage of high nutritive value for conversion into dried grass pellets for poultry feed 240
22. Types of *Poa pratensis* grown at Weibullsholm, S. Sweden 241
23. Growth habit of red clover at Macdonald College, Montreal 256
24. Production of silage and seed of white clover S100 in Breconshire 257
25. Sugar beets ready for overwintering in the field prior to taking seed in the following season 272
26. Effect of daylength on sugar beet 273
27. Effect of daylength on sugar beet 288
28. Effect of daylength on sugar beet 289
29. Effect of daylength and temperature on florist crops 304
30. Effect of daylength and temperature on florist crops 305
31. Effect of daylength and temperature on florist crops 320
32. Leaf fall of the tuliptree and many others may be delayed when the photoperiod is long 321

PREFACE

This book is an attempt to bring together two different worlds; that of the plant biologist working in his laboratory or experimental plot, talking of reactions and after-effects and hypothetical hormones, and that of the cultivator of crops in farm, garden, greenhouse or forest. The writing of these chapters has been like acting as a reporter at a shadow conference at which plant scientists past and present have mingled with weather-wise farmers, gardeners with green fingers, and cultivators of all manner of crops in every cultivable latitude. I have attempted to bring out the views and experiences of all these people, in many cases using practically or actually their own words and jargon in order to report them accurately. I ask those who have been conscious or unconscious participators in this exchange to complain if they have not been understood correctly, or if undue emphasis has been given to less important points at the expense of the more important. I would also welcome information as to other examples of the relationship between developmental physiology and crop production which may have been omitted.

I wish to express my most sincere thanks to all those who have helped by providing information or illustrations, checking sections of the manuscript, and in seeing the book through the Press.

Imperial Bureau of Pastures and Forage Crops,
Penglais,
Aberystwyth,
Wales.

CHAPTER I

INTRODUCTION

All crops are at the time of harvest or utilization the result of different degrees and combinations of growth and development. The cereals and other crops in which the seed or fruit is the economic product are characterized by a completion of all reproductive processes. Crops in which the foliage or the root is the economic end product depend more on growth than on development for their optimal yield. The leafy strains of herbage plants have been selected because they exhibit maximal growth for the species concerned, although their ultimate yield and particularly their high nutritive value depend upon the progress of development up to a certain stage. Agronomic practices are generally adapted to ensure that conditions are optimal for those physiological processes concerned in producing the economic returns required, whether of grain or cut green fodder, green vegetables, root crops, green manure, tobacco or timber.

The study of the developmental physiology of all plants including crops is therefore of great economic significance, and it is the object of this book to bring together as much as possible of the available scientific evidence and practical experience in order to show how and when crops react to the environment, and to indicate how the nature of this reaction affects crop yields, distribution and general agronomic behaviour and techniques. This entails a discussion of a wide range of problems not generally related, from the complex biochemical reactions within plants and the formation and translocation of hypothetical flowering hormones to the matter of choosing sowing dates and methods for many crops and also to the management of leys and the comparative grazing habits of cows versus sheep or other animals.

Throughout the following discussion, the terms 'growth' and 'development' are used in a restricted sense which requires definition. Growth is the accumulation of dry matter or increase in size of a plant, development the progress towards reproduction by externally recognizable or invisible stages. The change from a state of growth to that of development (the equivalent of puberty in animals) is carried through under the influence of the factors of the environment. The decisive factors which control growth and development are temperature and light (its presence or absence); once these factors have had an opportunity of operating at the appropriate time and to the required degree, a further set of conditions, including such factors as the relationship between carbohydrate

and nitrogen, water relations, general internal metabolism and nutrition, and so on, can then operate and determine whether a plant shall ultimately be permitted to exhibit the vegetative growth or reproduction already latent within it. This is an over-simplification of the problems at issue which are shown to be more complex by many of the experiments and responses described in subsequent chapters.

Plants vary widely in their capacity to react to the environment, and in their need for precise doses of one or more factors before they can proceed to reproduction. The different strains of economic plants or the ecotypes of wild species are expressions of the degree to which the particular biotype concerned is adapted to the environment in which it is found, for the purpose of optimal growth or development. The breeding of leafy 'pasture' strains of herbage plants is based on the selection of types which do not find their environment optimal for reproduction and therefore tend to remain largely vegetative. Some crops or wild plants which are found over a wide range of latitude are not restricted in their requirement for temperature or appropriate length of day for sexual or vegetative reproduction; other species or varieties within a species will reproduce themselves only within a very restricted range of environmental conditions and are therefore equally restricted as regards geographical distribution.

Research on the developmental physiology of plants may be said to have begun with the experiments of the German investigator, Klebs, in the years preceding 1918. Earlier experiments and statements had been made but Klebs may be regarded as the initiator of the modern extension of this branch of plant physiology, the main thesis of which is that it should be possible to isolate the factors governing plant growth and development and then to expose plants to optimal doses of these factors under artificial experimental conditions, thereby controlling growth or development at will. Since the work of Klebs, experiments have been made in many laboratories on the reaction of plants to temperature either in the very early stages of development in a seed or seedling (the phenomenon which has come to be called vernalization) or in more advanced stages of growth, or to light in the form of definite lengths and alternations of daylight and darkness (giving rise to the term photoperiodism). As it is inadvisable at this stage of the research to attempt sweeping generalizations (too many have been made already), the reader is referred to the chapters dealing with these factors, where the complexity of the problems will be obvious.

Gassner, another German physiologist, was one of the early chillers of grain, giving cereals in the laboratory the amount and duration of low temperature they would normally receive in the field after being sown in the autumn in Germany. Then for some years the interest of agricultural

physiologists became transferred to the relation between light and darkness and growth and development, and in particular to the work and statements of the Americans, Garner and Allard and their successors, on the photoperiodic reactions and categories of plants. The interest in temperature was, however, revived and the attention given to developmental physiology as a whole stimulated by the elaboration by Lysenko and his associates at the Institute of Plant Breeding and Genetics, Odessa, of the technique of pre-treatment of seed known as vernalization. This technique is considered by the Russians to differ from that of Gassner in recognizing that a minimum of growth is essential during low temperature exposure to provide conditions in which development can take place. The theoretical principles which were elaborated from the experimental data quickly exerted a revolutionary effect on the whole trend of Soviet research in plant biology, expressed in a large number of scientific and agronomic articles dealing with theory and practical applications.

There has since the time of Klebs been a tendency for investigators to postulate a succession of phases in the progress of a plant through development to ultimate sexual reproduction. In some cases, these phases are stated to be recognizable in external morphology, in others not. Klebs recognized three developmental phases. Ripeness-to-flower was stated by him to be a qualitative phase not recognizable morphologically, but dependent upon the temperature effect in relation to assimilation and dissimilation. The initiation of flower primordia and the formation of inflorescences and flowers are quantitative phases, recognizable morphologically. Following his work on vernalization, Lysenko produced a somewhat rigid hypothesis which has come to be known as the theory of phasic development, and is the subject of considerable disagreement, if not complete denial, in countries other than the U.S.S.R.

Lysenko included the light reaction in his theory in the form of a photo-phase, but a more important development in the study of light as a decisive factor is that investigators of photoperiodic reactions and particularly of the classification of plants into short-day, long-day and other groups have now recognized that the placing of a particular plant in any of these classes is dependent upon the age of the plant and the temperature (and other conditions) obtaining at the time of the experiment. It does not necessarily follow that the photoperiodic behaviour of a plant will be the same under a different temperature.

A natural outcome of all this research on the relation of individual factors or groups of factors to growth and development has been the construction at the California Institute of Technology, Pasadena, of air-conditioned greenhouses in which *all* the factors of the environment may be controlled for experimental purposes throughout the life of a plant

from seed germination to maturity and the formation of a new seed crop. From research under conditions such as these it should ultimately be possible to recognize which factors of the environment are decisive and which play an accessory or incidental role.

Certain experiments have, however, shown that even this is not enough. The life of a plant does not begin with germination of the seed, but with fertilization of the female gamete on the mother plant. A plant displays the capacity to respond to the temperature of its environment in certain instances remarkably soon after fertilization, within 5 or 6 days in one case studied. This capacity is progressively lost with approaching dormancy, and is acquired afresh when dormancy of the ripe seed is broken and germination begins. This has wide practical implications, and makes it necessary to record the environment, and particularly the temperature, under which seeds have been produced.

There has been considerable difference of opinion as to whether development is a reversible process or not. Led by Lysenko, most Russian investigators claim that it is irreversible, but this view does not appear to be tenable in view of results obtained elsewhere. Experiments at South Kensington have shown that it is possible to vernalize grains of winter rye, and then to devernalize them by drying, or exposure to high temperature, or to anaerobic conditions. When devernalization has been completed, it is then possible to induce vernalization again by exposure to the requisite environment. This has considerable practical implications. If the temperature in the field in winter or early spring rises sufficiently to produce partial devernalization, this will possibly have an effect on ultimate time of flowering. Similar irregularities might be produced by the existence of totally or partially anaerobic conditions during a wet winter in a sodden clay soil; a state of partial vernalization in seed sown in such a field during an earlier part of the season and later exposed to vernalizing temperatures might be annulled by a subsequent period under anaerobic conditions.

Darkness plays an important but still somewhat obscure role as an environmental factor governing plant development. In its original form, photoperiodism was understood to entail a regular alternation of light and dark periods, but the rigidity of this alternation is not now accepted. An alternation of light and dark periods is apparently not essential for at least some of the long-day plants, as development is possible even if these are grown in continuous light. It would appear that darkness is an inhibiting influence in the development of long-day plants. Research on short-day plants does not yet show definitely that the converse is true for short-day plants, namely that these require darkness for development and only tolerate light. The situation here is complicated by the fact that development is not possible without growth, and growth re-

quires a minimum number of light hours for photosynthesis. American and Russian work is indicating, however, that it is darkness and not the photoperiod which activates development in short-day plants, and that it is not the magnitude of the proportion between daily darkness and light but the absolute length of the dark period which is important.

Different parts of a plant respond to the decisive factors of the environment and transmit the impulse received either to daughter cells formed subsequently, or to other parts of the plant by means of the movement of a substance thought to be of a hormonal nature. The growing points appear to be primarily concerned with the response to low temperature in plants reacting to this factor, either in the form of excised embryos, or on seedlings or mature plants during over-wintering. The leaves respond to the other decisive factor, light (in combination with optimal temperature), and transmit the stimulus to the growing point which they control, producing therein a vegetative or reproductive reaction according to the environment to which they are exposed. A reproductive reaction in a growing point need not be the expression of an optimal environment for its governing leaves at exactly the same time, since there exists what is known as a photoperiodic after-effect. In certain highly responsive plants, the exposure of one leaf for a very short period of appropriate daylength may lead to complete flowering of that plant even if it is subsequently removed to an environment not conducive to development.

Earlier investigations made and theories produced in the U.S.S.R. seemed to indicate that the vernalization reaction could be explained on a hormonal basis. It was thought that the pre-treatment technique associated with vernalization stimulated the embryo to activity without providing the requirements for normal growth, and it was further assumed that there would be a marked absorption of the growth hormones abundant in the endosperm. This increased concentration of hormone in the cells of the growing point was supposed to be responsible for the more rapid progress of these young cells through the first phases of development. This postulation has now become untenable in view of results obtained at the Imperial College of Science and Technology, London.

All investigators appear to be agreed that the responses associated with the photoperiodic reaction are transmitted from one part of a plant to another by means of substances of a hormonal nature. It has not yet been possible to identify accurately or to isolate this hypothetical hormone with a view to injecting it into the plant body and thus controlling its subsequent behaviour. Much has been learnt of this behaviour; it is for example claimed that the hormone can cross from one plant to another through a non-living diffusion contact represented by a thin

sheet of lens paper separating approach grafts. Investigators have also postulated the existence of different hormones or the same hormone in different forms at different times to explain the phenomena observed in this research. The names florigen and vernalin have been proposed for two of these, but until they can be identified more accurately definite conclusions cannot be made.

Since the vegetative and reproductive responses of a plant to the environment have a profound influence on the internal metabolism and biochemical composition, it is obvious that the economic value of the crop is directly dependent on the existence of an optimal environment as regards both decisive and accessory factors. When a cereal finds the environment optimal for reproduction, the straw contains small amounts of nutrients, everything having been absorbed or transferred by the maturing grain. Where conditions are below the optimum for reproduction, grain yields are lower and ripening more difficult, but the straw is of higher nutritive value for livestock. Growth continues longer due to the lower inhibitory effect of the development. Such empirical practices as the selection of lettuce varieties for production throughout the year in England, the cultivation of crops in frames and greenhouses, the management of grazing leys and the closure of fields for hay or herbage seed production have been found by a process of trial and error and agronomic experimentation, but are based ultimately upon the developmental physiology of the crop concerned. Optimal yield of a green vegetable or herbage plant at the proper time in the season depends upon a synchronization of its growth and/or development with the environment concerned. The varieties which have been found to be adapted to a particular environment after many years of practical experience are permitted by that environment to express themselves either in growth or development or a combination of these, and to produce the economic product required in maximum quantity and quality.

Plants are during their growth periods exposed to a number of adverse environments in the form of extreme heat, cold or drought, or to attack by fungous and virus diseases, insect pests, and so on. Their reaction to these factors and the degree of their susceptibility to them depend to a great extent on their developmental physiology. Strains resistant to attack by a particular fungus may owe much of their superiority over susceptible strains to a difference in their developmental and growth processes, in that maximum susceptibility to attack no longer coincides with the peak period of infection. Plants are palatable to insects as well as to domestic animals or human beings, and what is the highest nutritive value for the latter (optimal combination of growth and development) is frequently also suitable for the former; a change in the progress of development may lead to a reduction in damage by insect attack.

Winter hardiness in particular is closely linked with the earlier phases in the developmental processes; the relation between the degree of vernalization or the degree to which a plant has been exposed to the low temperature necessary for development, and the capacity of that plant to resist frost are of great practical importance in countries where varieties are selected for autumn sowing, and experience a considerable variation in the severity of the winter conditions to which they are subsequently exposed.

It is obvious to any farmer that a particular variety grows where it does because it is adapted to the environment and the type of management it receives. To the north or south of his particular area, he knows that other varieties are found to be better. When his own variety is moved to another latitude, it may not give a crop or may be in some other way markedly inferior to the variety grown in that latitude; it may even break up into a number of subtypes which had not been apparent in its original environment. It is claimed that, when varieties behave in this way, they are heterozygous as far as the different phases or stages of their developmental period are concerned. In one locality, the environment in which a variety grows prevents the expression of the real nature of what has been assumed to be a pure line; if this variety is moved to a different latitude, some forms within that pure line may find the new environment more suitable for reproduction, others less so, and a range of forms thus appears producing a mixed population.

The genetical aspects of the general problem of developmental physiology are complex and controversial. Attempts to study inheritance on the basis of genes for winter and spring habit, earliness and lateness and other morphological expressions of a physiological condition do not appear likely to provide any conclusive results. The Russian method of phasic analyses and breeding on the basis of length of developmental phase would appear to be too far to the other extreme, but some knowledge of the relative requirements of different varieties, and even plants within a variety, as far as the decisive factors of the environment are concerned may provide a basis for controlled breeding or selection of types adapted to a given environment. It would be interesting if a breeder of a crop with a reasonably wide latitudinal range could distribute the F_1 generation seed from a cross made for studying the inheritance of characters such as earliness or lateness among scientific colleagues working in different latitudes, in order that the segregation in relation to latitude might be observed. Ratios might differ considerably according to the degree to which each environment permitted the manifestation of the true nature of the material.

As research on all these biological problems proceeds and reliable data accumulate, progress is being made towards the final aim, namely the ability to control and direct the behaviour of plants. Already many

practices have been developed by farmers, market gardeners and others which are based directly upon developmental physiology, even though they may have been evolved without a full appreciation of the fundamental processes involved. Probably the most publicized practice of this type in recent years has been the method of pre-treatment of seed with low temperature which has become known throughout the English-speaking world as vernalization. Some workers speak of vernalization as also applying to treatment with short day, and the after-effect associated therewith, but it is advisable to confine the use of the term to pre-treatment with temperature.

When the method of vernalization was first described in English in the publications of the Imperial Agricultural Bureaux at Aberystwyth and Cambridge, it became the fashion to attempt to vernalize all manner of plants for many different purposes and using many variations in technique. Too much was expected of the method, and too many sweeping and dogmatic statements were made at that time. Now, although experiments such as those conducted at the Imperial College of Science and Technology, London, have provided data for a better understanding of the fundamental biological processes involved, the period of great expectations is past. In the years preceding 1939 there were rapid increases in the acreages sown with vernalized seed in Russia, but no subsequent data have yet been seen. The chief aims there were to avoid either the severe winter months or periods of excessive summer drought; vernalization was also used in connection with the cultivation of catch crops in regions where the combined lengths of the vegetative periods of the main crop and the catch crop are longer than the possible growing season. The method does not appear to have been applied to catch crop cultivation in Germany, where these crops have been so widely grown in recent years, but rather to exotic crops such as the soybean, which might have been of great industrial value.

Although vernalization might possibly have been thought to be of some value in the cultivation of market garden crops of high cash value in England, or in the extension of crop cultivation northwards in Canada, this has not been the case, cultivators preferring in general to use varieties adapted to their type of cropping or conditions. Only in India do investigators still seem to take an active interest in the method of pre-treatment, reporting experiments on rice, wheat, mustard, gram, *Crotalaria*, jute and other crops, and suggesting a central station or stations from which vernalized seeds might be obtained by cultivators. The outstanding claim made by the Indians is for a variety of rice, which when 'vernalized by short day' and not temperature showed a reduction in time to flower from 133 to 47 days, the shortest period yet reported within which winter varieties of rice will flower.

Progress is, however, being made in the study of the developmental behaviour of a wide range of crops. The American agronomists and plant breeders have built up a self-sufficient sugar beet seed industry on the basis of a knowledge of the reaction of this crop to the factors of the environment, and investigations at the School of Agriculture, Cambridge, are providing further fundamental data on the same crop. Other Cambridge investigators have reported on the photoperiodic behaviour of the potato varieties collected on behalf of the Imperial Agricultural Bureaux by an expedition to the Andes. Good progress has been made in a very detailed study of the physiology of the onion at the Imperial College of Science and Technology, London, and in the application of that knowledge in practice. The Russian workers have classified their varieties of wheat, barley and other cereals into different groups after making phasic analyses, and are basing their breeding work upon this knowledge.

The work on herbage plants in natural stands or as cultivated crops is still in an early stage but has already provided data of considerable interest. The work in progress on the species of the American range grass, *Bouteloua*, at the University of Chicago, is providing information fundamental to the distribution and migration of plant species, and to the whole question of ecotype formation which is of such importance in economic breeding of herbage plants. As data accumulate on the developmental behaviour of the grasses and legumes of sown seeds mixture, it will become increasingly possible to link the management of grazing, hay or seed leys with the formation of flower primordia, the translocation of hormones from leaves to growing points, and other abstruse phenomena.

Suggestions are made from time to time regarding the desirability of collaboration between meteorologists and plant scientists or naturalists in making phenological observations on the relation between weather or climate and the behaviour of plants. Many of the records which it is suggested should be made are connected with the processes of reproduction of a plant as expressed morphologically in such recognizable phenomena as shooting, flowering, seed formation and so on. The usual type of meteorological data do not, however, provide the necessary information for a correlation between seasonal trends in the environment and the growth or flowering behaviour of a plant. If it is finally agreed which factors of the environment are decisive in affecting growth and reproduction, the taking of records can presumably be adapted accordingly to give total number of hours below a certain temperature, photoperiods, dark periods, or periods of light effective for reproduction (down to bright moonlight according to some workers). Microclimates at plant height are also of considerable significance, as temperatures within a

dense stand are likely to be lower in hot weather than ordinary records might indicate. This provides data necessary for the location and management of seed crops, hay leys and dense stands in general.

CHAPTER II

GROWTH AND DEVELOPMENT

As this book is concerned throughout with the biological phenomena and manifestations of growth and development in plants, it is necessary first to define this restricted use of these two terms. The need to distinguish between them has been stressed more particularly by Lysenko, who states that it is now certain that they are not identical phenomena. Growth is an increase in size without any profound qualitative changes in the growing parts. Although the germination of seed and the subsequent formation of vegetative organs lead to an increase in their number, to the branching of roots and stems, and to the appearance of new leaves, these are regarded in this research as manifestations of growth, but not necessarily of development.

By development is generally understood the progress of a series of internal qualitative changes (with or without external changes) governed by the factors of the environment and which lead ultimately to the production of fruit, and, in annual plants, to death. It is, of course, possible to have very vigorous vegetative growth with little or very slight progress in development, and at the other extreme, there are the examples of vernalized seeds, which are arrested in their growth at an early stage, but induced to develop more rapidly.

It does not appear that any claims are made for a complete separation between growth and development, nor for any antagonism between them, although the numerous examples of reduced vegetative growth accompanying flowering have to be considered in this connection. From the work on vernalization, it appears that development cannot proceed in the absence of growth, and that the fundamental difference between Lysen ko's method and those of the earlier 'chillers' is that Lysenko insisted that growth must begin before applying the temperature treatment.

From these remarks, it follows that Lysenko's emphasis on the statement that the *rate* of development does not depend on the *rate* of growth is reasonable. This fact is actually the basis for the experimental technique that has been developed to study this whole question of the factors that govern the progress of a plant towards maturity, and of the after-effects produced by the application of one or other of these factors at an early stage in the life of a plant.

Reference should be made at this point to the work done in Great Britain between 1918 and 1925 on what was then called 'physiological predetermination' (Kidd and West, 1918 and 1919, and Tincker, 1924).

These studies were concerned with the question as to how far the physiological condition of a plant in the seed-stage (that is, in maturation, dormancy and germination) may exert a predetermining influence upon the whole subsequent course of growth and development.

Although the concept of the distinction between the vegetative and reproductive states in plants is not new in itself, since Klebs expressed similar ideas in 1918, the emphasis that has been placed on it in recent literature has undoubtedly indicated the need to be more explicit when talking of growth and development. 'The confusion between these two terms which is still frequent is absolutely inadmissible' (Maximov, see Aberystwyth, 1934).

Actual Age and Physiological Age

It follows that a distinction must also be made between the actual age of a plant expressed in time from sowing, or fertilization on the mother plant, and its physiological or developmental age. By the latter term would be meant the stage that the plant under investigation has reached in its progress towards reproductive maturity. This is expressed by the use of terms such as 'ripeness to flower', 'thermo-phase', 'photo-phase', and so on, or by the description of morphological characters such as 'the formation of flower primordia' and 'flowering'. As it is not possible always to decide the developmental age of a plant, it becomes necessary, in carrying out experiments on problems relating to development, to record or have available details of the precise environment under which the plant has existed since it began its life. It would thus be possible to say, for example, in experiments on the relative requirements of light and temperature, how many hours or days of either of these decisive factors a plant has received before an experiment begins. It may then be decided whether development may be assumed to have progressed at all, and also whether any combination of factors were present which might lead to a reversal of development, as this can actually occur.

The Carbohydrate-Nitrogen Relationship

Maximov states that the study of plant development may be said to have started with the work of Klebs, who was one of the first to attach particular importance to the factors of the environment, especially temperature and light, and the controlling influence they exert upon the developmental processes. In emphasizing the effect of external conditions, Klebs differed from Pfeffer, who believed that internal influences alone were operative.

Klebs was able, by manipulating the light and temperature of the environment, to maintain continuous vegetative growth, or to induce reproduction prematurely, and considered that this was due fundamentally to the balance between carbohydrates and soil nutrients (redefined as soluble carbohydrates and soluble nitrogen). This concept was revived by Kraus and Kraybill (see Oregon, 1918), who attempted to establish a causal relationship between the C/N relationship and vegetative growth and sexual reproduction in the tomato. In writing on the physiology of plant reproduction, Murneek (1939) states that almost all the supporting and some of the contradictory evidence on the relation between the C/N relationship and reproduction has come from analyses of plants in advanced stages of reproduction, that is, advanced in developmental age. Although Klebs and others have found that a relatively high carbohydrate content exists in plants that are already flowering and fruiting, it has not been shown that any type of balance is necessary for the *initiation* of the reproductive state. Murneek refers, however, to his own work (see Missouri, 1937) and that of Knodel (1936) and Asami and Ito (1937) which indicate that a relatively high *nitrogen* content may be associated with flower initiation.

As regards fruiting in particular, and as distinct from floral initiation and formation, it is probable that other proportional ratios of nutrients are just as important as the C/N relationship alone.

The Separable Phases Postulated by Klebs

As much of the difference of opinion that exists among plant physiologists is concerned with the recognition or otherwise of definite or indefinite phases in the development of a plant, it is desirable to quote the views of Klebs in some detail, as being one of the classic works in the new science of developmental physiology.

Klebs found in his research on *Sempervivum* (1918), which is described in detail in Chapter VI, that the process of formation of the inflorescence proceeds in three clearly separable phases, which he called the onset of the ripe-to-flower condition, the formation of the flower primordia, and the development of the flowering inflorescence.

The ripe-to-flower condition is regarded as the product of intensive C-assimilation with active transpiration and a relative limitation of uptake of nutrient salts. All the factors operate in the same direction, by increasing the concentration of C-assimilates and hindering the counter-reaction of vegetative growth. Under usual conditions, the increase of assimilation hinders the initiation of the 'ripe-to-flower' condition; if it is already present in a plant, it is destroyed by weak light. As is well known, increased humidity favours vegetative growth and operates

against ripeness-to-flower; the effect of an active uptake of nutrient salts is still more marked.

Klebs states that the idea that a one-sided increase of C-assimilation, especially of carbohydrates, governs ripeness-to-flower also explains the relation to temperature. Under intense summer light, temperature can be very high without adversely affecting the initiation of ripeness-to-flower. As the light intensity falls, however, the hindering effect of higher temperature on ripeness-to-flower increases. Spring light at a temperature of 20° C. plus an active uptake of water and nutrient salts can eliminate an already acquired ripe-to-flower condition, and rosettes can in this way be kept in a vegetative condition throughout the year. It is still easier to eliminate 'ripeness-to-flower' in the dark at higher or medium temperatures (even at 15° C.).

Klebs' interpretation of these results was as follows. It is not the absolute strength of the light or the level of the temperature that is the decisive factor, but the quantitative relation of assimilation to the temperature effect, which is manifested more especially in an increase in dissimilation. This is also regarded as explaining why a lower temperature of about 6° C. has an opposite effect. Under the low intensity light of a German winter or even after months without light, the ripe-to-flower condition is maintained. The lower temperature can even induce the initiation of this condition in a well-fed rosette in darkness, a result regarded by Klebs as being probably due to the gradual conversion of starch into sugar. Under such circumstances, light may to some extent be replaced by the lower temperature, a clear indication, according to Klebs, that under normal conditions light produces the ripe-to-flower condition largely through its assimilatory operation, which is dependent on its energy.

The second phase postulated by Klebs is the formation of flower primordia. It is stated that the initiation of microscopically recognizable primordia would appear to be dependent upon light, but it is not clear whether success may still be achieved when light is replaced by another factor.

It is again the energy of the light that is operative. Continuous strong artificial illumination must last for several days before primordia appear. The time required depends upon the extent to which the ripe-to-flower condition has increased in the spring under the influence of daylight at a lower temperature.

With interrupted illumination the number of light hours per day even at the higher intensities must be relatively great. Klebs found them to be less in his March experiments on *Sempervivum* than in those made in December, but even in the March series it was found that they should not be permitted to fall below 12 hours per day.

A simple relation between the number of light hours and light intensity does not appear to exist, as the dark hours have an antagonistic influence at medium temperatures of 20 to 25° C. A special characteristic of the light effect is the contrast between weak and strong refracted rays. The red rays stimulate the onset of flowering within wider limits of intensity, under both weak and strong light intensity; the blue-violet rays hinder the process, and ultimately cause a reversion of the ripe-to-flower condition. This question of reversal back from a reproductive to a vegetative condition is discussed frequently in subsequent chapters.

Klebs' conclusion with regard to his second phase is that it follows that the trophic effect of light is replaced by a blastic effect, and that this depends, not as in the fern prothallus upon a mere acceleration or retardation of elongation and cell division, but on a change of the ripe-to-flower condition into true flower formation or conversely into purely vegetative growth. As in the type of light used in his experiments the red rays prevail over the blue-violet, this had a greater stimulatory effect upon flower formation than diffuse daylight with relatively more blue-violet rays, while in direct sunlight this difference is not important.

Klebs' third developmental phase, the formation of the inflorescence, is completed in *Sempervivum* by the elongation of the axis, the formation of lateral branches (scorpioid cymes) and by the unfolding of the flowers. The whole process depends upon light, but more in a way similar to the acquisition of the ripe-to-flower condition. If the microscopically recognizable primordia are already present, the development of the inflorescence may proceed in the dark, particularly if a low temperature is applied (up to 6° C.), but the formation of flowers is very poor compared with cultures in the light. The later in May the experiment on the absence of light was begun, the better was the flower formation, due to the influence of the earlier light effect.

The light intensity necessary under continuous lighting and a temperature of about 20° C. for the formation of more or less normal inflorescences is higher than that required for initiation of flower primordia. According to Klebs, however, flowering depends, as does the acquisition of the ripe-to-flower condition, not so much upon the absolute light intensity as upon the relation of the nutrient-storing C-assimilation to the removing processes of dissimilation.

Again, under strong Osram light in winter, the inflorescence is never so strongly developed and rich in flowers as in daylight in June; even culture in a greenhouse during the winter under a low light intensity has a somewhat more favourable effect. This is stated to be due to the fact that the direct irradiation under Osram light leads to a gradual impoverishment in sugar and starch.

This research by Klebs and the postulation of a form of phasic

development contain at least a reference to most of the problems at issue in the study of the developmental processes in plants, and of the reasons for the transformation from a vegetative to a reproductive state: the effect of the decisive factors, light, darkness and temperature, alone and in combination, upon a series of phases or conditions, each one of which must be acquired before the next can begin; a hint of a light after-effect; evidence of reversal of development; the internal metabolic changes associated with vegetative growth or reproductive development.

It has already been noted that Klebs' three phases are not all of the same nature. Ripeness-to-flower is not recognizable morphologically; on the other hand, the initiation of flower primordia and the formation of the inflorescence and flowers are recognizable morphologically. Before referring to the phases postulated by Lysenko, which it will be noted are not necessarily all assumed to be manifested by external morphology, the work of Gassner and Tolmačev on the effect of low temperatures on plant growth and development will be described.

Temperature in Relation to Physiological Characteristics of Winter and Summer Annuals

The other notable paper published almost simultaneously with that of Klebs on *Sempervivum* was that by Gassner (1918) on the physiological characteristics of summer and winter annuals. Whereas Klebs was concerned primarily with light as the decisive factor, Gassner devoted special attention to temperature. As he considered that the shooting and flowering of winter cereals depend to a marked degree on their passing through a period of low temperature, experiments were conducted to determine (1) the principles underlying the effect of low temperatures on flower production, and (2) further details regarding (*a*) the co-operation of the temperature of germination, and temperature and other conditions during the course of vegetation, and (*b*) the significance of the vegetative period in understanding the relative peculiarities of summer and winter Gramineae.

Gassner sowed the seed of cereals in sand at different dates between January 10th and July 3rd, and subjected them to the following temperatures during germination: 1 to 2°, 5 to 6°, 12° and 24° C. Selected seedlings were subsequently placed in pots and then planted out. Tables and graphs in his article show (*a*) date of sowing, (*b*) temperature during germination, (*c*) 'appearance above ground', when the young leaf had reached a length of 20 to 25 mm., and (*d*) shooting. The crop plants used were Petkus winter rye and Petkus spring rye. The results may be summarized as follows.

The temperature during germination had no influence on shooting of

spring rye, the plants that had been germinated at the temperatures quoted above all shooting at regular and uniform intervals. In winter rye, only the plants germinated at 1 to 2° C. exhibited shooting regularly throughout the whole vegetative period. Plants that were germinated at 5 to 6° C. only shot regularly if their 'appearance above ground' had occurred before the end of April, and those germinated at 12° and 24° C. only if they had appeared above ground before the middle of April and the end of March respectively.

Some plants did not shoot at all, but of those which did, the plants that had appeared above ground simultaneously attained shooting all the sooner, the lower was the temperature at which they had been germinated. Thus, plants which appeared above ground in the middle of March and which had been germinated at 1 to 2° C. shot about 9 days, 21 days and 41 days earlier than those that had been germinated at 5 to 6° C., 12° C., and 24° C. respectively. The illustrations in Gassner's article show the further difference that plants germinated at a low temperature not only reached the shooting stage more rapidly but also more regularly than those germinated at a higher temperature.

Gassner's conclusions regarding the physiological difference between summer and winter rye were as follows. Summer rye is practically independent of any need to pass through a cold period before it can achieve shooting (Blütenauslösung). The shooting (Blütenbildung) of winter rye depends on its passing through a cold period either during germination or at some stage subsequent to germination.

Gassner made some remarks with regard to the correlation between winter hardiness, sugar content and flowering. Without going into any great detail with regard to the problem of death of the plant cell through cold, he stated that the following may be quoted as definite facts:

(1) The growing of winter plants at a low temperature induces increased winter hardiness;

(2) Low temperature is a condition for the 'release of flower formation';

(3) Cultivation in a low temperature increases sugar content; it may be assumed that winter hardiness and sugar content are in a causal relationship, while the 'release of flower formation' depends on sugar content;

(4) Winter hardiness and the cold-requirement, so important for flowering, are correlatively connected.

It is not proposed to digress from the main subject at the moment to deal with the relation between winter hardiness and reproductive development; this aspect is discussed in Chapter XIII.

In connection with Gassner's results, it should be noted that he was concerned more particularly with the first phase of Klebs. Some of his

grain which germinated at a low temperature had acquired thereby the 'ripe-to-flower' condition. The grain or seedlings which had this property could not be distinguished morphologically from those which had not, but the difference between them became apparent in their subsequent behaviour, with special reference to flowering.

Gassner did not, like Klebs, specifically suggest that a plant must necessarily pass through any series of phases or conditions, each of which shall be governed by any particular set of environmental factors. Neither Klebs nor Gassner seem to consider that processional, regular development is inherent in a plant, but that this depends on the way (this being inherited and transmissible) in which a plant responds to the sum total of all external factors; that is, that the developmental rhythm is a product of the specific, inherited reaction method of the organism and of the sum total of all environmental factors.

Photoperiodism and Research by Garner and Allard

A few years later, Garner and Allard (1920) published an account of their studies of the effect of different lengths of daylight on plant growth and development, and initiated a new branch of plant biological research. On the basis of this research, some examples of which are discussed in Chapters VI and VII, they concluded that the different species of plants require for their normal development a certain ratio in the length of day and night, and named this phenomenon 'photoperiodism'. Ljubimenko has since pointed out that this definition describes only the changing of periods of light and darkness, but not the dependence of plants upon them, and proposes the alternative term 'photoperiodic-adaptation'. The earlier term has, however, remained in general use.

Garner and Allard, and subsequent investigators of photoperiodism also, have used the acceleration, or retardation or hindering of flower formation as a criterion of the effect of changed length of day, although the reaction of growth behaviour in terms of production of green mass, and of storage functions in terms of tuber formation and other characters was also studied. It was found that certain plants would flower much earlier if grown in an artificially shortened day, others if grown in an artificially extended or continuous day. The first group of plants, the so-called 'short-day' type, are mostly from the low latitudes north and south of the equator, where the day generally lasts for 14 hours fairly uniformly throughout the whole year, and in some regions for 12 hours only. The other group, the so-called 'long-day' type, have a shorter vegetative period in northern latitudes in the Northern Hemisphere and in southern latitudes in the Southern Hemisphere, where the days in summer are long.

Thus, it is possible to make the generalization that, in the majority of cases, the natural vegetation of the tropics is composed of short-day plants, while that of the temperate zone is composed of long-day plants. The degree to which the indigenous or introduced cultivated plants would be expected to be successful would depend on the group to which they belonged, and to the existence within them of biotypes adapted to the conditions of a new latitude. In this latter connection, the fact that the different varieties of one and the same crop may have different day-length requirements is of some importance.

The Gramineae may be quoted as examples of long- and short-day types among economic plants; those of the temperate zones (wheat, rye, oats and barley) are primarily long-day plants, while those whose home is in equatorial latitudes (millet and maize) are short-day plants. Yet the zone of cultivation of both types has been extended into the zone of the other.

Also, from an economic point of view, it is important whether the cultivated plant concerned is being grown for the products of reproductive development, for example, the seed or fruit yield, or for the products of vegetative growth. If one is, for example, moving short-day plants towards the north, it would be expected that yield of seed would decrease and that of green mass increase (maize for silage in Canada). This would be the natural reaction unless varieties were chosen with a low photoperiodic response, or were of the neutral type recognized by Garner and Allard. It is, therefore, of primary importance to know the photoperiodic reaction and requirements of the separate varieties being studied or introduced.

Experiments on these and other aspects of photoperiodism and of the phenomenon known as the photoperiodic after-effect are discussed in more detail in later chapters. In this consideration of the biological basis of plant development and of the transition from a vegetative to a reproductive state and vice versa, reference has already been made to several different interpretations, in which no serious attempt has been made to correlate the various decisive factors of the environment. For example, Gassner was concerned primarily with temperature and its effect on development if applied at a very early stage in the life of a plant, namely, shortly after germination. The photoperiodism school are primarily concerned with light and its effect on the transition from a vegetative to a reproductive condition. Their experimental material has generally been of such a nature that it would not be possible accurately to describe its 'physiological age', and to say whether it was in some kind of 'ripe-to-flower' condition before the experiment began, or for that matter whether the acquisition of any ripe-to-flower condition, as understood by Klebs, was necessary for that particular species and variety.

Photoperiodic reactions are considered by Lang and Melchers (1943) to be due to the working together of at least two separate processes each dependent on light in different ways. The two simplest possibilities are (1) the working together of one process positively dependent and one negatively dependent on light, of which the one or the other or even both are capable of summation to a limited degree, or (2) the working together of one process positively or negatively dependent on light and one process independent of light, of which that dependent on light must always be capable of summation to a limited degree. This second possibility is considered to agree with the fact that in *Hyoscyamus niger* the release of flower formation depends on length of day and 'the primary and secondary processes' participating therein. The critical length of day is that at which the effect of the primary processes is just cancelled by that of the secondary processes. The primary processes may be identical with the formation of the hypothetical flowering hormone, the secondary with the processes of dissimilation which attack, directly or indirectly, the assimilates requisite for the formation of the flowering hormone.

Writing on the subject of photoperiodism in 1936 Gregory stated that it must be admitted that the whole problem is still obscure; in such cases, there is a temptation to have recourse to the possible effects of special hormones, recalling the organ-forming substances postulated by Sachs. Since the hormones themselves have not yet been isolated, Gregory considers it may be futile to speculate as to whether they may be 'accelerators' or 'inhibitors' of flower formation, although such hypotheses may be useful in directing research into profitable channels. 'That the work of Garner and Allard has opened to investigation one of the most fascinating fields of plant physiology must be admitted, and moreover, a field particularly attractive, as within its limits all the resources of morphological, biochemical and horticultural sciences will have to be invoked to furnish an explanation of the complex phenomena encountered.'

Reaction to photoperiod is not confined to plants, and it is in connection with research on animals that some discussion on terminology has arisen (Greulach, 1945). The first report on experiments on the influence of photoperiods on animals was that of Marcovitch on plant lice (1923), but comprehensive studies did not begin until a series of papers by Bissonnette (1931) began to appear. From this work the term 'photoperiodicity' developed, to apply not only to reproduction controlled photoperiodically, but also to pelt cycles, plumage cycles in birds, and also migrations. Since the term 'photoperiodism' has been extended to cover aspects of the phenomena other than true reproduction, the terms are synonymous. Presumably the two terms will continue to exist side by side.

Number-of-Leaves as Indicator of Ripeness-to-Flower

One of the most important aspects of this research is the need for discussing some outward expression of the inner physiological state of a plant. It has already been noted that the ripeness-to-flower postulated by Klebs was not thought to be recognizable morphologically. However, Purvis (1934) and later Purvis and Gregory (1937) put forward their number-of-leaves interpretation.

First, in a study of the reaction of Petkus winter rye to temperature at germination and to varied daylength, Purvis reached the following conclusions (among others) regarding the exact time in the life history of a plant at which the change from vegetative growth to reproduction takes place:

(*a*) in assigning a plant to its correct photoperiodic category, the time of formation of the flower primordia should be considered rather than the time of emergence of the inflorescence;

(*b*) in winter rye, the differentiation of flower primordia is subject to an interaction between daylength and the temperature during germination, which factors determine both the minimal number of leaves formed before differentiation of flower primordia begins, and the rate of growth of the meristematic tissue.

The concept of ripeness to flower suggested by Klebs was accepted and was identified with the stage in development at which the 'minimal leaf number' had been laid down. In this paper, this number was stated to be seven or eight in spring rye, and was thought to be about twelve in unvernalized winter rye. In both the spring and winter varieties grown in short days, it reached twenty-two, as it did also in unvernalized winter rye grown in long days.

These conclusions were modified in the second paper; it was then seen that a quantitative relation exists between the duration of the vernalization treatment and the length of the vegetative phases, and that the number, twelve, applied only to winter rye vernalized for the particular period (4 weeks) used in those earlier experiments.

In the experiments reported in 1937, the effects of varying preliminary periods of low temperature and short days on subsequent development were observed. Both treatments resulted in acceleration of flowering.

With the low-temperature treatment, an exposure for 4 days leads to a definite response and the magnitude of that response increases with the duration of treatment up to a limit of 14 weeks, after which winter rye is indistinguishable from spring rye in its flowering behaviour. With increasing exposure to low temperature, the 'minimal leaf number'

necessary before the ripe-to-flower condition is achieved is reduced from about twenty-five to seven.

With preliminary treatment with short days (10-hour), the magnitude of the effect on flowering increases with length of treatment up to 6 weeks, but longer exposures retard flowering. The minimal leaf number falls to sixteen after 6 weeks' treatment and increases again with longer exposures.

In both spring and winter rye there is a minimal leaf number, seven, which cannot be further reduced, and a maximum, twenty-five, which cannot be further increased. The primordia between the 8th and 25th are indeterminate and can produce either leaf or spikelet; this is related to the structure of these initials, which are double, consisting of a flowering branch (spikelet) with a subtending bract, either of which may be inhibited according to the length of day or the temperature during germination.

Melchers (1943) also uses leaf number as an indicator of the release of flower formation (Blütenauslösung), stating that the method as developed by Purvis should be generally useful for plants with terminal flowers or inflorescences, such as *Hyoscyamus*. The advantage of this indicator lies in the fact that the values compared depend primarily upon the initiation of the primordia as such, and not on such indefinite characters as the appearance of visible buds or flowers and other growth phenomena. *Hyoscyamus* has also the advantage, as compared with several other plants such as the cereals, that leaf primordia and flower primordia are distinguishable at the earliest stages of development (see Fig. 1 in Melchers, 1937). This investigator always determines the number of leaves newly formed from the beginning of the experiment up to the first flower, or to the end of the experiment, and describes this value as leaf increase. A direct relation between leaf number and time of flower formation has also been established by von Denffer (1939).

CHAPTER III

GROWTH AND DEVELOPMENT (*cont.*)

Further Developments in Methods of Pre-treatment of Seed

Continuing the work of Gassner, Maximov treated seedlings with low temperatures and thereby influenced the whole of their further development. Winter cereals which, when sown in spring, did not normally reach the heading stage, headed and flowered normally when the seedlings had been exposed to a short period of chilling. It was found to be possible to determine the further course of development during the early stages of the growth of a plant, by treatment with appropriate temperatures and a given periodicity of light. This method was still, however, applicable chiefly to laboratory trials and greenhouse production, owing to the fact that the treatment was applied to seedlings.

At the All-Union Congress on Genetics in Russia in 1928, two papers were read which to a varying degree brought the earlier research of Gassner into the realm of routine agronomic practice. It was realized that the germinating grain of winter cereals require a certain quota of low temperature for their optimal development, that they usually receive the requisite amount while growing slowly in the open in the winter, after autumn sowing, and that the more the sowing date is delayed the less likelihood is there of the plants flowering and reaching maturity sufficiently early for harvesting in the following season. The important point in this process is that the germinated grain were growing slowly, and this was made the basis of the new methods of giving grain the necessary degree and duration of low temperature while in the laboratory or the barn.

It so happened that the Proceedings of the above Congress, published in 1930, contained, in addition to one of the early papers by Dolgušin and Lysenko (1929) on pre-treatment of seed with low temperature, another paper on the same problem by Tolmačev (1929). This author almost achieved a simultaneous solution of the problem of vernalization of winter cereals.

The objective of this new Russian research on pre-treatment by low temperature was to maintain the early seedling condition for as long a period as possible, and yet to break dormancy and permit growth to start very slowly. This was presumably done because it was considered that the temperature during or just after germination is the effective

factor in inducing subsequent flowering, and also because the grains might still be sown in a normal way, after treatment, a practice that would be impossible if seedling development were permitted.

In order to retard the growth of winter wheat, Tolmačev applied incomplete soaking; by keeping such seed for 2 months at a temperature of 0° C., he obtained plants which produced ears in the first year when sown in spring, even after the latest date of sowing. In experiments on sugar beet, the same investigator observed that seed soaked and exposed to low temperature produced plants with a considerably increased percentage of flowering in the first year. On the other hand, plants of sugar beet kept from autumn onwards throughout the winter in a warm conservatory, with electric illumination, were unable to form flowering stalks and fruit in the next year. Repeating the treatment each year, Tolmačev was able to maintain plants in a state of vegetative growth for 4 years. If, however, one of these plants maintained in an artificially perennial condition were transferred in winter to a cold conservatory, it proceeded to produce abundant fruit in the following summer.

This behaviour can, as will be seen later, be readily explained on the basis of Lysenko's hypothesis, but Tolmačev brought forward what Maximov describes as 'a peculiar theoretical interpretation'. According to this explanation, winter cereals will not ear nor sugar beet flower until a definite active phase has been completed in their 'stem plasm', a definite work must be done and a sufficient amount of products of disintegration must be accumulated. In spring plants, the 'stem plasm' is ready for its function at the time of seed maturity. Those conditions which stimulate the accumulation and preservation of the products of disintegration, for instance, low temperature, also stimulate fruit bearing, and, on the contrary, the absence of the accumulation of the products of disintegration during the intensive growth under the influence of light and high temperatures depresses stalk formation.

Origin of Method of Vernalization

Reviews of the theoretical bases of the method of vernalization and the hypothesis of phasic development have been published by Whyte and Hudson (see Aberystwyth, 1931), Maximov (see Aberystwyth, 1934), the Imperial Bureaux of Plant Genetics (see Aberystwyth, 1935), Whyte (1939), McKinney (1940), and other authors. The following discussion is based largely upon the review by Maximov (see Aberystwyth, 1934).

After stating that the method of influencing the development of agricultural plants evolved by Lysenko at the Institute of Plant Breeding and Genetics, Odessa, is one of the most significant achievements in plant

physiology during recent years, Maximov proceeds to ask: What is vernalization?

First, it is a practical agricultural method of affecting plant development in such a way that winter plants bear fruit in the first year, when sown in spring, while late-flowering plants become early-flowering. It is also one of the greatest achievements in that new trend of plant physiology which, not being satisfied with the most detailed possible objective description and interpretation of phenomena occurring in living organisms, makes an effort actually to control these phenomena by subjecting their progress to the active will of man.

Dealing first with the method of vernalization as proposed by Lysenko, Maximov states that this is extremely simple and easy to perform. It is based essentially upon the fact that the soaking of seeds transmutes them from a state of rest to a state of active life; at the same time, however, complete absorption of water (imbibition) is not permitted, in order that growth may be prevented from proceeding at full speed. These partially soaked (imbibed) seeds may for a fairly long time be retarded in growth at the initial stages of germination, when the tip of the root of the embryo has just penetrated through the seed coat. This retardation of growth makes it possible to subject the seeds or grains to low temperature during the particular period necessary for bringing this factor to bear upon the developmental processes of the variety concerned.

The first investigations at Odessa were concerned with the 'conversion' of winter forms of cereals into spring ones, or more precisely, with the induction in them of the ability to ear in the first summer after being sown in spring. In these initial experiments the principal factor of vernalization was the influence of low temperature. Partially soaked and therefore slowly germinating grains of winter cereals were exposed to a temperature little above 0° C. for 15 to 60 or more days, the period varying widely according to the variety used. The resultant material had acquired the properties of spring plants; the grains could be sown in spring and produced a yield of grain in the same summer, frequently even earlier than so-called spring varieties of the same crop sown simultaneously.

Lysenko then recognized a different class of crops which required not low, but increased temperature during the vernalization treatment before a similar result could be achieved. These he called the thermophilic plants, including in the group, millet, soybean, and cotton. It was stated that the slowly germinating seed of these crops must be exposed for several days to a temperature of 20 to 25° C. or even 25–30° C., after which they would acquire the ability to pass to the stage of fruit bearing in a shorter time after sowing, even in a cool climate under temperatures

at which such a transition in unvernalized plants would be retarded, or even impossible.

Principles of Theory of Phasic Development

In the 4 or 5 years up to and including 1934, Lysenko (1935) formulated the theoretical conceptions upon which this method of pre-treatment of seed was based, as follows.

(1) Growth and development are not identical phenomena.

(2) The entire process of the development of an annual seed plant consists of individual *étapes* or stages.

(3) The stages always proceed in a strict sequence and a subsequent stage cannot set in until the preceding stage has been completed.

(4) Different stages of development of the same plant or crop require different environmental conditions for their completion.

In much of the English literature on this subject, the word 'phase' has been used in the place of the word 'stage', as the latter term appeared to be already in wide use in connection with purely morphological manifestations of growth, for example, tillering stage, stage of 50 per cent flowering, etc. Thus arose the term 'phasic development' to describe all aspects of the theory underlying the method of vernalization.

LYSENKO'S FIRST POSTULATION

The distinction between growth and development has already been discussed at the beginning of Chapter II. It is sufficient to say here that it is the basis of Lysenko's method and theory, and that he expressly confines his distinction to the *rate* of growth and development, the former meaning the rate of accumulation of dry matter, or increase in size of the plant, the latter meaning the rate of progress through the stages of development as recognized by him. The necessity in vernalization experiments of dealing not only with seed that has already been soaked, but more particularly with seed that has begun to germinate, appears to indicate a certain interrelation between growth and development.

Passing to the remaining three of Lysenko's theoretical conceptions as to the progress of development, the following paraphrases Maximov's detailed analysis of each individually (1934).

DEVELOPMENT BY STAGES OR PHASES

The second of Lysenko's postulates, that the entire process of development consists of individual stages or phases, is clear only in connection with the first statement regarding the difference between growth and development. In studies of plant morphology and phenology, different

stages or phases of plant development have frequently to be described. The terms which are used to record physiological observations upon the growth of cereals include such 'stages' as the appearance of shoots, tillering, stalk formation, shooting, earing, flowering, milk, wax and complete ripeness or maturity, etc. In experiments with other plants, different stages are recorded, such as the appearance of the first or second leaf, branching, budding, flower unfolding, etc.

From Lysenko's point of view, all these 'stages', or at least most of them are actually only externally visible milestones in the process of growth. Some of them do not in any way reflect qualitative changes which may be occurring in a plant, for instance, such 'stages' as the first or second leaf, tillering, branching, etc. Others, however, are indirect and frequently belated reflections of these internal changes, for instance, such 'stages' as stalk formation in cereals or budding in some other plants, which indicate that the processes preparatory to a transition towards reproduction have been, or are about to be completed. Actual 'stages (phases) of development' may not be directly associated with any morphological changes, and profound internal developmental changes may be revealed in external morphology only under definite environmental conditions. For instance, vernalized seeds do not differ in any way from unvernalized seeds in their external appearance or their internal anatomical or cytological characters; only when they have been sown in the field does the sharp difference which has existed in their internal development become apparent. Special methods have been adopted at the Institute of Plant Breeding and Genetics, Odessa, to detect the completion of a definite phase of development by means of internal biochemical characters (see p. 76).

STRICT SEQUENCE OF PHASES

The third of Lysenko's postulates is the existence of a strict sequence in the progress of individual developmental phases. If for some reason any one developmental phase has not been completed, most frequently because of the absence of the environmental conditions required, the stage subsequent to it cannot commence. Lysenko suggests (1934) that there are five such phases, but only two of these have received detailed attention. The first is that which may proceed in a plant when the embryo has just begun growth; this Lysenko called 'the stage of vernalization', but in view of the confusion of this term with the actual method of vernalization, it has become the practice to call this phase the 'thermo-phase'. The most important factor for the completion of this phase is a definite temperature. Only when the thermo-phase has been completed may the plant enter upon the light-sensitive phase (or phases). Lysenko called the phase following the thermo-phase the photo-phase, and noted

that some plants require light for its completion, while others require darkness. Different varieties of one plant require varying amounts of these factors. It is stressed that in addition to the potent factors (temperature for the thermo-phase, and light for the photo-phase), there should be a definite combination of the other environmental factors, although these play only an accessory part. From Lysenko's point of view, therefore, the entire development of plants represents a chain of consecutive processes, not a single link of which can be either omitted or transposed.

REQUIREMENT OF ENVIRONMENTAL FACTORS

The fourth and last of Lysenko's postulates is that each of the hypothetical consecutive stages of development requires for its completion a definite set of environmental conditions, which vary widely for different stages and for different plants. It is upon the correct manipulation of these conditions (a given temperature treatment in order to induce the plant to complete the thermo-phase, a type of light treatment suitable for the light-sensitive phase or phases, and so on) that the method of vernalization has been based.

REVERSIBILITY OF PHASIC ADJUSTMENTS

Lysenko has also stated that the 'phasic readjustments' that occur during the development of a plant may be arrested by external and internal factors, but they cannot regress in the opposite direction. The tissues in which the vernalization response is localized do not lose the properties acquired during the pre-treatment with low temperature, if grown under conditions that prevent further development towards maturity. Vernalized seeds can be stored for considerable periods, without loss of their vernalized quality, provided the tissues that have acquired the vernalized or ripe-to-flower condition are not damaged in any way. Rejuvenation of a plant as a whole is admitted, but not rejuvenation of a particular tissue.

The evidence brought forward by other investigators shows, however, that reversal of development can take place. This particular problem is connected with the localization of response to environmental factors, and the transference of the stimulus so acquired to other parts of the plant. The evidence on this aspect suggests that, at least as far as light response is concerned, the leaves react to the duration of light and transmit the response to the growing points. If the plant is of a short-day type and is growing in short days, the leaves will transmit a reproductive response to the growing points, which will proceed to develop reproductive organs. If such a plant is transferred to long day, the response trans-

mitted from the leaves to the growing points will be of a vegetative nature, and will cause a reversal of development, or more correctly a return to a vegetative condition in the growing point and the organs formed in the vicinity.

Evidence has also been produced to show that exposure to high temperature causes a loss of the vernalized condition acquired during previous pre-treatment with low temperature. Supporters of irreversibility of development would argue in this case that the meristematic tissue containing the response has been damaged and that any further development would presumably have to be carried out by other meristematic tissue that had not been exposed for an equally long period to the decisive environment and therefore not so advanced phasically or developmentally. As, however, devernalized tissues can be revernalized and flowering may be quite normal (see p. 69), this criticism does not appear to be valid.

Internal Development and External Morphology

Two hypothetical successions of stages or phases have now been considered. Klebs recognizes one stage, that of ripeness to flower, and two stages of a different nature, both external expressions of the progress of development, namely the formation of flower primordia, and the formation of the inflorescence and flowering. Lysenko's phases are all of the first type, similar to 'ripeness-to-flower', and may or may not be expressed in external morphology at the same date. The argument for a series of phases without external manifestation is supported by the evidence for after-effects of both temperature and photoperiodic treatment, it being assumed that a plant in an early stage of growth may pass through one or more qualitative phases which become manifest externally only at a considerably later stage in its life. If this is so, then the appearance of shoots or the beginning of flowering of a cereal plant on any particular date does not necessarily mean that the environment in the days immediately preceding that date was the ideal one for inducing development towards maturity. Part or all of the required influence or amount of environmental factors may have been acquired at a much earlier date.

Under natural conditions and in the absence of laboratory controls, it is very difficult to decide whether and to what degree one or other of the decisive environmental factors is operating at any particular time. In a winter wheat, for example, presumably the first potent influence is the low temperature of the winter months; not the average temperature but the total number of hours during which it is below the critical requirement for that particular variety. With the advance of spring, low tem-

perature is replaced as the dominant factor by length-of-day, combined with increased temperature.

It is possible to diagnose when a plant has acquired the preliminary 'ripe-to-flower' condition or received the requisite amount of temperature (see p. 31), and it may ultimately be possible to recognize at least in a general way the subsequent course of internal development in terms of external behaviour. Recognition of the early stages of development such as the time of formation of flower primordia requires detailed microscopical studies.

Another example of a correlation between development and morphology is provided by the research of Sapegin (1940), who studied the determinative periods in the formation of the wheat ear, with particular reference to the times that are most suitable for the various types and rates of nutrition or irrigation. Sapegin made microscopic studies of organ formation in some forty varieties of wheat in order to establish the periods or stages that determine the formation of the individual parts of the spike. It is stated that this study was made during the photo-phase; this means that all the plants used had already received the full quota of low temperature required by the different varieties to complete the thermo-phase. The study also continued into the phase following the photo-phase, which has been called the gametogenic phase.

According to Sapegin, the photo-phase is divisible into the preparatory and executive stages. With the onset of the preparatory stage, leaf primordia cease to form, this process having occurred chiefly during the preceding thermo-phase. During the preparatory stage, the growing points show no morphological changes, but the conditions then prevailing determine the number of spikelets that are actually formed during the executive part of the photo-phase.

The preparatory period, which lasts according to the variety from 3 to 4 (in early forms) to 8 to 10 days (in late forms), is followed by the executive stage during which the spikelet primordia are initiated; this process continues for 3 to 7 or more days according to variety and conditions. Later, according to Sapegin, the plant reaches a turning point, when it ceases to require long photoperiods, and when the internodes of spike and stem begin to elongate rapidly and elongation of the tip is accelerated. This period, coinciding with the beginning of floral initiation, may be regarded as the beginning of the gametogenic phase.

Both the rapidity of floral organ formation and the number of flowers per spikelet are determined by environmental conditions. Under normal conditions, four florets are formed. Any further increase leads to the production of undersized grain. The number of grains per spike may be increased by increasing the number of spikelets per spike. The number of spikelets is determined by the rapidity of their formation, 2 to 4 days

on the average, and on the other hand by the duration of the photo-phase and the organ-forming activities associated with it. If the photo-phase and particularly the preparatory stage is prolonged, the number of spikes formed is increased. Optimal conditions of water supply and appropriate nutrition during this period are considered to be of the utmost importance, and every attempt should be made to harmonize the type of nutrition with the requirements at different developmental phases; this aspect is discussed in more detail in Chapter XII.

Krenke (1940) has stated that the presence of scale-like leaf primordia under the spikelets of wheat and barley indicates the age of the plants concerned, but Sapegin (1941) does not agree, stating that they belong rather to vernalized tissue. The organs become neither spikelets nor leaves, probably because the physiology of the plant is essentially altered by its entering the light phase. The character of organ formation in the first days of that phase may assist in determining its initiation with an accuracy of 1 to 3 days, by noting certain phenomena in relation to the location of the organ in regard to leaf sequence.

The Joint Action of Environmental Factors

It is probably safe to say that most physiologists and agriculturists agree that every plant has its own specific requirements of temperature and light in the presence of which it proceeds most rapidly towards reproduction and maturity. Lysenko's theory of a sequence of distinct phases is not, however, generally accepted. No direct criticism of this theory has, however, been published, as far as is known. It is probable that such a criticism, if published, would concede that it may well be possible in the laboratory to guide a plant to maturity by giving it first one factor, and then another, but that under natural conditions it has not yet been proved that a plant reacts first to temperature, and must complete the thermo-phase before being able to react to light. There may rather be quite a considerable overlap, if not joint action, of these two major environmental factors.

A number of the papers discussed in subsequent chapters describe studies of more than one factor, acting at successive periods of development, or simultaneously. It may be appropriate at this stage to refer to some German work on this subject, which has led up to the hypothesis of Kopetz, and the opinions of this investigator with regard to the relationship between growth and development. There appears to be a certain degree of misunderstanding among German physiologists regarding Lysenko's hypothetical succession of phases. Adler, for example, in reviewing the nature of short-day and long-day plants (1940), states that Lysenko distinguishes between a thermo-phase and a photo-phase, and

that it is Lysenko's opinion that chilling or vernalization is successful only if the plants obtain long-day conditions in the photo-phase. It is also stated that Rudorf finds that plants from grain vernalized at low temperatures do not shoot if grown subsequently in short day. 'Therefore, short day results in such a great inhibition of development in long-day plants that chilling is unable to eliminate it' (Adler). Harder has found that many long-day plants cannot be influenced by chilling, for example, many varieties of summer cereals, a fact already noted by Maximov and Krotkina (1930).

Adler points out, however, that among the long-day plants in which development is also dependent upon low temperature, there are again groups of types. It is already known from the results of Lysenko and Rudorf that some plants require chilling followed by long day; Harder and Störmer (1936) find that some plants behave in the reverse manner; the long-day plants, *Sinapis alba* and *Agrostemma githago*, show only a very slight reduction in period of development when chilling is followed by normal long day (4·8 per cent). If chilling is followed by a 9-hour short day, however, there is a sixfold acceleration of flower formation (30·6 per cent). The effect of cold is six times as great in short day as in long day. The group of long-day plants may therefore be subdivided as follows:

Long-day plants, the development of which
- cannot be accelerated by cold
- can be accelerated by cold
  - only when followed by long day; with short day only slightly or not at all (cereals)
  - mostly when followed by short day; with long day only slightly or not at all (*Sinapis*)

Harder and Störmer (1936) have brought forward the following explanation for this behaviour. Both types of long-day plants are liable to inhibitions of flowering which can be weakened or removed by treatment with long day or low temperature. In the case of mustard, this inhibition is relatively weak, having been already removed by the action of long day. As there remains nothing more for the low temperature to remove, its effect is therefore nil. In short day, on the other hand, the flowering inhibition is already so attacked by cold that it is almost removed. The action of cold is, however, assumed to be somewhat weaker than that of long day.

In the cereal species, on the other hand, the flowering inhibition is more difficult to remove. Low temperature is not effective as alone it is

too weak. Long day has a greater effect and alone can remove the greater part of the inhibition. That part which remains is removed by the joint action of both factors (see also Purvis, 1934, who found in winter rye that both short days and low temperature at germination caused an increase in the rate of growth of the apical meristem, and that short days also favoured the development of leaves; together they caused an extension of the meristematic cylinder and an increase in leaf ridges).

Sinapis and the cereals of Northern Europe may be regarded as two extreme types. Low temperature can remove the inhibition of flowering even when long day is absent, although not entirely. In cereals, the absence of long day results in so great an inhibition that chilling has no effect.

Harder admits another possible explanation. It can be assumed that a plant requires for the development of flowers a certain minimum length of time, which cannot be shortened but can probably be increased. In *Sinapis*, long day appears to be able to provide sufficient of the impetus required for this shortest possible period of development; low temperature cannot improve upon this result. According as long days are removed, however, the capacity of low temperature to influence development increases. In cereals, on the other hand, long day alone cannot provide the required impetus and must be supplemented by low temperature.

Harder and Störmer (1936) showed that white mustard (*Sinapis alba*) responded to temperature of germination best in short-day conditions. An exhaustive comparative study of vernalized mustard and oats made by von Denffer (1939) under a series of daylengths artificially maintained showed that this different behaviour of these two plant types occurred in the time between initiation of flower primordia and flowering. The relative shortening of the purely vegetative phase from germination to the visual appearance of flower buds in mustard, and shooting in oats, was on the other hand approximately the same for all daylengths (from continuous light down to 12-hour day) as compared with control plants which had not been vernalized.

The increase in duration of vernalization led in both mustard and oats to a gradual shortening of the vegetative phase, which asymptotically approached a limiting value. This occurred in winter oats (var. Eckendorfer) after 80 days' treatment, in mustard after 50 days' vernalization. The limiting duration of the vegetative phase after optimal duration of vernalization was dependent upon the daylength under which the plant was grown; being minimal in continuous light, maximal in short days. The extension of daylength leads in both plant types to a gradual shortening of the vegetative phase, and again approaches a limit value. The limiting duration of the vegetative phase under optimal photoperiod is dependent upon the duration of vernalization.

The leaf number on the main shoot of oats is directly related to the development, as McKinney and Sando showed for wheat, and Purvis and Gregory for Petkus winter rye; the same direct relation between leaf number and time of flower formation was established also in *Sinapis alba*. The results can be interpreted without difficulty along the lines of the flower hormone hypothesis of Purvis and Gregory (see p. 159).

Results from an exhaustive study of the relation of these major environmental factors to growth and development in the onion are given in detail on p. 300.

Although no attempt is made in this book to discuss all the factors governing plant *growth*, brief reference may be made to the influence of the natural environment, in which light, temperature and soil moisture are the chief operating factors. In Iowa, full summer sunlight does not appear to have any direct effect upon growth (Thut and Loomis, 1944), although indirectly it increased growth by increasing photosynthesis and raising the temperature. Growth was reduced by excessive temperature and by internal water deficits developed under the combined effects of sunlight, high absorptive capacity of the air and decreasing soil moisture percentages. Plants in Iowa make more growth in the daytime when temperature is the limiting factor, and more at night when moisture is limiting. The interaction of these two factors frequently produces a double peak of early morning and evening growth.

In order to reproduce the results obtained from the study of the complex interrelationships which exist between plants and their total environment, Went (1945) has introduced multidimensional models to present the multidimensional causality concerned in the growth of tomato plants under conditions in which the most essential conditions for growth are controlled and the necessary qualifications for the condition of the plant are known. 'Such interrelationships between growth rate and night temperature on the one hand, and modifying factors on the other hand can be expressed in multidimensional graphs, which stress the complex causality existing between these factors. Although biologists are used to the complexity of living material, they seldom have had the means of adequately expressing complex interrelationships, since environment could not be controlled sufficiently.'

Hypothesis of Kopetz

This investigator has developed a different interpretation of the relation between growth and development, and of the causes underlying the change from one condition to the other (Kopetz, 1936, 1937a and b). His hypothesis follows on from Harder's statement that a plant requires up to the time of flowering a certain, minimal time of development,

which remains constant for the race. This type of development, Kopetz has called 'pure vegetative development', v_r. Once the plant has passed through this phase it can proceed to reproductive development, unless inhibitions of development are present. On this basis, total development G =vegetative development V plus reproductive development R. In this it will be noted that, at least in terminology, we are departing from the rather rigid and yet indefinite distinction between growth and development noted earlier in these chapters.

If any factor such as unfavourable length of day is present to inhibit development, the plant is unable to flower until the inhibiting factor is removed. The period of time which exceeds the measure of 'pure vegetative development' Kopetz has named 'luxury vegetative development', v_l, presumably to apply to those periods when development is marking time under the influence of an inhibitor. The luxury figure can vary between nil and a maximum (? infinity), according as to whether any inhibitions are present and how long they remain operative. V is therefore $v_r \pm v_l$, in which v_l =maximum to zero.

According to Kopetz, there is for every plant, after the 'pure vegetative period of development' has been completed, a specific length of day in which inhibitions of flowering disappear. (This early period of development bears a strong resemblance to that described by Klebs as 'ripeness-to-flower'). The plant is then ready for reproductive development and proceeds to flower. In long-day plants, it is necessary that this specific length of day be exceeded; in short-day plants, it must not be reached. Kopetz has named it the 'critical length of day', k.

Under natural conditions in Central Europe, for example, this critical daylength is reached once in spring and once in the autumn, these two occasions being called by Kopetz the 'first and second border regions'. A summer annual long-day plant finds its critical length of day between the first and second border regions; if it comes up as this period is beginning, its vegetative period must always be uniform, as v_r is constant and there are no inhibitions (v_l =o). If it comes up before the critical length of day is reached or exceeded, it must wait until this day arrives ($V = v_r + v_l$). If it comes up after the first border has been passed and second not yet reached, the plant must wait for the second.

Conditions are reversed in short-day plants, as inhibitions of development through unfavourable developmental conditions are assumed to disappear before the first border region is reached and after the second is passed. In neutral plants there are assumed to be no inhibitions due to length of day.

In developing this hypothesis, Kopetz has apparently not considered the other environmental factors, although it is admitted that dormancy of vegetation in winter limits the progress of development.

His critical length of day is related to the attunement of the embryo and the seedling, which indicates a fixation of the further course of development. When a long-day plant is growing between the first and second borders of critical daylength, additional illumination will be without effect. If darkening is applied during this period, development will be slower, if the remaining daylength is below the critical. If the same long-day plant be grown between the second and the first border regions (autumn and winter months), then any form of artificial illumination which brings the total daylight up to the critical daylength will remove the inhibitions and flower production can proceed. The converse is true for short-day plants.

Kopetz has continued his work by studying the effect of temperature on growth and development of table peas (1943). On the basis of experiments in sowing at different times and in shading, a new concept for evaluation, the so-called 'pure warmth sum', is proposed. This value, which may be regarded as a varietal constant, is obtained by adding together the daily average temperatures for the period preliminary to flowering. The determination of this value is possible in long-day plants only if no inhibition is to be expected through the factor length of day, and the plant is thus in the 'purely vegetative development' stage. If the plant is not at this stage of development, then the warmth sums determined—as has been demonstrated also in short-day experiments—will give variable values and be more or less useless. It may be assumed that in the interaction of the factors of length of day and temperature both values have a decisive influence on development, but the extent of this influence appears to be principally dependent on the point of time at which it is exercised. While under short-day conditions the inhibitive action of the length of day considerably masks the influence of temperature, when sowings are made under long-day conditions temperature alone may regulate development.

From this Kopetz has obtained points of view with regard to the description and selection of varieties, as a constant value which is independent of the place of growing, the time of growing and the temperature of the environment, can now be used for judging.

Effect of Development on Growth

The effect of developing flowers and fruit on vegetative increase has been demonstrated by Murneek (1924 and 1926). There is no doubt that these organs exert a conspicuous physiological control on the metabolism of the plant, although this has been noted more particularly when reproduction is almost completed, i.e. at the stage of fruit and seed formation.

At this time, the influence is exhibited by various degrees of inhibition in the subsequent growth of the plant.

Some work has been done, however, on some of the earlier very significant though less evident stages of reproduction which reveals quite a different phenomenon in operation with respect to their effect on plant metabolism. Instead of the inhibitory or retarding influence, as is exhibited during the formation of fruits and seeds, there are to be noted more or less specific stimulations of vegetative growth coincident with flowering and fruit setting (Murneek, 1937, 1939, and see Missouri, 1926).

Wittwer (see Missouri, 1943) has studied these stimulating effects of reproduction on vegetative growth and extension, with particular reference to two 'crucial' stages of sexual reproduction, namely, synapsis (chromosome conjugation in meiosis within the immature flower bud during gametophyte maturation), and syngamy (fertilization or gametic union in the embryo-sac). These stimulating phases were demonstrated in the cucumber, strawberry and sour cherry by the treatments of disbudding, deflowering, and defruiting. The following is a quotation of Wittwer's summary of his results, which are also shown in Figs. 1 to 8.

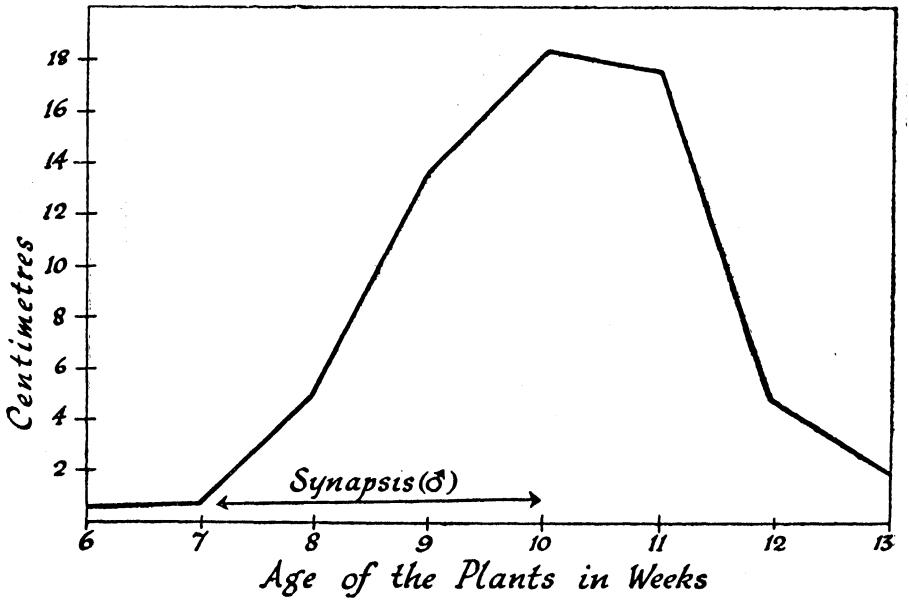


FIGURE 1

Weekly elongation increments in flower stalks of male spinach plants. No appreciable extension is evident in the flower stems prior to synapsis (chromosome conjugation in meiosis within the immature flower bud), noticeable growth occurring only after the initiation of this phase of sexual reproduction (Missouri, 1943)

Removal of reproductive organs (disbudding, deflowering, defruiting) at different stages of development, has demonstrated that a period of renewed growth, which arises, presumably, from increased metabolic efficiency of the roots and leaves, follows each of the above two crucial phases of fertilization. These intervals of accelerated activity in the plant

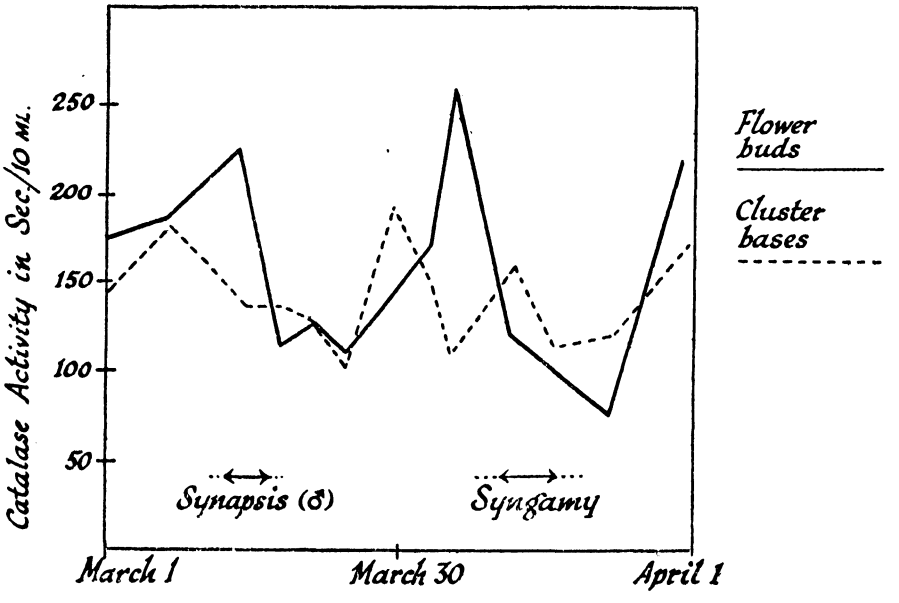


FIGURE 2

Catalase activity in flower buds of Kieffer pear during development. Two maxima and two minima are evident. Catalase activity is relatively low just before and at the time of synapsis in microspore (pollen) mother cells. A second minimum is reached with full bloom, at the time of or just after fertilization. There is a remarkable increase in enzyme activity following the two minima, and corresponding precisely with the post-synaptic and post-fertilization periods. Wittwer (see Missouri, 1943) states that the changes in catalase activity are due to internal factors related to reproductive development, rather than to the external environment directly.

are made manifest by increases in the vegetative extension, the production of fresh and dry matter, the absorption of soil nutrients, and the accumulation of photosynthetic products.

A rise in elongation increments and a change in movements of the flower stalk (pedicel) characterize the post-synaptic and post-syngamic periods in developing inflorescences. Generally two spurts in growth and alterations in movement occur, the one during bud development, the other following pollination. The two growth maxima are usually separated by a minimum, which occurs at full bloom.

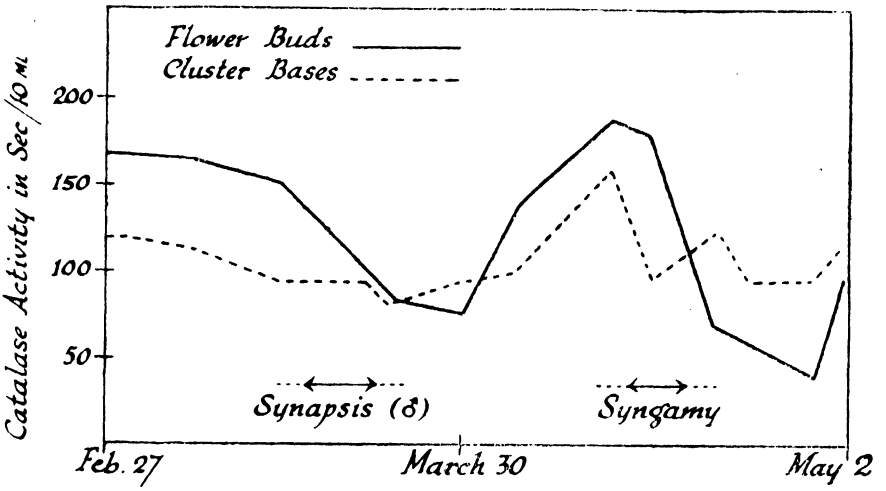


FIGURE 3

Catalase activity in flower buds of Vermont Beauty pear during development (Missouri, 1943)

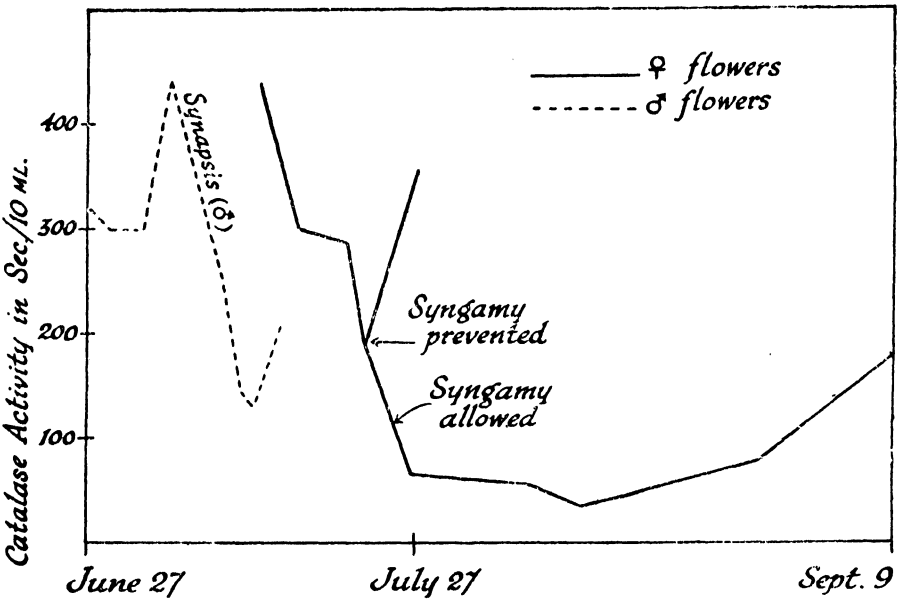


FIGURE 4

Catalase activity in the reproductive organs of maize during their development; the staminate and pistillate flowers are treated separately. Tassels show an increase in catalase activity following chromosome conjugation in the anthers, while ovules depict a remarkable increase following fertilization (Missouri, 1943)

Catalase activity in developing flowers and accessory reproductive tissue of the pear tree and corn plant exhibited two prominent peaks. The first increase followed synapsis in the microspore mother cells, the second occurred after nuclear fusion in the embryo sac.

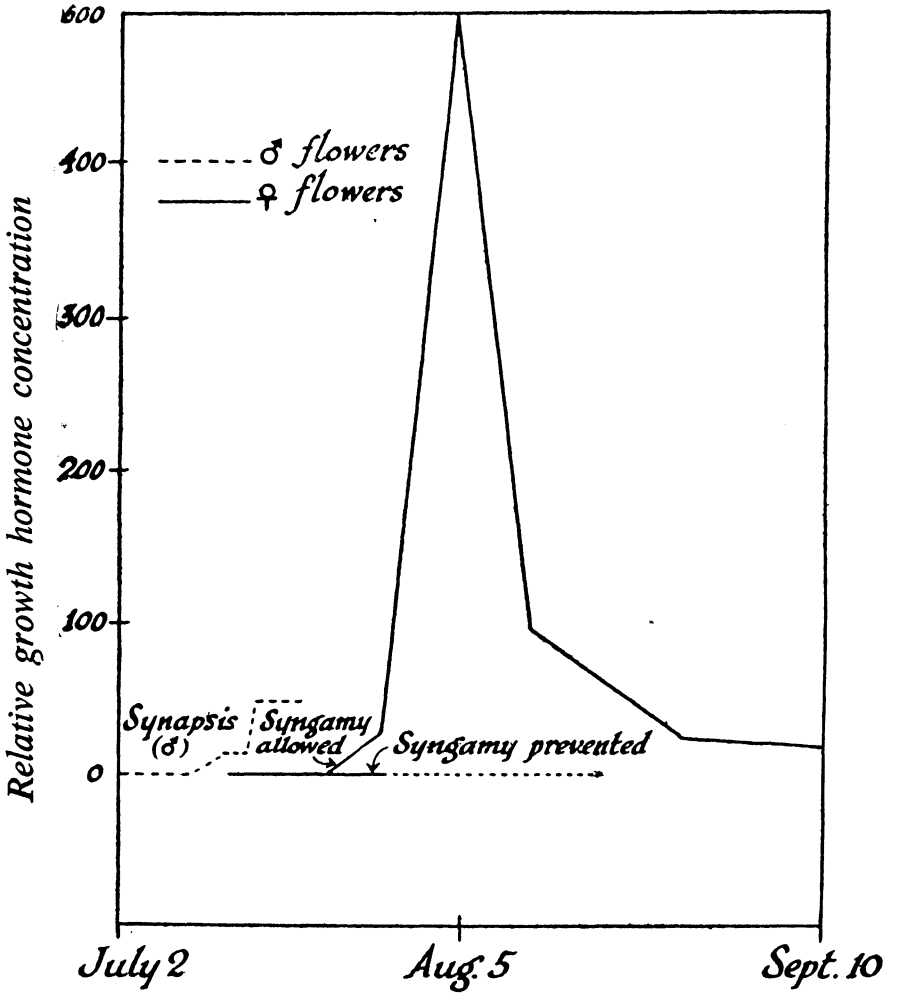


FIGURE 5

Changes in growth hormone content of the reproductive organs of maize during their development. There is complete absence of growth hormone in the male inflorescence prior to synapsis, and in the ovule before fertilization. A few days after chromosome conjugation in the tassel, and the union of gametes in the ear, growth hormones appear in considerable quantities in these structures (Missouri, 1943)

By alcohol extraction and bean seedling internode assay, an estimation of growth hormones in the reproductive organs of the corn plant during its development disclosed two maxima in their accumulation.

Following the initiation of chromosome conjugation in the staminate and fertilization in the pistillate flowers, substances possessing marked growth-stimulating properties were produced, the greatest concentrations being attained within the tassels 10 days to 2 weeks after the beginning of synapsis, and in the immature kernels an equal period subsequent to syngamy. The pre-synaptic stage in the male and the pre-syngamic period in the female inflorescences were distinguished by a complete absence of growth substances in the respective reproductive organs.

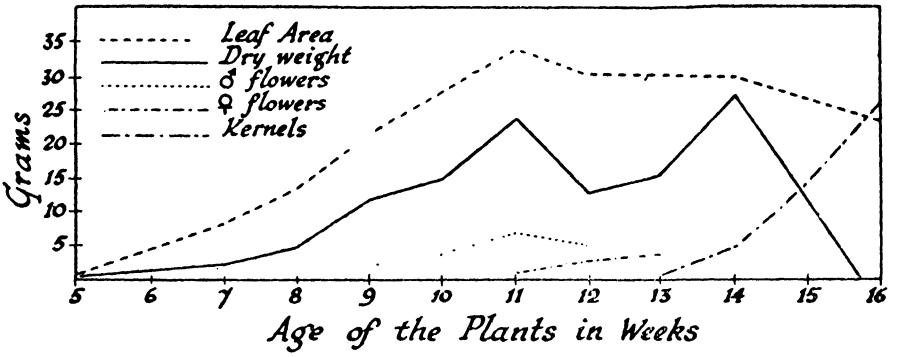


FIGURE 6

Weekly increment in dry weight of maize during its growth period. Interpretation by Wittwer (see Missouri, 1943) of earlier figure by Kreusler, Prehn and Hornberger (1879) apparently indicating that the processes of synapsis and syngamy are the causes of inception of the changes seen here and in Figure 7

It was revealed that the two maxima representing hormone accumulation correspond quite precisely (*a*) with the peaks in catalase activity and (*b*) with the spurts in growth following gametophyte and embryo inception.

Crude extracts of the immature corn kernels, applied in lanolin paste, were active in fruit setting and parthenocarpic fruit induction in the tomato. The percentage set, yield, and size of fruit were superior to that obtained by means of normal pollination and by the application of synthetic growth substances to flowers not pollinated.

A critical examination and new interpretation of data published in germane investigations revealed a striking correlation between (*a*) periods of greatest vegetative extension, accumulation of dry matter, absorption of soil nutrients, and carbon dioxide utilization, and (*b*) peaks in the production of growth stimulating hormones in the reproductive organs. These intervals of maximal increase followed closely in all cases the beginning of synapses in the flower bud and embryo initiation in the young fruit.

In their quantitative analysis of plant growth, Briggs, Kidd and West (1920) note that, in connection with the subsidiary maxima exhibited by the growth-rate curve, there is a significant correlation between the times of their occurrence and the recorded times of the first appearance of the male and female flowers of maize. It is a striking fact that when there is only one prominent subsidiary maximum the male and female

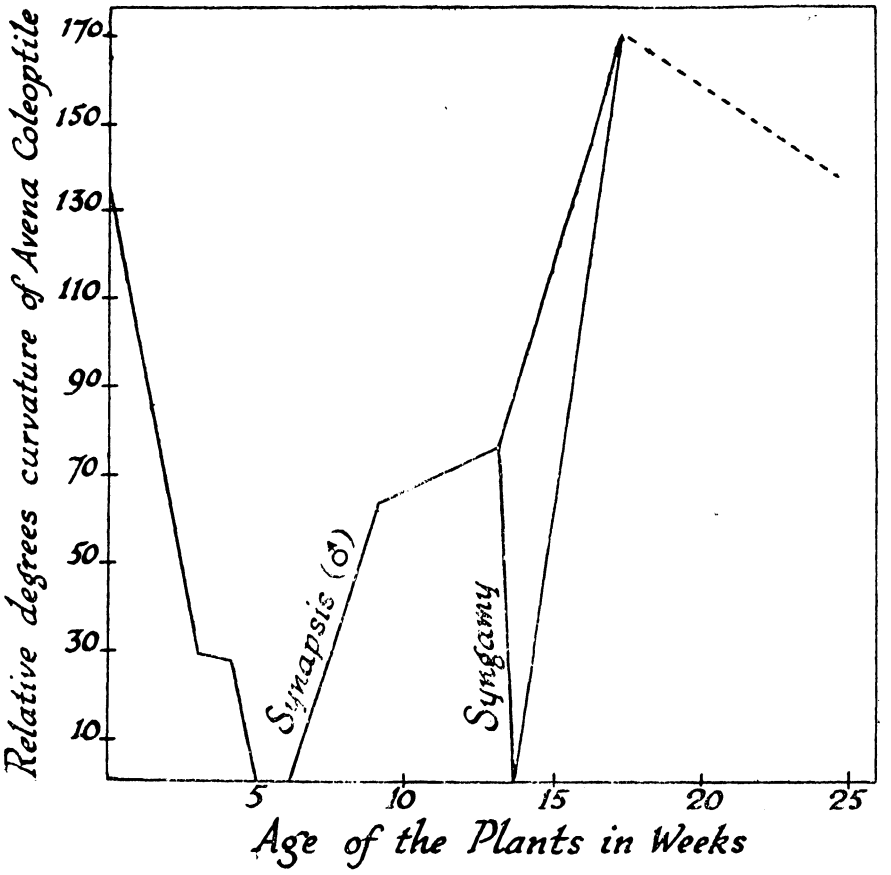


FIGURE 7

Changes in auxin content during the growth period of maize. Interpretation by Wittwer (see Missouri, 1943) of earlier figures by Laibach and Meyer, 1935, again indicating the effects of synapsis and syngamy

flowers appear together. Two alternatives are offered to explain these maxima and to correlate them with the appearance of male and female flowers in terms of assimilation and respiration.

The first is to suppose that at the recorded time of the appearance of the flowers there is a temporary increase in assimilation per unit leaf-area or a decrease in respiration per unit dry-weight, or a temporary

increase in salt absorption by the roots. The other alternative is to suppose that, during the early stages of flower development prior to the first record, the reverse conditions obtain, in other words, that the minima immediately preceding the record of the appearance of flowers is to be attributed to these reverse conditions. Since flower development is accompanied by an increased respiratory activity and also since there is no evidence that there is an alteration in assimilation per unit leaf area connected with flower formation, the safest conclusion seems to be that the minima are to be correlated with increased respiratory activity at these periods.

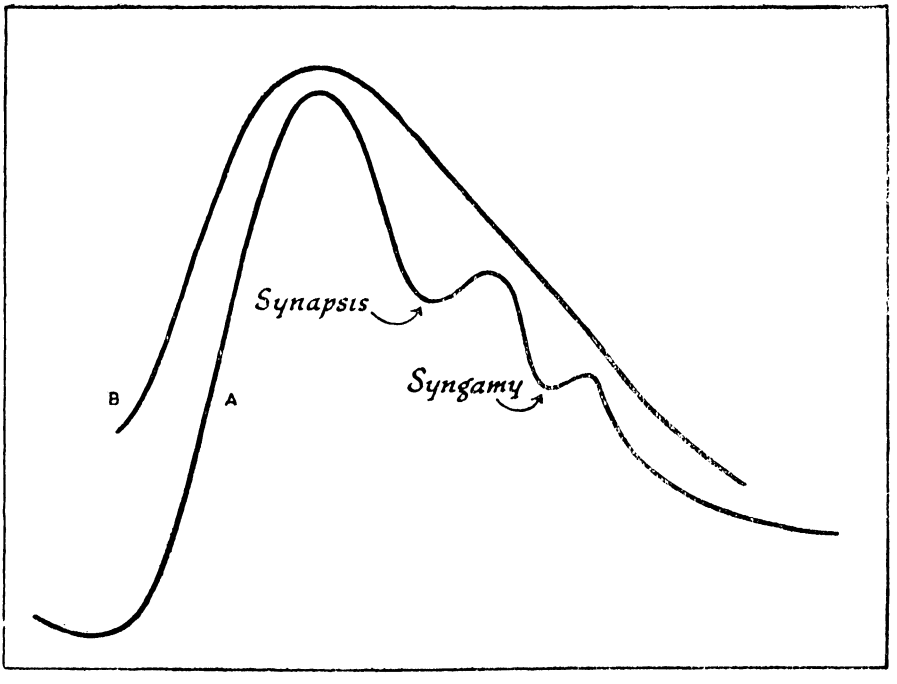


FIGURE 8

Weekly percentage increase in dry weight of maize during its growth period. A = dry weight; B = leaf area. Interpretation by Wittwer (see Missouri, 1934) of earlier figure by Briggs, Kidd and West (1920)

Fig. 8 gives the generalized form of the growth-rate curve for maize throughout its life-cycle. Although the broad form is that of a Sachs' grand period curve, it must be noted that it is not of this type, since the grand period curve as defined by Sachs is the curve of the actual increment per unit of time plotted against time and not of relative increment, that is, increment per unit of matter per unit of time plotted against time. On the broad form of the relative growth-rate curve for maize are superposed three secondary features, an initial fall, and two subsidiary maxima on the descending limb.

In the original curve the initial period A–B is the period before the assimilatory organs are able to counter-balance the loss in dry-weight due to respiration, and the rate of growth is consequently negative or nil. The phase B–C corresponds to a phase in morphological development during which the leaf-area per unit dry-weight increases to a maximum. The phase C–F covers the remainder of the life-cycle of the plant during which the leaf-area per unit dry-weight is continuously decreasing. The subsidiary maxima D and E coincide with the time of the record of the appearance of the male and female flowers respectively. The minima X, Y which precede these maxima, correspond with the earliest stages of flower development, and are possiblydue to increased respiration during that period. (See Briggs, Kidd and West, 1920.)

The incidence of the maxima is controlled by environmental conditions—not by the environmental conditions operating at the time, but by those obtaining at some previous stage in the life-history of the plant. The fact that the curve for leaf-area per unit dry-weight throughout the season (which has been calculated) shows a correspondence with the growth-rate curve indicates that the physiological basis for increased and decreased relative rate of growth is a corresponding change in the assimilating area per unit dry-weight.

Developmental Physiology and Taxonomy

This aspect has received study by means of transplant experiments, air-conditioned greenhouses (p. 81), investigations of ecotypes in relation to latitude (p. 216) and other methods of approach. It appears that the capacity of a species to migrate from one environment to another depends to a great extent on the occurrence, within its specific range, of ecotypes which are either day-neutral or adapted in some other essential way to different latitudes. When the migration takes place, any changes in reproductive behaviour in relation to the new environment may be reflected in different growth forms, although it does not appear to be claimed that these differences may acquire specific status.

The different behaviour of winter and spring varieties has long been the subject of research and discussion. Spring and winter forms of plants were originally separated into two distinct groups. In 1752, Linnaeus regarded winter and spring wheats as separate species; he classified the genus *Triticum* into five species of which the first two were *T. aestivum* and *T. hibernum*. Lamarck joined these two species and a third into one species, *T. sativum*, and later Darwin wrote that the difference between winter and spring plants is only one of time, a statement repeated by Lysenko: 'Sharply delimited groups of winter and spring varieties do not exist. Winter forms pass gradually into spring forms, and *vice versa*.'

The Russian outlook as to the application of the theory of phasic development to plant systematics is expressed by Kreier (1941), as far as the annual and biennial forms of *Hyoscyamus niger*, *Pyrethrum*, clovers, foxglove and *Poa annua* are concerned. The essential argument is that there is no hard and fast distinction between annuals, biennials and perennials, or between winter and spring annuals; intermediate forms can be found, and one type can be converted into the other under the influence of environment as determined by geographical location and ecological conditions. In general, a cold severe climate gives rise to biennial or perennial, and winter-hardy forms; and a mild climate to annuals, the seed of which germinates in spring producing plants which flower in the same year and are not hardy. Lysenko's phasic theory can be used for explaining how annuals can be changed into perennials, winter into spring annuals, and the reverse of these processes.

See also photoperiodism and taxonomy, p. 126.

Botanical Drosophilas

A number of plants are acquiring a place in research on developmental physiology equivalent to that long occupied by *Drosophila* in genetical investigations. Many references will be found in the following chapters to the use of cereals, soybeans, cocklebur and many other plants, but the interest now appears to be in species to which a mass production technique can be applied, thus giving greater statistical accuracy in interpreting results. In the recently developed work in air-conditioned greenhouses in Pasadena, California (Went, 1943 and 1944), spring annuals are used for experimental material, as they grow and mature rapidly and take up little space. A few thousand plants have been grown, many of them to maturity, in only fourteen 20″ x 20″ flats.

Laibach (1943) believes he has found a botanical *Drosophila* in *Arabidopsis thaliana*, a small, widely distributed Crucifer. It has a high degree of fertility: a vigorous plant can form 500 seed pods or more, each containing forty to sixty seeds. The duration of development is short, 30 days in early strains under optimal conditions. When cultivated, the plant has extremely modest requirements and needs very little space. On agar nutrient media in reagent glasses of ordinary size, one can grow them from seed to fruit-ripening in pure cultures. There is an extraordinary abundance of strains and, since the plants are self-fertile, pure lines can be obtained with ease. Summer and winter annual strains exist. In the winter annuals temperature, and in the summer annuals light (especially duration, to a less extent intensity), is the most important factor for flower formation. All the strains are long-day in type.

Micro-Dissection of Flower Primordia

It has already been indicated that differentiation of flower primordia is the first visible morphological sign that a plant has passed from a purely vegetative to a reproductive condition. There is now fairly general agreement that in a natural state this transition does not take place until a certain minimal number of leaves has been acquired by the plant. This does not, however, mean that no internal advance has been made in development. The Russians assume that development towards reproduction begins as soon as a plant or germinating grain is exposed to the low temperature applied in vernalization. The 'ripe-to-flower' condition recognized by Klebs is also development. In neither of these cases is the condition recognizable externally.

There are several studies of growing points of different species of plants. The work of Purvis has already been noted (p. 31). Plates 1 and 4 indicate the work of Sharman (1942) on both monocotyledons and dicotyledons. In a later paper (1943), the same investigator describes the technique to be adopted in micro-dissection of growing points, noting that the monocotyledons as a whole are not particularly easy material to handle. *Tradescantia* with its short apical dome and very sticky contents is difficult. The grasses are among the easiest subjects for study. Dicotyledons recommended are the privet (Plate 4) and the rose-bay willow herb (*Epilobium angustifolium*).

The following are detailed keys to Plates 1 and 4, from illustrations provided by B. C. Sharman, who has elsewhere (1945b) published a detailed morphological and anatomical study of leaf and bud initiation in the Gramineae:

Plate 1. Apices dissected from various species of Gramineae.

A=underground rhizome of couch grass, *Agropyron repens.*

B=vegetative shoot of wheat.

C=vegetative shoot of floating pond grass, *Glyceria fluitans.*

D=aerial vegetative shoot of *Agropyron repens.*

E=vegetative shoot of sweet vernal, *Anthoxanthum odoratum.*

F=vegetative shoot of Italian ryegrass, *Lolium multiflorum.*

G=young inflorescence of *Agropyron repens.*

H=young inflorescence of sweet vernal.

I=young inflorescence of six-rowed barley.

B and I are viewed in the plane of the leaves, the remainder perpendicularly to the plane of the leaves. The scale in D represents 0·5 mm. and applies to A—F. The scale in G also represents 0·5 mm. and applies to G—I.

Plate 4. Dissection of vegetative shoot of privet, *Ligustrum vulgare.*

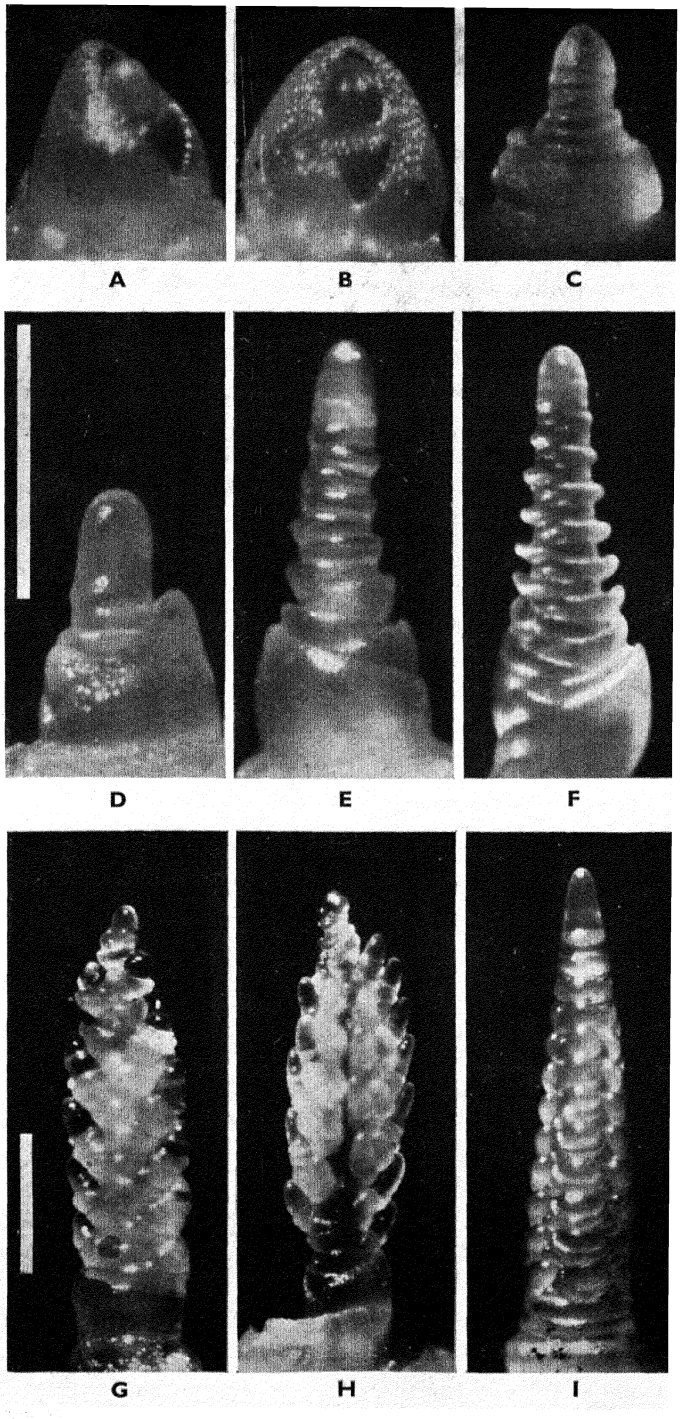


PLATE 1. Apices dissected from grasses and cereals (see p. 56). Photo: B. C. Sharman. The scale in D represents 0·5 mm. (1/50 inch) and applies to A–F. That in G also represents 0·5 mm. and applies to G–I.

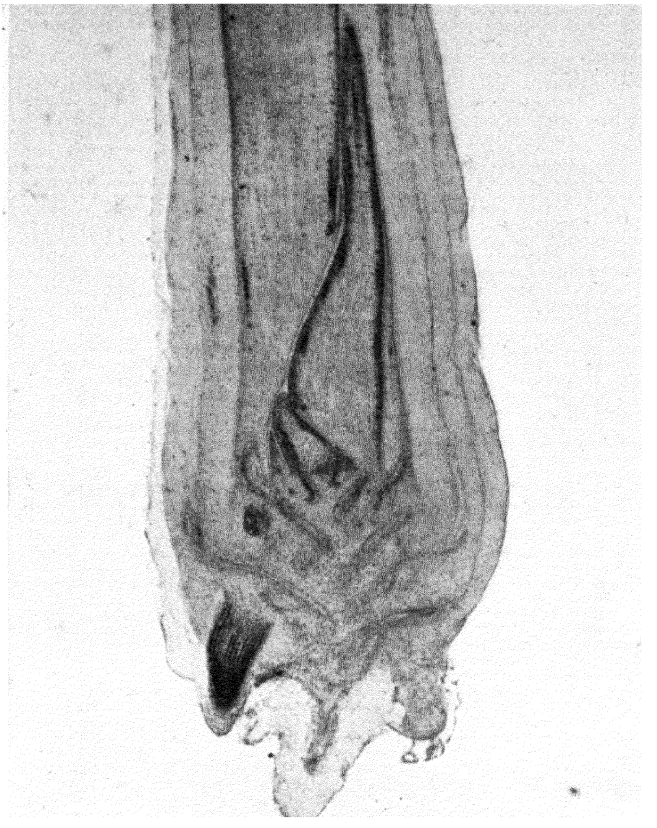


PLATE 2*a*. Longitudinal median section of a four-leaved onion seedling before bulb development (see p. 300). Photo: O. V. S. Heath.

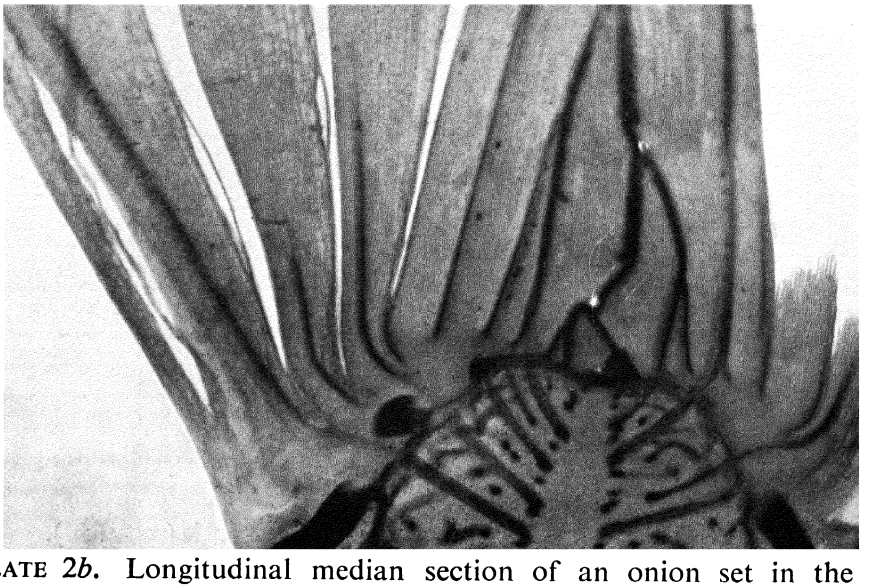


PLATE 2*b*. Longitudinal median section of an onion set in the vegetative condition (see p. 301). Photo: O. V. S. Heath.

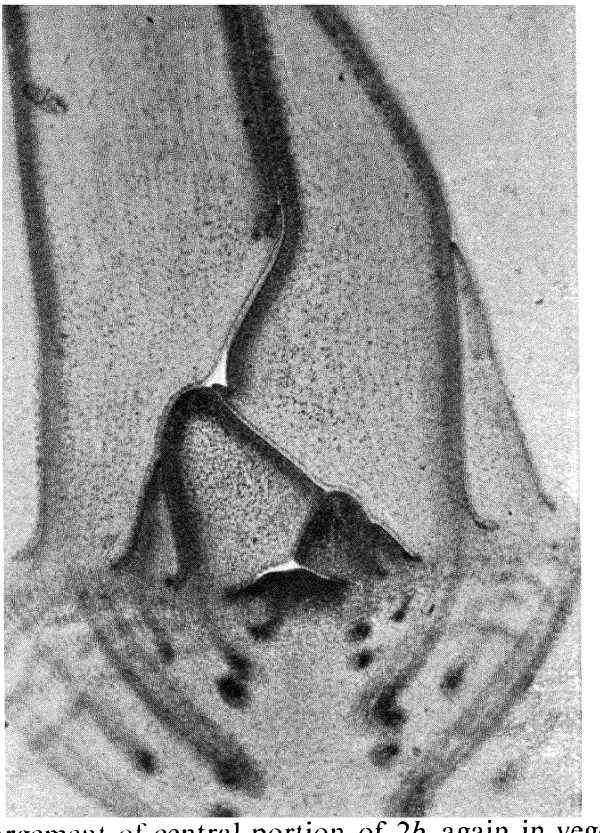


PLATE 3*a*. Enlargement of central portion of 2*b*, again in vegetative state (see p. 301). Photo: O. V. S. Heath.

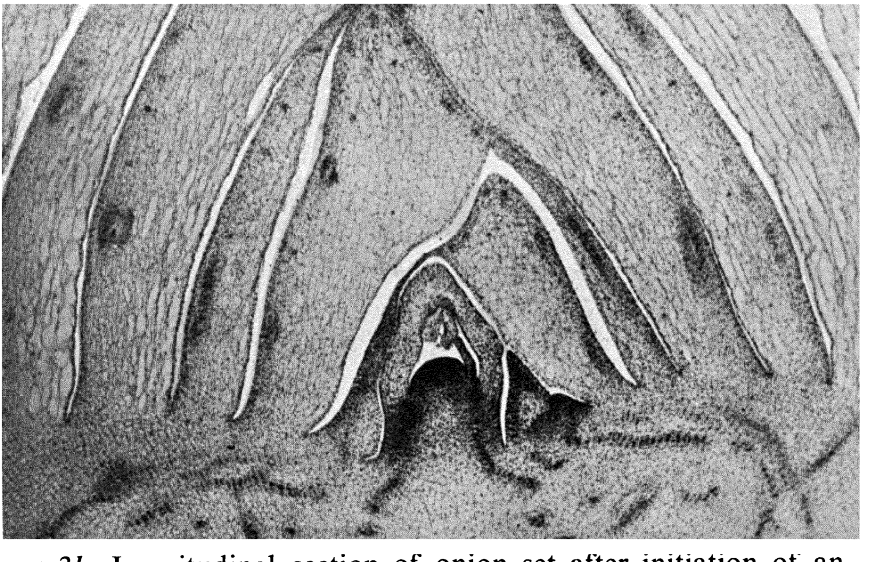


PLATE 3*b*. Longitudinal section of onion set after initiation of an inflorescence (see p. 301). Photo: O. V. S. Heath.

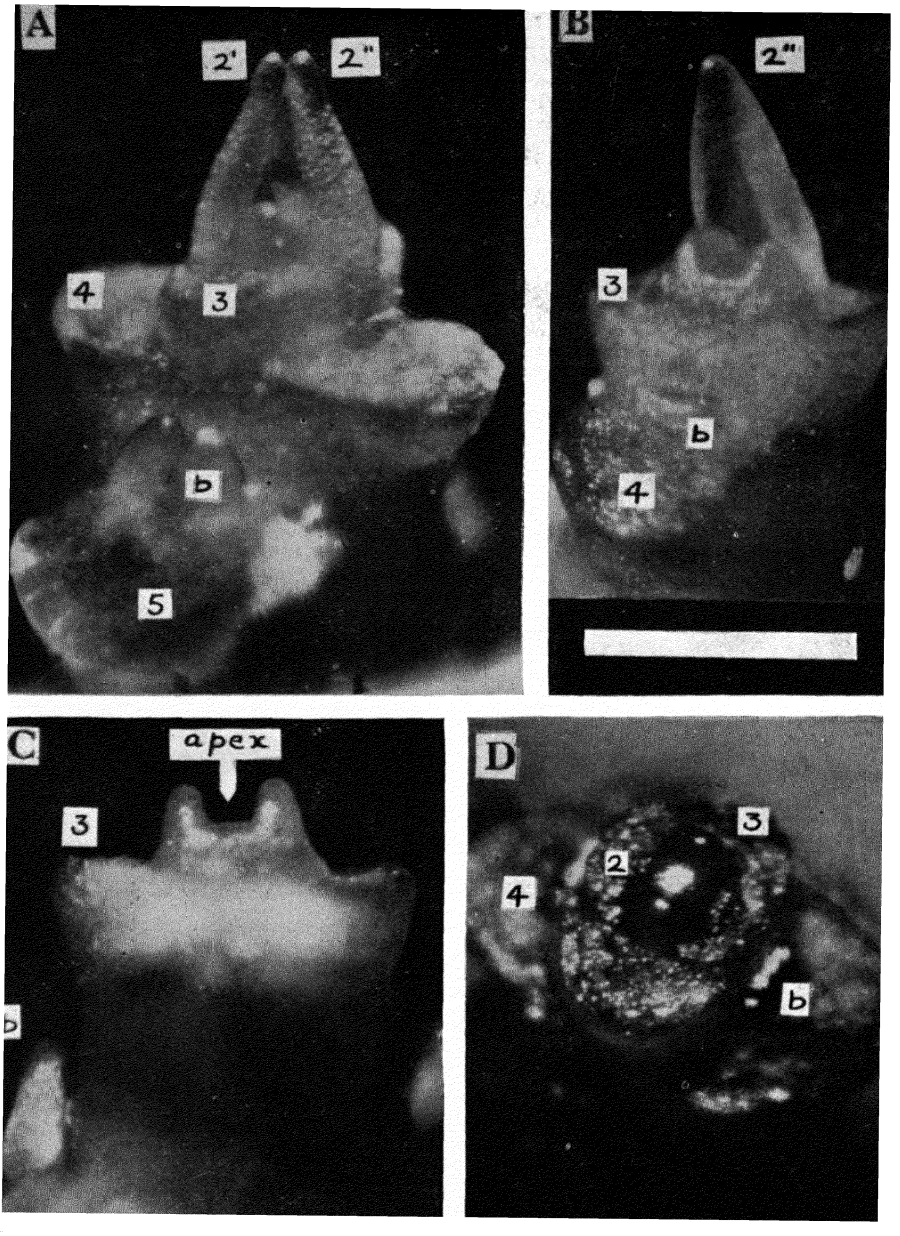


PLATE 4. Dissection of vegetative shoot of a dicotyledon (privet). (See p. 56.) Photo: B. C. Sharman. The scale below B represents 0·5 mm. (1/50 inch approx.).

*

A. 2′ and 2″ indicate the second pair of young leaves overarching the apex; 3, 4 and 5 are the shoulders left where leaves of the third, fourth and fifth pairs were attached; b indicates the first two leaves of bud in the axil of one of the fifth pair of leaves.

B. The same as A, with the young leaf 2′ removed and the whole shoot turned round a little. The first pair of leaf primordia are visible as small protuberances; b indicates a bud beginning to appear in the axil of one of the fourth pair of leaves.

C. The remaining primordium 2″ has been removed and the shoot is now viewed from the side. Only the first two primordia and the flat apex remain. The shoulder 3 indicates the former position of one of the third pair of leaves. b is one of the first pair of leaves of the bud in the axil of a fifth leaf.

D. An aerial view of C from above, showing the apex as a shining more or less rectangular platform between the first pair of primordia. 2, 3 and 4 mark the positions where primordia of leaf pairs 2, 3 and 4 were attached.

Scale below B represents 0·5 mm.

Cereals have been studied by O. T. Bennett (in addition to Purvis and others). In a first paper (1935) the early development of the barley spike is described and micro-photographed, but there are no notes as to date of appearance. The development of the wheat spike is described in a separate article (1936). Under the conditions of the experiment (variety and latitude), the growing point remains vegetative during autumn, winter and early spring. In the autumn, it produces only leaf initials, while in early spring, in addition to producing leaf initials the growing point elongates. The 'beginning of the reproductive stage' is marked by the appearance of double ridges, the upper of which produces the spikelet and its parts.

Experiments in Portugal have indicated the use of the micro-dissection technique in distinguishing between winter and spring forms of barley, and also in determining the vernalization treatments most favourable for different species and varieties before other environmental factors affect development (Almeida, 1942).

Noguchi (1929) has suggested a genetic factor to explain the elongated meristematic cylinder characteristic of perennial forms and the short dome or cone-shaped growing point characteristic of summer cereals. As regards minimum leaf number, Noguchi found that the average number of days after seeding before the initiation of flower primordia was 45 to 85 in summer cereals, but 145 to 175 in winter varieties.

Observing at the Ohio latitude, Evans and Grover (1940) found that the growing point of perennial grasses such as timothy remains vegetative during late summer and autumn and until April or very early May

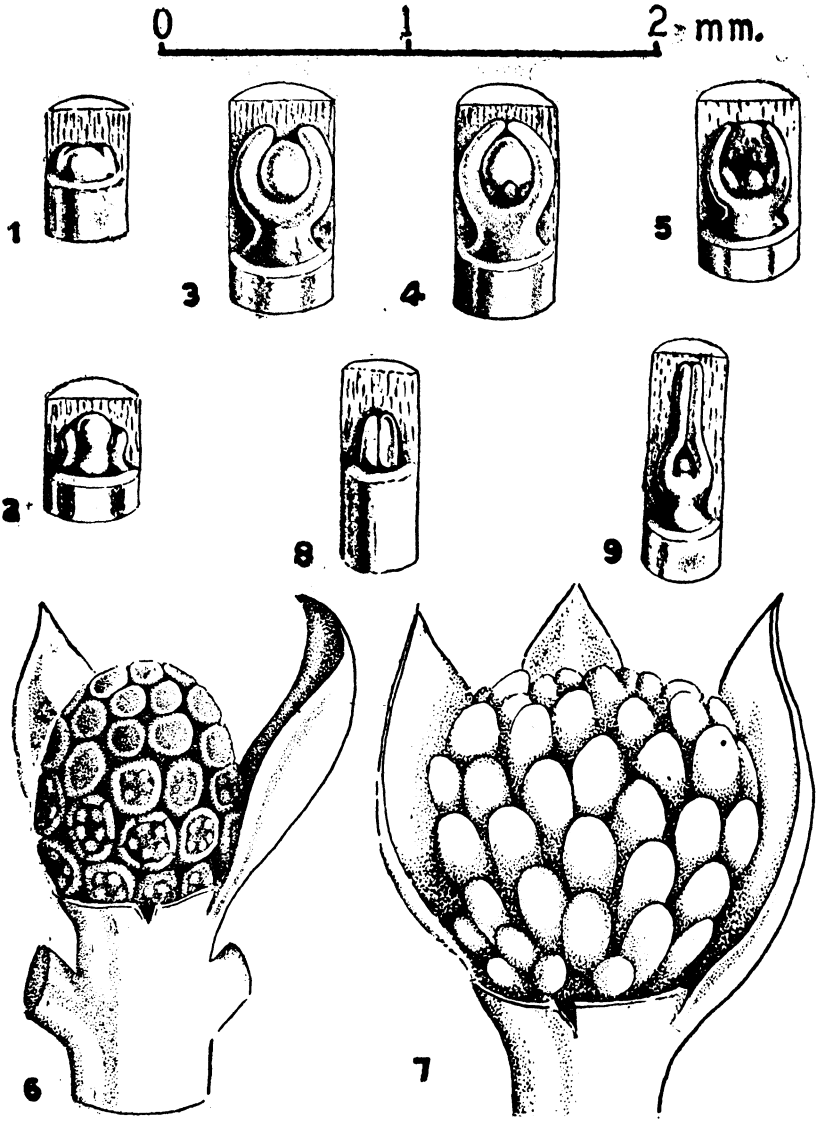


FIGURE 9

Apical growing point of *Baeria chrysostoma*, with front leaf removed leaving semi-circular scar. Diagrams 1 to 5 show successive stages of flower primordia; in all cases, two youngest opposite leaf primordia are separated by flower primordium, which has just initiated involucral bracts in diagram 4 and florets in diagram 5. Diagrams 6 and 7 show later stages; the two highest foliage leaves and two or three involucral bracts are removed to show flower head. Diagram 8 shows the growing point of a purely vegetative plant; only two leaf primordia are visible and the small apical meristem is hidden between them. Diagram 9 shows a growing point which has been kept at 28° C. in continuous light; the flower primordium has been initiated but is not developing further owing to unfavourable environment and has become overgrown by leaf primordia (Sivori and Went, 1944)

of the following year. In annual grasses, seeds of which germinate in early spring, the inflorescences originate and develop somewhat later than in the perennials. In describing and illustrating inflorescence primordia of the once-branched type (*Agropyron repens* and *Lolium perenne*) and of the multiple-branched type (*Phalaris canariensis*, timothy, tall oatgrass, cocksfoot, millet and *Euchlaena mexicana*), Evans and Grover note that the transition from the vegetative to the reproductive phase is usually marked by a sudden and vigorous elongation of the growing point and by an increase in its diameter. The further development of leaf fundaments is stopped. The protuberances or lateral swellings initiating the inflorescence then appear. Each of these represents a lateral growing point and may be regarded as the homologue of the primordium of a vegetative bud. Evans and Grover state that environmental conditions largely determine whether vegetative growth or reproductive development takes place, and they believe that, for many grasses, length of day is one of the most important of these conditions. Sharman (1945) doubts whether daylength has a marked influence on the change from vegetation to reproduction in perennial grasses such as ryegrass or sweet vernal. Timothy is vegetative under a short day and reproductive under a long day.

As a rule, each protuberance on a reproductive primordium, whatever its order, ultimately organizes a spikelet at its apex. There is a general tendency for spikelet formation to begin in the upper middle region of the young inflorescence, and to progress upwards and downwards. Further specialization is, however, more rapid in the distal region than in the central and proximal regions. Consequently, flowering and seed maturation progress from the apex towards the base of the inflorescence, in reverse order to the formation of primordia. The behaviour of growing points varies, of course, with the variety of grass concerned. Late pasture types will differentiate their primordia considerably later under natural conditions than early hay types.

Microphotographs of vegetative and reproductive primordia made during a study of the formative effects of environmental factors in the development of the onion are reproduced in Plates 2 and 3, and described on p. 300.

Internal Factors of Development

From the accounts given in these early chapters, and from those that follow in the chapters devoted to one particular aspect of the problem, it will be clear that there are many conflicting and inexplicable data, and that the interpretation of these has also produced a wide variety of hypothetical approaches to the real nature of plant development. So far

we have been concerned primarily with the more general aspects of the reaction of plants to the environment. All these must ultimately be correlated with, and will probably find their explanation in the internal physiology of the plant. The key to all these problems must ultimately lie in the discovery of the part of the plant that reacts to the factors of the environment, how this response is taken up, and how it is transmitted as a directional force or stimulus to other parts of the plant, thus leading to those external manifestations of morphogenesis which are recognized as indicating a state of vegetative growth or reproductive development.

CHAPTER IV

TEMPERATURE OF ENVIRONMENT

Temperature and Reproduction

Temperature affects the growth and development of plants in various ways. The actual existence and normal growth of plants are dependent upon the temperatures present during their vegetative period. Extreme temperatures outside the range to which a particular plant is adapted, for example, low winter or high summer temperatures, may have an adverse effect upon plant tissues and cause abnormalities in growth, or death.

Development of plants towards maturity is also affected by temperature. Scientific evidence on this relationship is not yet conclusive. It is known that some varieties and types of crop plants have a considerable requirement of low temperature for optimal development, and are therefore the 'winter' types that have to be sown at an appropriate date to permit the acquisition of their quota of low temperature in time for them to progress to maturity by a certain date. Other varieties have a smaller requirement of low temperature, this in some cases being apparently nil, and they can be sown in spring for production of seed in the same season. Other plants of lower latitudes appear to require not a low temperature, but a high one.

The requirement of the low temperature plants for low temperature is not a characteristic throughout their life. Apparently at later stages of their vegetative period they require high temperature combined with other necessary factors. For example, the reaction to photoperiods is governed to a considerable extent by the temperatures present at the same time. The latest work by Went (see p. 81) shows that temperature and in particular an optimal thermoperiodicity is the controlling factor in plant development, much more so than nutrition, photoperiod, water relations and so on (Went, 1944a).

It has been found possible to give plants their low temperature requirements while still in the form of slowly growing seeds; this has led to the theory that there is a definite succession of phases in the development of plants, and that the first phase in plants of temperate countries is a thermo-phase governed by low temperature. This is not generally accepted, and evidence has been produced to show that such plants can reach maturity after a considerable period, even in the complete absence of the low temperature considered to be essential for their thermo-phase.

The low temperature effect (thermal induction) connected with vernalization is of course of considerable economic significance, as yield and length of vegetative period are dependent to a great extent on whether the crop in question has had its quota of low temperature that favours optimal development.

The experiments reviewed below indicate the various viewpoints and the state of current research on this aspect of the problem. Most of the evidence is concerned with annual plants, but the same problems also apply to perennials, it being assumed that each year some parts of the plant that respond to the temperature of the environment, i.e. probably the growing points, require a certain quota of the temperature optimal for that species before it can proceed to maturity.

Early Work in the Soviet Union

Lysenko's first publication dealing with the influence of the thermal factor on the duration of developmental phases in plants was based upon experiments made with cereals and cotton at the Experiment Station at Ganja, Azerbaijan (Lysenko, 1928). In these experiments it was found that the time required for the completion of some of the recognized stages in the growth of cereals such as seedling emergence, ear emergence, full flowering, wax ripeness, etc., is inversely related to temperature; these phases are completed more rapidly at higher temperatures than at lower. It was noted, however, that, in spring and more especially in winter forms, the phase of 'shooting' (ear formation and elongation of internodes) does not always show this relation. With the increase in temperature under the conditions in which the crops are grown, this phase is in some cases initiated earlier, and in others takes place later or not at all; in the latter case, the plants remain at the tillering or rosette stage. Lysenko called this retention of the winter habit 'hibernalism, that is the property of plants to remain for an indefinitely long period at the phase of tillering without flowering stems'.

From this early work, Lysenko proceeded, in collaboration with Dolgušin, to study the property of hibernalism in cereals, and the nature of the difference between winter and spring forms, a subject examined at an earlier date by Gassner (see p. 26). The results of the experiments carried out for this purpose were presented to the All-Union Congress of Genetics, Selection, Seed Production and Animal Production in 1929 (Dolgušin and Lysenko, 1929).

A Study of the Winter Habit in Cereals

The results of experiments made on variation in sowing dates and

the natural chilling of slightly sprouted grains of rye, wheat and barley in snow have already been quoted in some detail in *I.A.B. Joint Publ. No. 1*, pp. 23–7. Here it will be sufficient to give a translation of the conclusions drawn by Dolgušin and Lysenko (1929). Abstracts of papers by other Soviet workers will be found elsewhere in *Joint Publ. No. 1.*

(*a*) Experiments on the time of sowing showed that there are no definite dates dividing winter forms from spring forms; the later the sowing, the larger is the number of cereals which retain the winter habit. For instance, when sown in the second half of April, or later under Azerbaijan conditions, not only all the winter and alternative forms, but also the majority of spring forms persisted at the phase of tillering.

(*b*) One of the main factors preventing shooting is the high temperature of the period subsequent to sowing. However, after a pre-sowing chilling of slightly sprouted or swollen seeds at 2·5° to 3·5° C. for a definite period (for instance, for Kooperatorka wheat, 38 days, and for winter barley, 28 days), winter cereals when sown at any time will proceed to the shooting stage. After such a pre-sowing treatment, the rapidity of shooting increases with the temperature of the period following sowing. Since a high temperature after sowing retards shooting in plants raised from unchilled seeds, the authors argue that in cereals the period from seed swelling to ear emergence covers at least two 'biologically consecutive' phases. The first of these does not produce any morphological changes in the plant and is directly related to the thermal factor, high temperatures prolonging its duration. The duration of the second phase (shooting) is, like all other phases, inversely related to temperature, so that the higher the temperature the quicker is the progress at this phase.

(*c*) Thus, the retardation of shooting observed in cereals subjected to a high temperature after sowing is due to the prolongation of the preceding phase; if the temperature of the after-sowing period reaches a maximum at and beyond which the preceding phase for a given variety of cereal cannot be passed, then this variety will behave as a winter form, i.e. will not ear (see, however, p. 67).

(*d*) Since the temperature rises with the approach of summer, it is observed in sowings of a collection of varieties that the later the sowing the greater is the number of varieties which change from the spring to the winter habit, i.e. the thermal maximum preventing the progress of the phase preceding shooting varies in different varieties.

(*e*) By comparing the records of temperatures during the authors' experiments with the length of the interval required for the progress of this

developmental phase, it was found that their relationship can be expressed by the formula

$$n = \frac{A}{B - t}$$

where n is the duration of the phase in days, B is the maximum temperature beyond which the phase will not progress, and t is the average daily temperature. A is the sum of the daily temperatures found by experiment to be necessary for the completion of the phase.

(*f*) The values of A and B are regarded as characteristic constants for different varieties of cereals; thus, for Kooperatorka wheat, A = 300, B = 12° C.; for *Hordeum pallidum* 419, A = 350, B = 15° C. These values, though not exact, closely approach the figures. Typical formulae for Kooperatorka wheat under two different environments would therefore be

$n = \frac{300}{12-3}$ = about 33 days as duration of phase where daily environmental temperatures average 3° C.

$n = \frac{300}{12-4}$ = 37·5 days as duration of phase where daily environmental temperatures average 4° C.

(*g*) Winter and spring varieties of cereals differ only in respect of the value of these thermal constants B and A, i.e. there is no virtual difference between spring and winter varieties. Every variety therefore is to a greater or less extent a winter form as determined by the value of its thermal constants. If during the after-sowing period the sum of differences between B and the actual temperature reaches the value A characteristic of the variety, then that variety will ear no matter when it is sown.

(*h*) To pass through the preceding phase winter cereals do not need a temperature of 0° C.; they can do so at a relatively high temperature provided the maximum B for a particular variety is not exceeded. The nearer the temperature approaches the maximum B, the longer will be the duration of this phase, as is seen from the given formula.

On this basis, Lysenko and his associates at the Institute of Plant Breeding and Genetics applied the method of chilling to slightly sprouted grain of cereals and seeds of other crops. In 1931 and 1932 Lysenko published instructions for treatment of seed by this method, which came to be known in countries other than the Soviet Union as vernalization (see Aberystwyth, 1933). Then followed the formulation of the principles and the theory of phasic development, already outlined in Chapter III. The Russian investigators interpret the change occurring during vernalization as a gradual qualitative change in the protoplasm, a conclusion

based on the possibility of partial vernalization of the thermo- and photo-phases. Results show that seeds may be partially vernalized, then removed from the treatment and later treated again, and that the degree of vernalization, or the extent to which the embryo plant has passed through the thermo-phase, is not lost in any way by the break in the treatment (provided the seeds are not in the meantime exposed to high temperature or other factors causing devernalization).

Related Research on Temperature in Great Britain

Apart from experiments on the vernalization of wheat, tomatoes and other plants made at various research centres in Great Britain and referred to in Chapters XVI to XIX, a series of studies has been made at the Research Institute of Plant Physiology, Imperial College of Science and Technology, London, by Professor F. G. Gregory, Dr. O. N. Purvis and others, on the experimental basis of vernalization and the sequence of developmental phases claimed by the Odessa school. Some of this British research comes within the scope of this chapter, but other investigations are concerned with aspects discussed elsewhere (pp. 95 and 152).

In 1934, Purvis published an account of an analysis of the influence of temperature during germination on the subsequent development of certain winter cereals and its relation to the effect of length of day. This study, which dealt more especially with winter rye, showed that length of day is interrelated with other conditions of germination in determining the subsequent flowering behaviour. Purvis and Gregory (1937) state that the omission of the length-of-day factor has not been given sufficient consideration by some investigators, a fact which 'is reflected in certain inadequacies in the hypothesis which Lysenko has put forward to explain the mechanism of vernalization'.

It has already been noted that the theory of Lysenko involves a concept of a series of stages or phases in the progress towards flower development, each one depending for its inception on the completion of the preceding stage. The decisive factor for the 'thermo-phase' in winter cereals is considered to be low temperature, without which Lysenko considers that no progress towards flowering can be achieved. In other words, winter rye should fail to flower unless and until the seed is subjected to low temperature for a certain fixed period. Purvis and Gregory (1937) state categorically that this is not the case, and that there is ample evidence to refute the claim.

Rejection of Hypothesis of Thermo-Phase

Reference is made in the first place to their own experiments (1934 and

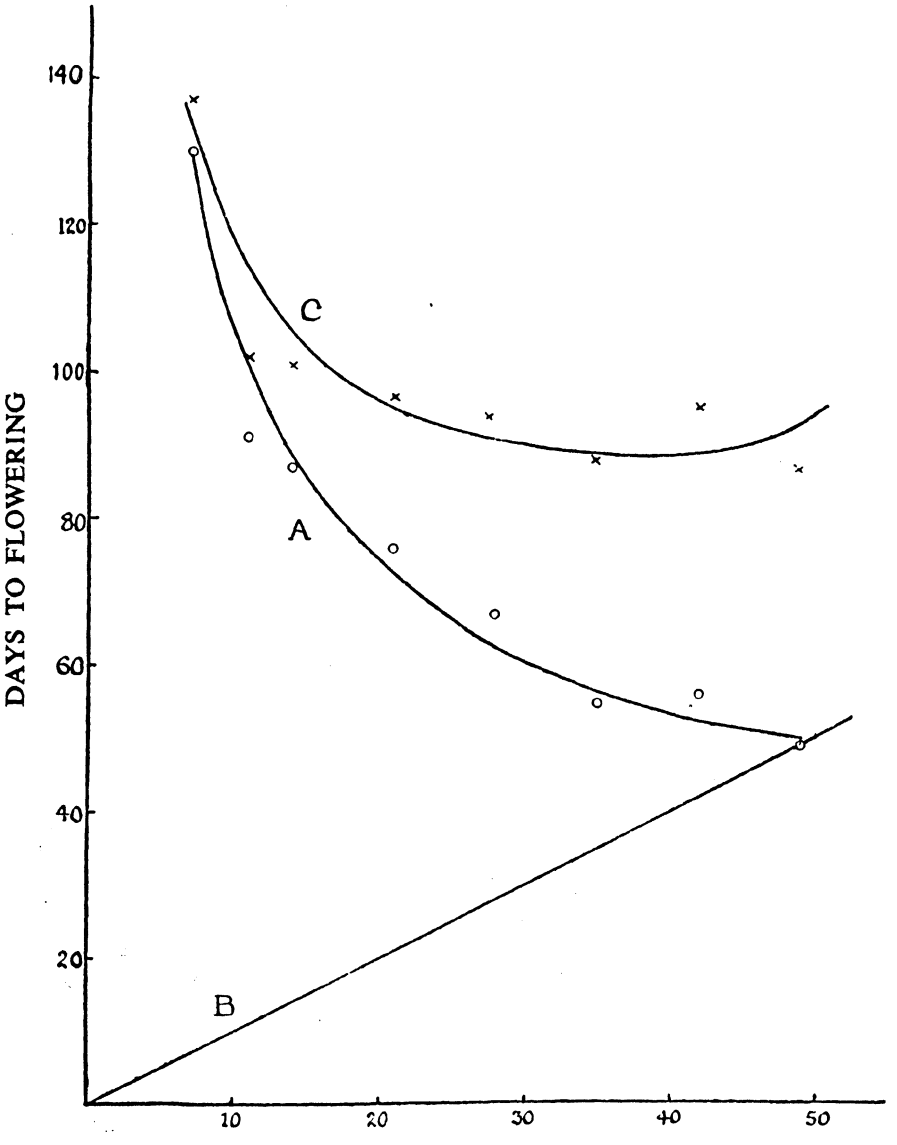


FIGURE 10

Vernalization of winter rye (Purvis and Gregory, 1937). Time to flowering (anthesis) from planting (A) and from beginning of treatment (C) after different periods of low-temperature treatment. There is little variation in *total* time with vernalization treatments of three to seven weeks' duration, while beyond this range the total time increases. Time from planting to flowering is a decrement curve approaching a minimum level with increasing exposures (A). The time of treatment is increasing in a linear series (B): the total time being the summation of these two curves culminates in a rising straight line (C) parallel to B. Such a curve exhibits a range of values which are, relatively to the original axis, almost constant over a considerable period.

1937) which show that preliminary subjection of seed to short days without low temperature 'accelerates the flowering of winter rye'. It is further stated that, even in the absence of any accelerating factor, winter varieties do not make the indefinite vegetative growth claimed by Lysenko and his associates, but come into flower under long days. As an example, the experiment of Lojkin (1936) on the wheat varieties, 'Leaps Prolific' and 'Turkey Red' is quoted; when these were sown without treatment, they came into ear in approximately 150 long days. Again, Vasiljev (1934b) is noted as having observed that five wheat varieties grown under continuous light at 20° C. came into ear in little over 150 days.

Purvis and Gregory state that it is the usual practice, in field experiments on vernalization, to plant late (in May in Great Britain) in order to avoid chilling by spring frosts; as a result of the long vegetative period, the plants are not ready to flower until the following October, when the natural daylength inhibits the final emergence of the ear. In such cases, flowering is recorded as having failed, but, as Purvis showed (1934), an examination of the growing points at this date reveals that in many cases flower differentiation has already taken place.

The same authors (1937) state that in their experiments 'Petkus winter rye, sown unvernalized on 17th March 1936, under a daylength increasing from twelve hours, came into ear in about 170 days and produced fertile ears and long straw, showing that failure to ear in plants sown in May is due to shortening days at the time at which the "shooting" stage is reached.' It is also shown that the effect of low temperature during germination is proportional to the duration of the treatment up to an optimum degree of acceleration.

These British authors therefore admit the possibility of thermal induction, the basis of the method of vernalization as originated at Odessa, but, by demonstrating an effect from the use of an initial period of short days, and the attainment of flowering in plants which have been denied the necessary low temperature, refute the existence of an obligate thermo-phase as such, or for that matter of any obligate succession of distinct phases as postulated by Lysenko. Lysenko's 'thermo-phase' is not considered to be obligatory for the initiation of flowering, but to be of a quantitative and not purely qualitative nature.

The postulation of two reactions by Purvis and Gregory (outlined on p. 159), one dependent mainly upon temperature of germination, the other on a photo-catalytic process, resembles in some respects the theory of phasic development, but the stages or phases are not regarded as necessarily consecutive.

'In winter cereals, flower initiation does not require the action of any special external factor, but it can be accelerated by either low-tempera-

ture germination or by an initial period of short days. In fact, if vernalization is defined as a treatment in early stages of growth which shortens the vegetative phase, one may speak legitimately of vernalization by short days as well as of vernalization by low temperature. It must, however, be emphasized that in either case a period in long days is necessary for flowering to be completed, and for this reason the winter cereals may retain their status as "long-day" plants' (Gregory and Purvis, loc. cit.).

Voss (1938) has also found that a thermo-phase is not obligatory in winter wheat. By the use of short day under conditions of constant high temperature of approximately +20° C., it was found possible to induce shooting in German winter wheats. The manner in which a variety reacts to treatment may differ within the variety under (*a*) combined cold and short-day treatment, and (*b*) short-day treatment alone, at high temperatures. Given a very long time of vegetation, winter wheat may be brought to flowering under continuous illumination and high temperatures. Since it is found that winter wheat can pass from the vegetative to the reproductive state most readily under the influence of different external factors, in particular low temperature and short day acting alone or in combination, Voss suggests a new definition of the terms 'winter wheat' and 'summer wheat'. 'Wheat varieties, which under a constant high temperature (approximately +20° C.), constant illumination (by natural or artificial light, as far as possible not $<$ 1,500 luxes), and otherwise favourable conditions in a hothouse do not exhibit the beginning of shooting within 4 to 6 weeks, are described as winter wheats.'

In experiments arranged to constitute three temperature series, namely, continuous high temperature, a daily alternation of 12 hours at 25° C. and 12 night hours at 4 to 6° C., and the seasonal temperature of Leningrad, Avakjan and Tagi-Zade (1934) found that no differentiation took place in plants kept at high temperatures irrespective of concurrent or subsequent daylengths, nor in plants kept at lower temperatures but grown in short (10-hour) day. The different nature of these two groups of plants was revealed when they were transferred to longer day. The growing points of the former failed to differentiate whereas those on the latter began to do so. This is considered to be due to the fact that plants kept at high temperatures failed to complete the first phase (to receive their low temperature requirement), whereas those grown after chilling in a short day failed to complete the second. Klebs would have said the latter were in a ripe-to-flower condition until they were removed to long day, after which they could progress to his second stage, the formation of flower primordia.



PLATE 5. Some of the earlier equipment of Garner and Allard at Arlington, Virginia, for their studies on photoperiodism (see p. 108). Photo: Bureau of Plant Industry, Soils and Agricultural Engineering, U.S.D.A.

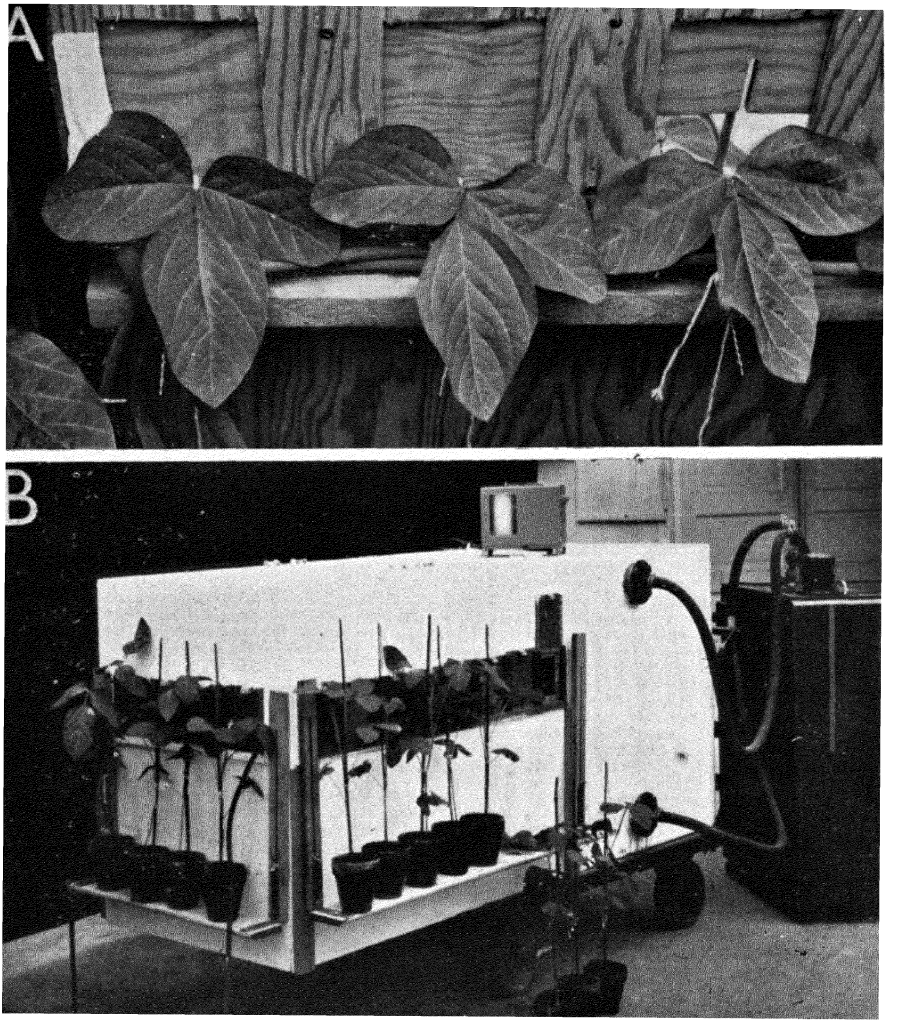


PLATE 6. Equipment for control of temperature and photoperiod for individual leaf blades (see p. 154). Photo: Parker and Borthwick, 1943.

Cause of Vernalization and Devernalization

Subsequent research by Gregory and others is concerned with various problems connected with the process of vernalization, but more particularly with the underlying cause of the phenomenon, and with the discovery of that part of the developing grain which actually responds to the treatment.

It may be considered possible that the mere check in growth caused by the low temperature employed is the chief factor. Maximov's interpretation (see Aberystwyth, 1934) of Vasiljev's data (1934a) led him to conclude that, when the time of low-temperature treatment is included with the length of the vegetative period, the time elapsing before ear emergence is no shorter in vernalized than in unvernalized plants. Vasiljev himself claimed this result only over a limited range of durations and methods of treatments. Purvis and Gregory (1937) proposed a simple explanation of this result, but, to test the statement of Maximov, sought a method, other than low temperature, to inhibit germination, and thus to prolong the period of germination. In this way it was hoped to separate the specific vernalization effect of low temperature from that of mere inhibition of germination, that is, that it is low temperature rather than restriction of growth which is the determining factor in vernalization. To separate these factors, anaerobic conditions were imposed during the period of high temperature treatment, and misconceptions have arisen as to the validity of the results on this ground (Gregory and Purvis, 1938, Whyte, 1939, Oljhovikov, 1940).

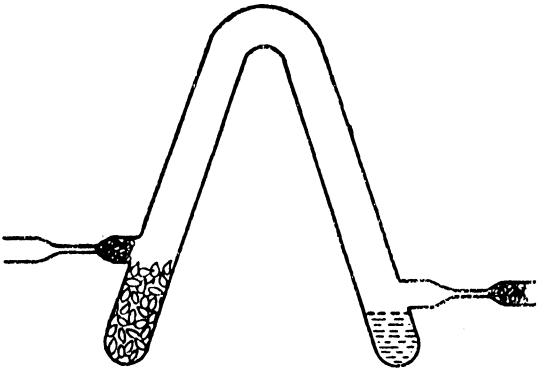


FIGURE 11

Use of anaerobic conditions in analysis of the vernalizing effect of low temperature during germination. Diagram of apparatus used for imbibing sterile grain of cereals with known volume of water under anaerobic conditions. (Gregory and Purvis, 1938b)

The anaerobic conditions and high concentrations of $C0_2$ which were employed for the purpose of prolonging germination at high temperature (Gregory and Purvis, 1938) also made possible a demonstration of what is claimed to be a quantitative reversal of the vernalizing effect of low temperatures by higher ones, as well as the complete inhibition of the low temperature effect in the absence of oxygen.

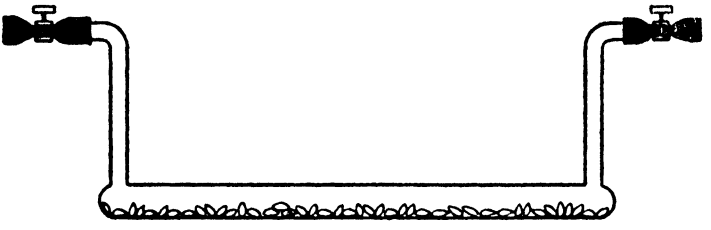


FIGURE 12

Apparatus used for exposing imbibed grains alternately to nitrogen and air (Gregory and Purvis, 1938b)

Results of four series with varying ratios of exposure to high and low temperatures (see Table from Gregory and Purvis, 1936) are considered to show that high temperature negatives the effect of low temperature progressively as the relative period of high temperature is increased. The control experiments are quoted as indicating that this effect is not due directly to the anaerobic conditions.

TABLE 1

Winter rye: total period at 1° C., 6 weeks in every case.

Treatment *Duration in air at 1° C.* *Duration in N at 20° C.*	*Days to anthesis from planting (average of those plants which eared).*	*Proportion of vernalized plants.*
1 : 1	Unvernalized	None
2 : 1	106	20 per cent
3 : 1	99	60 ,,
6 : 1	89	100 ,,
Control	71	100 ,,

A study made in the Pedagogic Institute, Moscow, is concerned with this same effect of high temperature. In order to check the destructive effect of high temperature (devernalization) on vernalized seeds claimed by Efeĭkin (see page 258), Tetjurev (1941) stored grains of winter wheat

(which had been vernalized at 0 to 3° C. for 56 days) at 30 to 35° C. for a period varying from 1 to 6 days. The grains were then sown. Plants from grains stored for 4 days or more failed to ear; in those from grain stored for 3 days, there was only 5 per cent earing; plants from grain stored for a shorter period as well as the vernalized control eared fully, while the unvernalized control failed to ear. Tetjurev concludes that, although the destructive effect of high temperature was evident after storage for 3 days or more, it still remains to be seen whether the grains are returned to their pre-vernalization state under the effect of high temperature, that is whether the process of vernalization is reversible.

In another experiment on devernalization, Gregory and Purvis (1938) found that a mature grain after being vernalized can be again devernalized by maintaining it in a dry condition at room temperature for 20 weeks, and therefore conclude that vernalization appears to be a reversible process. This reversal is slow and is not apparent at all until after dry storage for 6 weeks (see Table 2), nor does it occur when winter rye is kept in a moist condition at 1° C. for 6 months.

TABLE 2

Effect of Drying Vernalized Grain on Subsequent Development.

	Period of drying						*Unvernalized, sown dry*
	1 day	*6 weeks*	*8 weeks*	*12 weeks*	*14 weeks*	*20 weeks*	
Spike length in mm.	34·0	44·3	4·9	2·8	2·4	1·6	1·6
Tiller number per plant (10 plants per pot)	2·7	2·9	9·7	10·9	16·3	13·7	4·7
Stage of development: 'score' after 19 weeks' growth	51	49	26	25	21	20	19

These authors conclude from the results given in Table 2 that, as far as the stage of development in spike length or in the conventional 'score' units are concerned, complete devernalization has occurred, but that in the effect on tiller number an after-effect of the previous low temperature is apparent.

This effect is put forward as evidence for the scheme of vernalization already suggested by the same authors (Purvis and Gregory, 1937), and discussed on p. 159.

Filippenko (1940) also investigated the reversibility of vernalization

claimed by Gregory and Purvis (1938) and Efeĭkin (1939). Grains of winter wheat (Ukrainka and Lutescens) which had been fully vernalized were kept for from 5 to 10 days either in aerated water, or in water without aeration (partial anaerobiosis). Plants from vernalized grain stored in aerated water headed at the same time as those from vernalized but otherwise untreated grains. Vernalized grains kept under partial anaerobiosis showed delayed heading or perished altogether. Ascorbic acid and alcohol contents in the grains were investigated. Treatment in a condition of partial anaerobiosis caused a decrease in ascorbic acid and an increase in alcohol content (in the latter case, from 40 or 50 mg. per 100 grm. dry matter to 400 mg.). Filippenko considers that these factors have an effect in delaying further development.

The latest and confirmatory experiments on devernalization by high temperature are reported by Purvis and Gregory (1945). Petkus winter rye was vernalized for 42 days at 1° C. and the seeds were then subjected to a range of temperatures for varying periods of time (temperatures, 25°, 30°, 35° and 40° C.; durations, 1, 2, 3, 4, 5, 6 and 10 days). Petkus spring rye was subjected to similar heat treatments without previous low temperature treatment. Results obtained at 35° C. are given in Table 3; others will be published in a fuller article (the method of scoring is described by Gregory and Purvis, 1938).

TABLE 3

Effect of treatment at 35° C. before sowing on the rate of ear development (1) in winter rye vernalized 42 days at 1° C., and (2) in spring rye.

Duration of heat treatment	*Spring rye (unvernalized)*		*Winter rye (vernalized)*	
	'Score'	*No. of replicates*	*'Score'*	*No. of replicates*
0 (Controls)	123±0·12	(52)	100±3·0	(47)
8 hours	120±0·77	(48)	95±4·6	(44)
16 „	121±0·93	(53)	90±4·9	(35)
1 day	120±0·65	(62)	75±6·5	(35)
2 days	121±0·68	(47)	80±5·9	(39)
3 „	124±0·40	(55)	72±9·5	(16)
4 „	123±0·46	(49)	72±6·4	(33)
5 „	120±0·64	(42)	63±6·6	(35)

Purvis and Gregory draw the following conclusion from these data.

(*a*) Heat treatment of the seed is without effect on the flowering behaviour of spring rye, thus showing that there is no question of a lethal action. Spring rye heated at 40° C. for 14 days scored 120, substantially

the same as at 35° C. The reduction in score in winter rye is therefore not due to any injury effect, as is claimed by investigators who believe that vernalization is not reversible.

(*b*) A progressive and significant reduction in the score accompanies prolonged heat treatment of winter rye. The delay in flowering is then due presumably to the reversal of the vernalization effect. Complete devernalization did not occur. After treatment at 40° C. for 2 days the score was 79±8·0 (four times that of unvernalized winter rye) whereas a further day at 40° C. killed all the seed.

In a separate experiment, after the preliminary vernalization for 42 days at 1° C. and the subsequent heat treatment as above, the seeds were then revernalized by exposure to low temperature for a further 6 weeks. The effect on ear development is shown in Table 4. The scores are slightly higher than those of the control series vernalized for 12 weeks continuously. The efficacy of the high temperature devernalization in these experiments depends upon the duration of the previous low-temperature period and thus upon the 'intensity' of vernalization; this aspect is now being investigated.

TABLE 4

Revernalization of winter rye, after heat treatment, by a further period of 6 weeks at 1° C.

Duration of heat treatment	*'Score'*	*No. of replicates*
0 (Controls vernalized 12 continuous weeks at 1° C.)	112±1·18	(17)
8 hours	113±0·95	(48)
16 ,,	117±0·82	(41)
1 day	117±0·45	(42)
2 days	113±0·93	(39)
3 ,,	118±0·65	(54)
4 ,,	117±0·63	(54)
5 ,,	116±0·65	(55)

Location of Response to Thermal Treatment

In research on these aspects of the problem, two main questions are at issue. The first is the discovery of the part of the seedling undergoing temperature treatment during vernalization which actually responds to the treatment; the second is the determination of which part of the young seedling or growing plant it is that retains and transmits the vernalization effect. The latter question is referred to in Chapter IX, where it is

noted that the response is assumed to be retained in the meristem of the growing points. Investigations made by Gregory and Purvis and de Ropp (see refs. in Purvis, 1940) on the location of the response in the slowly growing seeds may be quoted as examples of studies on the former question.

Embryos of cereal grains, separated from the endosperm and cultured on a medium containing sugar, can be vernalized by exposure to a temperature of 1° C. in the same way as whole grains (see refs. in Purvis, 1940). In order to locate more precisely the tissues concerned in the process, Purvis (1940) mutilated embryos of Petkus winter rye in various ways before the vernalization treatment. The progress towards flowering made by each plant during 84 days from the end of vernalization, and the degree to which this was dependent upon the type of mutilation, are shown in Table 5.

TABLE 5

Treatment	*No. of replicates*	*Condition of plants 84 days after end of treatment*
A. Vernalized 6 weeks		
1. Whole embryos	7	All past anthesis.
2. Stem apex and fourth leaf primordium retained	2	Both with ears emerged.
3. Scutellum removed	2	One vegetative, one shooting.
4. Scutellum and shoot apex removed	2	No plants obtained.
5. Scutellum and roots removed.	2	One with ear emerged, one shooting.
6. Scutellum and coleoptile removed.	2	One with ear emerged, one vegetative.
B. Vernalized 2 weeks		
1. Whole embryos	14	All vegetative.

By making a comparison with plants grown from whole embryos vernalized for two weeks, Purvis considers that the vernalization treatment has accelerated flowering, but that the process was less effective than in the case of complete embryos. (More details of this research are given in Chapter IX, p. 149.)

After Purvis had demonstrated that the embryo alone is concerned in vernalization and that the response to low temperature is confined to this organ, and Gregory and de Ropp (1938) had shown that the isolated

embryo cannot be vernalized by low temperature in the absence of a carbohydrate supply, de Ropp (1939) made a more detailed investigation of the conditions obtaining in a grain of Petkus winter rye during the first few hours of germination. These studies were concerned with the effect which soaking grain for different periods of time has upon the growth and tropic responses of the excised embryo. It is stated that the rye embryo is a complete biological system capable of making normal growth without the acquisition of any growth substances from the endosperm. This introduces the arguments for and against the hormonal interpretation of vernalization, discussed in Chapter X.

Having already shown (Gregory and Purvis, 1938b) that the excised embryo of rye when supplied with nutrient salts and glucose responded to vernalization in the same manner as the whole grain and to a comparable degree (confirming their own and Russian statements that the locus of vernalization lies within the embryo), Purvis (1944) has examined the effects of vernalization on agar media containing varying proportions of carbohydrates and nitrogen. The general conclusions drawn by the British workers is that the large accumulation of blastanin found by Cholodny (see p. 161) in the endosperm of maize does not play any essential part in the vernalization process; the embryo is capable of synthesizing any hormones that may be necessary for vernalization from external sources of carbohydrate in the presence of organic salts, with possibly the aid of additional substances already present in the embryo before imbibition.

Purvis enumerates the factors which can possibly participate in the vernalization process as follows:

(a) the embryo and its constituents;
(b) the source of organic carbon;
(c) the source of nitrogen and the mineral salts;
(d) the effect of low temperature.

In preliminary experiments in 1939 with varying amounts of carbohydrates and nitrogen, a difficulty was experienced in that even on media containing little or no sucrose some degree of vernalization was apparent, and this applied only to a few individual embryos. It appeared that quite small amounts of sucrose were adequate for vernalization and that a source of this sugar may have been available within the individual embryo, either as stored sugars or starch in the tissues or as starch grains adhering to the scutellum. A technique was therefore developed involving periods of starvation for the embryos at high temperature to remove available sugar by respiration and this successfully reduced the variability of the low sugar series, although it raised a further set of problems requiring investigation. The scope of the eighth study from South Kensington is, however, confined to a consideration

of the effect on vernalization of varying the carbohydrate and nitrogen supply, the effectiveness of various carbohydrates in growth and vernalization, and to a discussion of the results obtained 'within the limits imposed by the unforeseen difficulties of the experiment'.

Diagnosis of Completion of Vernalization

It has already been noted that the 'ripe-to-flower' condition cannot be recognized by any morphological characters in the plant, and how Purvis applies the 'minimum leaf number' interpretation to the study of the differentiation of flower primordia; it is stated elsewhere (p. 40) how the Russian physiologists correlate internal development with external morphology.

In research on vernalization in particular, it would obviously be an advantage to have some reliable method whereby it would be possible to decide when an embryo is completely vernalized, without waiting for the seedling to grow and demonstrate by its flowering behaviour which duration and temperature of treatment was most effective. The earliest time at which this can be decided on a morphological basis is when the flower primordia begin to differentiate. Bassarskaja, however, claims that it is possible by tissue treatment and staining to distinguish between vernalized and non-vernalized tissues of an embryo in a grain immediately after the low temperature treatment (see Imperial Agric. Bureaux, 1935).

Slides containing longitudinal sections of an embryo were treated with 5 per cent ferric chloride for 2 to 3 minutes, rinsed in water, dried with filter paper and then flooded with 5 per cent potassium ferrocyanide. The growing point of vernalized seeds is stated to have stained an intense blue, whereas the unvernalized seed remained unstained, or became yellow or green. The absence of Prussian blue in cells of unvernalized seeds may be due to one of two causes: either the ferric chloride does not penetrate into the cells, or it is reduced to ferrous chloride in the tissues. As the latter suggestion is confirmed by the formation of Prussian blue on the addition of potassium ferrocyanide, Bassarskaja considers it possible that vernalization produces a change in the oxidation-reduction potential of the cells. Wort (see p. 261) states that he was successful in using the same technique.

Temperature and Photoperiodism

The reaction of plants to lengths of day (photoperiods) is discussed in Chapter VI, but in this and the following section it is desirable to consider the relation of temperature to the light effect.



PLATE 7. Effect of night temperature on growth of tomatoes (see p. 84 and Table 6). Photo: Went, 1944.

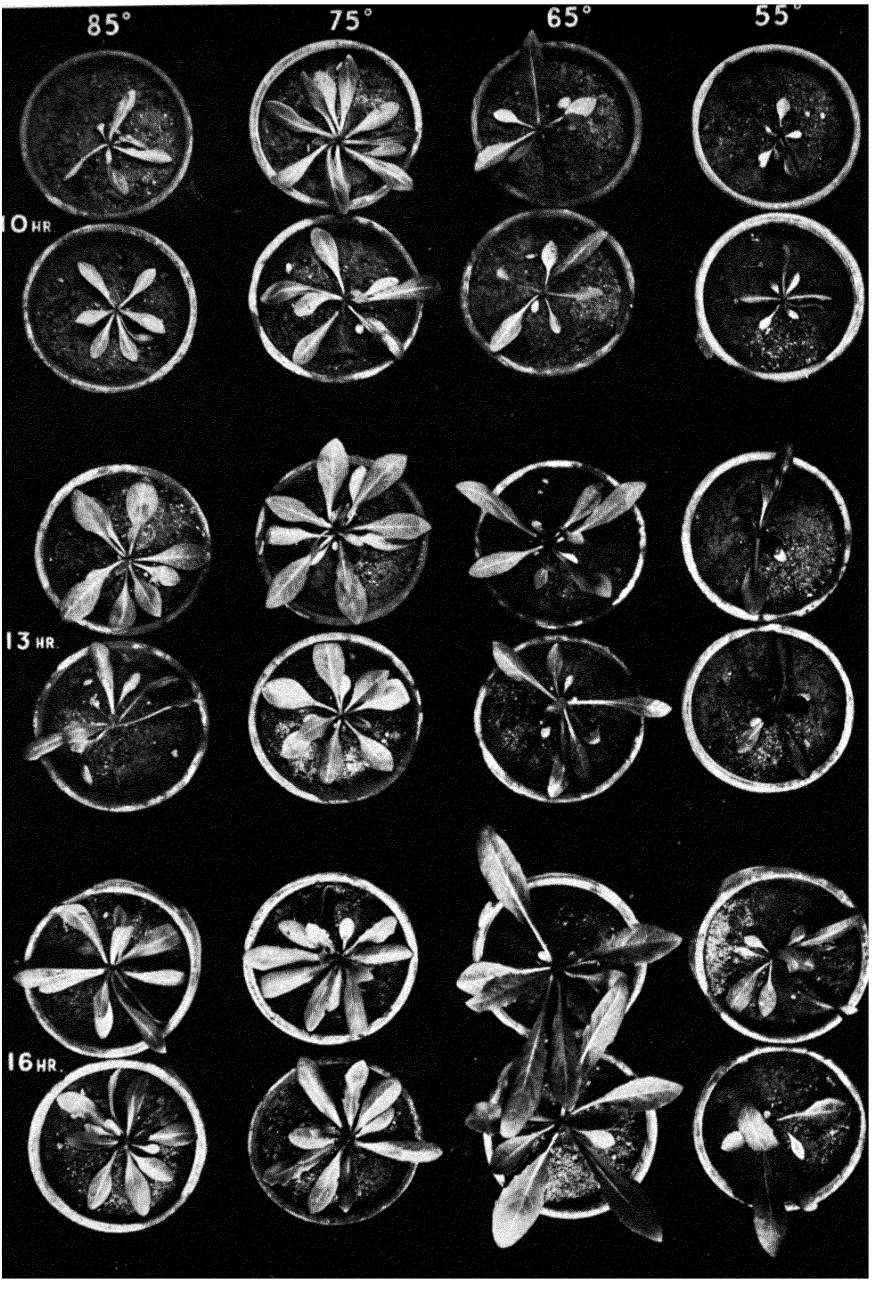


PLATE 8. Kok-saghyz seedlings after 29 days in growth chambers under conditions indicated. Only two or three small leaves present at beginning of experiment. Photo: Borthwick, Parker and Sculley, 1943.

Several workers on photoperiodism, notably Thompson (1939) and Hamner (1938), have stressed the need for correlating the effects of all environmental factors when studying the reaction of a plant to one particular factor. Thompson has stated that considerable confusion has arisen in environmental studies of growth type because of different methods of measuring response and disregard of other environmental factors. Not infrequently in studies of photoperiodism, temperature ranges are not accounted for, while it is known that some plants behave as 'long-day' plants at one temperature and 'indeterminate' plants at another temperature. When grown at optimal temperatures, plants may flower over a wide range of photoperiods. In studies of the effect of temperatures, no reference may be made to the light conditions.

In this connection, Hamner (1942) finds it necessary to modify Garner and Allard's classification of plants into long-day, short-day and other groups by saying that, in his own work, 'plants are considered as "long-day" or "short-day" plants if they fit Garner and Allard's classification under some set of environmental conditions and this particular set of conditions is assumed to prevail when the responses of such plants are discussed'. In this discussion, Hamner refers to certain responses, which it should be understood took place at a temperature between 65° and 75° F.

Some recent views and experiments on this aspect may be quoted.

In *Rudbeckia bicolor*, growth in height and sexual reproduction are initiated and maintained under a photoperiod exceeding 12 hours (Murneek, 1940). Reproduction can be induced by exposure to a certain number of long days, and floral organs will continue to develop and may function normally when transferred to short day. Stem elongation cannot be induced by but only maintained on long photoperiods. Growth in height stops as soon as plants are moved to short day. Murneek states that high temperature may be substituted for long day in the induction of *R. bicolor*, a species of more southern origin, but not in *R. speciosa*, a more northern species. Stem elongation is not fostered under short photoperiods by increase in temperature.

Parker and Borthwick (1943) studied the influence of temperature on the photoperiodic reactions in leaf blades of Biloxi soybean. When a leaf was held at 50° F. or lower during a 5-day induction period, floral initiation was greatly inhibited. At 70°–90°, such initiation was in general equal to that of the controls held at greenhouse temperatures, but at 90° or higher the extent of the initiation again was less. The inhibiting effect of low temperature on floral initiation in Biloxi soybean plant appears to be the result of its effect on the photoperiodic reactions occurring in the leaf blade during the dark period, rather than through its effect on translocation of a flower-inducing stimulus from the leaf to the terminal

meristems or its effect at the terminal meristems upon the differentiation and development of flower buds.

Temperature also has been introduced into the investigations of Rudorf and Schroeck (1941) on the photoperiodic reaction of a large assortment of soybean varieties at Muncheberg/Mark, and has been found to have a great influence on the strength of the reaction as measured by acceleration in flowering. It was also found that flowering can be greatly hastened by increasing the temperature in the early stages of growth. The effectiveness of treatment depends to a large extent on the temperature during treatment: with rising temperature flowering is increasingly hastened, independently of subsequent temperature and photoperiods. Under lower temperature also, photoperiodic treatment leads to the formation of the (still hypothetical) flowering hormone or to its preliminary stage, which cannot become operative, however, until there is a higher temperature. The variation in the strength of the reaction of different strains under lower temperature indicates a varying requirement of high temperature. The after-effect of treatment is expressed in morphological changes, difference in chlorophyll content (increased), dry matter content (slightly increased), and crude protein content (reduced) and in the number of flowers and grains formed (increased).

The percentage of seed stalks of turnips which develop at Cornell University in temperatures of between 50° and 80° F. varied inversely as the temperature. The longer the exposure to low temperature (15, 30 and 60 days), the higher was the percentage of seed stalks. Continuous exposure was more effective than alternating treatment. Low temperature is regarded as essential to flower initiation in turnips (Sakr, 1944). Photoperiods in excess of the normal daylength from March 3rd to May 1st had no appreciable effect on seed-stalk formation.

In view of these results which indicate, according to some interpretations, an obligatory thermo-phase, and to others an effect of photoperiods in association with temperature, Naylor (1941), has advised caution in interpreting results in terms of reaction to temperature or light. If conclusions are to be made regarding photoperiodic reaction, it is desirable to choose plants 'without a thermo-phase', that is which are not 'temperature-limited'. Dill (*Anethum graveolens*) and a variety of beet which differs from other beet varieties in this respect were selected for his own experiments.

Plate 5 shows a collection of seedlings of the Russian rubber-bearing dandelion, kok-saghyz, after they had been kept for 29 days in growth chambers at the temperatures indicated at the top and at daily photoperiods shown at the left. Only two or three small leaves were present on seedlings at the beginning of the experiment (Borthwick, Parker and Scully, 1943).

Plate 6 shows equipment for control of the temperature and photoperiod to which individual leaf blades can be exposed; A=interior of box showing leaves in position, B=exterior of box showing position of plants. In this experiment (Parker and Borthwick, 1943), each plant received photoperiodic induction (short days) at controlled temperature through one leaf inserted in the box, while the remainder of the plant received long photoperiods and fluctuating greenhouse temperature.

Plate 9 shows the effect of 16-hour photoperiods and several conditions of temperature on the growth of seedlings from four successive plantings of Wintex barley; the first planting is in the bottom row and the last in the top row (Borthwick, Parker and Heinze, 1941–2). In each case, an enlargement of the terminal of the main axis is shown at the right of the seedling from which it was dissected. The seedlings of the first column are 5, 10, 15 and 20 days old respectively, from top to bottom. Seedlings of second, third and fourth columns are all one week older than the corresponding seedlings of the first column. All seedlings were grown at 65° F. at all times except those of columns 3 and 4, which were transferred to 45° and 35° F. respectively, one week immediately prior to photographing.

Thermoperiodism

This term has already been used in the literature in connection with two different phenomena. Tetjurev (1940) has applied it to an alternation of low and high temperatures in the process of vernalization. Under natural conditions, seed are in many cases exposed to an alternation of temperatures favouring vernalization (night) with temperatures above the critical limit for passage through the thermo-phase.

Sprouted grains of winter wheat, Moskovskaja 02411, were vernalized at various daily alternations of low (0·5 to 5° C.) and high (15 to 20° C.) temperatures. In the first series, the seeds were kept under a daily alternation of high and low temperatures for 20 days and then continuously at low temperatures for 10 days; in the second series under daily alternations for 30 days and then at low temperatures for 10 days; in the third series under alternating temperatures for 40 days. The daily period of low temperatures ranged, according to the group within the series, from 2 to 24 hours. Complete heading, simultaneous with the control plants, was observed only in those plants which were vernalized at low temperatures for not less than 20 hours daily in the first series and not less than 22 hours daily in the other series (which received a total of not less than 880 hours of low temperature). Incomplete heading occurred in those plants vernalized at low temperatures for 20 and 18 hours daily in series 3; for 20, 18 and 16 hours daily in series 2; and for 18, 16, 14

and 12 hours daily in series 1 (which received not less than a total of 720 hours).

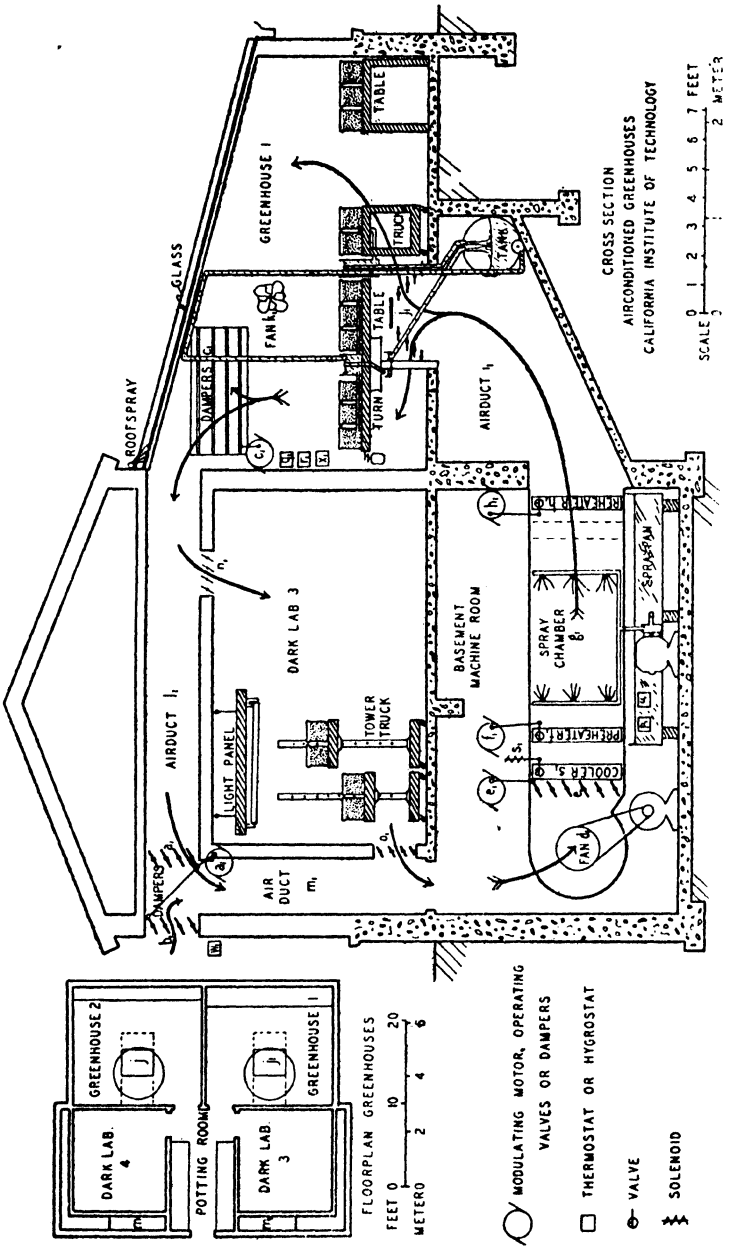


FIGURE 13

Air-conditioned greenhouse at the California Institute of Technology, Pasadena. Floor plan (left side faces north) and cross median section through house 1 and room 3. The usual discrepancy between plants grown in a greenhouse and those grown in the field is due to temperature differences in the two environments. By subjecting plants to a controlled temperature sequence similar to that of natural conditions, the same results and responses are obtained (see also Figures 14–18 and Plate 7) (Went, 1943)

Tetjurev considers that the incomplete heading he observed is due to a deficiency in the total number of hours at low temperature, and not to the shortness of the daily period of low temperatures, since in other experiments incomplete heading was observed in plants vernalized at low temperatures for 6 or even 4 hours per day. Grain can be fully vernalized

at alternating temperatures, but the minimum effective daily period of vernalizing temperatures (thermoperiod) has not yet been ascertained.

Using the special air-conditioned greenhouses erected at the California Institute of Technology (see Fig. 13 and Went, 1943), a series of experiments has been conducted which promise to emphasize to a greater extent than formerly the great and probably decisive role of temperature at all stages of a plant's life upon its development towards maturity. Complete air-conditioning of greenhouses by means of automatic controls was not perfected until about 1933. Simple arrangements such as ventilators, shades, various types of heating systems, roof sprayers and humidifiers helped to narrow the range of extreme fluctuations in temperature, but it was not possible to maintain even an approximation to constant conditions of temperature and humidity in relation to light intensity.

The principle upon which the temperature and humidity control of the air-conditioned greenhouses rest is as follows.

First, humidification of the incoming air in a spray chamber. In warm weather this cools the air to near the wet-bulb temperature. By controlled heating of the air in a pre-heater before it enters the spray chamber, the temperature of the saturated air, after passage through the spray chamber, can be maintained at any point above the wet-bulb temperature of the outside air. After the spray chamber the air passes through another heating element (re-heater), which brings the dry-bulb temperature of the air to the desired point. In one of the two separate air-conditioning systems a refrigeration machine can pre-cool the air before it enters the pre-heater, and, thus, either low temperatures or low humidities can be maintained in this system throughout the year. By maintaining a sufficiently rapid air movement through the greenhouses and by screening out part of the heat radiation of the sun through a thin film of water sprayed over the glass top of the houses the inside temperature does not rise much above the set temperature, even on warm sunny days.

Research in the greenhouses at Pasadena began with the determination of optimal growing conditions, and in the course of this work it was discovered that a subjection to different day and night temperatures gave better growth than the maintenance of a constant temperature. Changes in the external conditions were almost immediately reflected in changes in the growth rate of the tomato variety that was selected for experiment. During this work it was found that humidity, length of photoperiod, light intensity, mineral nutrition, root temperature, watering root medium, etc., could be varied within comparatively wide limits without significantly changing the rate of stem elongation and the setting of fruit. On the other hand, small differences in temperature caused significant

differences in growth and set of fruits. Closer analysis revealed the phenomenon of thermoperiodicity; optimal growth occurs in tomatoes when the temperature during the dark night period is lower than during the daily light period. The name, thermoperiodicity, is proposed by Went to include all effects of a temperature differential between light and dark periods on responses of a plant, whether they be flowering,



FIGURE 14

Effect of temperature and photoperiod on the California desert annual, *Baeria chrysostoma* var. *gracilis*, a botanical Drosophila. A = normal plant. B = grown at 22° C. in continuous light, 25 days after germination (Sivori and Went, 1944)

fruiting or growth. The phenomenon does not apply only to tomatoes, having also been noted in species of *Achillea*, *Potentilla*, many southern California annuals, and in hybrids of *Phalaenopsis amabilis*. In guayule (*Parthenium argentatum*), practically no rubber was formed in plants kept continuously at 26·5° C. or 7° C. but those exposed to 26·5° C. during the day and to 7° C. during the night formed an optimal amount of rubber (Bonner, in press).

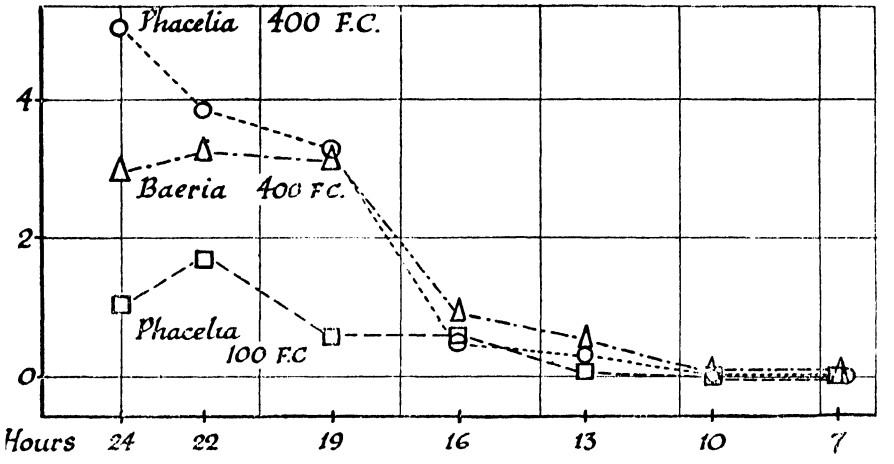


FIGURE 15

Relation between length of photoperiod (abscissa, in hours) and flowering of *Baeria chrysostoma* (triangles) and *Phacelia parryi* (circles = 400 foot candles; squares = 100 foot candles (Sivori and Went, 1944)

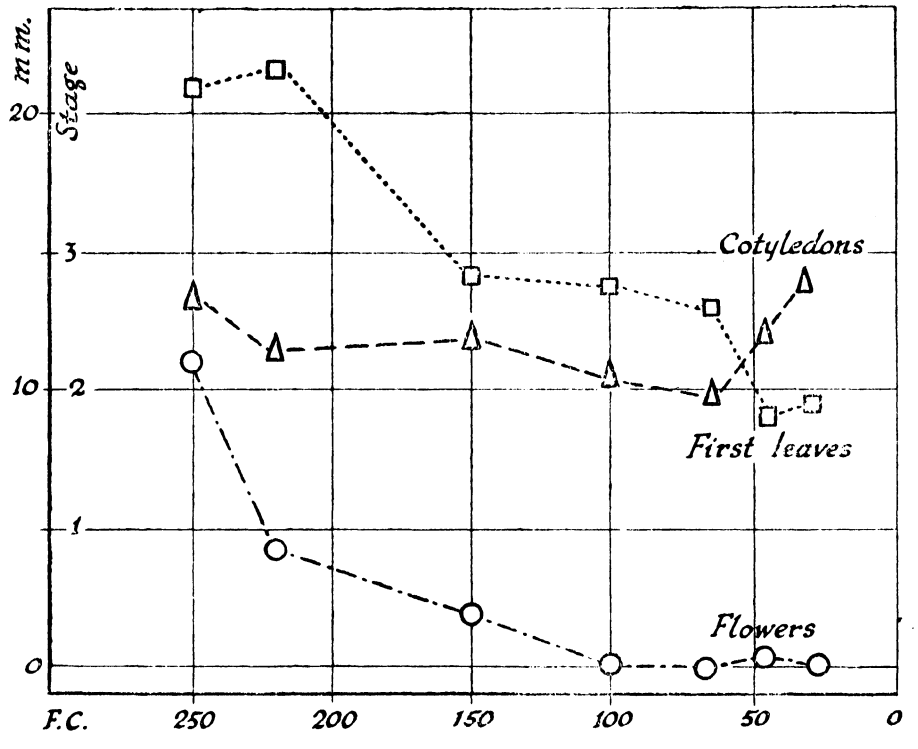


FIGURE 16

Length of cotyledons (triangles) and first leaves (squares) of *Baeria* plants grown at 22° C. and continuous light of different intensity (abscissa, in foot candles). Flowering also plotted (circles) in terms of stage reached (ordinate, O = vegetative) (Sivori and Went, 1944)

In Went's experiments (1944b), when tomato plants are grown in a constant temperature 24 hours per day, the optimal temperature lies well above 20° C. At 26·5° C. a steady growth rate of 23 mm. a day is reached when the plants are 30 cm. tall, which rate is maintained as long as the plants are kept trimmed to one stem. Plants grown at lower temperatures have consistently lower growth rates. But plants kept warm during the day (26·5°) and cool during the night (17–20°) grow more rapidly than any of the other groups (27 mm. a day). The lower temperature is effective only when maintained during the dark period.

Approximately the same temperature relation holds for fruit development. Fruit set is abundant only when the night temperatures are between 15 and 20°; with lower and higher temperatures during the night, fruiting is reduced in amount, or even absent. Artificial light when applied during the cool night period completely inhibits fruit formation. (See Table 6.) Plate 7 shows typical plants of groups A, B and C. All plants received a uniform day temperature of 26·5° C. The two plants at the left received a night temperature of 26·5° C., those at centre 10° C., and the two at the right 4 to 5° C. All plants were 20 cm. tall when treatment began on 20th October (metre stick at left); photo taken on 25th November (Went, 1944b).

TABLE 6

Growth of the tomatoes shown in Plate 7 during the period from November 3 to November 24, 1942. The last figures refer to other tomatoes grown in four gallons of gravel per plant, and watered automatically with nutrient solution three times daily.

	Temperature in C°.		*Stem growth in length in cm. in 21-day period*	
Group	*Day 8 a.m.–4 p.m.*	*Night 4 p.m.–8 a.m.*	*Individual plants*	*Mean*
A	26·5	4–5	Watered by hand, 8, 9, 10	9·0
B	26·5	10	Watered by hand, 20, 21, 21, 22, 22, 25, 27	22·6±0·9
C	26·5	26·5	Watered by hand, 40, 43, 43, 44, 45, 49, 50, 57	46·4±1·9
D	26·5	26·5	Automatic watering, 38, 39, 39, 43, 46, 46, 47, 47, 49, 49, 52	45·0±1·4

The conclusion reached as to the basic processes which cause and control thermoperiodicity is as follows (Went, 1944a):

The high optimal temperature during the day is due to the temperature effect on photosynthesis. The lower optimal night temperature is due to the interaction of two factors. Below 18° C. (in tomatoes) the actual growth process is limiting (tomatoes grow mostly at night). This has the typical temperature coefficient of a chemical reaction. Above 18° C., translocation of food (mainly sucrose) becomes limiting. The temperature coefficient of sugar translocation is less than 1. (This interpretation explains phenomena known to gardeners in connection with cool or warm nights—guttation, anthocyanin in growing tip, etc.)

The third paper in the series from Pasadena deals with the correlation between various physiological processes and growth in the tomato plant (Went, 1944c). Table 7 gives an indication of the type of data obtained at different day and night temperatures.

TABLE 7

Summary of the effects of day and night temperature on some physiological processes in the tomato. For the sake of comparison all processes or substances were graded from 1=very slow or very little to 5=very fast or very much. Temperatures in C°.

	Day temperature			*Night temperature*		
	8	18	26·5	8	18	26·5
Stem elongation when whole plant is subjected to the temperature indicated	1	4	5	2	5	4
Fruit growth	0	4	4	0	5	2
Stem elongation when only growing zone is subjected to the indicated temperature	–	–	–	(1)	3	4
Stem elongation when only roots are subjected to the temperature	–	–	–	–	4	4
Elongation of excised roots (White, 1937)	–	–	–	0	2	4
Translocation	–	–	–	5	4	2
Photosynthesis	2	4	5	–	–	–
Stomatal opening	–	4	4	–	0	0
Phosphate uptake	–	3	4	–	3	3
Sugar content of leaves in morning	–	3	3	–	2	4
Auxin content and production	–	5	5	–	5	5
Suction force	–	3	3	–	–	–

TABLE 8

Behaviour of Californian annuals (Lewis and Went, 1945).

Condition	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
Day temperature in degrees C. (8 a.m. to 4 p.m.)	19	19	19	19	19	19	19	19	19	19	26½	26½
Night temperature in degrees C. (4 p.m. to 8 a.m.)	19	19	19	19	19	7	26½	26½	13	7*b*	13	26½
Photoperiod in hours*a*	8	12	14	18	24	8	8	10	10	10	10	10
Baeria chrysostoma	57	69	47	40	32	B	0	0	103	–	97	0
Baileya multiradiata	–	–	–	–	B	–	0	–	–	–	–	X
Coreopsis californica	B	B	77	54	43	B	–	–	B	–	B	–
Eschscholtzia californica	–	–	–	98	56	–	–	–	–	–	–	–
Eschscholtzia lobii	B	B	99	59	72	B	–	–	–	B	–	99
Gilia tricolor	–	80	B	79	80	–	80	87	B	–	–	89
Godetia quadrivulnera	–	–	B	97	85	–	0	X	–	–	–	0
Linanthus montanus	–	–	–	74	56	–	–	0	–	–	–	0
Madia elegans	76	–	B	81	64	–	0	0	–	–	–	0
Mentzelia lindleyi	–	B	B	63	65	–	0	0	–	–	–	0
Monardella lanceolata	–	–	–	B	B	–	–	–	–	–	–	X
Oenothera deltoides	–	–	–	–	–	–	–	–	–	–	–	–
Phacelia parryi	–	B	65	43	33	–	–	B	B	–	B	–

Numbers represent days required for first flower to bloom.

B=flower buds initiated at the end of the experiment (103 days).

0=plants dead.

X=plants visibly unhealthy.

a The first 8 hours in conditions 1 through 7 are natural daylight; light for the additional hours was supplied by G.E. daylight fluorescent bulbs and Cooper-Hewitt lamps giving a combined intensity of 450 f.c. Conditions 8 through 12 were exposed to a natural length day which was approximately 10 hours during this experiment.

b From 4 p.m. to 8 p.m. the temperature was 13° C.

The possible application of thermoperiodicity to the cultivation of tomatoes in the open is discussed on p. 309. Plants planted out in the field in California in the middle of November and covered each day from 3 p.m. to 7 or 8 a.m. produced ripe fruits from April 1st onwards (Went, 1945).

The most recent report available on the work in the air-conditioned greenhouses at Pasadena is that by Lewis and Went (1945) on the Californian annuals noted above (including some potential botanical Drosophilas). The species used and an idea of the treatments given are indicated in Table 8.

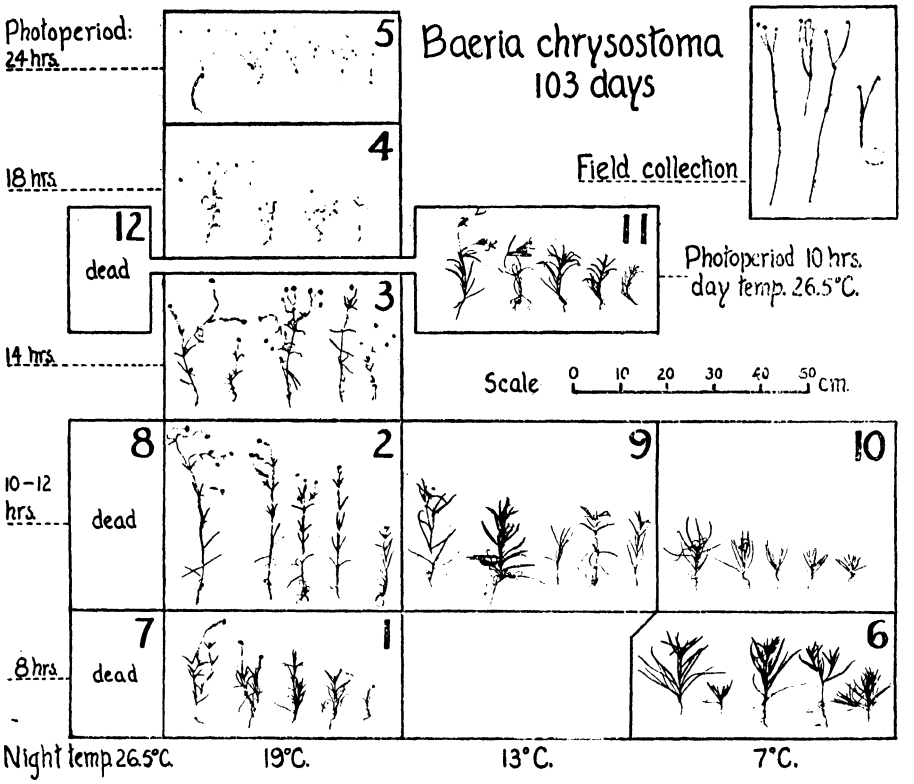


FIGURE 17

Relation between photoperiod and night temperature. Development of *Baeria chrysostoma*; plants harvested 103 days after sowing. For each condition, 6 to 10 plants are shown, representing the range of variability. Photo in upper right-hand corner shows the original plants from which the seed stock used was collected. For treatments and results see Table 8 (Lewis and Went, 1945)

Annuals were used because they complete their life cycle within a few months and differences in response between juvenile and mature plants can thus be observed in an experiment of 14 weeks' duration. All but two

of these annuals proved to be long-day plants. In several cases the size of the leaves is directly correlated with the length of the photoperiod.

Day temperatures seldom produce any differences in response, whether of flower initiation, size of leaves or rate of leaf production. Night temperature, on the other hand, has, in general, a pronounced effect upon the rate of leaf production and also upon leaf size. The rate of leaf production remains constant throughout the vegetative develop-

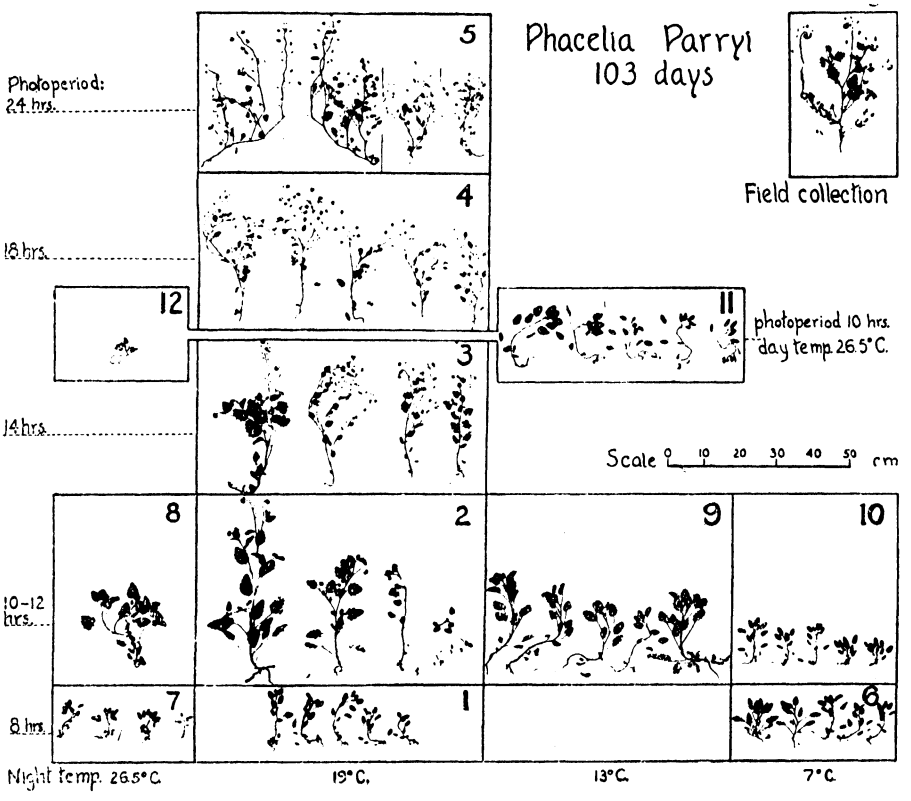


FIGURE 18

Relation between night temperature and photoperiod. Development of *Phacelia parryi*; plants harvested 103 days after sowing. For treatment and results see Table 8 (Lewis and Went, 1945)

ment of the plant so long as the night temperature remains constant. There is, in general, a shift in optimal conditions for the production of largest leaves.

The morphological modifications are of two kinds, namely differences in size and differences in habit. The differences in habit are attributable to differences in time of flower initiation. Comparison of leaves produced at a given node showed no differences in proportion, pubescence, venation or margin beyond those to be expected in a random sample from a

natural population. The modifications described are not of the kind or magnitude which would ordinarily influence a taxonomist.

It is obvious that under these conditions in which the entire environment can be controlled, a refinement on transplant experiments such as those of Bonner (1890, 1895, 1920), Hall (1932), Turesson (1922, 1925, 1930), Clausen, Keck and Hiesey (see Washington, 1940), and Marsden-Jones and Turrill (1935, 1937, 1938), in which the effect of different natural climates was investigated, an important advance will be made in the comparison of responses in nature with those in a greenhouse of the Pasadena type, and ultimately in studies of plant distribution and the nature of species. The natural environment of the transplant experiments that is now replaced is the sum total of numerous fluctuating and uncontrollable factors which vary from year to year; the morphological modifications induced by varied environments of this type cannot be attributed to any particular factor with any degree of certainty.

It might have been expected that Lewis and Went would have been able to correlate the response of their Californian annuals with their responses in nature and to find some of the factors effective in limiting their distribution, but this was not so. The limits used in the various treatments are stated to be not sufficiently wide. It is also considered that other factors such as water relations may be of greater importance than light and temperature. To analyse the factors which limit the distribution of a species, Lewis and Went state that it would be necessary to use a series of samples from different regions rather than a single sample, as was the case in their experiment, and it would be necessary to have a complete set of phenological and meteorological data of the appropriate type concerning the races under investigation.

CHAPTER V

DEVELOPMENT BEFORE SEED DORMANCY

Seed obtained from an ear on a parent plant only 5 days after fertilization has been found to be capable of germinating and ultimately producing perfectly normal plants. It is to be expected that a plant may from this very early stage in its life history begin to respond to the environment in which it finds itself while ripening on the mother plant. It is now well established both by observations made under natural conditions under wide variations of latitude and by experiments that it is possible for a plant organism to receive part or all of its low temperature requirement or to be vernalized during the period between the formation of the zygote and the entry of the ripe seed into a state of dormancy.

The discovery that developing seeds respond to environmental conditions while still attached to the mother plant makes it essential to give careful consideration to the environment, and particularly to the temperatures experienced before harvest. For example, the recommendations made regarding the duration of temperature treatment required for the vernalization of many crop plants may have to be revised. But more important is the possibility that the anomalous behaviour of some varieties when imported from one environment (particularly latitude) to another may be explained; a late variety may become earlier and an early one later according to the degree to which the old or the new environment provides the low temperature quota for the particular variety before the seed becomes ripe on the mother plant.

Two Russian investigators, Kostjučenko and Zarubaĭlo reported natural vernalization in varieties of wheat, and Gregory and Purvis independently demonstrated the fact experimentally. Later, the same Russian workers, as well as others, described the phenomenon in a number of crop plants. Some Russian investigators have referred to a phase preceding the thermo-phase, when conditions other than low temperature are claimed to be decisive; if such a phase exists, its completion might also be expected to occur before the seed becomes dormant.

Natural Vernalization of Grain During Ripening

In two Russian articles, and subsequently in an English translation, Kostjučenko and Zarubaĭlo (1935, 1936 and 1937) described the obser-

vations and experiments which led them to attach such importance to the possibility of vernalization during seed ripening.

EXPERIMENT AT HIBINY

In the spring of 1935, a comparative trial of several varieties of winter wheat was laid down at the Polar Experimental Station of the All-Union Institute of Plant Industry (V.I.R.) located at Hibiny. The grain used for this trial had been grown in two localities which differ sharply in environmental conditions, namely, Hibiny itself, at 67° 44′ N. Lat., and Kirovobad, at 40° 41′ N. Lat. There was a slight but not significant difference in the actual time of sowing, the Hibiny grain being sown on May 27th and the Kirovobad grain on May 31st. In both sowings, vernalized and unvernalized grains were used.

In September of the same year, a marked difference could be seen in the development of each variety, when the plants grown from grains of different origin were compared. Plants from Kirovobad grain, artificially vernalized, were then at the milk-ripe stage, while their unvernalized counterparts were at the tillering stage. Plants from Hibiny grain, also artificially vernalized, were almost at the stage of wax ripeness, while plants from the same grain, not artificially vernalized, exhibited partial or complete flowering (Fig. 1, *Herb. Rev.*, Vol. 5, p. 156); some of them had set seed in the ears of the main stem, while other tillers were at various stages of maturity.

Thus, these varieties of Russian wheat, generally regarded as winter forms, behaved as spring forms when grown from grain which had been ripened in Hibiny, whereas they retained their winter habit when grown from Kirovobad grain. Kostjučenko and Zarubaĭlo conclude that the Hibiny grains had passed their 'stage of vernalization' under the natural conditions of these northern latitudes, while the Kirovobad grains had not done so, and still required artificial vernalization before they could reach maturity in one season. It was assumed that the embryos of the Hibiny grain were vernalized by low temperature while still attached to the mother plant. An embryo which has not entered the dormant state may be as sensitive to vernalization as an embryo brought from the resting condition by soaking.

Dormancy, state Kostjučenko and Zarubaĭlo, is merely an interruption in the development of the plant organism, which begins on the mother plant and recommences as soon as the seed begins to germinate. Dormancy is characterized by a fall in the vital activity of the embryo to a minimum, and by a maximum increase in its insensitivity to environmental conditions.

EXPERIMENT AT PUSHKIN, NEAR LENINGRAD

In order to confirm their first observations and assumptions, Kostjučenko and Zarubaĭlo conducted another series of experiments in 1936 at the Experimental Station of the Institute of Plant Industry, Pushkin, Leningrad. The first objective was to ascertain whether the difference in development between seeds of different geographical origin observed in 1935 was due to the difference in the conditions under which the grain had been grown, or to other causes.

Results of a comparative trial in which grain of winter wheat varieties grown and ripened in Hibiny and Kirovobad respectively were sown together in the Leningrad latitude on 29th May 1936 fully confirmed the observations made at Hibiny in the previous year. Plants from Kirovobad grain, artificially vernalized for 20 days, did not ear, and passed the following winter at the tillering phase after having been in the field throughout the summer and the autumn. Plants from Hibiny grain, which had also received 20 days' artificial vernalization, eared in July of the same year.

EFFECT OF DATE WHEN GRAIN RIPENS ON MOTHER PLANT

In order to ascertain that this difference in development was actually caused by the effect of low temperature upon the ripening grain, and not

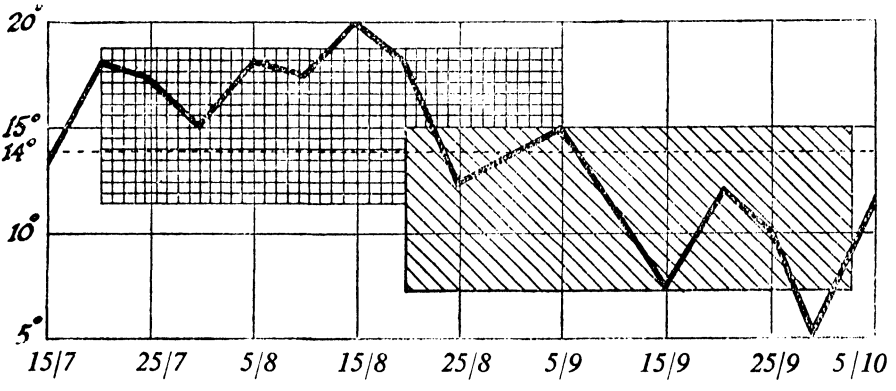


FIGURE 19

Relation of temperature during the ripening of seed in the ear of the mother plant to the behaviour of the subsequent plants. The mean 10-day temperatures during August to September at Pushkin, near Leningrad (Kostjučenko and Zarubaĭlo, 1937)

by differences in other factors, such as the length of day (characteristic of the widely separated latitudes in which the grain had been reproduced), grains of winter wheat raised in Pushkin in 1935 and which had ripened at different times were also tested alongside the grains from Hibiny and

Kirovobad. Early season grains ripened in Pushkin in August, late-season grains in September. The 10-day mean temperatures recorded during these periods are shown in Fig. 19. The authors recognize that the length of day was also changed, but note that, in the Pushkin grains, lower temperatures were linked with the *shorter* days of September, whereas in the experiments with grain of different geographical origins lower temperatures were linked with the *longer* northern day earlier in the season.

Grain from these early and later ripenings were sown at Pushkin in the spring of 1936 at the same time and on the same land as the grain reproduced in different latitudes. The grains which had ripened in the previous autumn at the lower temperatures showed a much reduced requirement for vernalization, as compared with those which had ripened at the higher temperatures of the early part of the period indicated in Fig. 19. It is, therefore, concluded that temperature is the decisive factor.

An examination of the temperature curve given in Fig. 19 shows that the early season grains ripened at mean temperatures above 14° C., while the late-season grains ripened at temperatures below that level. The authors conclude, therefore, that a vernalizing effect on ripening grain of winter wheat is produced by temperatures below 14° C. It should be noted, however, that this is a mean figure, and does not indicate the total number of hours during which the effective temperature for vernalization (probably lower than 14° C.) would be operative.

Early grains, ripened during August 1935, were left on the field and harvested at the same time as the late grain; they were thus subjected to the effect of low September temperatures, but were not affected owing to their fully ripe condition. Low temperatures are said to act only on ripening grain, which are in the milk-ripe or wax-ripe state, and contain an active embryo. Capacity to react decreases as dormancy approaches.

BEHAVIOUR OF GRAIN FROM HIBINY AND CRIMEA, WHEN GROWN AT PUSHKIN

The same investigators then proceeded to ascertain whether their results actually meant that vernalization was occurring, or whether it was a question of a shortening of the vegetative period in general. To decide this, spring varieties of wheat were tested alongside winter varieties, using grains raised at Hibiny and in the Crimea (Nikita Botanic Garden, Jalta, at 44° 31′ N. Lat.). The temperature at which the Hibiny and Nikita grain had ripened are shown in Fig. 20.

The varieties were chosen to include those not normally responding to artificial pre-sowing vernalization, as well as others which show a varying response. It was assumed that, if the ripening of grain (on the mother plant) at low temperatures can shorten the vegetative period as a whole, irrespective of the 'stage of vernalization' (thermo-phase), this reduction

must to a varying degree take place in the plants of all varieties grown from grain originating from Hibiny, irrespective of the length of the 'stage of vernalization'. If, on the other hand, vernalization has actually occurred, the vegetative period in plants from Hibiny grain should be curtailed only in those varieties with a relatively long stage of vernalization (that is, those requiring a large number of hours below the critical

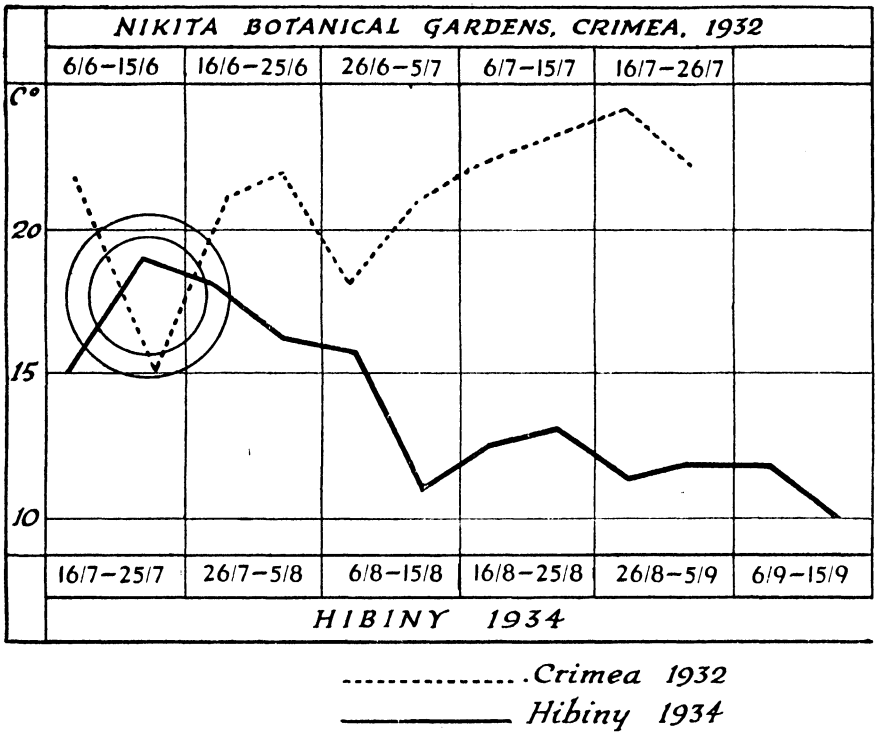


FIGURE 20

The mean 5-day temperatures at which the seed of the Hibiny (Northern U.S.S.R.) and Crimean reproductions in the experiments of Kostjučenko and Zarubaĭlo (1937) formed and ripened. Period of earing indicated by circles.

vernalizing temperature for that variety), and the reduction should be in proportion to the length of this stage. The results of this experiment are given in Table 9.

Varieties which do not normally respond to artificial vernalization show no response to the difference in the conditions under which the grain ripened. Varieties which normally respond to artificial vernalization also showed a reaction to the lower temperatures under which their grain had ripened at Hibiny. The authors therefore conclude from this and the other experiments that the vernalization of grain during seed ripening has been established.

TABLE 9

Acceleration in earing due to artificial vernalization and the dates of earing of plants from seeds of spring wheat of Hibiny and Crimean reproduction.

Name of variety or sample	*Acceleration in earing due to pre-sowing vernalization in days*	*Dates of earing*		*Acceleration in earing of plants from Hibiny seeds as compared with the plants from Crimean seeds*
		Plants from Hibiny seeds	*Plants from Crimean seeds*	
Tulun ZA/32 var. *ferrugineum*	1 (0)	June 30	June 29	–1 (0)
19576 Abyssinia var. *erythroleucon*	1 (0)	June 28	June 28	0
24390 India var. *pseudo-meridionale*	1 (0)	June 26	June 26	0
5466 China var. *erythrospermum*	5	June 28	July 3	5
14335 Iran var. *ferrugineum*	8	June 28	July 7	9
17342 Palestine var. *erythrospermum*	7	June 27	July 6	9
12605 Afghanistan var. *erythrospermum rigidum* (semi-winter)	20–30	July 2	July 30	28

Vernalization of Developing Embryos

Gregory and Purvis (1936 and 1938), after their experiments on the vernalization of excised embryos (p.152), studied the effect of vernalization on developing embryos and immature ears. Having shown that the vernalization process occurred in the embryo apart from the endosperm, it appeared possible to apply the low-temperature treatment after anthesis, while the embryo is developing, and before the onset of dormancy.

A preliminary experiment was performed in 1935, when the ripening ears were chilled by two methods.

(1) The ears together with several nodes of the stem were cut off and kept in water in a refrigerator for 5 weeks at 1° C. Control ears similarly treated were kept in a dark room at normal temperature until the grain ripened off. After the low-temperature exposure the treated ears were allowed to complete ripening at room temperature.

(2) The second method consisted in treating ears attached to the plant. The selected ears after anthesis were inserted into wide glass test-tubes, plugged with cotton-wool. In one set these tubes were placed in the necks of vacuum flasks containing crushed ice. The ears were thus kept at low temperature but did not come into contact with free water. Control ears were similarly treated and placed in vacuum flasks but without ice. The arrangement is shown in Plate IX, Fig. 2 of Gregory and Purvis (1938). After 24 days the ears were removed and allowed to ripen normally in the open air.

The ripe grains obtained from plants thus treated in 1935 were sown on 17th March 1936 in pots of sand, without further low-temperature treatment. Flowering was irregular, especially in those plants resulting from grain which had been treated in vacuum flasks, where the duration of the treatment was less than that known to be optimal for vernalizaing (see Table 10), and results sufficiently encouraging to warrant repetition of the experiment in the following year, when longer periods of treatment were used.

TABLE 10

Effect of Vernalizing Developing Ears of Petkus Winter Rye, 1935.

		Days from planting to anthesis in resulting plants	
Method of treatment	*Time of treatment*	*Ripened at 1° C.*	*Ripened at normal air temperature*
Cut ears in water	5 weeks	102	146
Attached ears in vacuum flasks	24 days	110	164

When a larger number of ears was treated in 1936, the ears were placed in a refrigerator while still attached to the stem, and in some cases whole plants were treated in this way. The period of chilling was increased to 45 days, and final ripening was carried out at medium temperatures. The ears were air-dried and the grain sown on 31st May 1937 without further treatment with low temperature.

The results shown in Table 11 indicate clearly the marked effect of the low-temperature treatment during the previous season, although Gregory and Purvis note that not all the treated grains had attained the vernalized state. Only 38 per cent of the treated grains produced plants with fully emerged ears, although others were approaching that stage.

In the last column of Table 11, the stage of maturity actually reached

TABLE 11

Vernalization of Growing Embryos in the Developing Ear of Petkus Winter Rye, 1936.

		Condition of plants 15 weeks after planting		
Treatment	*No. of plants*	*Stage of flower initiation*	*Stage of fully formed ears*	*Maturity in conventional units*
Vernalized	156	65 per cent	38 per cent	53
Control	49	49 per cent	0 per cent	24

is expressed in conventional units, which were derived from the approximate durations in days of the successive stages of morphological development reached by the spike of fully vernalized plants. The actual values employed are shown in Table 12.

TABLE 12

Conventional Units for Evaluating Stage of Development reached by Spike.

	Units
Simple ridges—very short spike	10
Simple ridges—very long spike	15
Double ridges	21
Ridges swelling	24
Lateral initials branching	26
Flower initials appear	28
Stamen	30
Stamen lobes appear	33
Awns growing	35
Spike elongating, stamens covered by palea	37
Spike emerged from last leaf	39
Anthesis	49
Past anthesis	49+number of days from anthesis to time of examination

Each plant was dissected at the time of examination; the stage reached by the meristem of the main axis was determined and allotted a 'score' on the basis of the figures in Table 12. The mean scores obtained by Gregory and Purvis are shown in the last column of Table 11.

Effectiveness of Chilling and Age of Developing Embryo

The results obtained by Gregory and Purvis on this point lead to the same conclusion as that reached by Kostjučenko and Zarubaĭlo with regard to the sensitivity of an active embryo and insensitivity of a dormant one. Gregory and Purvis (1938) dated the ears at anthesis and thus determined the age of the treated embryos. The results of the experiment, presented graphically in their paper, were grouped into 10-day classes covering the period from 5 days to 35 days after anthesis. The treatment is effective from the earliest stage of the development of the embryo, decreasing in intensity as beginning of treatment is delayed. Low temperature is therefore effective only while the embryo is actively growing, and ceases to be operative when the embryo becomes dormant. Gregory and Purvis conclude that the effect is quantitative depending on the duration of the exposure to low temperature, as had been shown to be the case in normal vernalization (Purvis and Gregory, 1937).

Further Studies on Immature Ears and Developing Embryos

An important result which probably indicates how early a developing embryo is fully sensitive to environmental conditions is that obtained by Gregory and Purvis (1938), who showed that seed obtained from ears removed from the parent plant as early as 5 days after anthesis germinated after being sown in the following spring. Completely normal plants were produced, although the individual immature grains were very small (4 × 1 mm.) and had apparently no reserves.

When winter rye was used, the plants grown from seeds having a range of maturity of 5 to 50 days showed no difference in the stage of development reached after 17 weeks. As the plants had not been vernalized, no ears emerged. In spring rye, on the other hand, a variation was found in the days from germination to anthesis varying from $51{\cdot}8 \pm 1{\cdot}17$ days (mean of ten plants) in completely matured seeds, to $62{\cdot}7 \pm 0{\cdot}91$ days (mean of three plants) in grain from ears removed 11 days after anthesis, the earliest removed ears to give viable grain. A decrease in the time taken to flower is correlated with maturity of the ripening grain. Gregory and Purvis suggest the possibility of partial devernalization of the very immature grains of spring rye.

Later studies made at the Research Institute of Plant Physiology, London, have been concerned with a more detailed investigation of the processes occurring in the embryo-sac of a cereal subsequent to fertilization, and of the conditions of formation and the subsequent growth of

dwarf embryos of rye. Nutman's account of the former investigation (1939) is concerned with the anatomical and cytological evidence for the formation of growth-promoting substances in the developing grain of rye. In a later paper, Nutman (1941) describes the formation of the

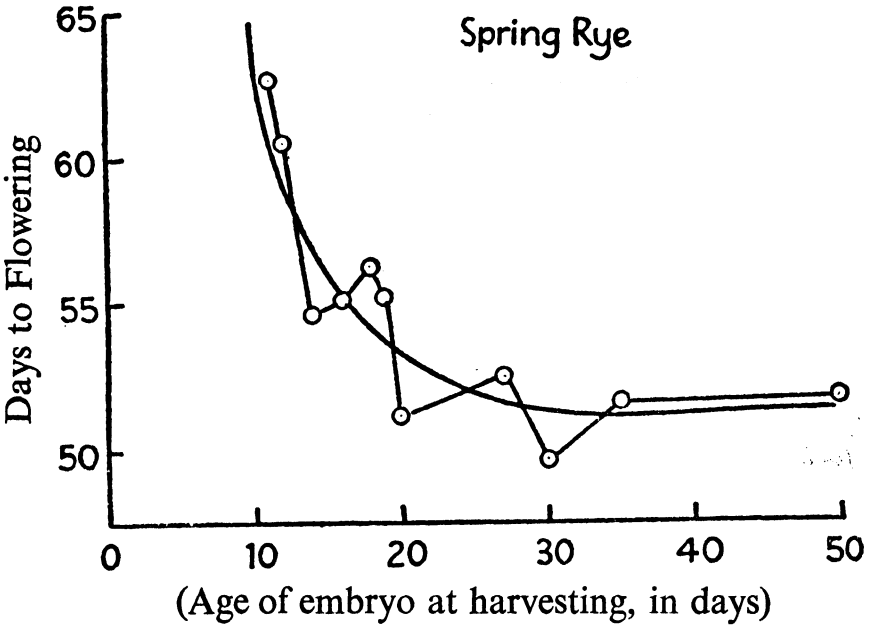


FIGURE 21

Flowering of plants from immature grains of spring rye. Relation between age of embryo at harvesting and time to flowering in resulting plants. Progressive decrease in time to flowering is shown with progressive maturity of the grain (Gregory and Purvis, 1938)

dwarf grain of rye in ears harvested at an immature stage, and compares the morphology and anatomy of dwarf and normal grains and embryos. He confirms observations made by Gregory and Purvis with rye, and earlier by Harlan and Pope with barley (1922, 1926) that ears removed from the plants as early as 5 days after fertilization produce viable grain.

Relationship Between Pre-Dormancy Vernalization and Varietal Composition

The facts so far established are considered by Kostjučenko and Zarubaĭlo (1937) to be of great importance in the setting up and interpretation of varietal tests. It is obvious that, in such tests, only seeds which have been produced locally for at least one generation should be used, and even here, the conditions under which they were formed and ripened

must be considered in order to avoid false conclusions. If the use of imported seeds is unavoidable, these same conditions should again be known fully. This is particularly important when dealing with plants from northern latitudes, where the period of seed setting and ripening frequently coincides with a season of low temperature. The same variety may in one year be early and in others very late, according as to whether the conditions during ripening in the previous season were such as to vernalize the developing embryos, that is, to provide them with their requirement of low temperature.

Even in less extreme latitudes, this factor has to be taken into consideration. It is possible to imagine that varieties of, say, Welsh oats might receive quite a considerable proportion of their requirement of hours of temperatures below the critical maximum, particularly if they had been formed at higher elevations under the temperate and frequently quite cool autumn temperatures of their home country.

If this hypothetical variety grown under such conditions is transferred in the form of grain to a different habitat, say, South Australia, it may appear in the first season to be a reasonably early variety, since the embryos are still in the partially vernalized (developmentally older) state produced by the environment while they were ripening in the Welsh hills. But when the next generation of grains is forming on the first generation plants grown from the imported grain, the conditions may be (theoretically) such as to preclude the possibility of natural vernalization of the developing embryo before dormancy. The variety which was generally regarded as early in Wales, and would have been recorded as early in the first generation in Australia, now acts as a later variety. If this example should be substantiated, and there is some evidence to this effect, it raises the whole question of locality for production of seed in relation to its place of cultivation, particularly with regard to wide changes in latitude or elevation between the two localities.

Pre-Dormancy Vernalization and Biological Characters

The most important aspect to be considered under this heading is the effect of natural, and particularly pre-dormancy vernalization, on the degree of winter hardiness of a particular variety. In Chapter XIII, the evidence is presented for the view that plants show a reduction in winter hardiness according to the degree of their completion of the thermophase, or according to the degree to which they have been vernalized. If this evidence is substantiated, then it is clear that, again, the possibility of pre-dormancy vernalization must be considered in making field or plot observations upon this character. Otherwise, say Kostjučenko and Zarubaĭlo, a variety may quite inexplicably be quite hardy over one

winter, due to absence of vernalization in the pre-dormant stage of embryo development in the preceding late summer-autumn ripening period, and yet non-hardy or only slightly hardy in other years, due to the fact that the embryos in the sown grain had already 'passed the thermo-phase' while still attached to the mother plant.

CHAPTER VI

LIGHT IN RELATION TO DEVELOPMENT

The Presence or Absence of Light

The literature is already voluminous on the relation between the presence or absence of light and the characteristics of plant growth and development. It will be possible here to refer only briefly to the main directions of this research, giving some of the classical work of Klebs and others, and quoting the conclusions accepted at the present day by reviewers such as Hamner (1944) and others. The full scope of the research on photoperiodism and related topics may be studied and an introduction to the literature obtained by reference to the articles by Garner, Arthur, Shirley and Popp in Duggar's *Biological Effects of Radiation* (1936), and in the articles of Burkholder (1936), Garner (1937), Allard and Garner (see U.S.D.A., 1940), Maximov (1938), Adler (1940) and similar reviews of the subject.

Formative Effect of Light in Reproduction

The notion has long been accepted that light of a definite wavelength and intensity has a formative influence upon the developmental cycle of a plant, particularly as regards the formation of reproductive organs, flowering and ultimate production of fruit. In discussing this question, Maximov refers to Klebs, whom he regards as the pioneer in the field of the physiology of plant development, in his classic research on the possibility of modifying development at will. The outlook of Klebs on the course of plant development has already been noted in Chapter II; it will be appropriate at this point to describe some of his experiments with *Sempervivum funkii*, in which he studied the effect upon the progress of plants towards maturity of continuous light of varying intensity, or of definite photoperiods, with or without control of concurrent temperature (1918).

The main interest was the time of flowering. If rosettes of *S. funkii* have become 'ripe-to-flower' in the course of the summer and the winter, the inflorescences develop under natural conditions in June of the following year. Klebs found that the flower primordia were first recognizable under the conditions at Halle at the end of April (April 26th to 30th). In the climate of Heidelberg, where the spring is on the average 14 days earlier, the flower primordia of the same Halle material never-

theless developed at the same time. This appeared to be an example of a definite inherited time of flowering, a contingency which Klebs considered improbable and rejected. Klebs had already determined that flower formation and time of flowering can be made to vary considerably, but had never been able to induce a ripe-to-flower rosette to form flowers during the winter, in spite of the fact that everything in the rosette was prepared for it (ripe-to-flower).

Klebs regarded it as useless to proceed with the inquiry until the insufficient winter light was supplemented; he therefore provided continuous light with Osram lamps, and showed that *S. funkii* could then be brought into flower throughout the winter months (Klebs, 1913b).

EXPERIMENTS OF KLEBS WITH CONTINUOUS LIGHT

In confirmatory experiments, Klebs used rosettes which according to age and previous treatment were judged to be ripe-to-flower, although no reliable indication of this condition is known. From late summer onwards, internal changes proceed slowly in rosettes ripe-to-flower, chiefly due to the lower temperatures of autumn and winter. Ripeness to flower increases progressively: a rosette which has been under continuous light in October requires about 5 to 6 weeks to the opening of the first flower, while in December and later only 4 weeks or slightly less are needed. It was, however, not possible further to shorten the time of development even with high light intensity in February and March. This varying degree of flower ripeness was also noted when the period of continuous lighting necessary for the first flower primordia to form was determined.

The ripe-to-flower rosettes were under continuous light for 2, 3, 4 and more days and then transferred to a heated greenhouse. Whereas in this greenhouse untreated rosettes ripe-to-flower did not come into flower, and indeed lost this capacity, nevertheless inflorescences were formed in such rosettes as had formed the first primordia after exposure to continuous light. Continuous light is, therefore, necessary only for formation of the first flower primordia.

In an experiment in which four Osram lamps provided an intensity of 200 candle-power at a distance of 40 cm., the rosettes illuminated in the greenhouse for 4, 5, 6, 7 and 8 days remained vegetative; exposure alone for 9 days led to inflorescence formation. This experiment was performed in November; in January and February, 4 days were generally sufficient, in March 3 days, and in April 1 day. The following table gives results of an experiment begun on February 20th; rosettes were placed 70 cm. from an Osram lamp of 1,000 candle-power; the average temperature was 25·4° C. (minimum, 24·7° C., maximum 26·2° C.), relative humidity 50 to 60 per cent.

TABLE 13

Continuous light—Days	*Behaviour in greenhouse on 25/4/14*
2	Rosette scarcely increased in height, vegetative
3	No elongation, four flowers in centre of rosette, besides two small rosettes
4	Axis slightly elongated, densely leaved, five stalked flowers, two rosettes
5	Axis distinctly elongated but still short, three whorls of open flowers, some rosette-like, two rosettes

The experiments show that 2 days are not sufficient; between 3 to 5 days the elongation of the axis varies with the duration of the illumination, but the flower formation may follow after even 3 days' exposure; moreover, vegetative transformations of the flower occur up to replacement by true rosettes.

EXPERIMENTS OF KLEBS ON LIGHT INTENSITY

Klebs placed rosettes of *S. funkii* of similar height under an Osram lamp of 1,000 candle-power at distances, reckoned from the middle of the lamp, of 80, 120, 160 and 200 cm. respectively. The average temperature at a distance of 80 cm. was 22·5° C.; at 200 cm., 19·8° C. The experiment began on December 27th, and Table 14 gives the results.

TABLE 14

Distance in cm.	*Light-strength in candle-power*	*Opening of first flowers, in days*	*Length of axis in cm.*	*No. of flowers and buds*	*Condition of the flowers*
80	1,560	31	9·2	8	Petals light pink
120	695	31	7·4	6	Petals whitish. Anthers almost sessile
160	390	42	9	7	Petals greenish with whitish sheen, thick rosette-like
200	250	47	14·8	8	No elongation of stem, only two open flowers, greenish white, the other buds atrophied
240	170	–	9·3	0	No inflorescence, all flower buds atrophied, not developing further

Klebs states that this experiment shows that the flower primordia were still formed at a distance of 240 cm., but that the development of the inflorescence, and especially of the branches and flowers decreases with a reduction in the light intensity. The stimulation of flower primordia requires under continuous lighting a lower intensity of light than does the elaboration of the inflorescence.

Klebs adopted a special dark chamber to determine the lower limit of light intensity; this consisted of a frame 2 m. long and 50 cm. high and broad, closed by black cardboard and black light-proof cloth, and provided with a small Osram lamp of about 10 candle-power at one end. The experiment continued from February 6th to March 2nd, when the plants were removed to the greenhouse. During the last 2 weeks, the light intensity was reduced to 6 candle-power. The temperature at a distance of 25 cm. averaged 21·2° C.; at 200 cm. 19·8° C. The results are given in Table 15.

TABLE 15

Distance in cm.	*Elongation of axis up to 7/3/14 in cm.*	*Condition of inflorescence on 7/3/14*	*Behaviour in greenhouse after 7/3/14 on 24 to 25/4*
25	9·5	3 flowers open, corolla whitish	
50	10	small flower buds	Axis 12 cm., densely leaved, four open red flowers
75	10·5	only leaf-buds visible	Axis 12·2 cm., 2 normal flowers, 3 atrophied, 3 leaf rosettes
100	16·6	ditto	Axis 17 cm., several flowers, little developed, also rosettes
125	9.5	ditto	Axis 10·5 cm., rosette of leaves; 1 stem with an open flower and a rosette
150	7·4	ditto	Axis 8·4 cm., a terminal rosette with a central flower head and a small rosette
175	9·5	ditto	Axis with vegetative terminal rosette
200	10	ditto	The same, below the terminal rosette 2 small rosettes

When placed at a distance of 25 cm. from a light of intensity approximately 160 candle-power, the rosette ripe-to-flower succeeded in forming a few open flowers; at 50 cm., small buds were still visible but at

greater distances apparently only leaves. The flower primordia had, however, differentiated, so that flowers were still formed in the greenhouse, although the vegetative transformation was increased. The light intensity at a distance of 175 cm. (about 3·2 candle-power) was too low, and according to Klebs represented almost the lower limit for the formation of primordia, clearly too low for the normal formation of the inflorescence.

In both series of experiments the elongation of the axis accompanied the reduced flower formation. Klebs notes in this connection that the results differ from those obtained with too short continuous illumination, as in the latter case the elongation of the axis was more suppressed than flower formation. There is thus a difference in the effect of light, according to whether the duration of light of high intensity is too short, or whether the intensity of light during longer periods is reduced too far.

Continuous illumination was not provided in the greenhouse and under natural conditions, but instead an alternation of light and darkness, and Klebs then proceeded to investigate the number of hours per day of Osram light necessary to produce flower primordia.

EXPERIMENTS OF KLEBS ON NUMBER OF LIGHT HOURS PER DAY

From several experiments, Klebs concluded that the number of light hours per day which are necessary for the stimulation of flower formation changes in the course of the winter and spring in accordance with the increase in the ripe-to-flower condition observed in his other experiments. A 12-hour light period in December or January, or a 10-hour period even in April is not sufficient for flower formation. Even if the light period in January is increased to 18 hours, 10 days are still insufficient to initiate the first flower primordia; further, the period of development up to the unfolding of the first flower is longer than with continuous illumination.

Klebs notes the probability that in *Sempervivum* there is no simple relation between intensity and time of illumination. The flower primordia may be formed under continuous illumination of even 4·4 candle-power, equivalent in a 24-hour period to 106 metre-candle-hours. On the other hand, the light intensity in his experiment with discontinuous lighting was about 2,000 candle-power, equivalent in a 12-hour period to 24,000 metre-candle-hours, but this was not sufficient to induce the formation of flowers. Klebs concludes that the time of flowering does not depend only upon the amount of light, but that the interruption caused by the interval of darkness has some kind of inhibiting influence; after some weeks of exposure to 12-hour periods, this duration of darkness may even destroy the ripe-to-flower condition entirely. Darkness is regarded as stimulating an antagonistic process, but this appears to be decisive

only at medium or higher temperatures; darkness combined with lower temperature has the opposite effect, maintaining and even promoting the ripe-to-flower condition.

Rosettes ripe-to-flower exposed from January to March to a lamp with an ebonite plate 1 mm. thick interposed (transparent to heat rays) did not form flower primordia, and in 2 to 3 weeks the ripe-to-flower condition was lost. Some rosettes ripe-to-flower were placed in a dark thermostat at a constant temperature of 15° C. from December 23rd. On every other day from January 12th onwards, a rosette was brought into the light room. The rosettes came into flower; those which had been in darkness at 15° C. for 32 and 34 days already showed a vegetative transformation of the inflorescence, and after 36 days of darkness the short elongated axis bore a terminal rosette. When a series was placed in a thermostat in darkness at 30° C. on January 27th, the ripe-to-flower condition was lost after 16 days, in other experiments even earlier.

With discontinuous lighting and a temperature of 22 to 25° C. also, the darkening has a slow action inimical to flower formation, of such a degree that the retarding influence of 12 hours of darkness per day is stronger than the promoting effect of 12 light hours. Klebs considers that it is very probable that it is the dissimilation processes which change the balance of internal factors in favour of vegetative transformation. The opposite effect of lower temperature is regarded as supporting this view.

When rosettes ripe-to-flower are placed in a darkened ice-chest (4 to 6° C.) at the beginning of April, before flower primordia are formed, the ripe-to-flower condition is fully retained. The darkness does not exert any retarding influence. When subsequently exposed to light during the summer, rosettes produced inflorescences even after 3 months' darkness. The lower temperature directly promotes the maintenance of the ripe-to-flower condition.

Ten 2-year-old rosettes were placed in the dark on June 6th, while still not ripe-to-flower; until October they were in an ice-chest which was refilled every 2 days. From October onwards no more ice was added, but the temperature remained below 10° C. throughout the winter. The dish was placed in the light on March 11th, after 9 months of darkness. The nine rosettes remaining alive came into flower during April, quite an unusual time for *S. funkii*. The axis of the inflorescence was very short, frequently quite reduced; in addition to the flowers, new rosettes appeared.

Klebs considers that the lower temperature, besides effecting a reduction in dissimilation (respiration, etc.), had probably also operated in the same direction as in the experiment of Müller-Thurgau with potato (1882, 1885), in which an accumulation of reducing sugar occurred after low temperature. It is regarded as conceivable that the ripe-to-flower

condition was gradually attained in the rosettes which were still vegetative at the beginning of the experiment.

Klebs stresses the fact that flower primordia have not yet been observed to arise in total darkness. If rosettes with quite immature primordia (beginning of May) are placed in an ice-chest, there follows in the darkness some elongation and even an unfolding of some white flowers. The formation of the inflorescence and especially of the flowers is clearly dependent upon light intensity, as in weak light the flower buds atrophy or do not pass beyond the initial stages. Klebs states that this is, however, connected with the temperature which is operative at the time.

At the conclusion of this section of his article, and before proceeding to discuss the spectral composition of light (notto be dealt with here), Klebs returns to his original question as to whether and why *Sempervivum funkii* forms its flower primordia under natural conditions at a fixed time at the end of April. A certain understanding of the question, if not a definite solution, is claimed. From March 21st onwards, that is, from the date of equal day and night, the amount of light gradually increases until it reaches the level required for the stimulation of flower primordia, with a still relatively low average temperature. After the middle of April, the essential internal changes in the rosette are progressing, and at the end of the month the first primordia appear.

Reference has already been made to the way in which Klebs interpreted his results in general (p. 24). Having observed the varying effect of light, darkness and temperature at different stages of development, he concluded that the process of formation of the inflorescence proceeds in three clearly separable phases: the onset of the ripe-to-flower condition, the formation of the flower primordia, and the production of the flowering inflorescence. 'All three developmental steps show a dependence upon light, but in varying degree and sense.'

Photoperiodism

The next tentative formulation of the action of length of day on sexual reproduction in plants was published by Garner and Allard in 1920. Their experiments with tobacco, soybean and other species indicated that, of the various factors of the environment which affect the plant, the length of day is unique in its action on sexual reproduction. Except under extreme ranges such as would adversely affect normal functioning, differences in temperature, water supply, and light intensity merely exert accelerating or retarding effects on sexual reproduction. The seasonal length of day may, however, have definite effects, initiating or inhibiting the reproductive processes, the effect being characteristic for different species.

Garner and Allard formulated this action in the following broad terms: 'Sexual reproduction can be attained by the plant only when it is exposed to a specifically favourable length of day (the requirements in this particular varying widely with the species and variety), and exposure to a length of day unfavourable to reproduction but favourable to growth tends to produce gigantism or indefinite continuation of vegetative development, while exposure to a length of day favourable alike to sexual reproduction and to vegetative development extends the period of sexual reproduction and tends to induce the ever-bearing type of fruiting.'

The term *photoperiod* was introduced to designate the favourable length of day for each organism, and *photoperiodism* the response of an organism to the relative length of day and night.

Garner and Allard's experiments with soybeans included four varieties showing a range in type from early to very late when maturing under normal conditions in the latitude of Washington, D.C. When planted in the field during the month of May, the average number of days from germination to flowering was approximately 27, 56, 70, and 105, respectively, for the varieties Mandarin, Peking, Tokyo and Biloxi, the last-named showing no open flowers until early September. Some facts regarding the effects of reduced light exposure on these four varieties are given in Table 16. (See also Plate 5.)

When the daily illumination consists of a single exposure of 12 hours or less, the usual duration of the growing period from germination to flowering is only slightly shortened in the early variety, Mandarin; the shortened duration is, however, increasingly marked as the normal growing period increases, so that, in the very late variety, Biloxi, the reduction amounts to three-fourths of the time required by plants grown under the full daylength during the summer months. In effect, state Garner and Allard, all varieties become early maturing under artificial conditions of a 12-hour day, and there is then only a slight difference in the time required by the four varieties to reach the flowering stage.

A further reduction in the length of the light period below 12 hours has no further effect in shortening the vegetative period; there is apparently a certain minimum period of light exposure, below which reduction has no further action in hastening the onset of flowering. Garner and Allard also concluded from their results that for each variety a certain minimum period of time (generally one of vegetative activity) must elapse from the beginning of the stimulating action of the reduced light exposure before the flowering stage can be achieved. They consider that the data in Table 16 indicate that this formative period is approximately 21 days in Mandarin and Peking varieties, 24 days in Tokyo, and 26 days in Biloxi, although under suitable conditions these periods might possibly be shortened further.

TABLE 16

Number of days required by soybeans to reach the flowering stage under daily light exposures of different lengths.

Length of daily exposure	*Mandarin*			*Peking*		
	Date of germination	*Date of transfer to dark house*	*Time from germination to blossoming*	*Date of germination*	*Date of transfer to dark house*	*Time from germination to blossoming*
			Days			*Days*
10 a.m. to 3 p.m., 5 hours	May 17	May 20	23[1]	May 17	May 20	23[1]
9 a.m. to 4 p.m., 7 hours	do.	do.	21	do.	do.	21
Do.	—	—	—	do.	June 7	22
Daylight to 10 a.m. and 2 p.m. till dark, 8½ to 11 hours	—	—	—	June 19	June 19	40
6 a.m. to 6 p.m., 12 hours	June 16	June 11	21	June 16	June 11	21
Full daylight, 12½ to 15 hours	May 17	Control	26	May 17	Control	62
Do.	June 16	do.	28	June 16	do.	51
	Tokyo			*Biloxi*		
10 a.m. to 3 p.m., 5 hours	May 17	May 20	24[1]	May 17	May 20	27[1]
9 a.m. to 4 p.m., 7 hours	do.	do.	24	do.	do.	26
Do.	do.	June 7	27	June 15	June 24	28
Daylight to 10 a.m. and 2 p.m. till dark, 8½ to 11 hours	June 19	June 16	62	June 19	June 16	79
6 a.m. to 6 p.m., 12 hours	June 16	June 11	28	June 16	June 11	28
Full daylight, 12½ to 15 hours	May 17	Control	73	May 17	Control	110
Do.	June 16	do.	66	June 16	do.	90

[1] In those cases in which the plants were placed in the dark house after they had germinated, only the period elapsing after they had been transferred is taken into account, rather than that beginning with the date of germination.

Garner and Allard also observed that it is not merely the total number of hours of light received daily by the plant that induces the above-mentioned marked reduction in the duration of the vegetative period, but that the degree of continuity of that exposure plays an important part. The breaking of the daily light period into two separate exposures, but with a total daily exposure to light averaging 9 or 10 hours, has very much less effect in inducing early flowering than a single daily exposure of 12 hours; in later varieties, the effect was of little significance.

The results are considered to show clearly that, as far as sexual reproduction is concerned, the Mandarin soybean is adapted to a relatively long day, since the time required to reach the flowering stage during the long summer days cannot be greatly reduced by artificially shortening the length of the daily exposure to light. Biloxi, on the other hand, is a distinct 'short-day' variety; with a daily light exposure of 12 hours or less, it flowers almost as early as Mandarin, whereas the control plants refuse to flower during the normal long summer days. Garner and Allard note that all four varieties would behave similarly when grown under a 12-hour day such as prevails at the equator.

Photoperiodic Classes

In this original work on the effects of different light periods, the data available (see also Garner and Allard, 1923) for classifying plants according to the nature of their response were limited; very few grades in length of day were investigated owing to the lack of facilities for detailed investigation of small changes in length of day. Conclusions in the earlier papers were based mainly upon tests involving a comparison between very short days, obtained by the special type of house constructed at Arlington Experimental Farm, Virginia (see Place 5), with the full length of the normal day of that latitude, or the very long days obtained by the use of artificial electric light. It was, therefore, not possible to assess with any degree of accuracy the upper or lower limits for flowering in the members of the two groups discriminated.

It has since become possible to adopt a stricter control of daylength, adjusting durations by half-hour steps from 8 to 10 hours of light daily up to the longest day of summer, and even to light periods of longer duration, by utilizing artificial light after sunset. This later phase of the experiments (Allard and Garner, 1940) has led the authors to what they consider to be a better understanding of the concept of long-day and short-day plants, and now makes it possible to classify many species into the two groups.

Allard and Garner state (1940) that it is obvious that plants must be subjected to lengths of day ranging from continuous illumination down

to 8 or 10 hours of light by half-hour steps at least, to determine the upper and lower limits (critical photoperiods) of flowering, if indeed such limits actually exist. This has not always been found practicable and the possibility is envisaged that many plants that undergo delayed flowering in longer days may perhaps cease to produce flowers altogether in very long days approaching continuous illumination.

The originators of photoperiodism find it difficult to formulate 'a satisfactory, workable, and all-inclusive definition' that may be used to separate clearly the long-day from the short-day plants. If response to daily light periods which decrease progressively from continuous illumination be taken as a basis, a long-day plant is regarded as one that ceases to flower or shows delayed or less profuse flowering with decreasing daylength, whereas a short-day plant is one that begins to flower or shows hastened or more profuse flowering when the length of day is sufficiently shortened. This fact remains true even if it is recognized that there is a pronounced overlapping of the upper limits of flowering of plants of the short-day group with the lower limits of the long-day group. 'These contrasting behaviours at the present time appear to be dependent upon fundamental differences in the physiology of the two groups, and may be so regarded until further investigations have proved otherwise'.

Allard and Garner (1940) now recognize also two further groups of plants in addition to the two chief classes discussed above. One group appears to be little affected by length of day, and has been called the indeterminate or day-neutral group; plants in this group flower readily under all lengths of day. A few plants have been found that will flower only between certain limits of length of day, the arbitrary figure given being 'between 12 hours and 16 hours of daylight'.

For a list of the species which have so far been classed in one of the four photoperiodic groups by Allard and Garner, reference should be made to their most recent publication (1940), containing the results of their many observations upon the behaviour of a large number of species in relation to varying daily light exposures, and also to the list given by Adler (1940) summarizing the position up to that date, but published before the above Bulletin.

In classifying plants into groups or classes, it must always be stated whether this is done in relation to reproduction or some other character. Some confusion with regard to the potato is noted on p. 284. There is also the example of Little Turkish tobacco (Dennison, 1945). Although daylength has no effect on flowering date, a number of growth responses can be seen. Under short days, the size and number of flowers are reduced. Differences in vegetative vigour between plants grown in 6·5 and 14-hour days are thus direct results of the photoperiod. Under



PLATE 9. Seedlings from four successive sowings of barley grown in 16-hour photoperiods and different temperatures; last planting in top, first in bottom row. Enlargement of terminals shown at right of seedlings from which dissected (see p. 79). Photo: Borthwick, Parker and Heinze, 1941–2.



PLATE 10. The effects of photoperiod may be localized. The half of each plant which is blooming received a relatively long photoperiod each day, the other a short one of but 10 hours. Photo: Bureau of Plant Industry, Soils and Agricultural Engineering, U.S.D.A.

short days vegetative growth is slower, but tends to continue longer despite flowering. Stems are shorter, and leaf area smaller at first, but after flowering the leaf area surpasses that in long days. Carbohydrates are less mobile under short days and tend to accumulate in the leaves. Root growth is poor especially during the period of stem extension. Total water uptake is not influenced by daylength despite the differences in plant size.

Photoperiodic Reaction and Geographical Distribution

The relation between photoperiodic reaction and the natural habitat of plants is obvious. Short-day plants inhabit tropical and subtropical regions, where daylength varies round about 12 hours daily by some 2 hours throughout the year. The long-day plants, on the other hand, normally inhabit higher latitudes in which they are exposed during their vegetative period to long days with considerably more than 14 hours' continuous daylight. As Maximov has pointed out, however, the vegetative season of a plant habitat may vary considerably with altitude above sea level. Work on the photoperiodic response in relation to the place of origin of plants has been done by Kuznecova, Razumov, Dorošenko, Rudorf, Kopetz and others.

Change in Photoperiodic Class with Advancing Age or Season

Reference has already been made to the statement of Klebs that the number of light hours per day which is necessary for the stimulation of flower formation changes in the course of the winter and spring in accordance with the increase in the 'ripe-to-flower' condition which had been observed in other experiments. Other authors have referred to similar observations; Sapegin (p. 40) recognizes a division of the photophase into a preparatory and an executive sub-stage. Eguchi (1937) performed experiments based upon the supposition that there may be two different stages in the course of flower formation, first, the stage of differentiation of the bud, and second, the stage of development of flowers, both stages responding to different lengths of day. Experiments were conducted with sixteen different species of plants; plants of the same kind were grouped into two plots, one being exposed to photoperiodic treatment before differentiation of the flower bud, and the other being exposed to the treatment after the flower bud had been differentiated.

Eguchi gives the results of experiments with short-day treatments. Some plants hitherto regarded as short-day types were tested under

short-day conditions (9-hour day). The differentiation of the flower bud was accelerated and the flower opened fairly early, but, if these plants were transferred to long-day conditions (24-hour day) after completion of flower bud differentiation, further development took place rapidly and flowering occurred earlier than in those plants that remained in short day. Eguchi concludes that there are two stages with different reactions to the photoperiod in the course of flowering, the first being the stage of bud differentiation, and the second the stage of blooming. A similar phenomenon has been observed in long-day plants, and Eguchi considers it probable that investigators have been misled by results such as these in their classification of plants as long or short-day types (see, however, Gregory and Purvis, 1936, who state that 'the problem of photoperiodism may therefore be considered not as concerning conditions leading to flower formation but as concerning failure to flower').

As Eguchi claims that there are three types of response within each of his two stages, there is thus a total of nine different types varying according to the mode of reaction during these two stages. An attempt has been made to designate these nine types in such a way that 'SL' indicates that a plant is a short-day type for bud differentiation and a long-day type for the subsequent stage of flowering, and so on. Table 17 shows the classification of the species used on the basis of these nine groups (see also Loehwing, 1939).

It is not known how reliable is the evidence that the later stages of flowering are actually *promoted* by *short* days in some plants; it is appropriate at this point to refer to the importance of micro-dissection of plants to determine the actual stage of flowering reached, as stressed in the work of Gregory and Purvis, and by Hamner (1944) who states: 'it would be helpful in much of the experimental work in this field if the investigators would examine all of their plants by micro-dissection (Hamner and Bonner, 1938, Borthwick and Parker, 1938, Snyder, 1940, Mann, 1940, Lang, 1942) to determine what stages of floral development are especially affected by the treatments used. This is especially true when an attempt is made to classify the photoperiodic responses of a given plant. In some cases, plants have been called short-day plants if blossoming occurs at an earlier date when the plants are grown under short photoperiods as compared to long photoperiods even though flowering takes place fairly rapidly under both conditions. Differences of only a few days in the time of flowering have been considered significant. This practice leads to confusion when comparisons are made between such plants and the responses of others which remain strictly vegetative for a long period under one set of conditions and produce flowers and fruits very rapidly when transferred to another.'

The present view on the use of the photoperiodic classes of long-day,

TABLE 17

New classification of photo-periodic type	*Classification of photo-periodic type hitherto used*	*Sign of photoperiod effective on two stages*		*Plant belonging to each type*
		Time of flower bud differentiation	*Subsequent development to flowering*	
SL plant	Short-day (Strawberry *Primula*) long-day (*Cineraria*)	S	L	Strawberry *Primula malacoides* *Cineraria hybrida*
LL plant	Long-day	L	L	*Silene pendula* *Chrysanthemum leucanthemum* Spring barley (two varieties tested)
LS plant	Unknown	L	S	*Physostegia virginiana* *Boltonia latisquama*
SS plant	Short-day	S	S	*Glycine max* *Pharbitis nil* *Cosmos bipinnatus*
LI plant	Unknown	L	I	*Phlox paniculata* Lindl.
SI plant	Short-day	S	I	Late varieties of rice (three varieties tested)
IS plant	Short-day	I	S	*Chrysanthemum articum*
IL plant	Long -day	I	L	Spinach, Wheat (five varieties tested)
II plant	Independent	I	I	Pepper (*Capsicum frutescens* Linn.) Early variety of rice (one variety tested)

L=Long-day. S=Short-day. I=Independent of daylength.

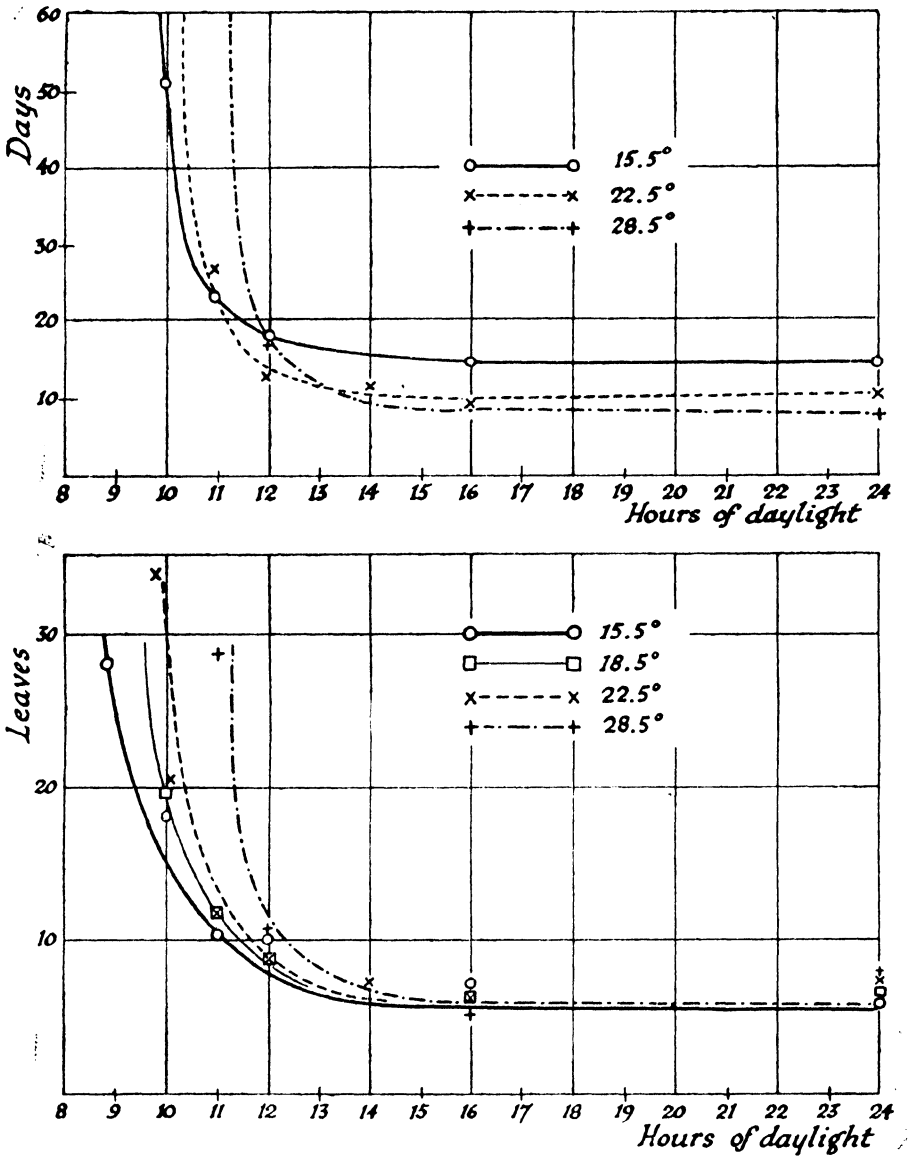


FIGURE 22

Dependence of the photoperiodic reaction of *Hyoscyamus* on the temperature. Upper graph = time of shooting; lower graph = leaf increase (Lang and Melchers, 1943)

short-day and other types of plants introduces a number of qualifications into the original definition. Plants are now considered (Hamner, 1944) as long-day or short-day plants if they fit Garner and Allard's classification at some definite *age* and *temperature*, and these particular conditions are assumed to prevail when the responses of such plants are discussed.

Reference may also be made to the 'phasic' outlook on development, in which it is postulated that a winter plant has a requirement of temperature which has to be met before it can respond to light, to Lysenko's

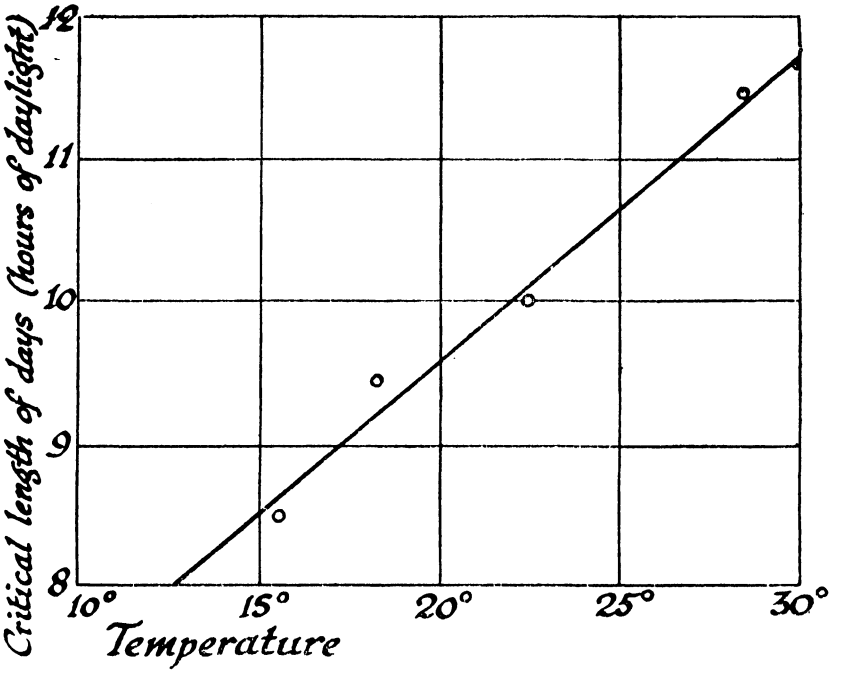


FIGURE 23

Dependence of the critical length of day on temperature in *Hyoscyamus niger* (Lang and Melchers, 1943)

original claim that long-day species are at their optimum in continuous day and short-day species in continuous night, and to the postulation of some type of intermediate phase between the thermo-phase and the photo-phase, when it is claimed by some that darkness may be the decisive factor.

The Photoperiodic After-Effect or Photoperiodic Induction

Between 1923 and 1927, Egiz conducted experiments on questions relating to photoperiodism in soybeans and maize at the Acclimatization Station at Detskoe Selo (1928), probably the first experiments to show that it was possible to treat short-day plants with specific photoperiods while they were at the seedling stage, and that the effect of the treatment became evident only at a much later stage of their life. The work of Egiz, Razumov and subsequent investigators thus brings pre-treatment by

light into line with the parallel pre-treatment with temperature, known as vernalization. Obviously it is not possible to treat seeds with light in the same way as temperature, since seeds, even though germinating slowly, do not contain the photosynthetic mechanism whereby they may

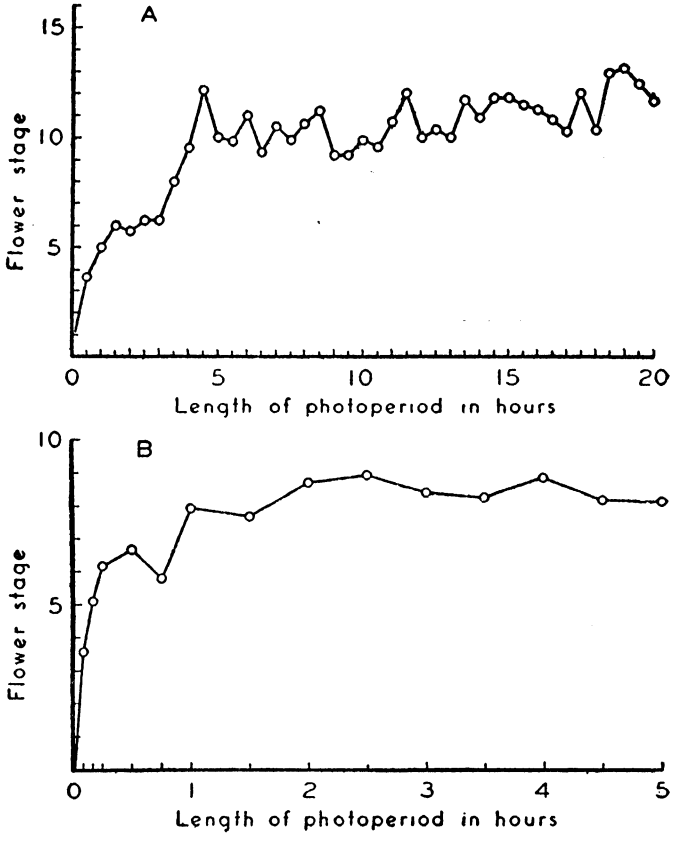


FIGURE 24

Photoperiodic after-effect in the highly sensitive plant, *Xanthium pennsylvanicum*. Effect of varied lengths of photoperiod (single photoinductive cycle) on nitiation and development of flower primordia. A = medium light intensity; B = high light intensity. Moderate temperature. Since the usual divisions of flowering stages into formation of inflorescence primordia, flower primordia, etc., are not sufficiently precise, an extensive scale for recording floral stages has been found to be necessary; see original paper (Mann, 1940)

respond to light treatment. If, however, short-day plants are exposed to short days during an early part of their life, or long-day plants to long days, they may be 'induced' to flower in due time even if transferred from the optimal length of day; hence the terms, photoperiodic after-effect or photoperiodic induction.

It has already been stated that Lysenko considers that long-day plants

require light at the photo-phase and only tolerate darkness, while short-day plants require a certain quota of darkness and only tolerate the intervening light intervals of normal days. The most recent reviewer of this problem (Hamner, 1944) agrees that there appears to be no evidence

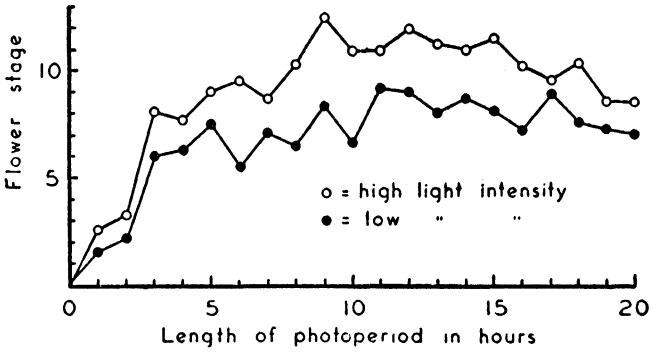


FIGURE 25

Effect of varied length of photoperiod (single photoinductive cycle) at two light intensities on initiation and development of flower primordia in *Xanthium* (Mann, 1940)

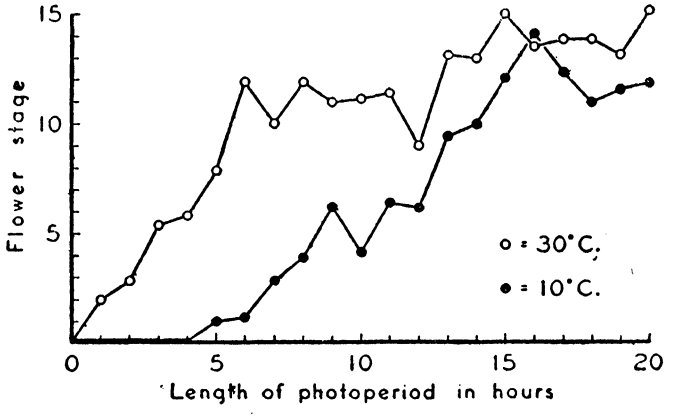


FIGURE 26

Effects of varied lengths of photoperiod (single photoinductive cycle) on initiation and development of flower primordia in *Xanthium* at two temperatures (light intensity = 2,000 to 3,000 foot candles) (Mann, 1940)

to show that long-day plants, in order to be stimulated to flower, require an exposure to darkness. Flowering will result when they are exposed throughout their growth to continuous illumination. As long-day plants do not flower in short days, the problem arises of the reason for this failure: are the dark periods too long, or the photoperiods too short? This question of the relative influence of light and darkness arises again with short-day plants: the evidence now available does not, according to

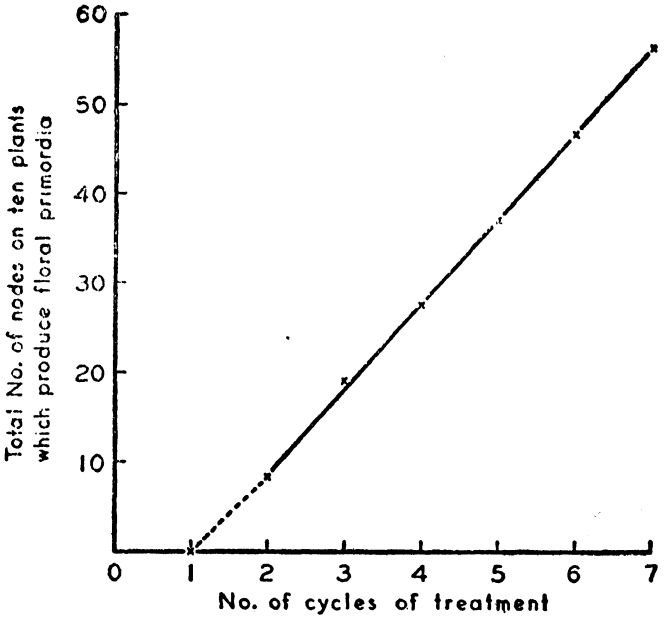


FIGURE 27

Effect of number of cycles, each consisting of a 9-hour photoperiod and a 15-hour dark period, on number of floral primordia produced by Biloxi soybean (Hamner, 1940)

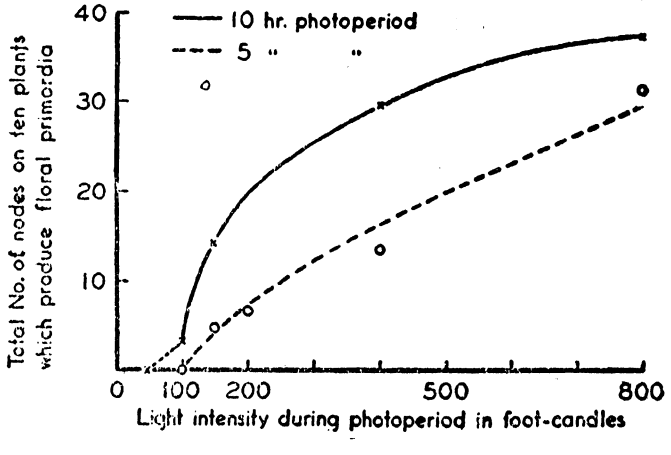


FIGURE 28

Effect of duration and intensity of light during seven photoinductive cycles on subsequent initiation of floral primordia by Biloxi soybean (Hamner, 1940)

Hamner, support Lysenko's statement that these plants require continuous darkness for development. The photoperiodic stimulus to flowering in some and perhaps in all typically short-day plants is brought about during both the light and dark periods.

The relation between light and darkness, and reproduction is one of

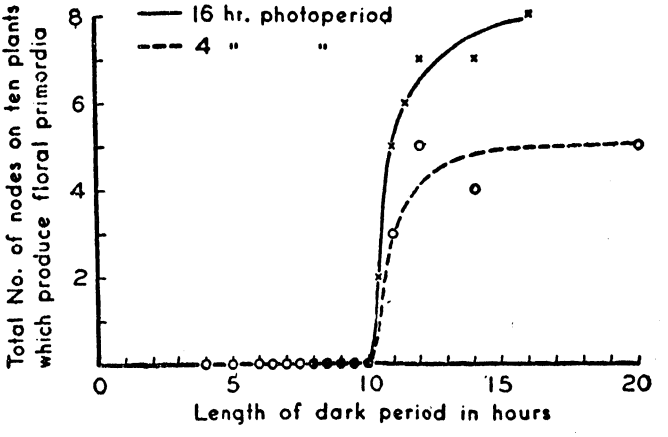


FIGURE 29

Effect of length of dark period of photoinductive cycle upon number of flower primordia produced by Biloxi soybean. All plants received seven cycles, each consisting of a 16-hour or a 4-hour light period and a dark period as indicated. There is a certain minimum length of dark period below which flowering will not take place regardless of the length of the light period (Hamner, 1940)

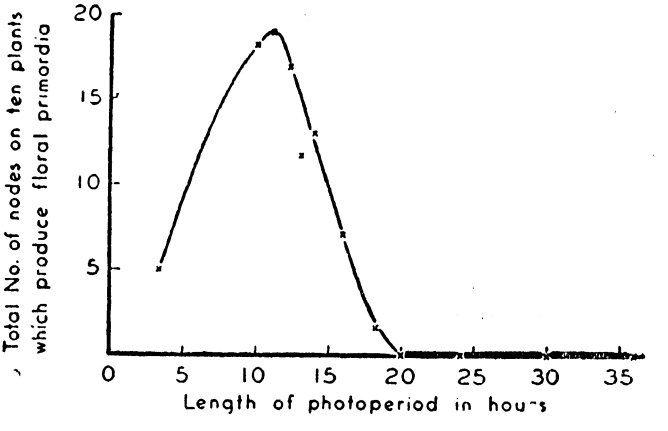


FIGURE 30

Effect of length of photoperiod upon number of floral primordia produced by Biloxi soybean. All plants received seven cycles, each consisting of a 16-hour dark period and a period of light as indicated. There is an optimal length of photoperiod at about 11 hours which results in the greatest flowering (Hamner, 1940)

the chief problems of current research on photoperiodism, and is dealt with more fully on pp.128-139. To quote Hamner again, the present opinion appears to be that under natural seasonal conditions flowering in both long-day and short-day plants is determined by the length of the 'night'. In short-day plants flowering seems to be stimulated by a long dark period while in long-day plants flowering tends to be inhibited by a long dark period. In both groups the effective length of the dark period may be shortened by illumination with light of very low intensity (Garner, 1936, Burkholder, 1936).

The question of the photoperiodic after-effect also introduces the large problem of the physiological processes that occur in leaves. Current research is now concerned with the isolation of a hormone or other substance controlling flowering (see Chapter XI). One of the latest Russian studies on the subject is that by Moškov (1941), who carried out experiments to show (*a*) the inadequacy of the explanation that the photoperiodic after-effect is due to the accumulation of, and the return to vegetative activity to the exhaustion of the reserve of flowering hormones, and to obtain (*b*) new data which might elucidate the role of the physiological processes that occur in leaves before, during and after photoperiodic treatment. The 'return to vegetative activity' mentioned under (*a*) above introduces the question of the reversibility of the photoperiodic after-effect.

In place of the hormonal interpretation worked out by Čaĭlahjan (1937) and discussed in Chapters X and XI, Moškov considers that his own data show that the photoperiodic after-effect may be attributed to physiological changes which arise in the leaves while they are under the optimal photoperiodic conditions for the plant concerned. Whatever may be the nature of these processes, they appear to have such an effect on the vital activity of the leaves that the plant is enabled to form flowers and fruits under any photoperiodic condition.

While under short day, the leaves of short-day plants pass a certain phase in ontogeny, thought to be an irreversible one, in which they have acquired the power of bringing into flower the growing points under their control. When certain plants revert from flowering to vegetative growth after the photoperiodic after-effect has become apparent, this is due, according to Moškov, to the influence of leaves exposed to a shorter treatment with optimal photoperiods and not those involved in the above process of ontogeny. When these new leaves have reached their normal size, they take over from the lower leaves, by mere reason of their proximity to the growing point of the stem, and direct its further development. In experiments with various plants, Moškov always found that the leaves direct the growing point towards the formation of reproductive organs, but did not observe direct transmission from one leaf to

another of any qualitative changes produced by optimal photoperiodic conditions.

It is therefore considered obvious that the photoperiodic after-effect is due to those changes that occur in leaves when they are under optimal photoperiodic conditions and which alter the influence they exert on the development of plants. Any subsequent return to a vegetative state is due to the formation of new leaves which have had a different course of development (less advanced) from those first formed. Moškov therefore considers it unnecessary to resort to theories of photoperiodic accumulation in order to explain the photoperiodic after-effect.

Phasic Development and a Photo-Phase

It is obvious that investigators have for some time been tending towards the view that plant development is based upon a sequence of ill-defined phases, the progress of which is governed by one or more environmental factors. Such a sequence in development has been expressed in more dogmatic terms by Lysenko. His theory of phasic development has already been outlined on pp.36-38, and the thermo-phase has been discussed in Chapter IV; Lysenko considers that the thermo-phase is followed by a phase in which light becomes the decisive factor, accompanied by accessory factors such as temperature, humidity, etc.

It has already been stated that, until the changes involved in the thermo-phase have been effected, the plant is supposed to be incapable of continuing in development towards ultimate reproduction. These changes in themselves are not, however, sufficient to enable reproduction eventually to be initiated. Before this can occur in wheat and other long-day cereals, for instance, it is claimed that a further stage is necessary immediately following the thermo-phase. This new stage can be effected only after the thermo-phase has been completed, and also requires a set of fixed conditions, differing from those required by the thermo-phase.

For instance, the thermo-phase in winter wheat can be passed only, according to the phasic development school, under conditions of reduced temperature, with sufficient moisture and aeration; light and darkness play no decisive part in this phase. The next phase, on the other hand, can be effected only (in long-day plants) under conditions of long day, or better still, of continuous illumination, combined with high temperature.

Lysenko quotes the experiment of E. P. Meljnik, who grew winter wheat Novokrymka 0204, vernalized and unvernalized, under high summer temperature conditions, such that the unvernalized plants were not exposed to the low temperatures required to pass the thermo-phase

under natural conditions. Although the unvernalized plants had every condition favourable for their development, they did not come into ear, while the vernalized plants produced seed normally. If, however, these same vernalized plants were grown in a 10-hour day instead of continuous light, they also entirely failed to come into ear and apparently remained in the same condition as the unvernalized plants. When some of these vernalized plants were then transferred at different times to continuous light, they immediately proceeded to form ears, regardless of the length of time they had been exposed to shortened day. The unvernalized plants did not come into ear, no matter how long they were kept in continuous light.

It is obvious, however, that this does not necessarily prove the existence of a *photo-phase*, but merely shows that winter wheat is a long-day plant. It is on the other hand not clear from the literature on photoperiodism whether it is necessary for such a plant to receive first its quota of low temperature before it can respond to light. The arguments for and against phases, either externally visible or of an internal cryptic nature only, are discussed again in Chapter VIII.

When the practice of vernalization by temperature was first brought forward, investigators produced results to show that it was also possible to vernalize plants by appropriate treatment by light, without first permitting the plant material to pass the thermo-phase. The experiments of Čaĭlahjan are quoted on pp. 33-5 of *Joint Publ. No. 1* (Imperial Agricultural Bureaux, 1935), and those of Gregory and Purvis are described on pp. 65-8 of the present book. When such experiments are successful, the supporters of the theory of phasic development claim that the plants concerned must have had the necessary temperature for passing the thermo-phase either during their early seedling stages, or even while still attached to the mother plant before the onset of dormancy. One of the Russian experiments quoted in this connection is that of Avakjan and Tagi-Zade (1935). These workers based their conclusions on the differentiation of the growing point, and found that plants kept at high temperatures failed to obtain their requirement of low temperature and therefore to pass the thermo-phase, while those (long-day) plants that were kept first in low temperature and then in short day failed to receive the light (or alternation of light and darkness) necessary for completion of the photo-phase.

Photoperiodism and Photosynthesis

Little work appears to have been done on a comparison of the photosynthesis of long-day and short-day plants. Although it might be expected that, since the relative length of day and night has a decisive

influence on development, photosynthesis might be the cause of the phenomenon, Garner and Allard (1920), Gaertner and Braunroth (1935) and Fabian (1939) among others have shown that minimal intensities of light (according to Fabian 0·5 lux) and indeed even moonlight can have a decisive influence on the course of development of the plants treated, although they cannot have any significant effect on carbon dioxide assimilation. Bode (1942) concludes that light appears to operate not only through the assimilation apparatus, but also that the chlorophylls must probably be regarded as perceptors, as the capacity to respond to photoperiodic stimuli corresponds approximately to the spectral absorption of the chlorophylls (Katunskiĭ, 1937, and Wallrabe, unpubl.).

Using the particularly responsive short-day plant, *Kalanchoë blossfeldiana*, Harder and von Witsch (1941) showed that the CO_2 content of the air must be essential for the formation of the 'flowering hormones'. Plants of which one leaf was placed in a celluloid chamber through which air was passed and which was kept in a 9-hour (short) day flowered after 4 weeks had elapsed. When air free of CO_2 was passed through the chamber, however, no inflorescence was formed even after 12 weeks. Bode asks the question whether the CO_2 of the air has a direct effect on the plasms, or whether one is not recording an influence of photosynthesis as development is dependent both on CO_2 and on light, and quotes Harder and von Witsch: 'it is shown that for the production of flowering the presence of the current photoperiodic conditions is not sufficient, but at the same time photosynthesis must take place in the leaf receiving the impulse'.

In Bode's own experiments on *Kalanchoë* (1942), assimilation and respiration in plants grown under varying lengths of day were tested by the manometric method. Plants which had grown in short day from germination onwards, and also plants which were not subjected to short-day treatment until some time after germination, exhibited considerably increased photosynthesis and respiration at the time of flowering. Conditions are still more extreme at the bud stage. After fruit setting, photosynthetic activity again decreased considerably. Through short-day treatment, an increase in the content of colouring matter was produced.

Bode gave individual leaves the following treatment. One leaf of plants in long day was darkened daily by setting over it a small bag impermeable to light, in such a way that this leaf received a 9-hour (short) day, while the other leaves of the plant received long day. The result of these measures is that the leaves of the same row as that containing the bagged leaf assume largely a short-day character and are distinguished therefore by increased succulence, while the opposite leaves are hardly influenced at all. The plant forms after a certain time an inflorescence which under slight impulse (bei schwachem Impuls) is normal on the bag side, but

exhibits proliferation on the opposite side (Harder, von Witsch an Bode, 1942).

This research and that of other German and Russian workers reviewe by Bode is linked with that already discussed in Chapter III (effect c development on growth), and in Chapter XII. It is also desirable t refer to the light and dark reactions of photosynthesis discussed b Briggs (1941), work which shows that during short days the light reactio will operate during shorter intermittent periods, (for example, 9 instea of 15 hours) while the dark reaction operates continuously. A specula tive suggestion has been made that the shift in relative periods of opera tion of these reactions might lead to secondary reactions connected i some way with the reactions involved in photoperiodism. Temperatur is, however, an important controlling factor, and the whole problen leads on to a consideration of modern advances in the biochemistry o photosynthesis, which is beyond the scope of the present review (see however, Franck and Gaffron, 1941).

Photoperiodism and Taxonomy

The photoperiodic reaction of plants has been used to distinguis species and varieties in taxonomic studies. Two examples may be given

The only wild native bean in the eastern United States is the so-calle Kidney Bean, *Phaseolus polystachios*. It is a rather rare species of ric deciduous woods of the Coastal Plain and the Piedmont. Although it name suggests that it belongs to the species-assemblage represented b *Ph. vulgaris* L., Allard (1943) considers that, for the following reasons its affinities may be nearer the assemblage of scarlet runner beans repre sented by the species *Ph. coccineus* L.

The varieties of *Ph. coccineus* tested by Allard and others tend t flower most freely in long days, and show no, or reduced, flowering in daylengths of 10 hours. If flowers are developed they are usually sterile or form fruit very late in the season.

Ph. polystachios becomes a dwarf, bushy, completely flowerless plant in a 10-hour day; it is intermediate in its photoperiodic behaviour since flowering occurs only within a definite range of daylengths. It is definitely not a short-day plant, flowering being favoured by long days which do not exceed a certain limit. There are, on the other hand, few if any of the varieties of *Ph. vulgaris* assemblage which show long-day tendencies or find lengths of day of 10 or 12 hours unfavourable to flowering.

In short photoperiods, the roots of varieties of *Ph. coccineus* usually show strong tuberization and *Ph. polystachios* has shown similar tenden cies, both in the field and when long-day conditions favourable to flowering are denied the plants. Both *Ph. polystachios* and *Ph. coccineus*

are hardier than members of the *Ph. vulgaris* assemblage. In England the scarlet runner beans sometimes overwinter by virtue of their tuberous roots, and the wild bean of the eastern States has become a perennial species for the same reason. Allard's conclusion is that these characteristics combined with the hypogean behaviour of the cotyledons (cotyledons of *Ph. coccineus* and *Ph. polystachios* remain buried in the soil, those of *Ph. vulgaris* do not) indicate that *Ph. polystachios* is more closely allied to the *Ph. coccineus* assemblage than to the kidney beans, *Ph. vulgaris*.

The second example is that of *Alopecurus myosuroides*, a Central European grass species that occurs mostly within the adventitious flora in Sweden (Johnsson, 1944). This species possesses all the properties of an allogamous species; enforced self-fertilization is attended by reduced seed setting of varying degree in different plants; different inbred species may be very unlike in habit. Some families are on an average fairly vigorous, others show considerable depression in vitality. Non-flowering plants are very frequent, and belong to two main types: (*a*) vegetatively very feeble, sub-lethal plants, and (*b*) vegetatively luxuriant but with few or no flowers.

These Central European plants have been taken from a relatively short day and cultivated in Sweden, considerably to the north of the range of the species. Johnsson suggests that special short-day forms have differentiated out within the species. When a short-day form is transferred to a latitude with a relatively long day, a protracted vegetative development without fructification is to be expected. The contemporaneous occurrence of forms neutral to the influence of length of day and showing a normal behaviour as regards vegetative and reproductive phases during cultivation under relatively long-day conditions is not considered by Johnsson to be surprising.

The opposite behaviour of forms of *Poa pratensis* from northern Sweden when moved south is illustrated in Plate 22, and the relation between this behaviour and the breeding of pasture types of herbage plants is discussed on p. 254. (See also Olmsted on *Bouteloua*, p. 216.)

CHAPTER VII

DARKNESS AND DEVELOPMENT

Requirements of the Photoperiodic Classes

Views and experiences have differed considerably relative to the role of darkness in growth and development. Klebs noted a retarding effect of darkness, which in one experiment proved stronger than the stimulative or promoting effect of light, when 12 hours of darkness alternated with 12 hours of light. The work on photoperiodism has been based upon the assumption that short-day plants at least require a definite sequence of dark and light periods in the course of every 24 hours. Recent work already referred to has indicated that this rigid alternation of light and dark periods is not essential for at least some of the long-day plants, as development is possible even if these are grown in continuous light. This is bringing the research on photoperiodism into line with the hypothesis of the photo-phase as put forward by Lysenko, who, as already noted, states that long-day plants require continuous light and only tolerate darkness. It appears that other workers would state that darkness is an inhibiting influence in the development of long-day plants.

Research on short-day plants is, however, not yet indicating definitely that the converse is true for short-day plants, namely that these require darkness and only tolerate light. The situation with regard to short-day plants is complicated by the fact that development is not possible without growth, and growth is not possible until a minimum number of light hours is available for photosynthesis. This makes experiments to prove whether or not darkness is the controlling factor in development of short-day plants rather difficult to conduct. In the experiments described below, the American work, and the Russian experiments based on the theory of phasic development do appear, however, to suggest rather strongly that it is darkness and not the photoperiod which activates development in a short-day plant such as the cocklebur used by Hamner and that it is not the magnitude of this proportion but the absolute length of the dark period which is important. The experiments of Hamner, Razumov, and others to be described also suggest simple ways of adapting this research in agricultural and particularly horticultural practice.

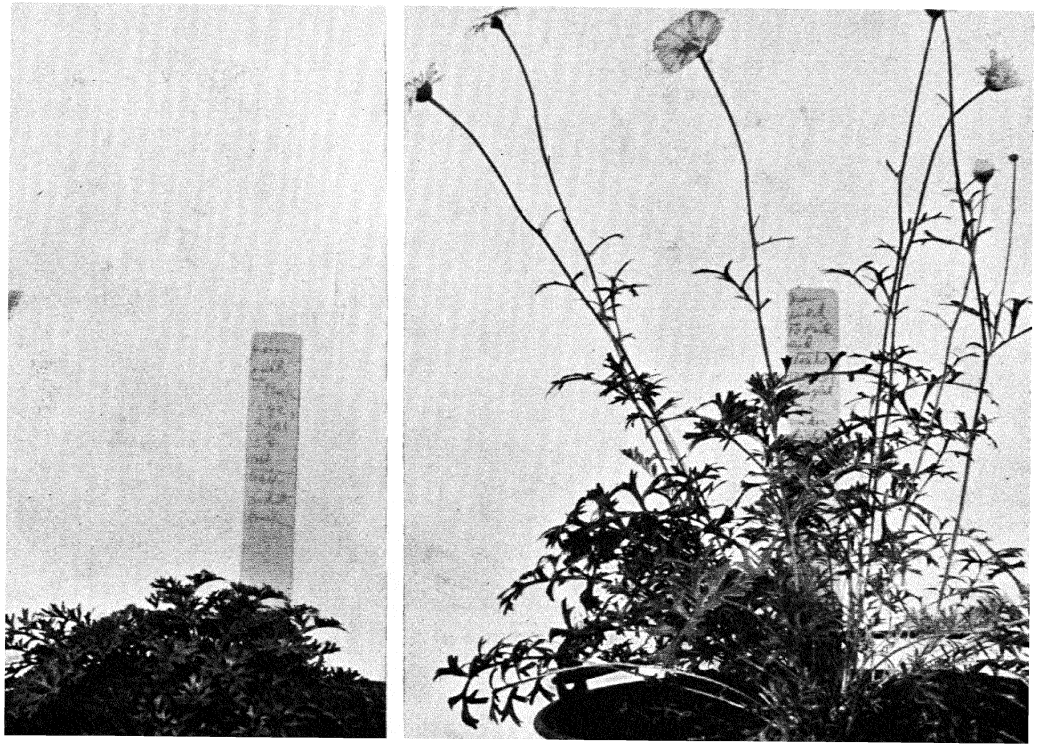
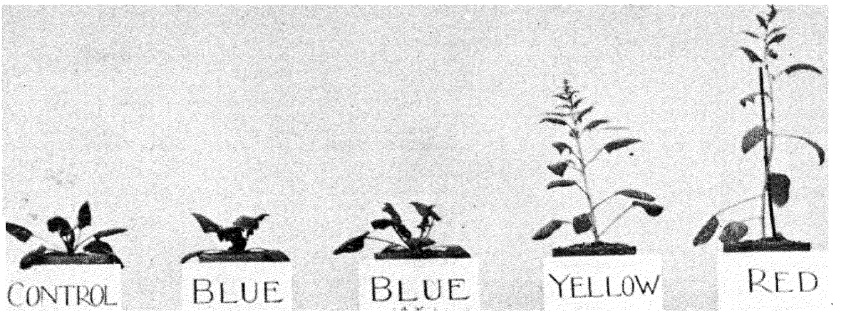


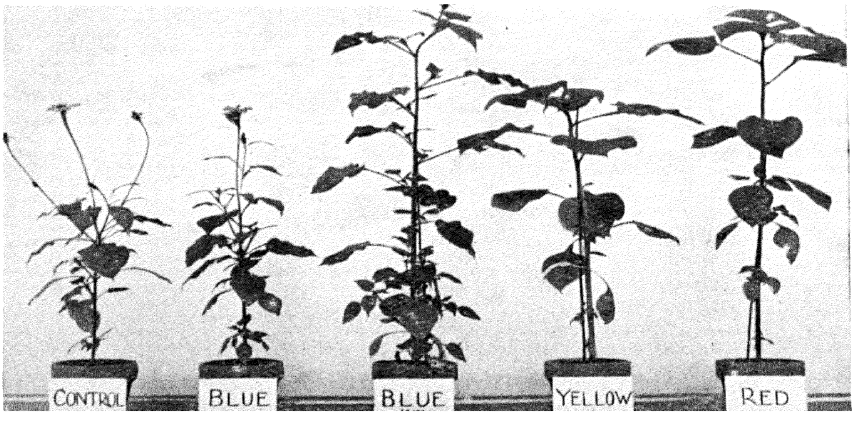
PLATE 11. Pyrethrum produces flowers (source of insect powder) only when grown where photoperiods are long; if days remain short, the plants remain as rosettes. Photo: Bureau of Plant Industry, Soils and Agricultural Engineering, U.S.D.A.



(*a*) *Spinacia oleracea* var. Nobel. Photo: 37 days after irradiation.



(*b*) *Soja max* var. Mukden. Photo: 73 days after sowing.



(*c*) *Tithonia speciosa* under various wavebands of irradiation.

PLATE 12. Effect of various wavebands of supplementary radiation on photoperiodic response. Photos: Withrow and Withrow, 1940.

Experiments on Cocklebur

The short-day plants employed in these experiments were the soybean and the cocklebur, *Xanthium pennsylvanicum*; results with the latter will be discussed here, on the basis of the summary given by Hamner (1942). Plants of *Xanthium* will remain vegetative for months and may attain great size without differentiating a single floral primordium if grown in cycles consisting of photoperiods of 16 hours (or more) alternating with dark periods of 8 hours (or less). Provided such a plant is beyond the seedling stage and has produced one or more fully expanded foliage leaves, that is it is ripe-to-flower, it will initiate primordia and develop flowers very rapidly when transferred from the above cycle to one containing dark periods of more than 9 hours alternating with photoperiods of less than 15 hours.

Xanthium is one of the more remarkable examples of the efficiency of the photoperiodic induction already described in Fig. 24; a vegetative plant may be 'photoperiodically induced' by transferring it from the unsuitable conditions of long day and exposing it to a *single* short day. It will then flower even if kept subsequently under long-day conditions. Since a 'short day' consists of two portions, a relatively short photoperiod followed by a relatively long dark period, it becomes desirable to know whether one portion of the 24-hour period or both are determinative.

Hamner and Bonner (1938) found that the effective part of the short day was the relatively long dark period, a vegetative plant transferred from long day being induced to flower by exposure to a single long dark period. The effectiveness of this dark period depends, however, upon the illumination which the plants had previously received under the long days. Many experiments have shown (Hamner, 1940, Hamner and Bonner, 1938, Mann, 1940, Snyder, 1940) that an effective photo-inductive cycle for *Xanthium* must include a photoperiod of about 30 minutes or over (the length required being dependent upon light intensity) followed by a dark period of more than 8¼ hours. The above sequence is not reversible; the photoperiod must precede the dark period. Under natural conditions where 24-hour cycles prevail, photo-inductive cycles occur only during the relatively 'short days' of the year when 'nights' of more than 8¼ hours are prevalent.

The effectiveness of the light period is dependent to a certain extent upon its duration. Fig. 24 indicates that the rate of floral development at two light intensities increases with increasing duration of photoperiod at each intensity up to a certain point, beyond which the rate remains constant. At high light intensity (10,000-ft. candles) maximum rate occurs

after 1 hour's exposure, while at medium intensity (2,000 to 3,000-ft. candles) 4 or 5 hours are necessary. At low light intensities (10-ft. candles) a photoperiod of many hours' duration is not effective in causing floral initiation (Hamner, 1940). At high light intensities, a degree of effectiveness is reached which is appreciably higher at all durations than that reached at medium intensities.

The relation between length of photoperiod and temperature has been studied. At 30° C. the maximum rate results after about 5 hours' exposure while at 10° C. the maximum is not reached until photoperiods of about 15 hours are used. The maximum rate of development reached at

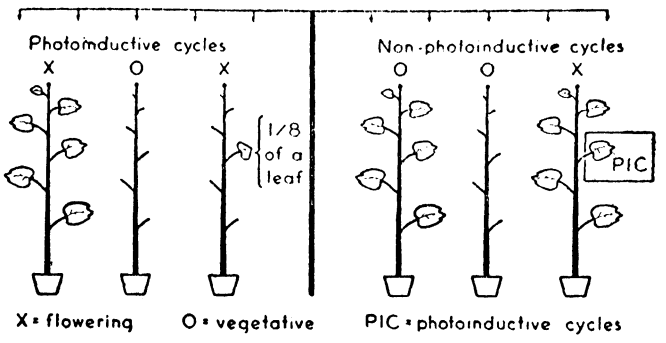


FIGURE 31

Responses of *Xanthium pennsylvanicum* to treatment with photoinductive and non-photoinductive cycles, that is, to cycles of light treatment which do, or do not cause a change to a reproductive state. In all cases, plants were grown in non-photoinductive cycles until they had developed three or more fully expanded foliage leaves. All plants are assumed to be in a vegetative condition at the start of the experiment. Various degrees of defoliation were carried out. On the extreme right is a plant of which only one leaf was exposed to a light environment appropriate for reproduction, and which nevertheless flowered (adapted from Hamner and Bonner, 1938)

each temperature is approximately the same (Fig. 26). Thus the effectiveness of the photoperiod of any particular photo-inductive cycle increases with increasing duration up to a certain point; here a maximum level of effectiveness is attained which remains fairly constant as the photoperiod is progressively increased in length. The rate at which this maximum level of intensity is reached is rapid at high light intensities and relatively slow at medium light intensities or at low temperatures.

The important conclusion drawn by Hamner, particularly with regard to the work of Razumov described below, is that, regardless of the length of this photoperiod or the intensity of the light preceding exposure to darkness, a continuous dark period of at least 8½ to 9 hours is necessary for the inducing of formation of flower primordia. Two dark

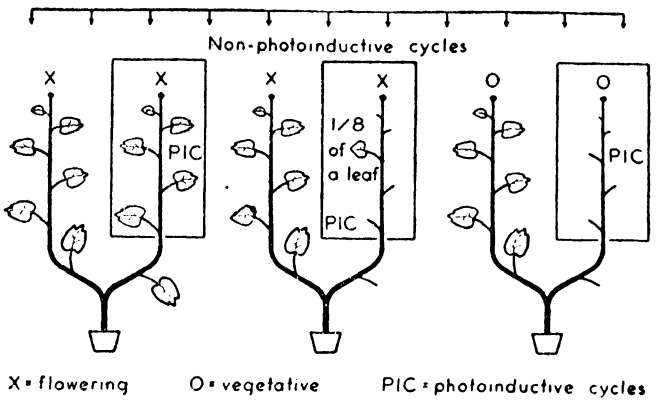


FIGURE 32

Responses of two-branched plants of *Xanthium*, one branch receiving photoinductive cycles, while the remainder of the plant is exposed to non-photoinductive cycles. Both branches flower provided the branch which is exposed to short day possesses more than one-eighth of one mature leaf (adapted from Hamner and Bonner, 1938)

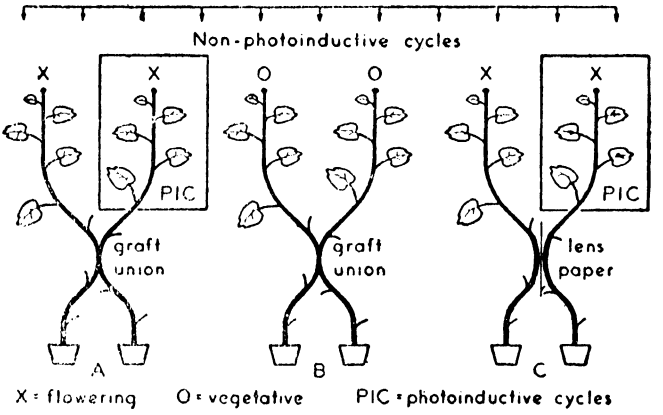


FIGURE 33

A. Responses of *Xanthium* plants which have been approach-grafted, the top of one plant being exposed to photoinductive cycles while the other plant of the pair is exposed to non-photoinductive cycles, showing the transfer of the flowering stimulus across the graft from one plant to the other.

B. Responses of similar grafted plants, both plants being treated to non-photoinductive cycles.

C. Responses of two plants similar to A, but in which the actual union of tissues at the injured surfaces is prevented by placing lens paper between the two plants. The flowering impulse is nevertheless transferred to the plant in the environment unfavourable for flowering, and flowering takes place normally (adapted from Hamner and Bonner, 1938)

periods of 6 hours' duration separated from one another by as little as 3 minutes of light of low or high intensity are completely non-effective. In order to be effective, the long dark period must occur soon after a previous exposure to an 'effective photoperiod'. If, previous to treatment with a long dark period, plants are exposed for several hours to light of low intensity (10-ft. candles) or to several short cycles of 3 minutes of light and 3 hours of darkness, they do not leave their vegetative state. Hamner concludes therefore that some type of determinative reactions take place during both phases of a photo-inductive cycle, and also that there is an interaction among them.

Experiments on Perilla

Moškov (1939) refers to Garner and Allard's research which showed that short-day species, which flower rapidly under equal lengths of light and darkness (12-hour periods), will not flower at all if the same dosage of light and darkness is alternated at shorter intervals, namely in periods varying in length from 6 hours down to 5 or 3 seconds. Long-day species on the other hand form no flowers when given 12-hour days, but do flower when darkness and light are changed in quick succession. Moškov states that these facts establish two fundamental principles, namely (1) that photoperiods have been interpreted properly as the daily ratio between the intervals of light and darkness, not as daylength or night-length independent of one another, and (2) that a characteristic photo-periodic reaction cannot be obtained if dark periods are interrupted, while an intermission of the daily period of light by darkness has been found to produce no influence on the flowering time of either short- or long-day plants. Moškov considers it probable that part of the light-requiring processes can be accomplished in very short periods of the day, or is not interrupted by temporary darkness, or is finally capable of summation by the addition of the individual short periods. Then, however, another part of the process requires long daily periods of darkness which must not be interrupted by light; this part progresses only slowly and is incapable of creating a summative effect or of advancing by degrees when interrupted.

Moškov began experiments on *Perilla ocymoides*, most of the varieties of which flower in daylengths of 3 to 16 hours; there is no considerable difference between the photoperiods within this range as regards effect on budding and flowering. In daylengths of 2 as well as of 17 hours, *Perilla* practically fails to flower, and the question therefore arises as to the minimum daily amount of darkness and light indispensable for this species to complete its full cycle of development. As the object of the experiments was to prove that the length of day and night requirement

of *Perilla* is as high as 3 to 4 hours of light and 8 to 9 hours of darkness, while the rest of the daily period matters little, 20-day-old plants of *Perilla* were subjected to a photoperiodic test for 20 days according to the plan shown in Table 18.

TABLE 18

No. of variant	*Series*	
	First Photoperiods	*Second Photoperiods*
I	3 hours of light and 21 hours of darkness every 24 hours	4 hours of light and 20 hours of darkness every 24 hours
II	15 hours of light and 9 of darkness every 24 hours	16 hours of light and 8 hours of darkness every 24 hours
III	3 hours of light and 9 hours of darkness every 12 hours (i.e. two photoperiodic cycles a day)	4 hours of light and 8 hours of darkness every 12 hours (i.e. two photoperiodic cycles a day)

Moškov regards the behaviour of Series I as indicating that 3 hours of light in the photoperiodic cycle represents the minimum below which it is not possible to go. The somewhat better development of variant III compared with variant I is regarded as indicating that either there exists some definite ratio between the requirements of darkness and light, or the processes occurring in light increase by addition and end by producing a summative effect.

In the second series, only plants from variant I, given 4-hour days, produced ripe fruit. Plants from the 16-hour-day variant were nearer to flowering than those receiving 3-hour days, but they did not start flowering and formed only a few buds. Plants of variant III resembled those of variant II.

Moškov concludes that 8 hours of darkness, whether following 16 or 4 hours of light, are insufficient for full development and profuse fruiting. The requirement of *Perilla* is only 9 hours of darkness and 4 hours of light; whether the remaining 11 hours are passed in light or the darkness is of no consequence for the processes which prepare the plants to enter the reproductive state. This distribution of the remainder of the daily period between light and darkness is not without influence on the yield of seed. In speaking of the minimum intervals of light and darkness in cycles suitable for the development of short-day plants, Moškov considers that the length of the dark periods should be two and a half or three times that of the light periods. Other experiments by the same investigator have indicated that minimum daylengths can be broken by

short periods of darkness without detriment to development while an intermission of the minimum periods of darkness by light disturbs the development of short-day plants, even though it does not change the total number of dark hours.

On the basis of the minimum requirement in daily ratios of darkness and light, Moškov was successful in these experiments in inducing flowering in short-day species by alternating light with darkness artificially in order to create two photoperiodic cycles instead of one within a 24-hour period, results which he considers apply in agricultural and horticultural practice.

Effect of Intermittent Light

The latest Russian work is by a supporter of the phasic development outlook, Razumov (1941), who prefaces his account of experiments with the statement that the inevitability of an alternation of light and darkness for short-day plants is discernible only in the fact that growth is not possible without light and consequently a green plant does not develop if it does not receive its quota of light for growth. As already noted, it is difficult to show that actually only the dark period in each cycle conditions the processes of development, as any attempt to maintain a plant for a long period (24 hours or more) in complete darkness will obviously lead to an interruption of photosynthesis and consequent failure. For the same reason, a short-day plant such as millet flowers later in a 2- or 3-hour day than in an 8- or 10-hour day. For this reason only is an alternation of light and darkness necessary for short-day plants; development in these plants proceeds, according to Razumov, entirely during darkness, and the statement to this effect by Lysenko is considered as being confirmed.

Razumov used a number of short-day and long-day plants, but dealt primarily with millet. The experiments were concerned with the inclusion of dark periods during the day and of light periods during the night. The dark and light periods were of varying duration and were interpolated at different times during the light and dark treatments respectively.

The differences between the reactions of short-day and long-day plants are fundamental, states Razumov. Very short intervals of light (up to 15 minutes) in the middle of the night exert a strong influence on the development of both groups of plants. When grown in a daylength of 10 or 11 hours, millet behaved as in continuous illumination when the period of darkness was so interrupted, whereas oats behaved as if it were under the influence of long day rather than of short.

In one set of experiments, the short-day plants received 8 hours of light daily, but the dark period was interrupted by a single light interval

asting a half-hour, and 1, 2 or 3 hours respectively, so arranged that the ıight was divided into two equal parts. The inclusion of even extremely hort intervals of light in the middle of the night had a considerable ffect on short-day plants. Several short-day plants (millet, *Perilla*, *Chrysanthemum*) were grown in 18- and 9-hour days with 15-minute ight intervals in the middle of the night. No plant in the 18-hour day lowered or eared. In a 9-hour day and unbroken night, development vas very rapid, but a 15-minute light interval in the middle of the dark ɔeriod caused a delay in panicle emergence in Pamir millet of 15 days, n Mongolian and Western Chinese millet of 40 days, and delayed lowering in *Perilla* by 35 or 42 days (according to variety), in *Chrysanhemum* by 30 days and in *Crotalaria* from India by 10 days.

As this effect is observed from introducing a light interval in the dark ɔeriod, while a dark interval in the day has hardly any effect on millet, t is concluded that processes of development take place in the dark in hort-day plants.

Razumov recommends that these results be used in agriculture and ıorticultural practice, when crops are grown under electric light or in aylight supplemented by electric light. Electric current may be econonized by introducing comparatively short intervals in the middle of the ight in such a way that the amount of darkness before and after the ght intermission does not exceed the limit necessary for a given plant, ɔr example, 6 or 7 hours for millet.

Borthwick and Parker (1938) have shown how this same treatment an be applied to Biloxi soybeans, and Emsweller, Stuart and Byrnes 1941) have used it to delay the blooming of chrysanthemums. Plants of oybean were grown in 16-hour days until the beginning of the experiıent, then transferred to 8-hour photoperiods and given 0, 1, 5, 15 and 0 minutes of artificial illumination of about 160-ft. candles at the midoint of the 16-hour dark period. After 4 days of treatment all plants /ere returned to 16-hour photoperiods for about 2 weeks, after which ıey were dissected. No flower buds were formed after a treatment inolving interruption by light, but were found on all plants receiving 6-hour dark periods without interruption.

Biloxi soybean forms flower primordia at all growing buds when the ntire plant or a single leaflet is exposed to a minimum dark period of 0·5 hours for two or more daily cycles. These dark periods must be ontinuous; even 30 seconds' interruption prevents formation of flower rimordia. A study has been made (Parker, Hendricks, Borthwick and cully, 1945) of the effectiveness of light at various wavelengths in preenting floral initiation; a special spectrograph has been designed /hich is unique in that the spectrum is wide enough to permit irradiaion of fully expanded leaflets yet maintains spectral purity at high

intensity. Floral initiation can be suppressed by interruption of the dark period with light of sufficient energy from any region of the visible spectrum, but two regions show maximum efficiency: one in the yellow, orange and red, and the other in the violet near 4,000 Å. The overall response curve, which strikingly resembles but is not identical with the curve for photosynthetic utilization of carbon dioxide, indicates that the chloroplast pigments of the leaf are associated with the reaction caused by interruption of the dark period. Carotenoids are apparently not involved since they have different absorption maxima. These investigators consider that energy may be absorbed by the chlorophyll and transferred to a reaction leading to the destruction of a material determining floral initiation. The response of *Xanthium pennsylvanicum* in the red is similar to that of Biloxi soybean.

The varieties of chrysanthemum (Mrs. H. E. Kidder, Josephine Byrnes, Cornelia, and Gold Coin) used by the other investigators were exposed to normal photoperiods, with two interruptions (one at 10 p.m. and the other at 2 a.m.) or one interruption at 11.45 p.m., the light breaks being provided by 45-minute exposure to Mazda light at 32- to 60-ft. candles.

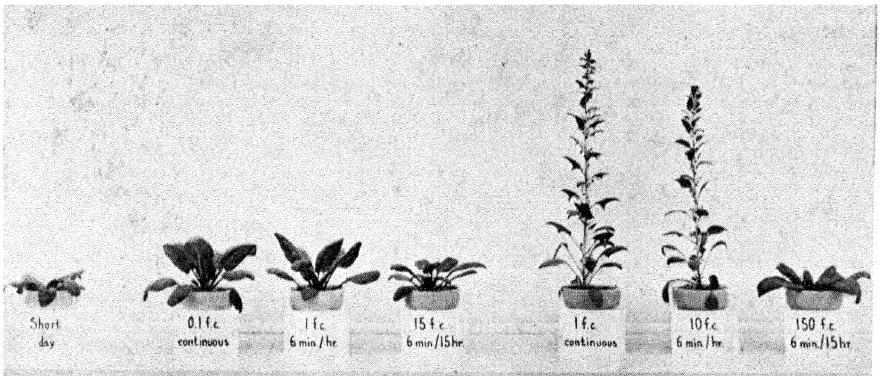
One light period delayed the variety Mrs. H. E. Kidder for 29 days, and Josephine Byrnes for 32 days; two light breaks delayed them for 20 and 26 days respectively. On December 10th, none of the Cornelia or Gold Coin plants that had received any light during the dark periods since the experiment began on September 6th were blooming.

As a result of interrupting the dark period, plant height was less in all varieties except Gold Coin than that of plants receiving unbroken darkness, even though the former plants remained vegetative and accumulated far more total dry weight than did those receiving no interruption. Two light breaks were somewhat more effective than one for increasing dry weight although not so effective in delaying blooming or retarding elongation.

The German investigators, Harder and Bode (1943) also found in their work with *Kalanchoë blossfeldiana* that an interruption of the period of darkness by switching on light temporarily had a marked effect on flowering, phyllody and leaf succulence.

Conclusion

This research leads on naturally to the more complex problems connected with the internal causes of flowering discussed in Chapter XI, and to a consideration of the evidence for the existence of some substance controlling flowering, possibly of a hormonal nature. If such a substance exists it must be formed in light conditions in long-day plants and in darkness in short-day plants. The action of the light breaks noted above



(*a*) Effect of varying supplemental irradiances and length of dark period on the growth and flowering of Nobel spinach.



(*b*) Flowering response of Nobel spinach to intermittent irradiation on constant time cycles.



(*c*) Flowering response of Nobel spinach to intermittent irradiation on constant irradiance cycles.

PLATE 13. Effect of intermittent irradiation on photoperiodic response (see p. 137). Photos: Withrow and Withrow, 1944.

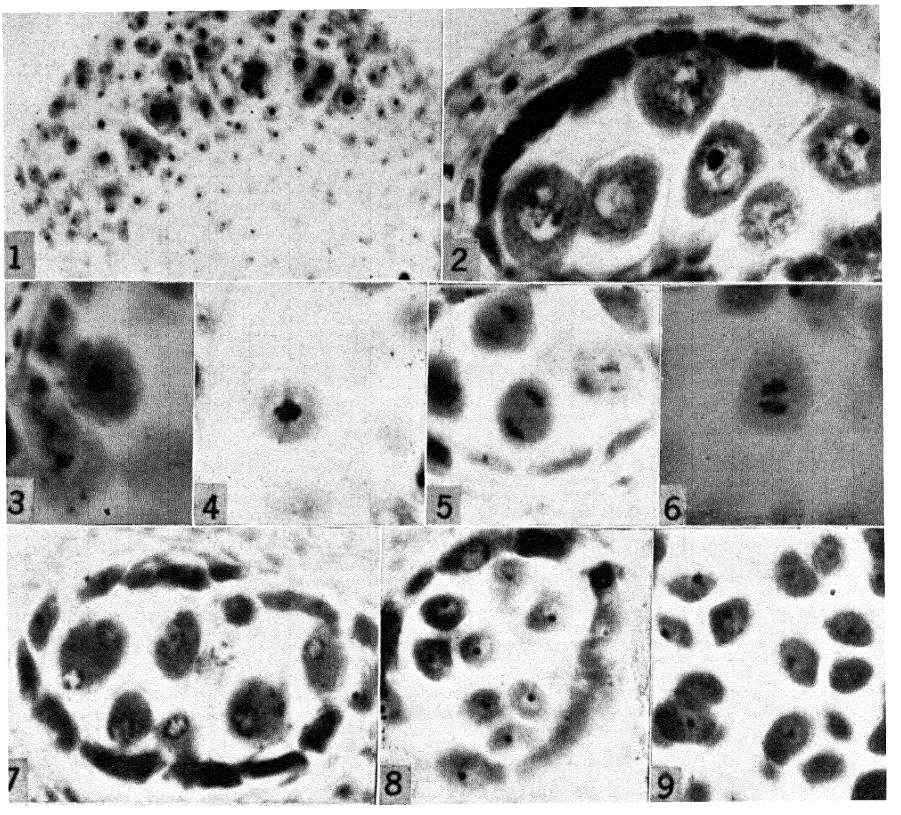


PLATE 14. Effect of photoperiod on microsporogenesis in Biloxi soybean (see p. 146). Photo : Nielsen, 1942.

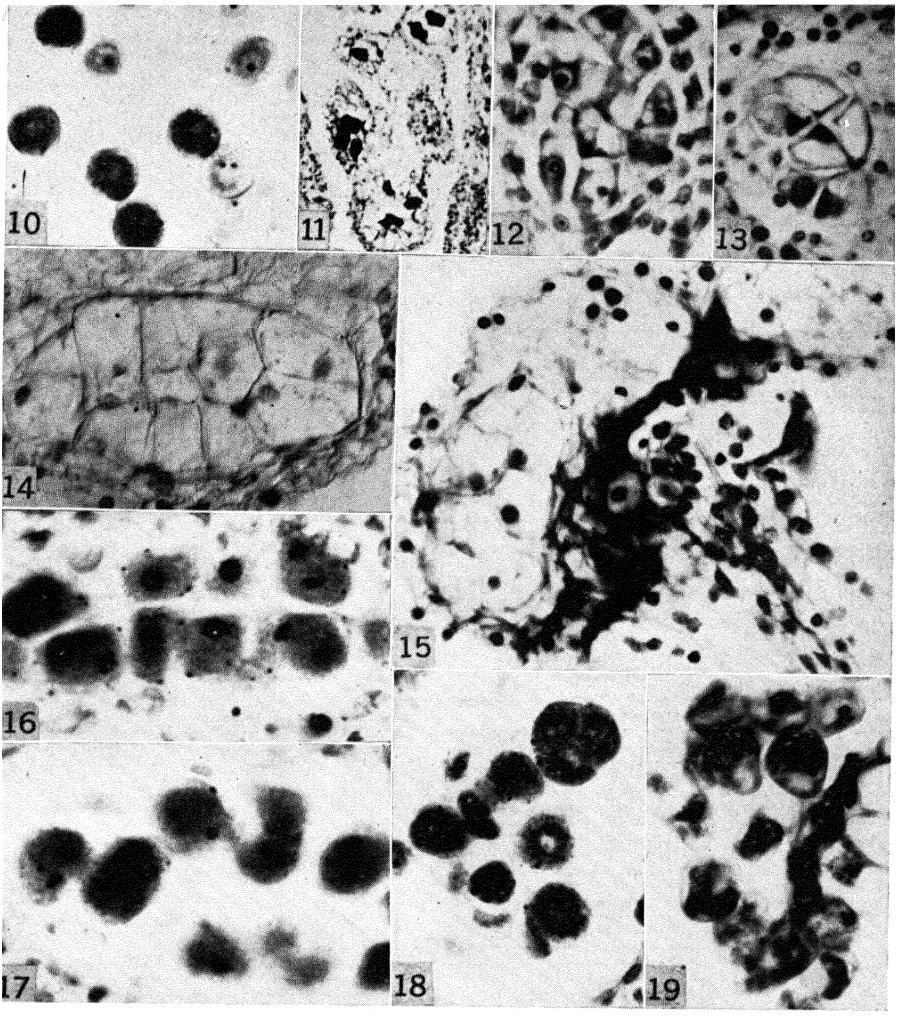


PLATE 15. Effect of photoperiod on microsporogenesis in Biloxi soybean (see p. 146). Photo: Nielsen, 1942.



PLATE 16. Light for an hour in the middle of the dark period delays the blooming of chrysanthemums (see p. 136). Photo: Bureau of Plant Industry, Soils and Agricultural Engineering, U.S.D.A.

must presumably be to inhibit the formation and/or translocation of this impulse from the leaves to the growing point, except when the dark interval (in short-day plants) is sufficiently long to permit its initiation and subsequent action.

To a reviewer concerned more especially with the phytogeographic and agronomic aspects of the problem, this clear distinction between long- and short-day plants is difficult to believe, both since there are all

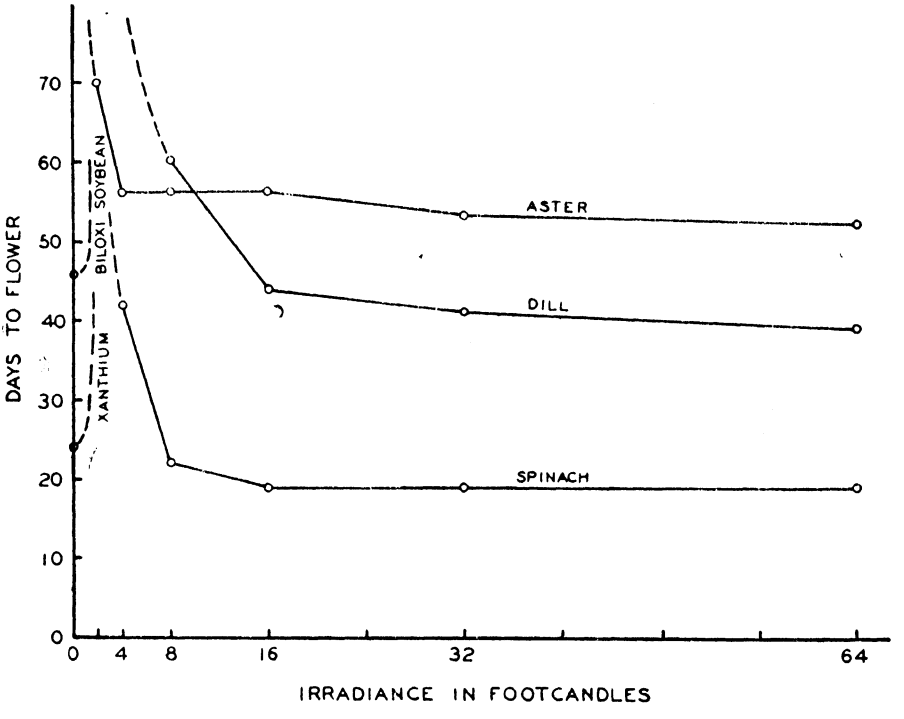


FIGURE 34

Effect of intermittent irradiation on photoperiodic responses. Flowering time of *Aster*, dill and spinach under the various irradiances of intermittently applied radiant energy. Broken lines indicate probable shapes of curves at low irradiances (Withrow and Withrow, 1944)

gradations between the long days of high latitudes and the short days of equatorial regions, and since there appear to be gradations also between the true long-day and short-day types of plants. It is not clear what the developmental requirements of those intermediate plants might be expected to be, if development is governed by light in one group and by darkness in the other.

Melchers and Claes (1943) consider that the results of their experiments on the induction of flower formation in the long-day plant, *Hyoscyamus niger*, in short-day conditions through inhibition of respira-

tion in the dark phases confirm their view that the secondary processes inhibiting flower formation in *Hyoscyamus* are identical with respiration processes (see p. 30). Respiration was inhibited by means of a N_2 atmosphere during the dark periods. With both 10 hours' light daily plus 5 hours' N_2 atmosphere, and 9·5 hours' light plus 8 hours' N_2 atmosphere, all the plants achieved flower formation, while the majority of the controls remained vegetative. Experiments have now begun to analyse the effect of weak light intensities on inducing or encouraging flower formation in long-day plants.

In addition to the studies on flowering hormones or related substances,

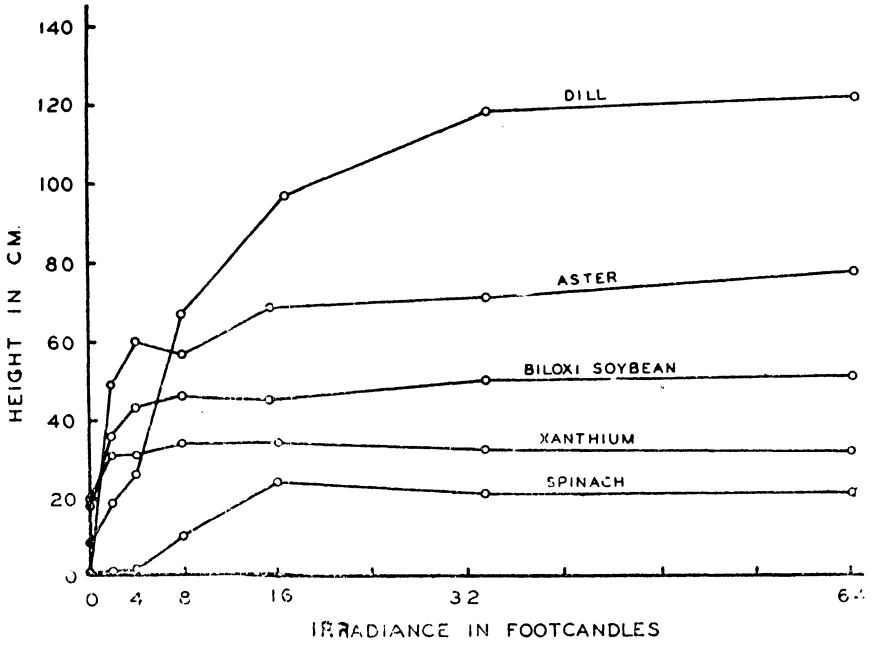


FIGURE 35

Height of plants under the various irradiances of intermittently applied radiant energy (Withrow and Withrow, 1944)

numerous other highly academic aspects are being studied. As an example the work of Withrow and Withrow may be quoted (1944), as an outcome of the work on intermittent radiation already referred to earlier in this chapter. These authors state that the investigators who have intermittently applied radiant energy in studying photoperiodism have used irradiances far above the point of saturation of the photochemical reaction and little attempt has been made to control the energy relationships per cycle. It has thus been difficult to interpret the results in terms of the inter-relationships between the photochemical and non-photochemical reactions.

The results of the experiments made by these investigators show that: (1) the region of saturation of the photochemical reaction for most of the plants used is in the neighbourhood of one foot candle, since further increases in irradiance failed to bring about corresponding increases in the photoperiodic responses; and (2) the greater the length of the dark period between irradiation cycles, the less the efficiency of the radiant energy in promoting the long-photoperiod responses, with the efficiency falling off rapidly when the dark periods were around 90 minutes or longer for spinach and Biloxi soybean. In all cases, continuous irradiation resulted in the highest efficiency.

From these results, a theory has been postulated concerning the kinetics of the photoperiodic reaction based on two relationships which appear to limit the photochemical reaction; namely (1) the relatively slow rate of the non-photochemical reaction which forms the substance to be photo-activated; and (2) the relatively low equilibrium concentration which this substance attains during long periods of darkness.

CHAPTER VIII

PHASIC DEVELOPMENT

Visible and Invisible Phases

The Russian plant physiologists support the theory of phasic development proposed by Lysenko (see p. 36). Most of the current experiments are based on this hypothesis and use the appropriate terminology such as thermo-phase, photo-phase and so on. On the basis of the fact that the rate of growth and the rate of development may be quite different, it is assumed that the thermo-phase may be passed while the plant is still a slowly growing seed, and the photo-phase while it is still only a young seedling provided it has a chlorophyll mechanism capable of photosynthesis. There is no reference to the number-of-leaves statement of Gregory and Purvis (p. 31). Presumably subsequent phases of development are also considered as able to proceed while the plant is still in an early growth stage. Whether or not these various invisible phases, which are stated to be always in a strict sequence, have been passed in any given plant will not become evident until later; if they have, the plant will flower.

The alternative view held by investigators outside Russia is based on a combination of invisible and visible (morphological) phases. It appears from the literature that the inward state or condition of ripeness to flower represents a first phase, which is not at the time manifested by external appearance of the plant. Subsequent phases, however, are based upon external appearance, even if micro-dissection may be necessary to diagnose the first of them. These phases or stages are generally regarded as the formation of flower primordia at the growing point (to be found by micro-dissection), the formation of flowers, flowering, the formation of viable male and female gametes (gametogenesis), and so on.

The exposure of slowly growing seeds to requisite low temperature (vernalization) and of plants of a certain age to requisite daylength (photoperiodic induction) is accepted in most physiological circles as able to influence subsequent development of plants towards reproduction, even if the plants being treated are, after exposure to the required temperature and daylength, transferred to conditions that do not favour development as such. Some authors talk of photothermal induction, suggesting that early treatment with temperature and appropriate daylength are necessary. This approaches very near to the Russian phasic outlook, although the dogmatic statement characteristic of Soviet

articles that there are separable and distinct phases dependent for completion on different factors would not be supported by non-Russian investigators.

It may well be that winter varieties may be induced to flower under *artificial* conditions by exposure first to the required low temperature and then to the required length of day. It is, however, doubtful whether a winter variety sown in the autumn and growing under *natural* conditions first responds only to low temperature until the thermo-phase is completed, when it clicks over into the photo-phase and begins to respond to daylength (combined with a high temperature).

Some investigators appear to consider that exposure to optimal daylength without any previous exposure, intentional or accidental, to low temperature, will cause plants to flower. Others are beginning to consider that temperature is the controlling factor throughout, overriding the effects of photoperiod, nutrition, etc.

A reviewer approaching this problem from the agricultural point of view feels that no definite conclusion can yet be made. The application of this research in agricultural and horticultural practice is, however, important; an understanding of the relation between development and the environment will make it possible to control growth and reproduction according to the crop concerned, whether it be a lettuce or cabbage (growth), a herbage plant at its most nutritive stage (just before shooting), or a cereal (development to reproduction, i.e. grain formation).

Extreme Phasic Interpretations

It will now be appropriate to indicate some extreme interpretations of development put forward by supporters of phasic development in the Russian sense. These theories and results of experiments should, however, be accepted with great caution, as the evidence is not yet in any way conclusive.

Phase or Phases Preceding Thermo-Phase

Some Russian work on *Brassica* spp. has shown that it is not possible to obtain any response to vernalization of seed of these species when treated in the usual way (partial germination and exposure to low temperature). Vernalization is effective, however, if applied to young seedlings. It is therefore concluded that this inability of the germinating seed to respond to temperature indicates that the thermo-phase does not begin until late, and that therefore there must be a pre-vernalization phase with special environmental requirements that are not yet known.

Following on the studies of the germination behaviour of seeds before

they are ripe, made by Noguchi on rice (1929), Harlan and Pope on barley (1922, 1926), Nutman on winter rye (1939, 1941), Culpepper and Moon on maize (1941), Modilevskiĭ (1943) has postulated the existence of three stages of development of the embryo up to ripening and harvesting of the grain. A characteristic of the first stage is that the unripe grain is completely devoid of the capacity to germinate, no matter how favourable the conditions. Modilevskiĭ states that this period has been determined as 9 days in spring wheat, while Nutman found it to be 5 days in winter rye.

With the beginning of Modilevskiĭ's second stage, the capacity to ger-

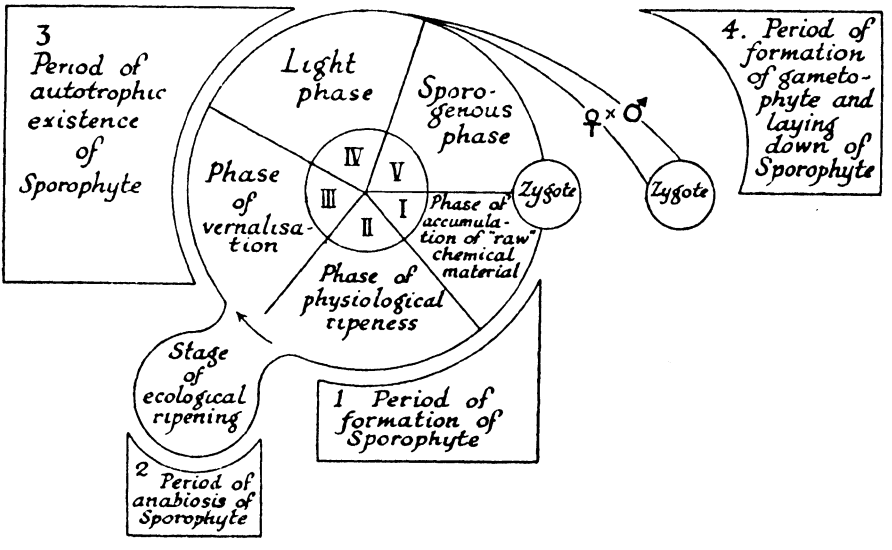


FIGURE 36

Diagrammatic representation of phases before and subsequent to seed dormancy, according to Modilevskiĭ (1943)

minate is acquired, although to make it effective a definite preparatory period (18 to 20 days in spring wheat) is necessary. This is thought to be due to the need for conversion of certain 'raw' chemical substances into substances which are necessary both to stimulate the development of the embryo and for its nutrition and growth.

The second stage of development of the embryo thus begins when the capacity to germinate first becomes apparent, and continues until a definite and 'sudden' change occurs. According to Modilevskiĭ, the grains and their embryos are more ripe at the end of the second stage, but they then seem to require a longer period in the moist chamber before they can germinate. The length of the second stage is defined as the period between the time when the capacity to germinate is first

acquired (end of first stage), and when the preparatory period required for considerably older developing grain to germinate begins to lengthen again. In spring wheat, Melanopus 069, the duration of the first stage is 9 days, and of the second stage about 21 days.

The third stage is characterized by further chemical changes in the ripening grain and finally by its drying into the ripe grain of commerce. The two parts of this stage may be separated at some point by actual harvesting. This third stage of development of embryo and grain is not essential to the development of the embryo into a new plant, being no more than an adaptation to certain ecological conditions. Embryos germinated at the end of the second stage may produce normal plants and yield (see Gregory and Purvis, p. 152).

Modilevskiĭ accepts the results of experiments on observations on vernalization before seed dormancy, but states that vernalization does not begin until the end of his second stage. It has been indicated in Chapter V that an embryo can begin to react to the temperature of the environment at the end of the first stage postulated by Modilevskiĭ.

Phases Following Thermo-Phase

Several exponents of phasic development have attempted to improve upon Lysenko's hypothesis or to explain discrepancies that have arisen by postulating new phases before or in the vicinity of the photo-phase. For example, the Ukrainian investigator, Eremenko (1936, 1938) found that for the first 12 to 15 days after the germination of vernalized winter wheat seed, the length of the subsequent vegetative period did not depend upon daylength during this time, that is that the photo-phase did not begin (no reaction to light) until 12 to 15 days after vernalization. From a number of experiments only one will be quoted, a pot experiment with the late-ripening spring wheat Hordeiforme 0802. The results given in Table 19 show that during the first 12 days after sprouting, the plants did not react at all; from the 12th to the 20th day they reacted only weakly to daylength by a change in the time of earing. The change of daylength from the 20th to the 35th day after sprouting had a marked effect on time of earing, but this became weaker from the 35th day after sprouting, when the plants had a well-developed stem. The unvernalized plants again reacted somewhat later than the vernalized ones to the change in daylength, the interpretation again being that part of the thermo-phase had still to be completed under natural conditions before the daylength could begin to act.

Eremenko's main conclusions are therefore that: (*a*) there is in wheat a biologically important transitional stage of development between the thermo- and the photo-phase; (*b*) this phase does not require the long

TABLE 19

Influence of light regime on the rate of earing in wheat, Hordeiforme 0802 (Pot experiment 1937). (Eremenko, 1936, 1938.)

From sprouting		*Short 10-hour days*											Short day throughout the experiment
		0	2	4	6	8	10	12	14	16	18	20	
Number of days from sprouting to earing	Vernalized	50	51	51	51	51	51	52	53	53	54	54	126
	Un-vernalized	54	55	54	54	54	54	55	56	56	56	56	130

From sprouting		*Natural days*															Natural day throughout the experiment
		2	4	6	8	10	12	14	16	18	20	25	30	35	40	45	
Number of days from sprouting to earing	Vernalized	119	128	121	133	127	120	114	111	112	108	104	74	59	53	53	50
	Un-vernalized	–	135	131	135	141	138	135	135	139	135	119	91	68	63	59	54

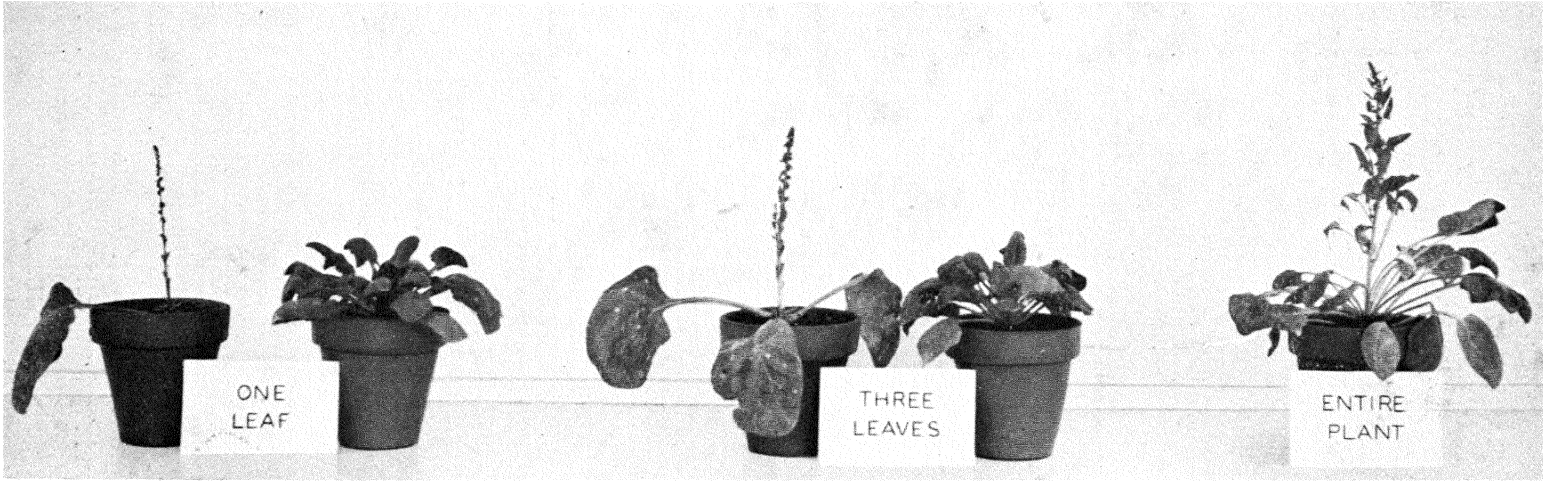


PLATE 17. Inhibiting influence of leaves on photoperiodic response of Nobel spinach (see p. 155). Photo: Withrow, Withrow and Biebel, 1943.

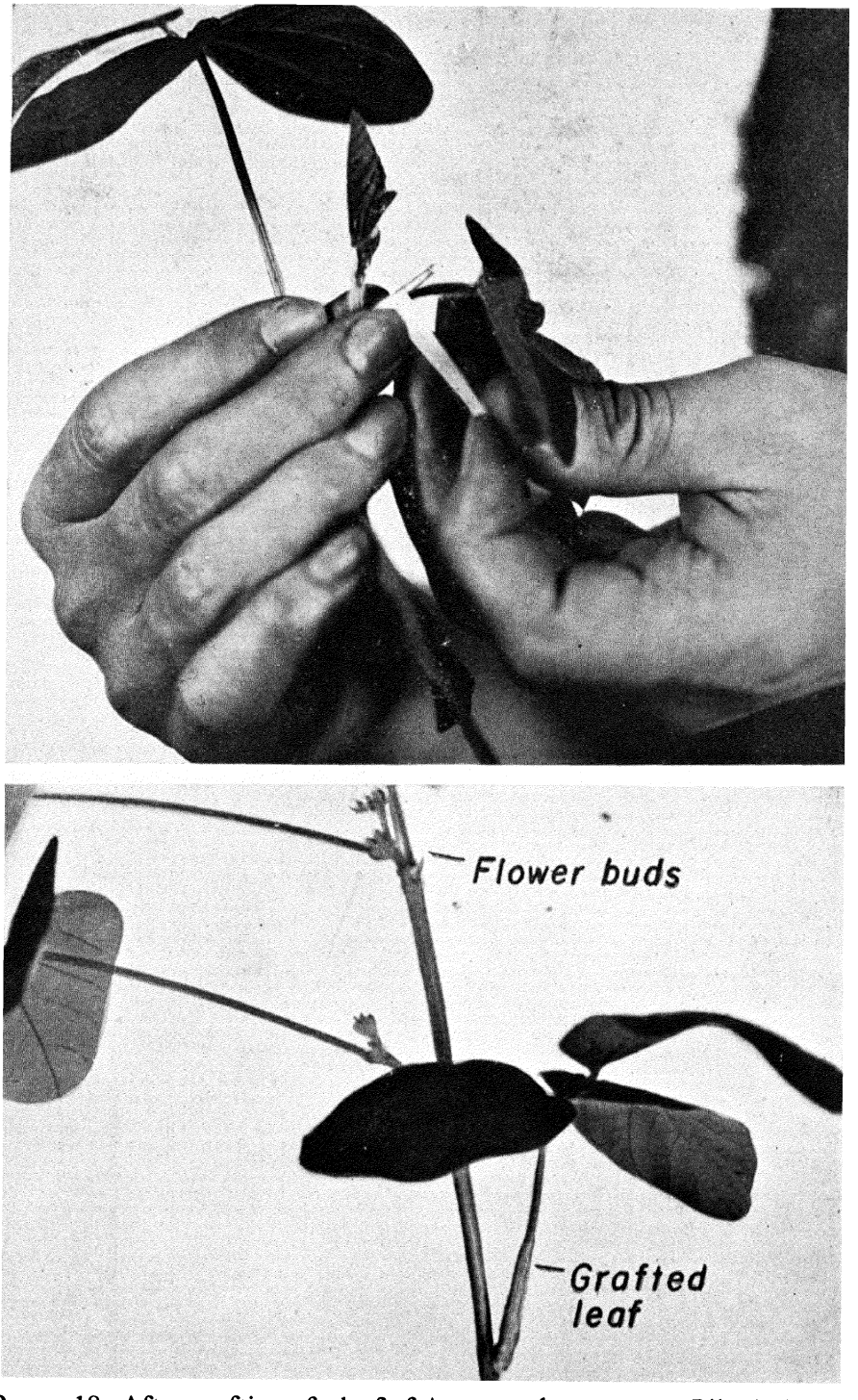


PLATE 18. After grafting of a leaf of Agate soybean on to a Biloxi plant, the latter has been induced to flower. Photo: Bureau of Plant Industry, Soils and Agricultural Engineering, U.S.D.A.

days essential for the photo-phase; (*c*) lack of differentiation of the rudimentary spike is a typical anatomical character of this period; (*d*) when wheat plants have passed this transitional phase and enter the light or photo-phase, they require continuous illumination or long day in addition to other factors, a short day retarding earing; (*e*) the beginning of the photo-phase is characterized by increased long-day requirement and differentiation of the rudimentary spike; (*f*) the end of the photo-phase corresponds with the beginning of stem formation when the differentiation of the main elements of the ear seems to be achieved; (*g*) at the end of the photo-phase, the requirement for long days appears to become reduced.

By utilizing the data obtained in experiments described in this and earlier chapters, Oljhovikov (Whyte and Oljhovikov, 1939) developed a theory based upon a succession of phases considerably more hypothetical than those put forward by the phasic development school. Reference is made to the concept that long-day plants may at a certain stage of their development require a short day (Wanser, 1922), and vice versa. The conclusion is therefore made that there is an identical sequence of phases in both long- and short-day plants, namely:

$$\rightarrow \text{thermo-phase} \rightarrow \text{dark phase} \rightarrow \text{light phase.}$$

This hypothesis is thought to explain the different requirements of long- and short-day plants noted in the previous chapter, namely, continuous light for long-day plants, continuous darkness for short-day plants. It is assumed that the long dark phase characteristic of short-day plants becomes reduced when one studies plants of longer-day latitudes, while the light phase becomes proportionately longer in the same direction, that is as one approaches the true long-day latitudes. Long-day and short-day plants are therefore seen merely as extreme variants in the same series, with the possibility of all manner of intermediate forms between them, as the two phases governed by darkness and light compensate one another.

The results obtained in experiments made by Wort (1941) are claimed to support a rigid distinction into phases, the existence of a dark phase before the photo-phase, and the division of the photo-phase into two parts.

The Formation of Gametes

This is a visible phase and is probably the most important from an immediate practical point of view, being the essential preliminary to the formation of fruit. It is therefore very desirable to know to what extent the environment affects this phase in the progress of a plant towards ultimate reproduction.

It has already been noted that there is a tendency among some workers to divide the light-responsive phase into two parts. The Russian investigators Kraevoĭ and Kiričenko (1935) consider that there is a phase subsequent to the photo-phase during which the pollen grains and female germ cells are formed. It is not clear, however, what the decisive factors for this phase are supposed to be.

The only recent Russian work found dealing with development after the photo-phase is that by Samohina and Ziherman (1941), who studied the effect of temperature on the rate of development of spring wheat after it had passed through the light phase. Plants were kept at: (1) 17 to 22° C. throughout the interval between the shooting (light phase) and ear-forming stages; (2) at 17 to 22° C. for 50 days and then at 5 to 8° C.; (3) at 17 to 22° C. for 32 days (10 days after shooting) and at 5 to 8° C. thereafter; (4) at 17 to 22° C. for 27 days (5 days after shooting) and at 5 to 8° C. thereafter; and (5) at 5 to 8° C. throughout. The daylength was maintained at 18 hours.

The rate of development was highest in (1); ear formation occurred in 53 and 103 days in (1) and (5) respectively. The slowing down of ear formation occurred principally after the stage of shooting (light phase) had been passed. The retardation of ear formation at low temperatures was not due to a reduction in the rate of growth but to the inhibition of development. Studying the changes at the growing point, these investigators found that for 16 days there were no appreciable differences among the five groups of plants, but these became obvious to an ever-increasing degree after shooting had taken place. Pollen sacs were fully developed in variant (1) in 70 days and in (5) in 50 days after shooting. Differentiation of the ear was therefore more rapid at the higher than at the lower temperatures, and actually ceased altogether in other experiments where the range of temperatures was 0 to 5° C.

There have been several studies in North America on the relation between the environment and the formation and viability of pollen. The experiments of Nielsen (1942) on Biloxi soybeans may be taken as an example. Three experimental series of plants were given photo-inductive treatments of from two to ten cycles, each consisting of 8 hours of natural daylight followed by 16 hours of darkness, that is the short days required by this variety for flowering. After induction, Series I and II were placed in cycles of long photoperiods consisting of 21 hours of light and 3 hours of darkness, and Series III in cycles of 16 hours of light and 8 hours of darkness. Floral buds from control plants and from the experimental series were collected progressively to obtain the various stages in development.

Among the control plants, those under short and natural photoperiods flowered normally and the reduction division preliminary to

pollen formation occurred, but no flowers were formed on those kept in long photoperiods. In the plants of the three experimental groups, floral structures developed normally until differentiation of the pollen grains in the anthers, after which there were abnormalities in meiosis associated with the photo-inductive treatment. In those plants that were given five or less photo-inductive cycles, reduction divisions in the anthers began, but the nucleus disintegrated in the prophase. In those plants given six or more cycles, the reduction division proceeded to a later stage before degeneration, in some cases as far as the formation of the resting nucleus of the tetraspores, while in a few instances pollen grains that were normal in morphology were formed (see Plates 14 and 15). Nos. 1 to 9 in Plate 14 are normal stages in the production of the pollen tetrads seen in No. 9, and the normal microspores in No. 10, Plate 15. Varying degrees of vacuolation and degeneration of microsporocytes and ultimately microspores are seen in Nos. 11 to 19 (Nielsen, 1942).

The number of photo-inductive cycles thus influences the degree and stage to which normal development of pollen grains may proceed. In addition, the length of the photoperiod following induction appears to be an important factor affecting the degree of sterility of the plants in these experiments, if they are compared with the results obtained by Borthwick and Parker (1938), who used the natural photoperiod following the photo-inductive treatments. These results seem to indicate that the visible phase or stage of the formation of male and female gametes (gametogenesis) has environmental requirements of light and probably also temperature that differ from those governing flowering as such. Flower formation can be induced by a given photoperiodic treatment, but these flowers will be sterile until the subsequent requirements of gametogenesis are also provided.

Further study of this stage in plant development has great practical significance. Investigations such as those of Poole (1932) and Sexsmith and Fryer (1943) show the relationship between the production of good and bad pollen throughout the flowering period and the degree of seed setting. Poole's conclusion is that fluctuation in the percentages of good and bad pollen in pure species is probably not influenced by external factors 'but by the physiological adjustments made to flowering and senescence'. Sexsmith and Fryer find no significant difference in pollen viability throughout the season on any one plant, but differences between plants may be highly significant. Their conclusion is that the seasonal variation in pod-setting cannot be due to changes in pollen viability. It would be interesting to know whether the wide variation in pollen viability between plants may be due to the fact that many plants are out of harmony with their environment as far as the gametogenic phase is concerned. It would also be desirable to know the relation

between abnormal ovule development and the seasonal variation in pod setting.

Reference has already been made (p. 46) to the effects of developing reproductive organs as vegetative growth. That research shifts the emphasis from the type of vegetative growth that is conducive to flower and fruit formation to the converse question, the effect of the complex processes associated with formation of gametes on the growth behaviour of the same plant.

CHAPTER IX

LOCATION OF RESPONSE TO ENVIRONMENTAL FACTORS

It has been shown that a plant responds to variations in temperature and light at different stages of its life, and that the character of that response decides whether the ultimate result will be vegetative growth or reproduction. It is now necessary to consider the evidence relative to the part or parts of a plant that respond to a given treatment and transmit that response to the meristematic tissue at a growing point, where a condition of growth or reproduction manifests itself.

The factors that influence development as distinct from growth appear to be temperature at varying times and levels, and light and darkness; the other factors of the environment, such as nutrition or atmospheric or soil humidity, play an accessory part.

The temperature responses include that associated with vernalization, of either a slowly growing seed or a grain maturing on the mother plant, and with thermal induction, and that associated with the photoperiodic reaction, which is dependent on the temperature occurring at the time of the exposure to light.

The light responses are those that occur during photoperiodic induction; in long-day plants they appear to be a reaction to light, in short-day plants to darkness. Is it the same or different parts of a plant that take up the stimulating effect of temperature and light and transmit them to the growing point?

The whole picture with regard to location of response is fragmentary and lacks cohesion. This is, however, only to be expected when the reaction of a plant to the various factors of the environment at different successive stages in its vegetative period has not yet been clearly demonstrated. If, for example, a long-day plant first reacts to low temperature, and then in the next phase to light coupled with high temperature, does this mean that the same or a different tissue is taking over the duty of directing the progress to maturity of the plant as a whole?

Again, it has been claimed that a plant may receive all its requirements of low temperature while still in the condition of a slowly growing seed. This would appear to indicate that whatever part or tissue of a seedling or young plant (growing through a winter under natural conditions) it is that responds to the low temperature of that season, the same part or tissue must be present within the much smaller space of a slowly growing seed. One must also take into consideration the fact that successful ver-

nalization of the light phase in growing seed has not yet been decisively demonstrated, but that a photoperiodic or light after-effect can be obtained from treatment of a seedling while still young, but with a certain minimum number of well-developed leaves supplied with chlorophyll.

Location of Response to Temperature of Vernalization

Lysenko (see Imperial Agricultural Bureaux, 1935) describes several experiments made with soybean and cotton to discover whether the changes associated with vernalization occur in the entire plant or only in localized sections. The following observations, which are not new, were made with soybean. When cuttings were taken at successive points along the stem, the plants obtained from them behaved differently; those from cuttings taken from above the point of insertion of the first flowering shoot all came into flower almost at once, while those taken from below this region were considerably delayed in flowering; the delay was greater according to the distance below the flowering shoot at which the cutting was taken.

The same phenomenon was observed in cotton plants which, after they had produced fruits, were kept in a greenhouse throughout the winter; in the following spring they began to form new leaves and sympodial branches in their axils, but again these sympodial branches were formed only in the axils of leaves which appeared above the point of insertion of the first sympodial branch of the previous year; below this point only monopodial vegetative branches were formed. This occurred even when the upper branches, that is, those above the first sympodial shoot, were removed, thus indicating that it was not a lack of nutritive materials that prevented the lower branches from forming flowers, but rather some quality of the cells composing them.

Two cuttings of soybeans were grown in continuous light, one having been taken from a sterile plant also grown in continuous light (a condition under which soybeans do not normally flower), the other from a plant that had been grown under normal conditions and which had flowered. The cutting from the non-flowering plant formed no flower buds during the whole time it remained in continuous light, while the other cutting from the plant that had flowered itself formed flowers rapidly and developed fruits.

From these experiments Lysenko concluded that the formation of reproductive organs is not governed by the supply of nutritive materials, nor by the position on a plant, but depends entirely on whether the cells of the tissue in question have undergone the particular changes that are necessary before reproduction can be initiated. The cuttings from successive points along the soybean stem flowered gradually earlier, accord-

ing as they were taken from points higher and higher up the stem, that is from younger tissue. This is regarded as indicating that the older the tissue, the less it has progressed in the direction of ultimate maturity. In other words, in the life of the plant and of its individual organs, there is a gradual completion of those changes which constitute the different developmental phases, in such a way that the changes are most nearly complete in the youngest tissue. The tissues of the lower parts of the plants had actually been longer under the conditions favouring the qualitative changes concerned, but their behaviour showed that they were as little changed as the tissues of a young plant which had never been under these conditions at all.

From this result, it is argued that the changes occur only in the cells of the growing point, occurring gradually until the limit, represented by the completion of the phase in question, is attained. Once the changes have occurred in the growing point, however, they are transmitted from that growing point to all cells formed later, so that a plant may be formed in which its different parts are at different stages of preparation for reproduction. Thus the position at which the first reproductive organs appear on a plant varies with the rapidity with which the qualitative changes, on the one hand, and the growth of the plant on the other hand progress under the particular conditions in which it is grown. Cotton is again quoted as an example. The first sympodial branches generally appear in the axil of the fourth to the sixth leaf, but plants have been observed which, when grown under conditions particularly favourable for the developmental phases but unfavourable for growth, have formed sympodial branches in the axil of the second leaf while others grown under the converse conditions may form 25 to 30 leaves without producing a single sympodial branch.

Another experiment on the localization of reaction to temperature was performed by Litvinov (1934) on soybeans. The object of this study was to test Lysenko's conclusion experimentally and to determine whether the complex of environmental conditions concerned acts directly on the cells of the growing points or acts on the whole plant, which then produces some internal stimulus that affects the cells of the growing point.

The growing points of young soybean seedlings were darkened by placing opaque black paraffin caps over them from the moment of germination, leaving the rest of the plant exposed to the natural long day of the Moscow latitude, and free to continue assimilation. A variety which was known to react markedly to vernalization was chosen for these experiments. As each set of leaves developed, the caps were removed to allow the internodes and the young leaves, which were quite etiolated, to extend, after which the caps were replaced. Caps were also

placed on the growing points of the axillary buds. As the last three leaves unfolded without any interval of waiting, the growing point was in continuous darkness for the last three periods, covering 9 days in all. Thus, during the whole period of the experiment, 28 days in all, the growing points received 492 hours of darkness, including the 60 hours of light (which is equivalent to 41 12-hour days) and 180 hours of light. During the same period the control plants and the illuminated parts of the experimental plants had received 168 hours of darkness and 504 hours of light. The variety used was known to require only 320 hours of darkness, when treated with an 8-hour day, in order to flower normally, so that the controls had received one-third the total amount of darkness received by the experimental plants, and one-half that required for flowering. On this basis they were expected to flower only by August 3rd, and flowering actually began between August 1st and 3rd. The experimental plants all flowered at about the same time, between July 31st and August 3rd, and no differences were noted in the further development of the experimental or control plants, although the yield from the experimental plants was slightly less.

The conclusion made was that the changes occurring during vernalization do not occur at the growing point in response to the direct action of the external conditions, but must occur in the whole plant; as they are probably of a chemical nature, Litvinov expects that these must in turn effect a specific change in the cells of the growing point.

Response of Excised Embryos to Temperature

Gregory and Purvis (1938) carried this type of experiment further back in the life of the plant, by removing embryos from the endosperm and exposing them to the temperature of vernalization. These investigators found that embryos of winter rye (variety Petkus) removed from the endosperm would germinate and grow readily on nutrient agar as used by Robbins (1922) for the culture of isolated root tips.

After some preliminary experiments, about fifty excised embryos were kept at 1° C. for 6 weeks; 5 days before the end of this period control embryos were excised and germinated at 18° C. to reach the same stage of development at the time of planting out. The more vigorous seedlings from both lots were planted in soil. In order to check the effect of a free supply of glucose in the culture medium during germination, a further lot of complete grains was sterilized and germinated on the same nutrient agar at both temperatures. The results are given in Table 20.

It is evident that the isolated embryos react in the same way to low temperature as do the whole grains, and the degree of reaction is the same. A total of eighteen vernalized embryos were grown to full maturity,

TABLE 20

Vernalization of Excised Embryos and of Whole Seeds of Winter Rye (var. Petkus).

Experimental Material used	*Excised embryos*		*Whole grain*		*Whole grain*	
Medium of germination	*Glucose agar*		*Glucose agar*		*Sand*	
Temperature of germination	1° C.	18° C.	1° C.	18° C.	1° C.	18° C.
Final leaf no.	9·4	> 21	10·5	> 21	11·5	> 21
Days to first anthesis	74	> 150	70	> 150	68	> 150
Mean time to anthesis (days)	89·3	> 150	81·2	> 150	68·5	> 150

and all had set seed before any of the unvernalized plants reached the shooting stage. Gregory and Purvis draw attention to the characteristic reduction in leaf number in the vernalized plants, and to the fact that the plants from excised embryos had only one less leaf than those from vernalized whole seeds. This apparent difference is regarded as possibly due to damage of the embryo and failure of the first leaf. A reduction in tillering was also noted in the embryos and whole grains germinated at 1° C. Normal ears were produced on plants grown from the excised embryos, although some of the plants resulting were smaller than the controls grown from whole seed.

So far, these remarks on temperature response have applied more particularly to annual plants that reach maturity within one season, but the question of location of response in the growing point acquires even greater importance in perennial species such as herbage plants, small fruits and trees. Adopting Lysenko's outlook regarding the growing point, it would be necessary for all the new (spring and summer) tillers of a perennial grass plant to be exposed during the following autumn and winter to the required temperature for the period necessary for the vernalization (passage through the thermo-phase) of that particular species before the growing points could take up and transfer the stimulus to the other parts of their own tiller, thereby producing ear formation under suitable subsequent conditions of light, etc.

Photosynthesis and Response to Light

Later sections support the fact that it is the leaves that respond to the photoperiodic effect, whether during the continuous lighting of a so-called photo-phase or the photoperiods of long or short days. The leaves are generally associated primarily with photosynthesis. It is desirable to know whether there is any connection between their photosynthetic activity and their response to light for the purposes of development. Parker and Borthwick (1940) have investigated this relationship (see also p. 185).

Photosynthesis of Biloxi soybeans was restricted, either by removing CO_2 from the air during the light period for 8, 6, 4 and 2 hours daily throughout the period of photoperiodic induction, or by reducing the light energy available by replacing natural daylight by a weak Mazda light. In these experiments, the number of plants forming flower primordia in long photoperiods following the induction, and also the number of flower primordia per plant were reduced according as the duration of restriction of photosynthesis was increased; plants deprived of photosynthesis produced no flower primordia.

In supplementary experiments, the cessation of the circulation of CO_2-free air during the dark period permitted the accumulation of CO_2 from respiration in amounts sufficient to cause floral initiation in CO_2-free air. In a reciprocal series of experiments, floral initiation was fostered by daily or continuous supplies of air enriched with CO_2. Plants receiving this CO_2-enriched air produced more flower primordia than the control. The authors conclude that active photosynthesis is indispensable in the photoperiodic response through its effect expressed within each individual leaf rather than through its effect on the plant as a whole.

Light Perception in Leaves and Transmission to Growing Point

This question has been frequently investigated, by various methods such as Garner and Allard's special light-proof cases whereby different branches of the same plant may be subjected to different constant light periods every day (Plate 10), or Loehwing's slit panel technique (1938), or by the special equipment evolved by Parker and Borthwick (Plate 6), Hamner (1939), or Withrow and others (1943), to mention only a few. In addition, there is the use of the grafting technique developed more particularly by Russian investigators, which is described in a later chapter.

The aim of the exposure techniques is to keep part of a plant in an

environment (daylength with or without controlled temperature) known to favour reproduction, and the remainder of the same plant in an unfavourable environment. It has been shown that one leaf of a normal plant kept in a favourable short photoperiod is sufficient to induce flowering in the short-day plants, Biloxi soybean (Borthwick and Parker, 1938) and *Xanthium* (Hamner and Bonner, 1938), even though the remaining leaves on the same plant are kept in an unfavourable photoperiod. In certain experiments involving two-branched plants or grafted plants, where one branch or plant is induced to flower while the other is held in an unfavourable photoperiod, the leaves on the latter branch or plant inhibit flowering of that branch or plant. In this case, however, the inhibitory effect is not carried over to other parts of the plant.

Withrow and others (1943) note that work of this type on long-day plants has not been very extensive. Knott (1934) found that the formation of flower stalks in varieties of spinach was not affected by the exposure of the bud to a favourable photoperiod, but only when the leaves were so exposed. Lang and Melchers (1941) noted that leafy biennial plants of *Hyoscyamus niger* which had been pre-treated with a low temperature of 5° C. flowered only in a long photoperiod and did not do so in a short photoperiod or in darkness. If, however, all leaves were removed from plants after the temperature treatment, they flowered in any photoperiod, short or long, or in darkness, indicating that failure of a leafy specimen to flower in a short photoperiod or in darkness is due to an inhibiting effect exercised by the leaves. This question was further studied by Withrow and others with Nobel spinach, an experiment which may be taken as an example of this type of research.

The flowering of intact plants with only a portion of the plant in a favourable photoperiod and of partially defoliated plants was studied. Intact plants with about nine leaves were given three different treatments; some additional leaves developed during the experiment. The treatments were:

(*a*) one leaf exposed to a 24-hour photoperiod while the remainder of the plant received a short photoperiod by covering with opaque rubberized cloth;

(*b*) three leaves exposed to a long photoperiod, remainder in a short;

(*c*) entire plant exposed to long photoperiod.

One leaf of a normal intact plant exposed to a favourable photoperiod (*a*) was not sufficient to cause flower bud initiation if the remainder of the plant was in short photoperiod. One leaf was, however, sufficient in the absence of leaves in an unfavourable photoperiod, indicating that leaves in an unfavourable photoperiod exert an inhibiting influence on flower bud initiation and development. Even if three leaves (one-third of the total at the beginning of the treatment) were in long day, the re-

mainder kept in short day exerted an inhibiting influence, counteracting the flower-forming stimulus initiated in those leaves which were in the long photoperiod. It would seem that there is quite a range in the stimulatory or inhibitory power of leaves of different plants in favourable or unfavourable environments. In some cases, the stimulatory effect from one leaf may be able to bring a whole plant into flower (examples of soybean and *Xanthium* noted above, and dill described by Hamner, 1939); in others such as spinach, the antagonistic action of the leaves in unfavourable photoperiods is too strong, even if one-third of the total leaves are in favourable daylengths (Plate 17).

Similar work of the following type has also been in progress in Russia, and has led on to the study of the transference of the stimulus from the leaves to the growing point, discussed in a subsequent chapter.

In experiments with *Perilla ocymoides* and the soybean, Ermolaeva (1938) noted that flowering was earlier when the leaves were exposed to a short photoperiod, and that this increased earliness in flowering was in direct proportion to the number of leaves that were so treated. Flowering was not induced when the terminal buds alone were exposed to short photoperiods; the photoperiodic response of the plants was not interfered with when the main veins of the shaded leaves were cut. When both leaves and buds were shaded, the growth rate was reduced. This author concludes that the primary functions in photoperiodic response are performed by the leaves, and that the effect of short photoperiods is transmitted from them to the growing point.

Psarev (1936) has shown, by exposure of different aerial parts of a plant to varying photoperiods, that the capacity to respond is inherent in all green tissues, but that the leaves are the main organs for performing this function. This author together with Čaĭlahjan and Moškov, all Soviet botanists, came to the conclusion, probably independently of each other, that the green leaves are the organs of perception for the photoperiodic stimulus, and that it is in the green leaves as affected by diurnal alternation of light and darkness of a certain duration that certain physiological processes arise, the action of which then spreads to the terminal buds, directing them either towards further vegetative growth, or towards the initiation and development of reproductive organs.

In chrysanthemums Moškov found that the younger uppermost leaves which had not yet reached maturity and the lowest ones which had completed their life cycle were least sensitive to photoperiods, while the intermediate four to six leaves were most active.

There may be different response to photoperiods as between the parts of a single leaf. Čaĭlahjan (1945) introduced longitudinal and transverse shading of the leaves of a short-day plant (*Perilla nankinensis*) and a long-day plant (*Spinacia oleracea*). When the *base* of a *Perilla* leaf is

exposed to short day, the transition of the axillary shoot to reproductive development is only slightly later than that of the shoot under the influence of a leaf entirely under short day. When, however, the *apex* of a leaf is exposed to short day the lag is very marked. The long-day zone (base) which separates the short-day zone (apex) is apparently a barrier to the transmission of the photoperiodic influence from apex to shoot. There is a similar barrier in the spinach leaf when its base is kept in short day and its apex in long day.

Before proceeding to discuss the internal factors of flowering, their nature, operation, and transmission from one part of a plant body to another, all questions closely following on the initial response to the environment, the practical application of this research on location of response to light should be noted in passing. It is probably most directly applicable to the use of herbage for grazing, hay, and seed production. It is common practice to close a field for hay or seed at a certain date, which is presumably subconsciously selected as one which will allow sufficient growth of leaf to respond to the normal length of day and transmit that stimulus to the growing point. What seems remarkable is the fact that more growing points (probably containing tender flower primordia) are not damaged by the treading of the grazing animals prior to closure.

CHAPTER X

HORMONES, GROWTH AND REPRODUCTION

The practical application of hormones is already well known in agriculture, horticulture and forestry in connection with the stimulation of rooting of plant cuttings (East Malling, 1939). As far as the present study is concerned, it is necessary to distinguish between those hormones which govern and direct growth processes and those concerned with progress towards reproduction. This whole branch of biological research promises to be of great value in practical work on crops that are manifestations either of growth or development or combinations of the two. The work on growth hormones will probably ultimately offer a complete explanation of such facts as bud formation, tillering habits of cereals and herbage grasses, the reactions of various types of herbage to grazing and cutting, and the eradication of weeds by cutting at optimal dates. Reviews of the scientific aspects are given in the *Cold Spring Harbor Symposia on Quantitative Biology* (Avery, Hamner, van Overbeek, and Zimmerman, 1942) and by van Overbeek (1944).

In addition to attempting an explanation of these phenomena, mainly matters of growth, investigators of the processes of development and reproduction have postulated that the photoperiodic stimulus perceived by leaves is transmitted to the growing point by means of a hormone-like substance. Many experiments made in Russia and the United States have been directed towards the discovery of a specific hormone of flowering, but although there is ample circumstantial evidence of the existence of a controlling substance, no one has yet extracted it from a flowering plant and used it to bring a non-flowering plant into flower.

Cholodny (1939) has stated that the preliminary data make it possible to hope that the introduction of phytohormones into the plant body at different stages of development may in future prove to be a useful method of increasing the productivity and of regulating the development of agricultural plants. As far as the hormonal treatment of seeds is concerned, the balance of evidence is now against any after-effect of the above nature (Templeman, 1939; Stewart and Hamner, 1942).

This substance that directs reproduction within a plant may be one hormone acting in different ways at different times, or different hormones, or a succession of hormones developing one from another and taking up control of reproduction in turn. The action is to perceive,

retain and transmit a stimulus from one part of a plant to another, where meristematic changes will be controlled in a certain direction according to the original environment producing the stimulus. This transference of stimulus may not be immediate, as a stimulus may be received at one time and not become fully obvious externally until a later date when an appropriate change in the environment has taken place.

In order fully to correlate the action of this hormone or hormone-like substance with development, it will be necessary to produce a hormonal interpretation of vernalization of seeds or of seedlings and its after-effect, and also of the photoperiodic reaction and its after-effect. It is, for example, now known that the photoperiodic stimulus is perceived in leaves, but it is not clear whether the temperature linked with photoperiodism has a primary effect on this or another part of the plant body.

Cholodny has produced a hormonal interpretation of the vernalization process; this will now be described, although recent results (Hatcher, 1945) at the Research Institute of Plant Physiology, London, show that it is not tenable in the form postulated (see p. 163). Cholodny put forward his concept on the basis of a belief that there is a deep organic connection between the temperature (vernalization) and light (photoperiodic) reactions of plants; he is also a supporter of the theory of phasic development.

Reference has already been made (p. 67) to the substance postulated by Gregory and Purvis, in their study of reversibility of vernalization, which is regarded as capable of producing either a 'flower-initiating' or a vegetative 'leaf-forming' substance according to the external conditions prevailing at the time. To explain the mechanism of the reactions of a germinating seed or seedling to low temperature or short day, Purvis and Gregory (1937) postulated the existence of a hypothetical 'flower-forming' substance, the effect of which on the labile primordia varies according to the factors to which the plant is exposed. Although stressing that the whole situation is not yet clear, they state that the following facts are established:

(a) The hypothetical substance is not preformed in the endosperm and transferred to the embryo, as the embryo isolated from the seed behaves similarly.

(b) The change can be reversed by high temperature. It appears possible that during vernalization some precursor of a 'flower-forming' substance accumulates in the embryo. This substance may be supposed to be translocated and accumulated in all growing points of the shoot, and when a critical concentration is reached induces flower initiation. The increasing rate of formation of primordia indicates that the substance increases autocatalytically. In spring rye about 2 weeks at normal summer temperatures after germination suffice to reach the critical

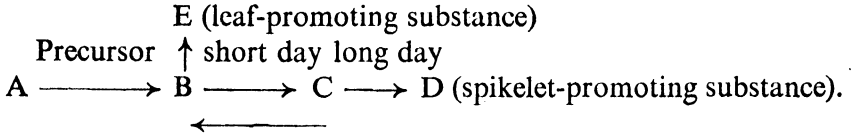
level, while in unvernalized winter rye somewhat less than 6 weeks are required.

(c) An oxidative reaction is involved in the formation of the substance, as anaerobic conditions completely inhibit its production during vernalization of winter rye and partially so in spring rye.

During vernalization the 'flower-forming' substance or its precursor increases in concentration so that the critical level is reached earlier, and thus spikelet initiation sets in earlier in the sequence of labile primordia, and a progressive reduction in leaf number occurs, finally reaching the minimum of seven characteristic of spring rye. The progressive effect of longer duration of low-temperature vernalization can formally be accounted for on these lines.

'The relations to daylength are more difficult to formulate. The outstanding problem here is related to the fact that in both spring and winter rye in continuous short days a maximum leaf number is found, which is approximately constant and independent of temperature of germination. In spring rye the "flower-forming" substance is already present in high concentration, but only in long days do the early members of the series of labile primordia form spikelets. It appears, therefore, that two stages are involved in the process. A precursor depends for its formation on a genetic factor in spring rye and on low temperature of germination in winter rye. This precursor accumulates in all the growing-points, increasing autocatalytically. A second stage in the process involves reactions depending on daylength.'

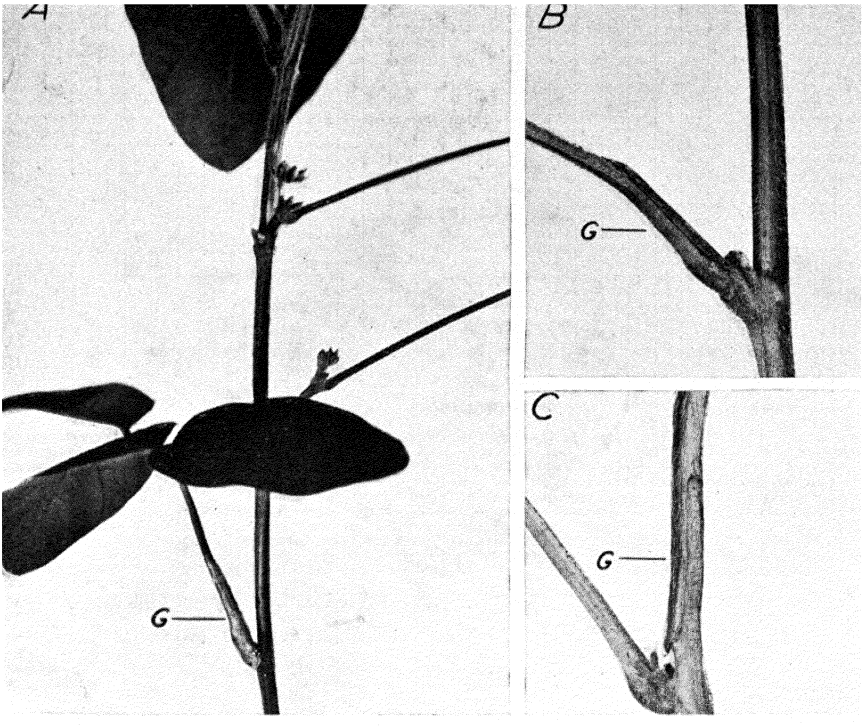
The relations were schematically represented as shown below.



The Internal Factors of Vernalization

The investigations of Schander (1934), Cholodny (1935), Laibach (1935) and others have shown that seeds contain reserves of various hormones received from the mother plant and concentrated chiefly in the endosperm or cotyledons. This reserve comes into action during germination, in the early stages of which the phytohormones are transmitted to the organs of the embryo that are beginning their growth and development.

Schander (1934) showed that the active substances contained in cereal grains at the very beginning of germination pass over to the embryo through the special elongated cells of the aleurone layer. Schander re-



(*a*) Splice grafts of petioles and stems. *A*. Agate leaf to Biloxi receptor. *B*. Detailed view of petiole-graft union. *C*. Detailed view of stem-graft union (G). Photos: Heinze, Parker and Borthwick, 1941–2.



(*b*) Splice grafts of Biloxi soybean and garden bean. *A*. Red Kidney scion on Biloxi stock. *B*. Biloxi scion on Red Kidney stock (G = graft union). Photos: Heinze, Parker and Borthwick, 1941–2.

PLATE 19. Technique of grafting.



(*a*) Vernalization of winter barley in Detskoje Selo, July 1935. Spring sowing. Left vernalized, right untreated (foreground). Photo: O. H. Frankel.



(*b*) Field experiments on vernalization of cereals at East Malling. Photo: F. G. Gregory.

PLATE 20. Vernalization of cereals.

gards these substances as being required for further development and growth of the embryo. Cholodny (1935) found that auxin or a related compound, which is accumulated in the endosperm during germination of cereal grains, is also transmitted into the embryo.

This auxin has subsequently been chemically identified as indole-3-acetic acid by Haagen-Smit, Leech and Bergren (1942). Thimann and Skoog (1940) have shown that it is rapidly liberated from its storage form in the endosperm by simple moistening or alkali hydrolysis, and in this respect differs from the auxin in leaves and stems, which is not liberated in this way.

Having found that auxin accumulates in the developing rye grain from the third week after anthesis, but almost entirely disappears as the grain ripens (Hatcher and Gregory, 1941), Hatcher (1943) continued the experiments on the auxin relations of the grain of rye, comparing this plant with maize as studied by Avery, Berger and Shalucha (1941 and 1942).

In 1936, Cholodny made the first attempt to reveal the nature of the internal factors which act upon the growing points during vernalization. According to his hypothesis, the embryo is stimulated to activity by the pre-treatment method, but lacks the capacity for normal growth, because of the insufficient moisture and low temperature accompanying the vernalization treatment; it absorbs from the endosperm the growth hormones that are contained there in great quantity. As these hormones are used primarily in growth, and as under the conditions of the vernalization treatment there is almost no growth, the concentration of the hormone in the cells of the embryo rises considerably above the normal for that stage of development. This increase of the intracellular concentration of the hormone in the growing points causes an acceleration in the progress of the meristematic cells of the young plant through the first phases of development, according to their hereditarily determined sequence. Thus, the interval of time that separates these first phases of development from the later stages, connected with preparation for fruiting, is shortened. The full result is that the whole cycle of plant development is completed sooner than it would be under normal conditions (Cholodny, 1936).

The experiment of Gregory and Purvis (1936, 1938) on the vernalization of excised embryos has already been described on p.152. Konovalov reported a similar experiment on Ukrainka winter wheat in 1937, and concluded that vernalization of embryos is possible without the endosperm taking any part, the latter acting merely as a source of nutrients. The embryos were, however, separated from the endosperm a few hours after soaking of the seed, and it is quite possible that some hormones could have passed from the endosperm to the embryo during that time. Schander had found earlier that the embryos in soaked seeds could

acquire their 'hormone charge' in a few hours and thus proceed in their development into normal plants.

Gregory and Purvis sterilized the seeds of winter rye before the operation and then cultivated them on nutrient agar under sterilized conditions. The plants derived from excised embryos which were vernalized after separation from the endosperm eared at the same time as the control series from seeds vernalized intact. Cholodny notes, however, that Gregory and Purvis sterilized their seeds by soaking them for 5 hours in a solution of calcium hypochlorite containing 1 per cent chlorine, and that therefore the enrichment of embryos with phytohormones at the expense of their reserves in the endosperm may have already occurred. Foreseeing this objection, Gregory and Purvis pointed out that inhibition of all seeds in a sterilized solution was made at room temperatures, regardless of whether the embryos were later excised or not, and whether they were vernalized or not. Therefore, the transmission of phytohormones into the embryo, in their opinion, could not be the cause of the difference noted in the subsequent development of plants from vernalized and unvernalized embryos. In the opinion of Gregory and Purvis, on the basis of this hypothesis, the difference then lies in the different effect of low temperatures on the subsequent action of the hormone which entered the embryo from the endosperm. The latest development in this research at the Research Institute of Plant Physiology, London, is reported by Purvis (1944), who has studied the role of carbohydrate and nitrogen supply in the vernalization of excised embryos of winter rye.

In discussing further Cholodny's postulation that the accumulation of phytohormones in vernalized embryos may be responsible for accelerating their development, Gregory and Purvis draw attention to some earlier data of Purvis (1934), from which it follows, in their opinion, 'that up to the stage of flower initiation developmental processes go on at the same rate in vernalized and unvernalized plants; thus, the leaf production rate is the same and there is no indication of earlier senescence in individual leaves in vernalized plants'. Cholodny wrongly considers that Gregory and Purvis seem to confuse growth and development, and states that accelerated 'ripening' may or may not be accompanied by accelerated growth of vegetative organs. In addition, he cites some later (though less thorough) observations of Sereiskiĭ and Sludskaja (1937) which revealed an unmistakable acceleration in the development of seedlings of spring and winter wheat following vernalization.

From these experiments, the conclusion may be made that, apart from phytohormone concentration, the development of the embryo must be affected also by the *duration* of the action of these substances, a conclusion which has been confirmed by Thimann and Lane (1938). Cholodny feels that it is desirable to introduce yet another correction into his

hypothesis, because of the rapid advance in the knowledge of phytohormones during recent years: 'It is hardly possible at the present time to doubt that the *qualitative aspect* of the complex of phytohormones acting upon the embryo is not also without its own effect upon the development of the embryo. The composition of that complex and the chemical nature of the active substances found in tissues of the embryo and of the plant developing from it undoubtedly change also under the effect of the external and internal conditions in which development is maintained.'

Cholodny (1936) considers that his working hypothesis is confirmed by some of his own experiments on pre-treatment of seed with various solutions of indole-acetic acid and 'blastanin' or embryo extract, as well as by some later experiments by Thimann and Lane (1938) and also by Čaĭlahjan and Ždanova (1938). These investigators found that a short treatment of growing seeds with increased concentrations of phytohormones affected the subsequent development of plants. In some cases it was observed that the growth of the vegetative organs was inhibited or accelerated; in others fructification was intensified and occasionally conspicuous curtailment of the vegetative period was recorded.

It has already been noted that the evidence is against any such after-effect from hormonal treatment. An example quoted by Hamner (1938) may, however, be mentioned; Wendt has taken out U.S. Patent No. 2,037,203/1936 for the application of acetylene to pineapple plants. Hamner states: 'the prompt differentiation of flower primordia and fruit development which ensue in treated plants as compared with non-treated plants which differentiate flower primordia many weeks and even months later is worthy of critical experimentation'.

The whole question of auxin production in the developing and ripe ear has been systematically studied and its relation to vernalization has been investigated by Hatcher (1945). This work has experimentally tested the hormone hypothesis of Cholodny and has shown this theory to be completely untenable. Preliminary reports have appeared in *Nature* (Hatcher and Gregory, 1941; Hatcher, 1943). The auxin content was determined by the standard *Avena* coleoptile test of Went (1928). The following salient points have been established. Mature cereal grains of different species vary considerably in total auxin content and concentration, giving a descending series: maize, oat, rye, wheat, barley. The auxin of the rye grain is located in the endosperm and chiefly in the aleurone: none could be definitely detected in the embryo itself. The auxin contents of spring and winter rye varieties are not different. The auxin is detectable in the embryo either during development or during germination either at normal or vernalizing temperatures. Auxin, far from being accumulated in the embryo of grain undergoing vernaliza-

tion as Cholodny supposed, is not concerned in the process. The other findings in this work are not of immediate concern and are therefore very briefly mentioned.

Free auxin appears in the rye grain in the third week after fertilization, accumulates during the next month to a peak value and disappears almost completely with ripening. A 'precursor' is present similar to that described in maize by Avery, Berger, and Shalucha (1941) and isolated by Berger and Avery (1944). This precursor releases indole-3-acetic acid on alkaline hydrolysis (optimal conditions *N*/50 NaOH). The precursor and free auxin appear at the same time and both accumulate to a peak value, up to which time they are present in a constant ratio of 2:1. During ripening the free auxin disappears at a greater rate, so that in the ripe grain of rye the ratio reaches a value of 80:1 precursor to free auxin. Spring and winter rye are quite similar in the matter of auxin production.

When prematurely harvested the same cycle of auxin accumulation and disappearance occurs, but the peak value is the lower the earlier the grain is removed from the plant. No auxin is present in the ear prior to emergence, and is then first formed in the anthers, where a cycle of accumulation and disappearance occurs similar to that in the carpel.

The shortening of the first leaf after low temperature treatment noted by Thimann and Lane (1938), and held by them to support Cholodny's hypothesis, has been shown to be quite independent of the vernalization process, for it occurs equally in spring and winter rye and is a different effect of low temperature.

The Actions of Phytohormones in Plants

According to Thimann (1941), there are several principal types of hormones so far known in plants: (*a*) hormones controlling flowering; (*b*) the substances belonging to the vitamin B group that are necessary for root elongation; (*c*) the auxins, a group of organic acids which exert their action on many phases of growth and development; (*d*) the wound hormone, or traumatic acid, and others.

Little is known about the first group, and the evidence that they exist at all is only indirect. It is with the experiments on photoperiodism in which the action of these flower-directing hormones has been studied that this and the following chapter deal primarily, but some reference must first be made to Thimann's review of the effect of auxin on growth, as expressed in elongation of stem and root, degree of tillering, bud development and similar reactions.

The control of shoot growth by auxin is much more immediate than the stimulation of root elongation by the hormones of the group (*b*)

above. The local application of auxin to almost any growing shoot causes, according to Thimann, a rapid local acceleration of growth, that is growth is directly and immediately dependent on the available auxin; tropisms are quoted as the most striking example of this phenomenon. On a given tissue a given amount of applied auxin produces less growth in light than in the dark, an indication of the mechanism of the extreme elongation of etiolated plants; light in some way alters the *sensitivity* of the plant tissue, for reasons that are still not clear.

It is possible to make the generalization that variations in shoot growth are directly and immediately referable to variations either in the rate of auxin supply or in the responsiveness to auxin. Variations in supply may have internal or external causes; as an example of the former is quoted van Overbeek's experiment on a dwarf variety of corn which differed genetically from the normal by a single gene, and which had an almost normal rate of auxin production but an increased rate of destruction. The example of zinc deficiency is quoted as an external cause, since the absence of this element in the nutrient solution causes a marked decrease in auxin content.

Among its numerous effects, nitrogen deficiency greatly reduces growth and also auxin content; Thimann draws attention to the fact that reduced growth is often associated with tendency to flowering, and raises the question whether 'flowering is in some way opposed by auxin supply'. Dostal and Hošek (1937) have shown that application of synthetic auxin to the stems causes flower buds to revert to vegetative shoot buds. Again Thimann raises a question: 'Perhaps the old association of flowering with high carbon/nitrogen ratios may receive its explanation along these lines'.

The response to auxin differs for different organs and different tissues within the same plant. While the elongation of shoots is in general promoted through cell enlargement, under certain conditions auxin may stimulate the cambium to divide and thus produce extra xylem; it may induce the cells of the cortical parenchyma, the cambium or the pericycle to undergo rapid division and form root initials, a procedure which is the basis of the hormonal treatment of cuttings.

One of the most important conclusions made as far as the study of plant development in relation to growth is concerned is that the formation of buds, and especially lateral buds, is powerfully inhibited by auxin. Dwarf plants become bushes or super-tillering when the terminal bud is defective in supplying auxin, and thus loses its power of inhibiting lateral bud formation and growth. Thimann discusses the evidence brought forward by Snow and others to explain this phenomenon, but concludes that none of it is so far decisive. It is suggested that it is possible that the optimum concentration of auxin in buds may be very low, and that even

physiological concentrations of auxin (those normally present in the plant) may be within the inhibiting range. Very low concentrations may conceivably promote bud growth, and Thimann states that there is good evidence that they do.

This section on hormones in relation to general growth of plants, as distinct from development as understood in these chapters, has been included to indicate one aspect of the complexity of the internal mechanism of a plant. Much has been said in studies on plant development relative to the increase or reduction in growth, expressed as plant mass, dry weight or any other character, which follows exposure of plants to one or other of the decisive factors of the environment. It is obvious that any measures taken to prevent a plant from advancing towards flowering, either by keeping it under an abnormally high temperature or under unsuitable photoperiods for an indefinite period, must necessarily have a considerable effect on the hormonal balance and mechanism within the plant (see also Thimann on auxins and inhibition of plant growth, 1939).

CHAPTER XI

HORMONES AND PHOTOPERIODISM

Nature of Flower-inducing Substances

From the evidence available, there seems to be no doubt that some flower-controlling substance does exist in plants. The experiments to be discussed in this chapter follow up the discussion in the two preceding chapters in being concerned with various attempts, by means of grafting or other methods, to discover the nature and action of this controlling substance. The first question that has to be decided is whether this substance might not be of a hormonal nature.

It is well known, for example, that various organic compounds are formed in the leaves and that these building materials are constantly being transferred from the leaves to the growing points. It may therefore be asked whether the 'flower-inducing substances' are not merely a complex of carbohydrates and nitrogenous compounds which in a certain combination are able to promote the initiation and further development of flower buds.

The Russian investigators, Čaĭlahjan and Moškov, are generally regarded as the originators of the idea of flowering hormones. Čaĭlahjan has produced one fact that may be used to contradict the above assumption.

By breaking the bases of *Chrysanthemum* leaves and excising a portion of the main vein 2 to 3 mm. long, Čaĭlahjan observed that the flower-forming substances were still transmitted from the leaf blades to the growing points, and not any less vigorously than from undamaged leaves. The injured leaves, however, remained throughout the experiment in a living and fresh condition, indicating that their conductive system was functioning more or less normally, and that the flow of manufactured plastic substances was still sufficiently vigorous. Ljubimenko and Buslova (1937) obtained different results with *Perilla ocymoides*, in which they investigated the extent to which shortening of photoperiods by darkening the leaves would affect the development of axillary shoots. It so happened that the short 7-hour photoperiods induced earlier flowering of these shoots. If the main vein of the darkened leaves was severed, however, the effect of darkening was eliminated, a result regarded as being due to the cessation of the flow of assimilates from the leaves with the excised veins.

An experiment arranged so as to prevent the translocation of plastic

materials from the leaves was made by Melchers, who grafted leaves of Maryland Mammoth tobacco on biennial *Hyoscyamus niger* plants in the first year of growth. During a 5-day contact between scion and stock with no fast union between them, the translocation of any large amounts of plastic substances from the grafted leaves to the tissues of the stock or vice versa would be unlikely. An exchange of substances of a hormonal nature would be much more probable, as hormones are known to diffuse readily throughout the plant body, regardless of dissections, in amounts sufficient to manifest their physiological potency.

Moškov removed blades of the upper four to six leaves from the short-day plant, *Chrysanthemum*, after it had been in continuous light throughout its life, and was therefore vegetative; leaf blades from other *Chrysanthemum* plants grown in short photoperiods and thus containing sufficient amounts of flower-forming substances were fixed to the petioles with the help of glass tubes containing water. The transferred leaf blades were changed daily. Some of the plants to which leaves had been thus transferred did form buds, under conditions in which, as in Melchers' experiments, the transference of large amounts of assimilates from the leaf blades to the petioles and stems would be improbable.

Hamner and Bonner (1938) found that the short photoperiod plant, *Xanthium pennsylvanicum*, could be forced to flower in long photoperiods if sufficiently close contact could be established between the stems of two plants, one in short photoperiods, the other in long photoperiods. Hamner and Bonner succeeded in achieving this by means of a non-living 'diffusion contact'. The bark as far as the cambium was removed from short portions of the stem of two plants grown prior to the operation in long photoperiods. The stems were then brought into contact along the injured parts, a thin sheet of lens paper being placed between them; this would not prevent the diffusion of soluble substances from one stem to the other, but would prevent their union; the place of contact was bound with raffia. The leaves of one of the plants were then removed and it was left in long day; leaves of the other plant received short day. Both plants flowered and produced fruit some time later (Fig. 33).

Withrow and Withrow (1943), however, working with the same plant, found that the floral stimulus crossed an inarch contact between an induced donor plant and a receptor plant only when tissue union was established and direct tissue contact was uninterrupted for more than 4 days. These investigators also found that the floral stimulus failed to be translocated downward from a leaf in short photoperiods through dead petiole tissue or through functional xylem cells. They found that the floral stimulus is translocated chiefly in the bark, both up and down the stem. These results confirm those of Moškov (1939), who failed to

secure transfer of the floral stimulus from the donor to the receptor in *Perilla* unless the scion had been kept on the stock more than 10 days. Tissue union occurred in 9 to 12 days and Moškov concluded that this was necessary before the transfer of the floral stimulus could occur.

In spite of these differences in results and views, and in spite of the fact that it has not yet been possible to induce flowering by injection of hormones, the views expressed in the literature appear in general to support the existence of some substance of a hormonal nature. Further results of careful experiments adapted to deal with such minute amounts as probably exist must be awaited. In the meantime, we have a choice between Čaĭlahjan's flowering hormone, or the substance postulated by Gregory and Purvis (p. 159), or the substances A, B and C postulated by Hamner (1942) as being concerned with adjusting the balance between growth and development according to their amounts and interactions.

Auxin in Plant Development

Čaĭlahjan attempted to investigate whether the transition to flowering is connected in any way with regular changes in the *concentration* of growth hormone (auxin) in leaves and tips of stems. He failed to extract growth hormone from the leaves, and was unable to detect its presence due to unsuitable technique. Instead of attempting another more sensitive method, Čaĭlahjan abandoned experiments with leaves and began to compare auxin amounts secreted in the basal parts of cut stem tips of different plants. It was possible to establish that in all plants, whether short-day or long-day, and regardless of their physiological state (flowering or vegetative growth), the amount of growth hormone increased according to the increasing length of the photoperiod experienced by the plant.

This fact has, however, little connection with the problem of the significance of auxin in the processes preparatory to flowering that occur in the green leaves. The fact that in all plants more auxin is secreted from cut tips in long photoperiods shows merely that the greater part of this substance is not produced in the growing point but in the leaves during photosynthesis. It is presumptuous to conclude that the growth hormone concentration does not affect the character and trend of development, as it is not known whether there is any definite proportion between the amounts of auxin secreted by basal parts of the cut tips, and its concentration in the meristematic cells; in his review Cholodny (1939) considers that there are no grounds for Čaĭlahjan's conclusion that 'flowering and fructation are independent of growth hormones'.

In Čaĭlahjan's own research and those of other investigators, some data can be found in support of the assumption that plants while pre-

paring to flower expend on the preparatory processes preceding that most important step in their ontogenesis a considerable part of the auxin produced by the entire body.

After discussing in detail one of Čaĭlahjan's experiments with millet, Cholodny (1939) is led to conclude that the manufacture of a flower-forming-substance in the leaves is probably connected with certain chemical transformations of auxin, a supposition which gives rise to a number of concrete problems within the scope of experimental test. 'If further investigations ultimately show that the substance stimulating flowering is of a hormonal nature, it will first be necessary to investigate its relation with auxin. At the same time, if it were found that the initiation and development of flowers involves also the participation of special plastic material elaborated in the leaves and transported to the growing point, it should be necessary to investigate the relation between growth hormones and corresponding chemical transformations.' Reference may be made at this point to the idea first expressed by Tschirch and later extended by Cholodny (1936), that hormones are regulators of enzymatic processes, and that through the enzymatic apparatus they may also affect the character of the organic substances manufactured in the cells.

It is now probable that the ontogenesis of plants as a whole depends to a certain extent on the regulatory activity of the growth hormones, their action on developmental processes being probably determined by two factors, their concentration, and qualitative differences in their properties. The type of response of a phytohormone also depends upon the internal environment, upon the state of the living substrate upon which this substance acts. With the extreme complexity of all these relations it is possible to visualize such a combination of conditions in which the same substance, for example, auxin acting upon the meristematic tissues of the growing point, may in one case divert development towards the formation of vegetative shoots, and in the other towards the initiation of reproductive organs.

This does not mean that phytohormones other than auxin may not affect these processes in one way or another, but it becomes more and more probable that the regulation of the processes of growth and development is a function not of a single substance, but of a complex of substances. Cholodny (1939) raises the question whether the flower-forming substances may not be a complex of several phytohormones, for example, auxin and vitamins of group B, which at a definite quantitative ratio acquire the faculty to divert the trend of development of the embryonic tissues of the growing points towards the initiation of reproductive organs.

Florigen and Vernalin

There is not at the moment sufficient evidence for a categorical denial of the existence of a special hormone of flowering—florigen or anthesin —as a definite chemical entity, but neither is there sufficient evidence of its existence. Čaĭlahjan in his book, *The Hormonal Theory and Plant Development* (1937), has enumerated the supposed differences between his flower-forming hormone, and auxin; the former he regards as being synthesized in green leaves, the latter as being manufactured chiefly in the growing points of stems. He considers that the movement of auxin in the plant body is always strictly polar, spreading only basipetally from tip of stem or root towards its base; the flower-forming hormone can be transmitted in all possible directions. Cholodny (1939) states that it is now known that auxin is manufactured in the leaves during or parallel with photosynthesis, and that several samples of non-polar movements of growth substances are known, in which they probably travel through the elements of the vascular bundles. 'It is, therefore, presumptuous to speak of differences existing between auxin and "the flower-forming substances".'

As further evidence of the fact that the transition from the vegetative to the reproductive state is very complex, reference should again be made to the experiment of Melchers (1939), on grafting of Maryland Mammoth tobacco plants on the biennial *Hyoscyamus niger* in the first year of growth. Maryland Mammoth (short-day plant) does not form flower-forming substance under long photoperiods. Nevertheless, when a tobacco scion (either entire defoliated stems or leaves alone) grafted on *H. niger* was exposed to long photoperiods, the stock flowered in about the same time as the stock of the control, the scion of which was in short photoperiods throughout. In this case no trace of floral initiation could be found on the grafted stems of tobacco plants grown in long photoperiods. To explain this result, Melchers resorts to the hypothesis of the existence of another flower-forming hormone, 'vernalin', the presence of which is first required for the elaboration of Čaĭlahjan's 'florigen'.

While deprecating an increasing accumulation of scientific names for hypothetical substances, Cholodny (1939) feels impelled to conclude from Melchers' data that, for the transition from the vegetative to the reproductive state, several, and at least two different substances must be present in the tissues as apparently no single substance possesses the faculty to induce floral initiation. Cholodny regards this as supporting his own hypothesis that the initiation of organs of sexual reproduction is determined by the action upon embryonic tissues at the vegetative tip, not of a single specific 'flower-forming substance' alone, but of a certain

complex of phytohormones (auxin, vitamin B, and others). Such a supposition may be regarded as more probable since different plants and the same one plant are endowed at different phases of their development with a different capacity to synthesize and accumulate hormones or vitamins.

On this basis, it is possible to interpret Melchers' results as follows. In the growing tips of the biennial *Hyoscyamus niger*, the organs of sexual reproduction are not laid down in the first year of development, because one or several links in the complex of phytohormones required for flowering are lacking. On the other hand, it is just these substances necessary for flowering that are present in sufficient amounts in the tissues of the tobacco scion and which are transmitted to the tissues of the stock. The scion probably requires some other substances which it cannot form in long day and which cannot be supplied by the stock.

Results such as those obtained by Hamner and Bonner (1938) on the effect of various substances of the vitamin and hormone group upon the initiation of reproduction may not contradict this view, as to compound such a complex mixture is not a simple task.

Relation Between Light and Flower-Inducing Substances

According to data obtained by Moškov and Čaĭlahjan, the flower-forming substance manufactured in leaves is of the same kind in both long- and short-day plants. If this is so, it must be asked why different plants require different photoperiods for the transition from vegetative growth to reproduction. Čaĭlahjan considers that the 'hormone of flowering' is synthesized in the leaves under the effect of solar energy, but at the same time states that this substance 'originates under that duration of diurnal light to which the species in question was adapted: the plants of tropical and subtropical countries flower and fruit in short photoperiods, and the plants of higher latitudes in long photoperiods'. Such a conception does not agree with our knowledge of photochemical reactions, and a case may be visualized in which a substance originating in the leaves of short-day plants under a 10-hour photoperiod disappears completely when a little additional light is given, and exactly the same compound is not formed in the leaves of long-day plants in 10-hour day, but suddenly appears with a small increase in the duration of light.

Cholodny proposes two alternatives to this supposition: (*a*) it may be assumed that the flower-forming substance is synthesized in leaves under any duration of day and night, but that, under the influence of photoperiods, this substance is not formed in equal amounts and that, on the other hand, different amounts are required by long-day and short-day

plants to complete their preparation for flowering and the change-over to a reproductive state; or (*b*) for flowering either group of plants requires the same amount and concentration of 'flower-forming substance' but that the rate of its accumulation in the leaves may not be the same; its elaboration may be slower in long-day plants, with the result that they require longer durations of light.

Lysenko (1932) claimed that millet (short-day plant) may achieve flowering in long photoperiods and even in continuous day, if slightly germinated seeds are first treated with darkness for 5 days at 25 to 30° C. and in reduced moisture conditions. Moškov (1940), found that, if *Chrysanthemum* is given 10 short (10-hour) days, it will flower subsequently even in continuous day. As this 10-day period represented 140 hours of darkness, an attempt was made to replace the action of ten short photoperiods with continuous darkness for 3 to 12 days, the plants then being transferred to continuous light. As no plants flowered, the influence of continuous darkness was in this case not equivalent to the influence of an alternation of light and dark periods.

We have already referred to the experiments of Hamner and Bonner (1938) who studied whether it is photoperiods or darkness which determine floral initiation in *Xanthium pennsylvanicum*, a plant with a critical photoperiod of about 15·5 hours and hence a critical dark period of 8·5 hours. If the photoperiods are the decisive factor, then flowers must be laid down in any photoperiod shorter than 15 hours, and no flower will appear in a photoperiod longer than 15 hours, regardless of the amount of darkness. If the dark period is the decisive factor, flowers will be formed in any period of darkness exceeding 8·5 hours, and none in shorter periods of darkness, regardless of the accompanying photoperiod. The conclusion drawn was that 'the flowering response of *Xanthium* to short photoperiods depends primarily upon reactions directly related to the dark period', and that consequently biochemical reactions in leaves of this species, which lead to the synthesis of substances inducing flower initiation, occur not in the light but in the dark.

Cholodny concludes that only more or less hypothetical suppositions are possible with regard to the nature of these reactions to light and darkness. For short-day plants, light may acquire the significance of a factor promoting the destruction or oxidation of the active compounds formed in darkness, while on the other hand, certain compounds may arise in leaves exposed to light which may inactivate the 'flower-forming substance' manufactured by the same or other leaves in darkness.

'The very diversity of the possible suppositions in this field suggests how far we are from any satisfactory decision as to the nature of the biochemical and physiological reactions connected with the effect of photoperiods on plants. No matter how this question will be solved in

the future, it is necessary to remember that at the basis of the different photoperiodic response of different plants there lies their hereditary constitution, particularly their genotype, formed in the evolution of the species in question in relation to the natural-historical conditions of its existence' (Cholodny).

Movement of Hormones Within Plants

Čaĭlahjan (1940) has investigated the way in which his hypothetical flower-promoting hormones move along the leaves, the stems and the roots. The plant used was *Perilla*. It was found that the hormones which are formed in leaves exposed to a reduced period of daylight are able to pass from them to the flowering shoots not only along the veins but by way of the leaf parenchyma. When a main vein of a leaf is cut, only the nutrients which are required for the vegetative growth of shoots and the formation of dry matter are hindered in their passage from the leaves where they are formed.

In the experiments with stems, the top 10 cm. was cut off and a strip from the remaining lower part of the stem was split downwards to the base. The shoots on the main part of the split stem were cut off, while the leaves were retained, those on some plants being exposed during the whole experiment to a full, those on others to a reduced, period of daylight. From the strip of stem split away, retaining some of the cortical and woody tissues, all but a few small leaves were cut off, only the shoots being left intact. Some of the strips were bent over and rooted in a separate pot, but the connection between the parent plant was maintained. Whether the shoots had been rooted or not, it was observed that they were able to form flowers, instead of vegetative growth, only when the leaves on the main part of the stem had been exposed to a reduced period of daylight.

The tops of some plants were not cut off, but a strip was split downwards, a large leaf left intact near the top of it, and all other leaves and shoots lower down the strip removed. As before, some of the leaves were exposed to long, others to short, periods of daylight; while the main part of the stem, all but the smallest leaves on which were removed and only the shoots retained, was always exposed to a full period of daylight. Some of the strips were rooted in separate pots.

It was observed that a flowering shoot was produced from the bud nearest to the leaf exposed to short periods of daylight, and others followed in succession down the strip and up the main part of the stem. When one of two shoots lying nearer to the leaf was cut off, the onset of flowering in the shoot next to it further away was hastened. The quantity of hormones required to induce flowering in a given number of shoots

was determined by the leaf area and the amount of exposure to daylight. A lack of the hormone resulted in a part or all of the shoots being vegetative.

The purpose of the experiment with roots was to discover whether the hormones produced in the leaves could pass by way only of the roots to the axillary shoots and induce them to flower. The top of each plant was cut off and the stems split longitudinally downwards until the only connection between the two halves of the plant was the unsplit lower portion of its main root. The root systems of some of the plants were immersed in a nutrient solution; those of others were left suspended in somewhat damp air inside empty flasks. Three large leaves were retained and the shoots cut off on one half of each plant, while the shoots were retained and all but a few small leaves cut off on the other. With the exception of the control plants which were exposed to a full period of daylight, the three large leaves on one half of each split stem were exposed only for a short period of daylight. The hormones formed by the leaves on one half of the stem were able after some delay to pass down that half stem, by way of the main root and up the other half stem where they induced flowering. The rate of passage was the same whether the roots were in solution or in the air.

There are many other preliminary data from research on perception of stimulus and its translocation to another part of a plant. For example, old leaves in short-day plants have an inhibiting effect, the rate of transfer of stimulus may be relatively slow, transmission of stimulus may be seriously delayed by local applications of low temperatures or narcotics, and the partner plants in a graft union need not necessarily be of the same species or photoperiodic class (references in Hamner, 1944).

As already noted, this research has great prospects of usefulness in practice. In addition to the possibility that a hormone may ultimately be isolated and made available for injection to produce flowering, there are many other less obvious relationships. In grazing management, for example, the degree of defoliation must affect the supply of flower-inducing substance to the growing point; in a hay crop, it would be interesting to know whether differences between species in degree of aftermath production are linked with specific differences in hormonal behaviour and translocation. Similar data would be useful in developing optimal methods and times of cutting for weed control.

The practical application of research on the growth-regulating substances in plants has been fully reviewed by van Overbeek (1944), who deals with abscission, fruit set, bud inhibition, rooting and general growth promotion. A recent note in *Nature* (10.2.45) reviews the attempts to influence fruit set in fruit crops and vegetables, which have so far

had varying degrees of success. Greene (1943) finds that growth substances applied as sprays, lanoline pastes and injections to apples failed to increase fruit set. Similar negative results are reported by Pomeroy and Aldrich (1943), using naphthyl acetic acid on orange and grapefruit, although with the Marsh grape-fruit used, pollen of other grapefruit varieties did increase the set of fruit; on the other hand, Roberts and Struckmeyer (1944) found that aqueous solution of β-naphthoxyacetic acid and 2:4 dichlorophenoxy propionic acid sprayed on tomato flowers induced fruit setting. Favourable results from the use of these sprays were also found with pumpkins, outdoor cucumbers, egg-plant and *Nicandra physaloides* but not with apple (nine varieties), greenhouse cucumbers, peppers, potatoes, or strawberries. In field experiments by Murneek, Wittwer and Hemphill (1944) on snap beans, using naphthylacetamide and naphthoxyacetic acid applied as a spray every second or fifth day, increases in fruit yields were obtained in hot years, but decreases in cold years, emphasizing the importance of environmental conditions in determining the nature and extent of response to the treatments.

The new use of growth hormones in the control of weeds is an interesting side issue to this general problem. Growth responses are induced in weeds which eventually result in their destruction. In some cases, the weeds are excited to such activity as to grow themselves to death.

CHAPTER XII

RELATIONSHIPS OF DEVELOPMENTAL PHYSIOLOGY

The physiological processes that occur in plants during vegetative growth or reproduction are of great significance in connection with the yields and nutritive values of crop plants. Although crops such as green vegetables or herbage plants are primarily manifestations of growth, they are in a varying degree also dependent upon a certain amount of development before they can reach their maximal nutritive value. The protein content of herbage is probably at its highest when a grass is in a very active state of growth, and is at the same time providing a developing ear (possibly before shooting) with building materials.

For maximum production of grains in an annual cereal, growth processes are allowed to proceed to their end, until such time as the developmental processes and building of the grain exercise a completely inhibitive effect upon growth and the plant bearing the ripe fruit dies. Where optimal environmental conditions are available for fruiting, the straw is of little value, everything having been supplied to the grain. Where conditions are below the optimum, grain yields are lower and ripening more difficult, but the straw is of higher nutritive value for livestock. Growth has continued longer owing to the lower inhibitory effect of the development, and less building material is supplied to the grain.

The striking of an appropriate balance between growth and reproduction is the basis of good management of grassland for grazing or hay production. The breeder of herbage plants produces for grazing purposes strains called 'pasture types', that is types that find the environment suitable for growth but not optimal for reproduction. The best pasture ryegrass of Great Britain (Aberystwyth S.23) is a very 'shy seeder' because it is out of its true developmental environment. This variety has, however, a high nutritive value. It presumably finds the environment suitable for just that degree of development that stimulates active metabolism and growth and produces a high nutritive value.

It would appear that, if the carotenoids, carotene and xanthophyll, are taken as indicators, the maximal nutritive value is to be obtained just at the time of flowering; this has already been noted many times in studies of time of cutting hay for maximal yield and nutritive value. Murneek (1939) reports that when plants have become reproductive through exposure to an appropriate photoperiod, there is an increase in

carotene and xanthophyll content of the leaves (Table 21). The concentration of these carotenoids seems to reach a maximum at the time of flowering after which there is a reduction (Table 22). The lower amounts of carotene and xanthophyll in the nodes of Biloxi soybeans when fruit is present suggest that the carotenoids are moved to the reproductive organs or changed into some other compounds (see also p. 182).

TABLE 21

Concentration of carotenoids in vegetative and reproductive plants at approximate time of flowering.

	Milligrams in 10-gram sample of leaves	
	Carotene	*Xanthophyll*
Cosmos		
Vegetative (long day)	0·95	1·5
Reproductive (short day)	1·17	1·85
Salvia		
Vegetative (long day)	1·85	2·50
Reproductive (short day)	2·07	2·80
Soja		
Vegetative (long day)	1·10	1·52
Reproductive (short day)	1·49	2·00

TABLE 22

Carotene and xanthophyll in leaves of soybeans.

	Milligrams in 10-gram sample
Vegetative (long day) plants	
Carotene	0·32 → 0·46 → 0·65 → 0·76
Xanthophyll	1·1 → 1·96 → 1·57 → 1·25
Reproductive (short day) plants	*Flowering*
Carotene	0·35 → 0·43 → 1·26 → 1·07
Xanthophyll	1·2 → 2·1 → 2·44 → 1·77

Much of the herbage literature now appearing deals with the carotenoids of grasses and legumes, and the relation between this research on the production of nutritive herbage and that on developmental physiology is obvious.

Investigations on plant physiology and metabolism at different de-

velopmental phases or while exposed to controlled environmental factors have not yet reached a stage warranting definite conclusions. The scattered works to be discussed in this chapter begin to give an indication of the picture, and its possible application to the production of optimal yields of grain, or green mass for forage or green manure, and to the optimal utilization of fertilizers or other cultural measures.

Physiological, Biochemical and Anatomical Conditions in Vernalized Seeds

Since enzymatic processes are very active during the period of germination, it was natural that studies should be made of their behaviour in relation to vernalization. Whether any change which may be noted in their activity is governed ultimately by the concentration of hormones present depends upon the confirmation of Cholodny's hormonal interpretation of vernalization (see p. 161). The studies on enzymes in relation to vernalization made by Richter and his associates and Demkovskiĭ, and on the iso-electric point by Richter, Gavrilova and others are described in the early reviews of vernalization (*Imp. Agric. Bur.*, 1935).

Ovečkin and others (1936) studied the biochemical changes in winter wheat grains during vernalization. Grains were vernalized at 0 to 1° C. under normal air conditions, and also on a 0·003 per cent concentration of chloroform or ethylene chloride. Samples were taken on every sixth day and records made of respiration rate, sugar content, catalase activity, content of mono-amino-acids and reduced glutathione, and of the percentage of fully vernalized grains that grew when planted out of doors. The presence of chloroform or ethylene chloride reduced the percentage of fully vernalized grains; the respiration rate, catalase activity, and content of reduced glutathione were all lower in grains vernalized in ethylene chloride. The reduction-oxidation processes are intensified during vernalization, but there is no relation between content of sugars and mono-amino-acids and vernalization.

Sapožnikova (1935) analysed vernalized seed of *Lupinus angustifolius*. The content of reducing sugars in seeds treated at 6 to 7° C. increases with the progress of vernalization, a fact regarded as suggesting an increasing activity of the enzymes acting on carbohydrates; however, the content of reducing sugars gradually falls in seeds vernalized at 4 to 5° C. The amount of active enzymes rises with vernalization at 6 to 7 °C. to a maximum on the last day of treatment; they increase less rapidly with vernalization at 4 to 5° C. during the first 12 days and then fall. The control of active enzymes is measured by their activity at 35° C. The protease content in seeds vernalized at 6 to 7° C. was found to rise to a climax on the day of sowing, while in those vernalized at 4 to 5° C. its

changes were indefinite. The activity of catalases, peroxidases and respiration varied in the different series. Marked activity of catalases and peroxidases is a feature of vernalized lupin seeds that give rise to plants with a reduced vegetative period, and this character is stated to be useful for distinguishing vernalized from unvernalized seeds.

From determinations of nitrogenous substances (total N, insoluble and soluble N, amino-N, amide-N, and ammoniacal N) in seeds and plants during vernalization and in those under conditions which prevent vernalization, Konovalov (1938) found their behaviour to vary considerably. When vernalization was prevented, the disintegration of the proteins extended to the end products, whereas during vernalization the proteins retained their form, but became more readily soluble. This worker concludes that nitrogenous substances appear to be re-synthesized during vernalization, and regards this transformation as a distinctive feature of the vernalization process.

Paševič (1940) found that vernalization induces changes in the protein substances of the wheat germ affecting both their colloidal state and their amino-acid content.

Physiological Conditions in Plants Grown from Vernalized as Compared with Unvernalized Seeds

In some early studies on the effect of vernalization on the rate of accumulation of dry matter, Konovalov (1936) found that vernalized plants of wheat and lentils accumulated more dry matter per unit of time than the unvernalized control, and the yield of organic matter was consequently increased. More recently, Konovalov and Popova (1941) found that the synthesizing capacity of vernalized plants is higher than in the unvernalized controls. By the time of earing, vernalized plants contained 26 per cent more organic matter than those from soaked and germinated seeds and 52 per cent more than plants from seeds sown dry.

Konovalov (1944) has continued his work at the Timirjazev Institute of Plant Physiology, Moscow, on the effects which vernalization of seed exerts on the growth and physiological processes in the leaf relevant to the yield of grain or seed ultimately produced. The chief concern in these experiments has been productiveness of a plant as governed by the intensity of photosynthesis, the extent of its leaf area, and the duration of activity by the leaves.

The intensity of photosynthesis was not materially affected by vernalization, but the interval between emergence of the leaf and its death was shortened. The factor most closely connected with yield was the leaf area of a plant, and it was this which was markedly affected by vernalization. The successive emergence of leaves was more rapid with than

without vernalization, and each leaf reached its maximal size sooner. A growing leaf uses much of the products of metabolism for its own use; vernalization has the advantage of hastening the growth of leaves and ensuring its early completion, after which the products are released for the benefit of the embryonic ear. It was noticed that the content of nitrogenous substances in the lowest leaves was diminished after the leaves had ceased to increase in size.

The synthetic activity of the leaves reached the maximum sooner in vernalized than unvernalized plants, and, after remaining stationary for a while, gradually decreased. The accumulation of dry matter was, likewise, more abundant in vernalized plants. Consequently there was more material available for translocation to the developing ear, thus accounting for the well-being of vernalized plants which is to be especially observed during a dry season.

The yield of late-maturing wheat in Konovalov's experiments was increased by vernalization because, although tillers were reduced in number, their ears bore better and more numerous spikelets, as well as more numerous and heavier grain. In the early maturing varieties the good development of the ears could not compensate for the reduced number of tillers, and vernalization did not therefore increase the yield.

A similar result is reported by Buzovir (1936), who made experiments over two seasons with varieties of winter and spring wheat and a variety of millet; at the beginning of vegetative growth in winter wheat and throughout the vegetative period in the other plants, the rate of elaboration and accumulation of dry matter was greater in vernalized plants. The accumulation of carbohydrates was also greater in vernalized plants, particularly during the period from jointing and stem elongation to milk ripeness.

In experiments made by Zaĭceva (1939), with spring and winter wheats sown with vernalized and unvernalized seeds, it was found that the chlorophyll content increased as the plants advanced towards sexual maturity, reaching a maximum of over 6 mg. of crystalline chlorophyll per grm. of leaf weight in either variety, by the time of heading or thereabouts and falling rapidly thereafter. In rapidity of development, the spring wheat was somewhat ahead of the vernalized winter wheat. No such regularity was noted in unvernalized winter wheat plants that remained at the tillering phase, the chlorophyll content varying from the beginning of tillering between 3 and 4 mg. of crystalline chlorophyll per grm. of leaf weight, the highest figures being obtained in the leaves nearest to the spikes. Advance in development is considered to be the chief factor causing this conspicuous variation.

Physiology and Biochemistry in Relation to Response to Light

A considerable amount of work has been done on the physiology and biochemistry of plants in relation to the photoperiod in which they are grown; readers are referred to Burkholder's review (1936), and the literature quoted therein. As regards enzymatic activity in relation to light as distinct from the temperature relationship described earlier in this chapter, mention should be made of the experiments of Knott (1932 and 1926), who investigated the catalase in spinach before and after lengthening the photoperiod, and found a rapid response as exhibited by an increase in the enzymatic activity following a change to long days, that is to conditions favouring reproduction. In the second paper, Knott reported a decrease in catalase in the apical portion of the stem of spinach and *Cosmos* when the plants changed to a reproductive type of growth. If vegetative growth was resumed, a higher catalase activity was restored.

Murneek has made a detailed study of the metabolic changes associated with the photoperiodic reaction, and quotes over two hundred references to literature in his paper (see Missouri, 1937). The exposure of plants of *Soja max* to a 7-hour day (in comparison with a 14-hour day) resulted in induced sexual reproduction, retardation of growth in height, greater accumulation of dry matter, and higher nitrogen metabolism and nitrogen concentration; under a 14-hour day, vegetative development was continuous and no flower buds were formed. In the plants in both long and short day, the total coagulable, proteose, basic, ammonia and humin nitrogen increased upwards from the base of the stem to the tip, while nitrates, amide and amino-N decreased in the same direction.

Murneek does not ascribe any specific dynamic function to any group of nitrogenous substances as regards the initiation of floral organs, and considers that the evidence available indicates the action of a specific flower-producing hormone.

The plants in short day maintained a higher rate of respiration at the time of the photoperiodic treatment than those in long day, and a change over from long- to short-day exposure also increased respiration. As a result of the curtailed growth in the plants under short day, nitrogen and carbohydrates accumulated in the vegetative parts, and at the time of full flowering there was a relatively higher accumulation of carbohydrates than nitrogen in the leaves. In plants under long day, according to Murneek, these substances are used for supporting vegetative growth, and in the plants under short day for sexual reproduction. The buds, flowers and young fruits were comparatively rich in carotene; this sub-

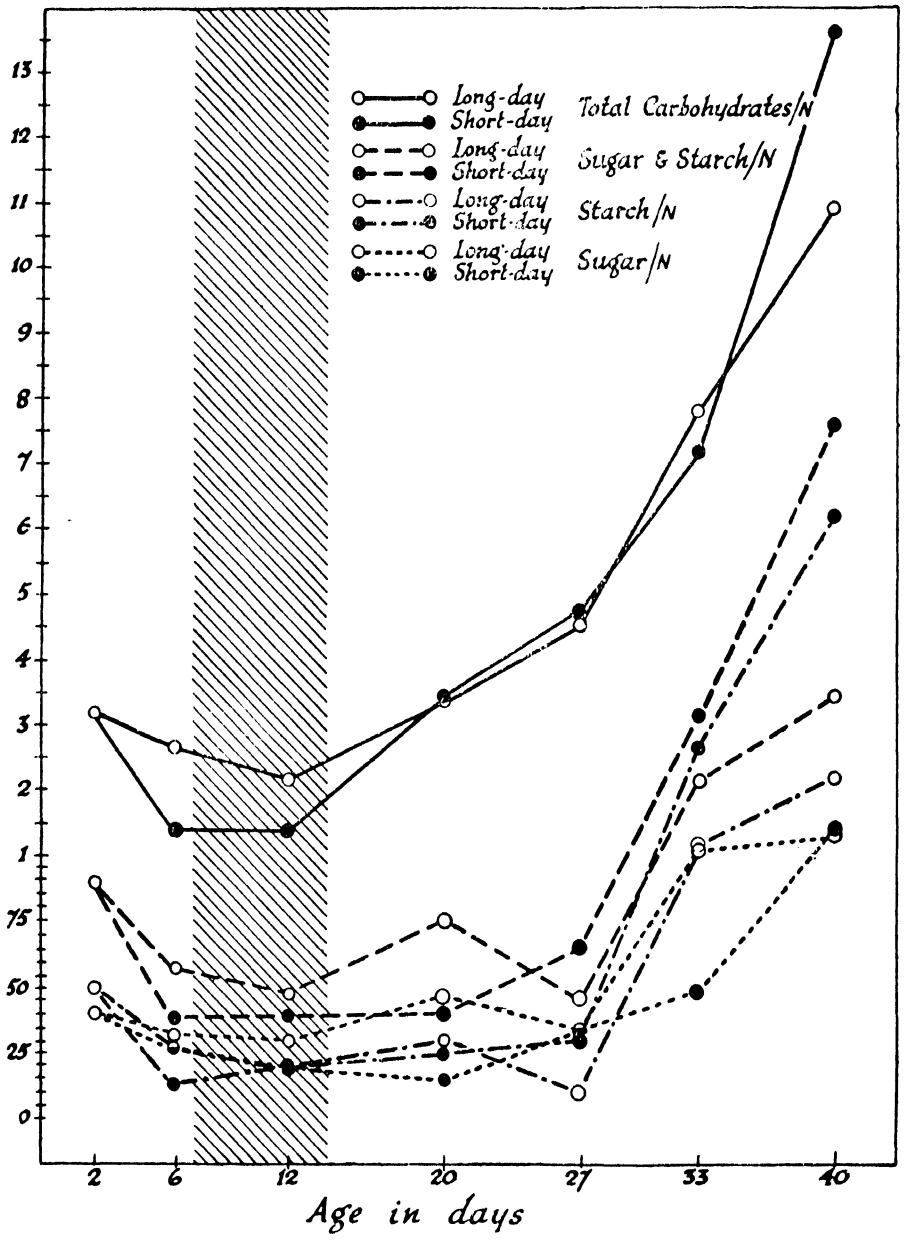
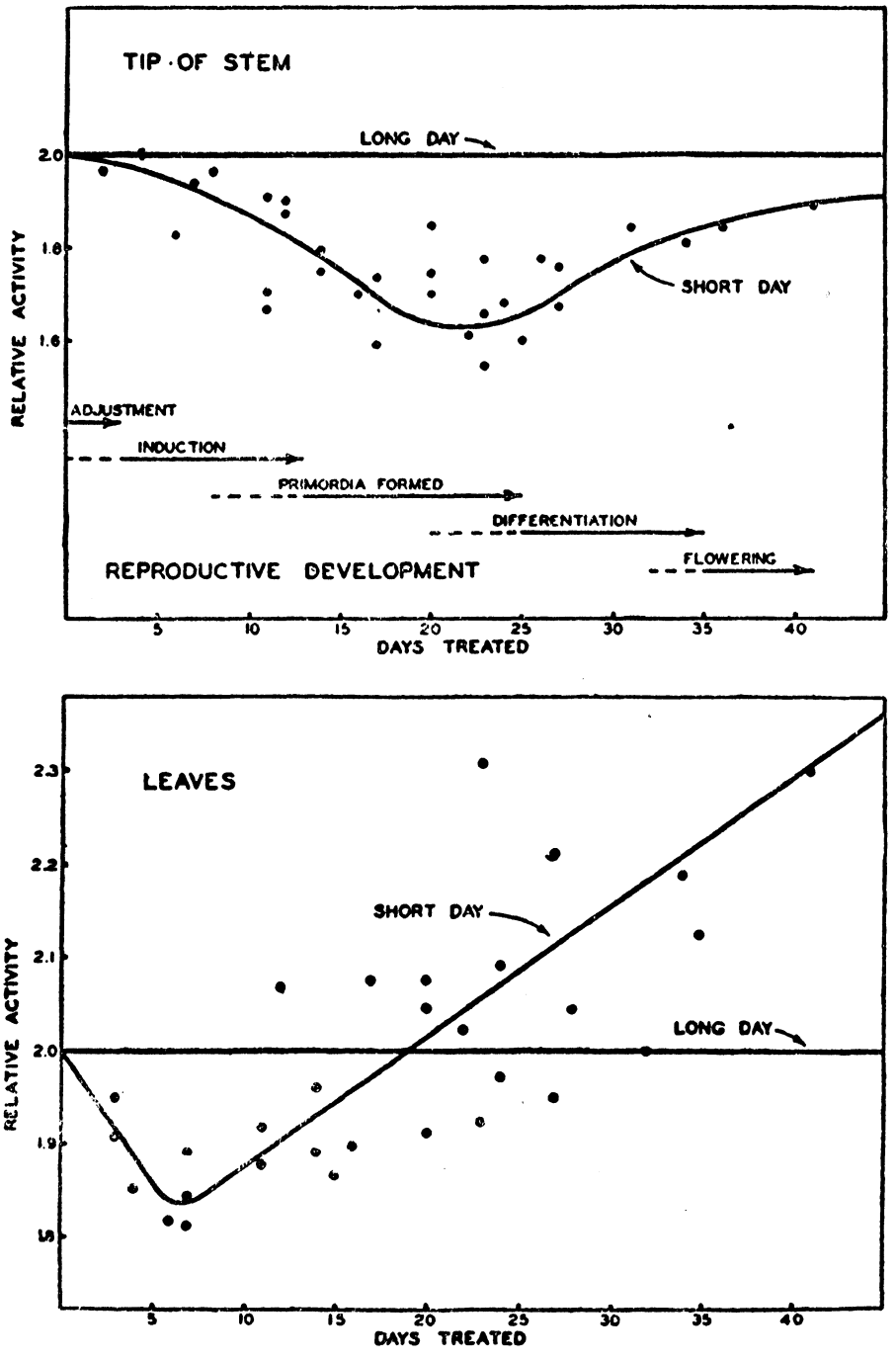


FIGURE 37

Carbohydrate/nitrogen ratios and photoperiodism, in the stems of Biloxi soybean, a plant reproductive in short day. Maximal flower induction period shaded (Murneek, 1939)



FIGURES 38 & 39

Relative catalase activity in short-day Biloxi soybean plants, expressed as log. per cent of long-day plants (Murneek, 1939)

stance, together with xanthophyll, reached a maximum concentration in the leaves of plants under the 7-hour day at the flowering stage, and decreased subsequently.

Parker and Borthwick (1939) studied the carbohydrate and nitrogen metabolism of soybean plants of the Biloxi variety in relation to exposure to photoperiods; the plants for these biochemical studies were first grown in a daylength which would promote the initiation of flower primordia, and were then transferred to 8, 13 and 16-hour photoperiods; the control lot had been grown in 16-hour photoperiods throughout.

One week after the transference, the total nitrogen and soluble non-protein nitrogen were higher in the 8-hour day series than in the controls. Carbohydrates were lower than in the controls, although the starch in the leaves was higher. The total nitrogen in both leaves and stems of the 16-hour transfers became similar to that of the controls, and the 13-hour transfers approached the 8-hour ones as the season advanced. The soluble non-protein nitrogen showed the same relationship in the stems, while an abrupt rise was noted in the amount of ammonia in the leaves and stems of the 8- and 13-hour transfers at pod formation.

Parker and Borthwick found that the amount of soluble carbohydrates in the transfer groups was apparently correlated with the length of the photoperiod. Starch accumulated in the leaves and stems of the 8- and 13-hour transfers when pods began to form.

Two groups of plants upon which flower buds had been initiated and which were subsequently grown at photoperiods just above and just below the critical showed progressive deviation from each other in their carbohydrate and nitrogen metabolism. Those grown below the critical became similar to the 8-hour transfers, while those above the critical became similar to plants that had been kept in a vegetative state by continuous cultivation in a 16-hour photoperiod.

A paper by Eremenko (1936) may be quoted as an example of a Soviet work on the relation between length of day and nitrogen metabolism, that is the C/N relationship which has already been discussed in relation to plant development on p. 22, and which Eremenko considers should not be regarded as a regulator of development, but as a function of the processes of growth and development.

In Eremenko's experiment, the vegetative period was most shortened when the soybean plants were grown in a 10-hour day; the exposure to short day of plants grown up to flowering in an 18-hour or normal day also increased their rate of development. Plant height and dry matter content were reduced by the reduction of the vegetative period. The soluble carbohydrate content (chiefly monosaccharides and less notably maltose and sucrose) was higher in plants grown in short day. A negative correlation was noted between soluble carbohydrate content and

the rate of development. The total nitrogen and nitrogen of proteins fell with ageing of the plants. The highest N and protein-N content was found in plants grown in short photoperiods; consequently, the C/N ratio increased with age of plants.

Development of the apical bud was retarded in plants grown in short day, although the leaves continued their functions normally and assimilated a large amount of carbohydrates. As the reproductive organs are formed early in the soybean, a considerable part of the nutrients migrate into the roots; the ratio between overground and underground parts was therefore smaller in plants grown in short day.

The experiments of Katunskiĭ (1939) are concerned with the relation between the accumulation of organic matter (weight of dry matter per plant) and the photosynthetic activity of plants during their growth and development. The long-day plants, *Avena sativa* var. *byzantina*, *Phaseolus vulgaris* and *Hordeum vulgare*, and the short-day plants, *Panicum miliaceum*, *Soja hispida* and *Cannabis sativa*, were grown under light conditions that were equally favourable for photosynthesis, but differed in relation to the photoperiodic reactions of the plants, namely, a 10-hour day, supplemented by light of an intensity below the critical value for photosynthesis for 0, 6, 8 and 14 hours.

Katunskiĭ found the accumulation of dry matter to be a very complex biological phenomenon, being determined not only by the duration and intensity of the 'working hours' and energy of respiration, but also by the rapidity of development and the relative development and growth of plant organs, with which is associated the distribution of assimilates. The relative significance of these factors in relation to the amounts of organic matter ultimately produced varied considerably, being determined by the hereditary nature of the plant and the conditions of growth. In the experiments, four out of ten plants (*Phaseolus* and *Pisum* in 10-hour day plus 14-hour supplementary light, and *Soja* and *Panicum* in a 10-hour day) produced the maximum weight of dry matter under conditions of the most rapid development; this high productivity was considered to be associated with the vigour of the reproductive organs.

Photosynthetic activity and energy of respiration were also studied in relation to rapidity of development in plants that were grown under the appropriate photoperiodic treatment for 10, 20 and 30 days, and then transferred to seasonal day. Photosynthesis and respiration energy were found to increase with the rapidity of development in both long- and short-day plants, if the appropriate photoperiodic treatment was continued long enough to affect the rapidity of subsequent development. Katunskiĭ states that these conclusions were confirmed in tests of photosynthesis and respiration during the vegetative period in *Perilla*, *Chry-*

santhemum, cucumbers and potatoes, these processes increasing with the advance of plants in their development.

Nutrition and Reproduction

Most farmers and horticulturists are already quite aware of the fact that, once they have provided for the basal nutrient requirements for their crops under their own soil conditions, the balance can be tilted in one direction or another by the application of a particular fertilizer at an appropriate stage in the growth of the crop to provide better growth or reproduction.

The literature on the different rate of absorption of mineral elements by plants at different stages of growth is noted by Maximov in his *Plant Physiology* (1938); it is stated (p. 266) that most annuals absorb the greater part of the requisite salts before the flowering stage, while in corn all the nutrients required for further development are already accumulated in the stem at the time of flowering, when their further absorption ceases almost completely. Maximov also notes that there is a difference in the rate of absorption of individual elements during the development of plants, and describes the absorption of calcium, potassium, magnesium and phosphorus by plants such as oats and peas.

Sugar beet requires nitrogen throughout its vegetative period; a critical time is during intense development of the assimilatory apparatus (four to seven pairs of leaves). The elimination of nitrogen has a harmful effect on yields of root and leaf at all developmental stages. The supply of nitrogen during the second half of the growth period causes an increase in cell colloids. In the absence of nitrogen, the uptake of phosphates and potash is reduced (Demidenko, 1945a).

If potassium is excluded from the nutrient medium of sugar beet during early stages (four to seven pairs of leaves), yields are reduced and quality of crop impaired (Demidenko, 1945b). The period of intense sugar accumulation (seven to ten pairs of leaves) is critical as far as potash is concerned. Leaf area is reduced by potash deficiency; if it is excluded from the nutrient medium during the growing period of the plant, the amount of colloids in the cell sap is increased. If potassium is deficient during the second half of the vegetative period there is an increase in the percentage of soluble nitrogen. The period of maximum absorption does not coincide with the critical periods in potassium nutrition.

Nitrogen supply and photoperiod are related in their effect on flowering, growth and stem anatomy in a number of long-day (*Scabiosa atropurpurea* and spinach) and short-day plants (*Tithonia speciosa*, Biloxi soybean, *Salvia splendens* and *Xanthium pennsylvanicum*). The

external nitrogen supply is not, like photoperiod and temperature, a determining factor in determining floral initiation or vegetative growth, but has a considerable effect on time of flower bud appearance and flowering in some species (Withrow, 1945). Abundant nitrogen produces taller and heavier plants, but with the same nitrogen supply plants in a long photoperiod are taller than those in a short photoperiod. Flowering plants have a higher percentage of dry matter and a higher top-root ratio than vegetative plants; nitrogen does not alter the direction of this response. Limitation of nitrogen has a marked effect on the anatomy of the stems.

The general question of the relation of mineral nutrients to flower development has been discussed by Loehwing (1940), who reviewed the sequence of physiological events antecedent to and concurrent with flowering, which are stated to consist, first, of a change in the internal water balance, followed in turn by altered translocation and redistribution of nutrients. As far as the general progress of plant development is concerned, however, the problem is rather as expressed in a recent paper by Čaĭlahjan and Lukovnikov (1941), who studied the limits within which the rate of development can be influenced by mineral nutrients, in order to reconcile the present conflicting views; (*a*) plants have been reported to show very different rates of development according to vernalization and photoperiod, and at the same time to respond only very slightly to variations in the supply of mineral nutrients, and (*b*) under natural conditions of growth, mineral salts have a very considerable influence on development.

Čaĭlahjan and Lukovnikov find that, under favourable light conditions, development is not affected by varying the mineral ration; no amount of mineral matter will bring plants from a vegetative to a reproductive state. When plants are developing towards sexual maturity under favourable photoperiods, however, the conditions of mineral nutrition naturally become an important factor in plant development. At that time, the authors did not claim that this result applies equally to the respective photoperiodic groups.

Further work by Čaĭlahjan (1944) has been concerned with nitrogen in relation to flowering and fruiting. It is stated that the oat plant (long day) when grown in the long days of Moscow flowers earlier if lower quantities of mineral nutrients are provided, while millet (short day) flowers and fruits sooner if more mineral nutrients are made available. A study was made to discover to what extent these two opposite reactions are exhibited by other plants, and which elements actually have the determining effect. Oats, blue lupin, Illini soybean and buckwheat were grown under favourable light conditions. Čaĭlahjan finds that they are divisible into three groups:

(*a*) plants which start flowering sooner, the lower the mineral supply (oats);

(*b*) plants which start flowering sooner, the higher the mineral supply (millet and blue lupin);

(*c*) plants which flower simultaneously irrespective of nutrient supply (buckwheat, soybean).

Čaĭlahjan gives some preliminary data regarding nutrition rich in nitrogen, but attempts no conclusions. Nitrogen stimulates accumulation of dry matter and growth in all plants, inhibits flowering and fruiting in some (mustard and oats), accelerates those processes in others (the short-day plants, *Perilla* and millet, and the long-day plants, lupin and lettuce), and has no influence on these processes in buckwheat, soybean and hemp. The following statement is proposed as governing the use of nitrogenous fertilizers in agronomic practice: 'in the case of an excess of nitrogen, nitrogenous fertilizers delay the progress of individual phases of development in some plants, and on the contrary accelerate the development of others.' The application of nitrogenous fertilizers should therefore be regulated according to the phase of development of the crop concerned.

It has now become possible, according to Čaĭlahjan (1945), to group plants according to the reaction of flowering to changes in nitrogenous nutrition, as follows:

I. Nitronegative plants, attaining flowering sooner when given little or no nitrogen, or grown on a soil low in nitrogen (varieties of wheat, barley, oats, white mustard, spinach, lucerne, white clover, *Salvia splendens*, *Clarkia elegans*, *Pelargonium hortorum*, *Iberis amara*).

II. Nitropositive plants, flowering earlier with normal or supplementary nitrogenous nutrition, or on soils rich in nitrogen (millet, maize, *Setaria italica*, *Perilla nankinensis*, sunflower, tobacco, cotton, *Capsicum annuum*, lettuce, *Lupinus angustifolius*, different varieties of *Chrysanthemum indicum* and *Ch. mepho*, *Tagetes erecta*, *Xanthium pennsylvanicum*, *Tinantia fugax*, *Kalanchoë blossfeldiana*).

III. Nitroneutral plants, with a constant flowering date, regardless of nitrogenous nutrition (buckwheat, *Cannabis sativa*, soybean, *Phaseolus vulgaris*).

Development and External Morphology

The experiments of Stankov (1938) may also be quoted as an example of a claim for a direct correlation between phase of development and organ formation, and the type of mineral nutrition, and the effect adjustments in this relationship may have on the yield of grain from cereals. Stankov states that the yield of a seed plant, which depends upon num-

ber of spikes on an inflorescence, number of spikelets on a spike, and 1,000-grain weight, is a morphological expression of suitability of the environment for development, and can be co-ordinated with developmental phases as follows (Sapegin, 1938):

Thermo-phase	Number of leaves
Photo-phase	Number of spikes in an ear and spikelets in a spike
Gametogenic phase	Number of fertile florets
Embryogenic phase	Number of grains in an ear and spike, and 1,000-grain weight

The initiation and expression of these parts were investigated with deficient, optimal, and excess amounts of N and P in water cultures, with different combinations of N, P and K in soil cultures, and with different amounts of N, P and K in complete mineral nutrition under field conditions; special attention was devoted to the ratio between N and P.

It was found that the thermo-phase lasted 15 days in wheat and 6 days in barley and that its progress was not affected by type of nutrition, all variants having the same number of leaves. The length of the photo-phase and consequently the rate of differentiation of the apical meristem varied according to the N/P ratio, being retarded when N/P = 5/250 and accelerated when N/P = 250/5. This in turn affected the number of spikes, which varied in water cultures from 9·9 (N/P = 5/250) to 16·2 (N/P = 250/5); in soil cultures from 13 to 17·2 (lack of N) to 20·1 to 21·6 (NPK-N); and in field tests from 9·4 to 13·4 with increasing N in the nutrients supplied. The number of fully developed florets increased also with the increase of N/P, and caused a corresponding increase in the number of spikes with two and three florets.

Stankov found that the gametogenic phase depends upon the inclusion of phosphorus in the nutrition; the percentage of fertile florets increased from 66 (in absence of P) to 90 (with P in nutrition), a result regarded as indicating the importance of P in the nutrient supply towards the end of development. Maximum seed setting (86 per cent) in specially arranged water cultures was obtained when the N/P ratio was varied as follows: 5/50 during the first two phases noted above, 250/5 during the third phase, and 5/50 during the fourth phase. In spite of this conclusion, the author admits failure in finding a balance of nutrient supply which would secure at the same time the largest number of spikes in an ear and a maximum percentage of seed setting.

The number of grains in an ear and spike also varied with the nutrition during the fourth phase, being eleven in the series without fertilizers, and twenty-four in the presence of N; a similar result was noted with 1,000-grain weight, which was 31·6 in absence of fertilizers and 36·0 with NPK.

Stankov notes that the location of the grain on the ear is of importance, as the protein content and vigour of derived plants varied for this reason; the correlation between shape of ear and type of nutrition has not yet been studied.

There are many more Russian papers dealing with the adaptation of fertilizer supply to developmental phase, which can be regarded as experimental confirmation of some of the practices that have long been employed by agriculturists and horticulturists to produce the maximal and optimal yield of the product in which they are concerned, whether it be cereal grain, tomatoes, lettuces or early-bite grass, at the most appropriate season of the year.

The occurrence of maximal infection by fungous diseases and insect pests at a time when the part attacked (whether it be the green herbage or the developing grain) has reached a peak in nutritive value or protein content is a phenomenon that is observed with several crop plants. It is perhaps obvious that herbage or grain that is highly palatable and nutritive for animals or human beings should also be most acceptable to grazing insects or most suitable as a medium for the rapid growth of fungi.

Resistance to Low Temperature and Winter Hardiness

Bibliographies on the very extensive literature on the low temperature relations of plants have been compiled by Harvey (1935 and 1936); 600 publications on the nature of the cell changes which occur during hardening and of the protection which they afford have been critically reviewed by Levitt (1941), while Scarth (1944) has discussed studies on cell physiology with relation to frost resistance, dealing especially with the research of the group at McGill University, Montreal.

Scarth recognizes three main types of injury due respectively to: (1) intracellular freezing; (2) the mechanical effects of freezing and thawing when ice is extracellular, and (3) the physico-chemical effect of dehydration. The first occurs at the moment of rapid freezing of the tissue. The second is inferred to occur during fluctuations of temperature and is actually observed on rapid thawing. The third occurs at the critical low temperature which marks the limit of frost endurance of the cell. The last, according to Scarth, appears to be the commonest cause of death of the plant, or of part thereof.

Before giving the outlook of the Russian workers as expressed by Tumanov, it is appropriate to quote from Scarth's critical review of the literature, and to give the conclusions reached by the McGill group in their research on the phenomena connected with hardening, namely, osmotic pressure, bound water, permeability and the physical state of protoplasm including different regions of the protoplast.

Scarth on the Mechanism of Resistance

The mechanism of resistance is sought by first discovering what other characters are associated with hardiness and then inferring and if possible observing if and how they oppose the action of frost. Since there are several modes of injury, one may expect to find several resistance factors but may also hope to discriminate between the more important ones.

Certain phases of development of the plant and its cells, especially those of maturity and dormancy, are very commonly correlated with

resistance. But though active growth in higher plants at least is not associated with great resistance, some degree of resistance and growth is not incompatible, while true dormancy is often unaccompanied by any resistance, although it would seem that any correlation between a particular phase of development and hardiness depends on the morphological and physiological characters of the cell which are commonly but not necessarily associated with that phase.

The one morphological character which seems to bear a relation to resistance is cell size. Very hardy plants or tissues have small cells, but such cells of course deharden without change in size so that the size factor can be of little importance unless associated with others.

Physico-chemical characters of the cell sap proved to be correlated with frost resistance are moisture content, sap concentration and sugar content, which form an interrelated group. Commonly the increase in sap concentration in hardening is partly due to water loss and partly and usually chiefly due to increase in total sugar. These factors might reasonably be expected to afford some protection, but as their correlation with resistance often breaks down other, more fundamental, factors must be found.

Study of the colloidal contents of the cell has been directed principally toward discovering whether hydrophilic quality accompanies hardiness. On the whole the evidence is against any necessary association of resistance with high pentosans, pectins, soluble proteins or other soluble nitrogenous substances. Several authors from Müller-Thurgau (1882) onward have reported an increase in the more soluble forms of nitrogen in plants exposed to hardening temperature, but the increase is not related to varietal differences in hardiness (Newton, 1924) and occurs also in tender plants that are injured by these temperatures (Wilhelm, 1935a, 1935b; Dexter, 1935). There is also no evidence in the literature that fats play any essential role.

Comparison of metabolic activity (e.g. respiration, photosynthesis and specific enzyme action) has generally shown that differences which tend to increase or conserve sugar promote hardiness, but has thrown no further light on the problem.

Protoplasmic properties have only lately become the subject of direct experiment in this connection. From 1931 onward (see Levitt, 1941), a number of Russian investigators have all agreed that cell permeability decreases with hardening. They estimated permeability from exosmosis, absorption of salts or turgidity. Exosmosis after freezing, as in the earlier work of Pantanelli (1919), was probably a measure of injury rather than of resistance and the other differences observed do not necessarily depend on permeability. The McGill workers are convinced that the relation of permeability to hardening is the opposite of that stated above.

A comparison of the physical state of protoplasm in hardy and unhardy cells was first made by Kessler (1935) and extended by Kessler and Ruhland (1938). They found an increase in viscosity with hardening. While the McGill group would qualify this conclusion, most of their results are not irreconcilable with those of these other workers.

CONCLUSIONS OF MCGILL GROUP

The three main types of frost injury mentioned earlier are opposed by the various hardening changes as follows (Scarth, 1944):

(1) Intracellular freezing tends to be prevented by increased cell permeability to water because this accelerates concentration of the cell sap by the growth of ice outside the cells.

(2) Mechanical injury during freezing and thawing with ice extracellular is principally prevented by the reduced 'structural viscosity' of the cytoplasm, or, at least, of its outer zones. Hardy cytoplasm preserves a more fluid or ductile consistency than unhardy when exposed to equal dehydrating force. The comparison was made on plasmolysed cells but is presumed to hold for cells dehydrated by frost. Further protection is usually afforded by increased osmotic pressure and in very hardy cells by high non-solvent space, both of which reduce shrinkage and distortion of the cells.

(3) Dehydration injury at the critical low temperature is prevented by reduced coagulability of the protoplasm—again notably of its ectoplasm.

(4) The protein fraction which is soluble between pH 5 and 7 is twice as great in *Robinia* bark in summer as in winter.

(5) Increased hydrophily of cytoplasmic proteins indicated by this chemical difference could conceivably account for all the protoplasmic hardening changes.

Tumanov on Hardening

The Russian plant physiologist, Tumanov, has reviewed his own and other Russian work in his *Physiological Bases of Winter Hardiness in Cultivated Plants* (1940). The following review is based on that by Oljhovikov in *Herbage Reviews* (1940), and deals with only two out of many problems covered by Tumanov, namely the nature of hardening, a question more of indirect application in plant development, and the relation between phasic development and winter hardiness.

Dealing first with hardening, it is recognized that a high degree of frost resistance is not a property which is always inherent in a given plant. In order to develop this quality, plants must undergo certain internal readjustments, processes which are not yet fully understood and

which are known under the general name of hardening. In many Russian investigations, chiefly by Tumanov, it has been found possible to establish two ecologically and physiologically distinct phases in the hardening of plants and to outline the factors concerned therein, with the result that plants hardened under laboratory conditions may now attain quite as high a frost resistance as they would in the open. This discrimination of the complex process of hardening into two phases is a distinctive feature of Russian research, 'hardening' in Western European and American research being said by Tumanov to apply only to the first of these two phases. The following are the general characteristics of the two phases recognized by Tumanov.

Tumanov (1936) and his associates claim that the first phase of hardening is acquired by winter plants (chiefly cereals) at 0 to 6° C. in light; the upper temperature limit is apparently determined by the temperature at which growth becomes more or less pronounced. Under these conditions plants rapidly accumulate large amounts of sugars (up to 30 per cent). Tumanov (1931) considers that hardening would be possible at alternating temperatures, for example, 10 to 15° C. during the day and down to freezing point at night. Assimilates would be rapidly manufactured and stored during the day, and growth arrested at night. Under these conditions, however, plants exhibit a conspicuous reduction in their ability to achieve the second phase of hardening, probably because of too rapid growth during daylight. The frost resistance acquired during the first phase of hardening is not generally very high, the lethal temperatures for wheat varying from −7 or −8° C. to −10 or −12° C. The rapidity with which this first phase of hardening may be acquired depends largely upon the environment; under laboratory conditions it may be fully acquired in 5 days or less.

The second phase of hardening is acquired only under much lower temperatures, in the vicinity of −2 to −5° C., and would appear to be based, according to Tumanov, upon different physiological processes. As under these conditions a process of dehydration occurs owing to the freezing of water in the tissues, this phase of hardening is similar in its effects to intensive wilting. The second phase progresses more rapidly, although excessive moisture in the environment of the plant may cause a considerable retardation.

Frost resistance is conspicuously increased due to this second phase of hardening; in Lutescens wheat, the percentage of survival was increased from 17 at −13° C. after the first phase to 96 at −17° C. after the second phase. Since the second phase may be initiated and proceed only when and if the first phase has been completed, it is stated that dehydration of tissues and low temperatures may become effective only in the presence of the protective substances of the first phase, and, as will be noted later,

while the plant is in a certain physiological state, or more precisely, at a definite developmental phase.

It is not known on what basis Tumanov assumes there are two clear-cut phases; hardening appears to be more generally recognized by other physiologists as a continuous process.

The hardening of woody plants is stated to be somewhat different, as the accumulation of starch usually begins in them in the second half of summer, when their growth is much reduced. On converting starch into protective substances (presumably sugar) during the autumn, woody plants also enter the second phase of hardening at still lower temperatures. The existence of a second phase has so far been demonstrated in plants that form sugars; it remains to be seen whether the second phase is acquired at all by woody plants in which oils and not sugars are the protective substances.

Winter Hardiness and Developmental Phase

In the research of Vasiljev (1934), Kuperman (1935), Timofeeva (1935), Kuperman and Zadoncev (1936), Saltykovskiĭ and Saprygina (1935) and others, it has been claimed that frost resistance is connected with phasic development. These experiments were made chiefly with winter cereals; frost resistance was found to be generally lower, and at times conspicuously so, in plants from vernalized seeds, that is from seeds with embryos which had, as far as could be ascertained, completed the thermo-phase, in the terminology of phasic development. The following percentage survival of wheat plants observed by Tumanov (1935) is quoted as an example:

TABLE 23

	Vernalized	*Unvernalized*
Ukrainka: early sowing	16	92
„ late sowing	12	94
Moskov. 02411: early sowing	7	93
„ „ late sowing	0	96

Tumanov and Ivanova (1935) found that both early and late sowings of vernalized grain of Lutescens wheat became depleted at higher temperatures (–11 to –12° C.) than sowings from unvernalized grain, and that generally the frost resistance was higher with the shorter periods of pre-sowing vernalization. After 20 days of vernalization of winter wheat and 15 days in winter rye, the frost resistance of the resulting plants was conspicuously reduced.

Special investigations conducted in the Leningrad region indicate the risks to which autumn sowings are exposed when the early autumn temperatures favour the natural vernalization of seeds after sowing. When Lutescens 0329, Moskov. 02411 and Minhardy had been sown at the end of August, they were found to have completed their thermo-phase on January 13th in 1934-5, on January 1st in 1935-6, and almost entirely by November 19th in the 1936-7 season.

Such a variation in time of completion of the thermo-phase cannot be attributed to variation in climatic conditions alone. A partial or complete vernalization as far as the thermo-phase may occur while the developing grains are still attached to the mother plant, and is also regarded as possible during prolonged drying on the field in a cold and wet season, when the seeds may be sufficiently imbibed to begin the slow growth necessary before development through the thermo-phase can begin.

Tumanov recognizes two possibilities resulting from the after-sowing vernalization in the open: (1) the seeds may be completely vernalized before the beginning of winter, (2) the vernalization of the thermo-phase may be completed either by the beginning of winter or during the winter. In the first case, especially when the plants have had an opportunity to grow for a considerable period, they would lose their ability to harden, and their resistance to frost would thus be much reduced. Some investigators believe, however, that frost resistance begins to fall in vernalized plants with the beginning of the photo-phase. Certain investigations have indeed shown that the capacity to resist frost falls rapidly when the plants are grown after completion of the thermo-phase under conditions which favour the progress of the photo-phase, namely high temperatures and long day. On the other hand, Tumanov states that a fall in frost resistance may also be noted when plants are grown under conditions not favouring the photo-phase, as may be the case with late autumn sowings of vernalized seeds.

Tumanov refers to his own investigations in 1936-7. When the plants were tested on November 2nd, and the thermo-phase was not completed until November 19th, frost resistance was found to be reasonably high; the percentage of survival in Lutescens 0329 at –12 to –18° C. varied from 98 to 84. When the plants were tested on December 14th, that is 25 days after the end of the thermo-phase, frost resistance had fallen, percentage survival varying from 85 to 27 at temperatures of –13 to –22° C. Before the tests were made, all plants had been kept under conditions which would ensure their hardening. In these investigations, the loss of the capacity to resist frost was observed only when plants were grown for some time after the completion of the thermo-phase; this was the case with winter rye, Vjatka, the percentage survival being

78 to 44 in the first test, and only 25 at –13° C. in the second test, while no plant survived temperatures lower than –15° C.

The situation is different when the thermo-phase is completed so late that no growth is possible before the plants are frozen. In Tumanov's investigations in 1935-6, when vernalization was completed by January 1st in winter wheats and by December 1st in winter rye, the percentage survival at –14 to –18° C. varied from 96 to 74 in Lutescens wheat and from 81 to 70 in Vjatka rye. Similar results were obtained in another experiment where the percentage survival was much higher after later sowings.

It may be noted at this point that Oleĭnikova has shown that the thermo-phase can be completed in the open during the winter under the snow cover in the winter conditions at Leningrad. Winter wheats were sown on November 17th, January 1st, February 1st, and March 1st and 31st in the open; from the beginning of April, the various series were transferred to greenhouses where the temperatures were such as to prevent any further progress through the thermo-phase by those plants which had failed to complete this phase in the open. Winter rye failed to ear only after the last date of sowing, and winter wheats after the last two dates. It is therefore concluded that, even in strongly 'winter' plants, the thermo-phase may be fully or partially passed during the winter.

Tumanov considers that the completion of the thermo-phase alone does not yet necessarily mean that frost resistance is markedly reduced, provided the conditions for subsequent growth are not present. Different conditions arise, however, under a deep snow cover or during a temporary thaw, when plants may resume active growth very readily and would thus have a reduced resistance to frost. Tumanov considers it possible that, after the thermo-phase, the growing point is capable during resumption of growth of changing the state of the protoplasm in all other tissues in existence at that time, and suggests a hormonal mechanism as the possible explanation.

Kuperman and Zadoncev (1935) showed that vernalized plants accumulated much smaller quantities of sugars than unvernalized plants, but Tumanov and Fedorova found that vernalized plants have sufficient amounts of sugars and that a sugar deficiency cannot be regarded as the reason for their lower frost resistance. The amount of sugars in vernalized plants first rose very slowly and later, in April, more or less rapidly, reaching 26 per cent on May 7th, or 10 per cent lower than in unvernalized plants, and similar to unvernalized plants before wintering.

Tumanov and Ivanova (unpublished) found that the exposure of vernalized plants to the conditions requisite for the second phase of hardening had no effect, although it is during this phase (of hardening) that plants should show a considerable increase in their frost resistance.

Tumanov therefore assumes that those changes that originate during vernalization cause the protoplasm to be readjusted in such a way that it loses the ability to undergo the appropriate changes during the second phase of hardening, regardless of the presence of protective substances, dehydration and low temperatures.

Winter Hardiness and Length of Thermo-Phase

The length of the thermo-phase in winter wheats varies from 18 to 57 days or more; in certain Scandinavian varieties, according to Beljdenkova, the thermo-phase was found to be longer than 75 days, and yet these wheats were only slightly winter-hardy in Šmelev's tests. Certain varieties which have a thermo-phase of similar length, for instance, Nebraska 60, Kooperatorka and Argentine 38 MA, or Kanred and Erythrospermum 714, show considerable differences in frost resistance. Winter rye has a relatively short thermo-phase and is yet much superior to many winter wheats in frost resistance. Tumanov therefore concludes that further investigations do not confirm the existence of that parallelism between the length of the thermo-phase and frost resistance first claimed by Buĭlina (1935), and believes that these characters have different physiological bases.

Tumanov does not imply that the thermo-phase is of little or no importance, for it is obvious that the longer this developmental phase, the longer duration of vernalization is necessary after autumn sowing, and thus the less is the risk of growth occurring after the thermo-phase has been completed. Further study is necessary before generalizations can be made on this point, particularly in view of claims such as those of Šestakov (1936) to the effect that some wheat and rye hybrids may retain a relatively high frost resistance when sown after vernalization and grown in continuous day.

It is obvious that date of seeding becomes important in connection with the character of winter hardiness. According to Tumanov, no definite conclusions may yet be made, as the question has proved to be much more complicated than was previously apparent, even when considered in relation to phasic development.

General Conclusions of Tumanov and others

It is stated that the application of the theory of phasic development has revealed a very considerable complication of issues connected with winter hardiness of plants. For instance, recent studies in hardening of plants have shown that frost resistance increases greatly during the second phase of hardening. In the presence of protective substances,

dehydration and low temperatures, the protoplasm becomes readjusted, with the result that its resistance to mechanical pressure becomes considerably increased. The ability of the protoplasm to become adjusted is considered to be during growth in plants that have completed the thermo-phase and in woody plants after the break in winter dormancy.

Hardening of plants is stated to be a reversible process, and evidently the loss of hardening may be traced to a resumption of growth; the second phase of hardening is very readily lost when the thaw begins. If, however, temperatures during the thaw are not too high and the plants do not reverse beyond the first phase of hardening, they may under favourable conditions revert to the second phase.

In his study of dehardening and rehardening of *Medicago* and wheat, Dexter (1941) obtained results which agree with those in studies of hardening in relation to phasic development, but makes the reservation that vernalization makes this (rehardening) less probable, although not impossible. The ability to reharden in these experiments was probably lost or much reduced at the stage of elongation of the main stem.

Rudorf (1938) also found that the resistance to cold is largely governed by the condition of the plants in the dormancy period before the thermo-phase is passed through. The more this internal condition is degraded by vernalization (analogous to the action of winter temperatures about 0° C.) the less is resistance to cold, although in this behaviour varietal differences may become apparent. When the thermo-phase has been partially completed hardening capacity is annulled in proportion to the length of the treatment. Rudorf considers that the different degrees of hardening capacity after graded treatment appear to furnish a further good distinguishing character for the evaluation of winter hardiness.

Tumanov's conclusion is that breeding and agronomic management offer the only practical means of avoiding damage by cold.

Winter Hardiness and the Light-Responsive Phase

Russian physiologists consider that the capacity to resist cold is lost if conditions at the end of the thermo-phase favour the progress of the photo-phase. Another experiment may be quoted; Vetuhova (1936) found that winter hardiness increased during the thermo-phase and remained high some time after the completion of vernalization, due to the fact that daylength was unfavourable for the photo-phase. A fall in winter hardiness early in spring was found to be related to the progress of the photo-phase, and particularly to the development of the rudimentary ear and of jointing. Changes were noted in the cell colloids; the amount of hydrophilic colloids and their water-binding capacity gradually decreased and coagulation occurred much more readily. These

colloidal changes are considered to be connected with changes in the protoplasm.

Rudorf (1938) chilled dual-purpose and summer forms of wheat and barley at 2 to 4° C. for periods ranging from 5 to 20 days, and grew them subsequently either in an 8-hour or a 16-hour day. In a third experiment, winter forms were chilled for periods ranging from 20 to 60 days at 1 to 3° C., and grown under the same two-day lengths. Without exception, resistance to cold in all varieties was reduced through the treatment in long day, even after chilling for 40 and 60 days.

Ivanov (1940) found that short days tend to increase frost resistance of citrus plants, long days to reduce it. This tendency was not expressed equally in all species tested, but appears to depend on varietal characteristics. The early lignification induced by short days is not alone responsible for increased frost resistance. It was found that the content of glutathione in the leaves decreases considerably as the daylength increases, and this is related with degree of frost resistance.

In a study of photoperiodism in relation to frost resistance in perennial plants, Moškov (1935) concludes that since photoperiodic conditions influence the whole life activity and all the principal characteristics of a plant, including such an important character as its capacity to resist frost, a plant should not be classed as day-neutral merely because daylength does not influence the transition from the vegetative to the reproductive condition. Presumably it is thought that one daylength may be optimal for reproduction, and another for other biological characters of a plant, such as winter hardiness. Moškov therefore disagrees with Garner and Allard's system of classification.

Breeding for Winter Hardiness

The methods and procedures adopted in the United States of America, Canada and other countries concerned with producing winter-hardy types do not come within our present scope, but the way in which the Russian plant breeders base their technique on the theory of phasic development deserves consideration. The work of Saltykovskiĭ and Saprygina with wheat can be taken as an example (1943 and 1944).

These investigators state that, although the breeding of winter-hardy wheats is of great economic importance, breeders have reached a bottleneck because of the great scarcity of winter-hardy forms among the world's wheat varieties, and because hybridization has seldom yielded 'transgressive' forms much exceeding the more hardy parent in winter hardiness. Saltykovskiĭ and Saprygina have already shown that when wheats are in the stage of tillering, in which they pass the winter if sown in the autumn, their resistance to cold is functionally correlated with the

length of the two developmental phases, the phase of vernalization or thermo-phase, and the photo-phase. Upon this interrelationship were based a cycle of experiments on the hereditary transmission of the winter habit and winter hardiness in wheat and wheat × *Agropyron* hybrids with the object of demonstrating the magnitude of the transgressions of winter hardiness in hybrids between spring and winter varieties.

The hybrid material consisted of fifteen combinations of spring and winter varieties of wheat (Lutescens 4952 × Kooperatorka, Lutescens 3483 × Kooperatorka and Milturum 321 × Kooperatorka) of which the parents had been selected to represent different lengths of developmental phases. It was found that by selecting and crossing wheat varieties as similar as possible in cold resistance but differing as widely as possible in the length of their respective developmental phases it is possible to obtain forms with greater cold resistance than their parents. All the hybrids were more winter hardy than Ukrainka, some approached the very winter-hardy variety, Hostianum 237, while one line even exceeded this in winter hardiness.

Another set of crosses was made with Lutescens 3483 × Erythrospermum 534 and Milturum 321 × Erythrospermum 534. Erythrospermum 534 has a poor cold resistance, being as much inferior to Kooperatorka as that variety is to Hostianum 237. The hybrids between Erythrospermum 534 and the two varieties of spring wheat yielded forms not merely more resistant than the two parents and Kooperatorka, but even more resistant than Ukrainka, that is a jump in grade of cold resistance over several classes of winter wheat varieties.

Saltykovskiĭ and Saprygina express their views on the evolution of winter-hardy winter wheats. In southern regions (south-west Asia, southern Europe), two basic biological types of wheat are used in winter sowings. The one type contains winter wheat with very poor cold resistance; they have a rather long thermo-phase and a short or moderate light phase. The second type contains spring wheats with a short thermo-phase and a long light phase; these ripen late if sown in spring. Crosses between the two biotypes give large and frequent transgressions of winter hardiness. If these biotypes were sown mixed (in ordinary farm practice) in a single population, it is believed that they would have good opportunity for spontaneous crossing, a phenomenon stated to be rather common in wheat. The spontaneous hybrids between winter wheats of poor winter hardiness and late spring wheats are thought by these investigators to represent one of the main initial paths followed in the evolution of winter-hardy spring wheats.

It is maintained that the first step in inducing frost resistance consists in the formation of structural parts of the most important organs and tissues which should survive the winter while still young anatomically

and physiologically. This first step in the development of winter hardiness has been termed the structural phase of resistance to the unfavourable conditions of hibernation. It is only young undifferentiated tissues that are capable of acquiring a maximum winter hardiness after passing the two subsequent phases postulated by Tumanov. The structural phase is more complicated and variable compared with Tumanov's phases, and is dependent on the climatic and agronomic conditions of growth.

The rate at which a plant ages depends on the length of its developmental phases; the shorter these phases, that is, the smaller the requirement of temperature and light for reproduction, the sooner does ageing set in. The differentiation of tillering nodes is also stated by the Russians to be related to these two developmental phases, and the tillering nodes play an important part in the safe overwintering of wheats. Thus shoots formed early in autumn are partially aged, but further late tillering causes rejuvenation. Thus tillering in grasses and cereals may be an adaptation to rejuvenate the organism and thus to create more winter-hardy tissue. This outlook has its application in planning dates of sowing of winter cereals, in relation to rate of growth in the autumn and the expected severity of the following winter, and in managing the grazing of pastures in the latter part of the year in regions where winter-killing is a problem.

Resistance to Drought in Relation to Development

The interpretation of the trends in the drought resistance of plants in relation to phasic development has been expressed by Skazkin (1940) in a paper to a Conference on Plant Physiology in Russia. Drought resistance is found to vary according to the physiological age of a plant, specimens being more resistant at an early period of their life (up to jointing or even up to tillering) than in the subsequent periods (earing to flowering). It is not possible to define morphological characters that separate these two periods. Resistance is found to fall with the beginning of differentiation of the growing point, which coincides with completion of the thermo-phase and an advance into the photo-phase. It may thus be assumed, according to Skazkin, that plants are more resistant at the thermo-phase than at the photo-phase.

The higher resistance to drought noted during the thermo-phase is thought to be determined by (*a*) a higher resistance to wilting and more rapid recovery therefrom, and (*b*) a greater ability to restore certain lost parts by invigorated tillering. During the photo-phase, the physiological state of the plant is altered, and the capacity to resist soil drought is changed.

After the photo-phase has been completed, the preparation of plants

for flowering and seed setting is an expression of profound changes in their physiological and biochemical state. During this period, the effect of drought upon the normal physiological processes is particularly marked; hydrolysis prevails over synthesis and the direction of biochemical processes is changed. High sensitivity to water deficiency during this period is connected with the progress of the reproductive processes.

Drought has a marked effect on yield of grain of cereals, even if growth of the whole plant is not seriously affected (Maximov, 1941). If drought should occur in the earliest stages of initiation of the ear, the number of spikelets (then to be seen as small protuberances on the embryonic ear) is reduced; if after the initiation of the spikelets, a proportion of the florets which can become fully formed on these spikelets is likewise reduced, although the number of spikelets may be normal. If drought occurs at a still later stage after the florets have been formed, the grain and other parts of the florets will suffer. The inability to appreciate how early in development drought can begin to reduce the yield of grain has caused many cultivators on irrigated land in Russia, for example, to apply water only after much irrevocable harm has been done.

Attempts are being made in Russia and India to subject seeds to a treatment analogous to vernalization, with the object of increasing their capacity to resist drought (Ljubinskiĭ, 1940). These pre-sowing treatments for increasing drought resistance have been elaborated by Henkel and his associates (1938) and also include the method of heating seeds at 80° C. for 4 hours (Vorobjev, 1915), Isip's method (1938), Pinčuk's method of treating beet seeds (see Pastuh, 1939), and others. According to Ljubinskiĭ, these methods of treating embryonic plants acquire greater interest in view of Krasovskaja's report (1940) that certain treatments may be applied with success during seed formation and ripening on the mother plant (analogous with vernalization before seed ripening).

This worker made preliminary studies with wheat which indicated that the degree of drought resistance depended upon the conditions under which the mother plant developed. The first generation from plants that had been exposed to drought, particularly if this were done during seed ripening, showed much improved resistance. The beneficial effect of this drought treatment depends also upon its intensity; extremely severe conditions suppressed the viability of the seed generations and resistance was reduced; moderate drought during seed setting had little, if any, effect on the resistance of the progeny. Krasovskaja found that selection of plants in respect of vigour of development of spikes under dry conditions proved to be a very efficient method of breeding for drought resistance.

Moškov (1939) writes that drought resistance, like frost resistance, is

determined by the whole of the physiological processes which take place before exposure to drought, and not only by those that take place after drought has set in. As frost resistance had been found to be related to photoperiodic reaction, it was natural to suppose that the same might be true of drought resistance. This theoretical consideration is, according to Moškov, supported by the changes in anatomy and morphology, which vary in one clone or variety from a xeromorphous to a hydrophilous structure, depending upon the photoperiodic treatment or environment. Moškov describes laboratory experiments in which soil drought was created artificially for some woody species that had received different photoperiods before being introduced into the experiment. All plants were grown out of doors in pots with optimal soil humidity, and not until watering was eliminated were they transferred to wilt in the hothouse. Before wilting began, all the pots were immersed in water to saturate the soil, after which the water supply was cut off until either the end of the experiment or the first cutting. The plants used were American cherry (*Prunus besseyi*), *Robinia pseudacacia*, lemon, and tea.

Plants of black locust were grown in pairs in pots and each given a different daylength. When drought set in on August 15th, three pots from each of the variants (13, 14, 15, and 16-hour photoperiods) were transferred to the hothouse. Fifteen days later, on August 31st, plants that had received 16 and 15-hour days had not only wilted, but most of their leaves had dried and fallen off, whereas the 14 and 13-hour variants were not at all affected by wilting. Moškov claims that plants of the 16 and 15-hour variants differed widely from the other two series; the 14-hour variants stopped growing while the seedlings in a 15-hour day continued to grow. The 13 and 14-hour variants were only half the size of the others and had poorer foliage. Although Moškov admits that the smaller amount of water lost by them is due to their smaller evaporation surface, he does not accept the probability that the whole effect observed may be explained on the basis of reduced evaporation alone. Certain structural peculiarities of leaves and shoots were also noted in the different variants, but no claim is made as to their dependence upon type of photoperiodic exposure.

A more definite characteristic was that, after water had been withheld from 15 to 30 days, the plants invariably wilted; in no case did they shed their leaves normally. The behaviour in response to repeated wilting was, however, quite different. A certain variant is described in which locust plants receiving 15-hour day experienced soil drought many times and not only once, like the other variants. The plants were also transferred to a hothouse when deprived of water supply. After the first wilting, as soon as their tops had lost their turgour, they were given water, which increased the soil humidity up to 75 per cent. The water supply was

interrupted again until loss of turgour again appeared in the tops, whereupon the supply of water was restored. When this procedure had been repeated on numerous occasions, the leaves of the plants yellowed and fell off in the normal way after growth had already been completed, a process which took 3 to 4 weeks. Thus, continuous and protracted wilting leads to destruction of plants, starting with the drying of their leaves and tops before growth is completed and normal shedding of leaves can occur. If weak wilting and watering are alternated, the plants remain alive and shed their leaves normally. Moškov concludes that plants seem unable to resist a steadily increasing soil drought, but a rapid rhythm of recurring soil humidity induces in them what he calls protective qualities that make normal growth and leaf shedding possible.

The evergreen plants, tea and lemon, like the deciduous ones, completed their growth quickly and shed yellowed leaves when wilting and watering were repeated. Moškov considers that no essential difference exists in this respect between deciduous and evergreen species. The latter can shed their leaves and restore their foliage, while the former can acquire an evergreen habit. With protracted soil drought, the leaves of the citrus plants dried, but remained on the trees. The highest resistance to soil drought was observed in lemon and tea plants that had received short 8 to 10-hour days. Best growth of the lemon was induced with a 12-hour day, and resistance to drought was greater than in variants receiving longer days, which were nevertheless inferior in growth. Moškov concludes that the resistance of any cultivated variety to drought is dependent not only on the photoperiodic conditions of a particular experiment, but also and for the same reason on the geographic latitude of its cultivation.

Resistance to Flooding

It is even suggested that resistance to the abnormal environment associated with flooding may be induced by pre-sowing treatment. Parija and Pillay (1944), working in India, exposed activated germ of paddy to a period of anaerobiosis at 30 to 32° C.; one set was then subjected to 2 to 5° C. Treated and control seeds were submerged (one lot after 60 days from sowing, the other after 85 days). It is stated that such treatment induces resistance to flood.

CHAPTER XIV

CROP PRODUCTION AND GEOGRAPHICAL DISTRIBUTION

General Application of Experimental Results in Agricultural and Horticultural Practice

As the fundamental knowledge of the processes of plant physiology is built up from the results of many scientific experiments on the development of plants such as have been described in the foregoing chapters, it will be possible to record many advances in the applied science of crop production and, above all, in the understanding and interpretation of many practical methods and phenomena which have not yet been given an adequate scientific explanation.

It may be said that the results of experiments in plant growth and development will be applicable in agricultural and horticultural practice in four chief directions:

(1) they will provide a clearer insight into the adaptation of plants to a definite environment, in which their development is governed by the decisive factors of temperature and light (length of day) in combination with the secondary factors of the environment;

(2) with the knowledge obtained under (1), it will be possible properly to locate the production of a particular crop species for seed, forage, green manure or other purpose in an environment which provides the necessary factors in a suitable quantity and quality, and at the correct time;

(3) it may be possible to breed new varieties of plants adapted to new environments or to select strains which are day-neutral or otherwise likely to be adapted to a wide latitudinal range;

(4) where economic production of the required plant products is not yet possible after adopting the measures noted in (2) or (3), it may be possible intelligently to employ (although generally on too small a scale) certain methods of manipulating the development and growth of crop plants in a desired direction by the use of methods such as vernalization by temperature and/or light, control of length of day, shading, hormonal treatment, and so on.

In all this work, it is obvious that care must be taken in deciding which growth forms and behaviours are due to the environment as understood in this book, and which to the agronomic management given to the

crop concerned. Martin Jones has, for example, at Craibstone, Aberdeen, converted red clover from a biennial to a perennial of at least 6 years' duration, by suitable grazing or cutting management. This is not due to any change in the light or temperature of the environment, but probably to the fact that the plants are not permitted to flower. Therefore the hormonal resources of the plants are maintained in the lower regions and prevented from becoming transferred to the flower and seeds; the hormones are therefore available for further growth from basal buds. Sukačev (1941) describes a similar change from biennial to perennial habit in *Trinia henningii*, which can if sown thickly be prevented from flowering by competition and maintained in a vegetative state for at least 4 years. This is stated to be due to competition for moisture and not light nor supply of mineral nutrients.

In the remaining chapters it will not be possible to cover the practical application of the knowledge of the processes of plant growth and development adequately, but it is hoped that this particular aspect of the general problem may be made the subject of exhaustive review by those of the Imperial Agricultural Bureaux concerned with crop production.

This chapter will be devoted to a brief consideration of some of the points that arise in connection with paragraphs (1) and (2) above, on the adaptation of plants to the environment as far as the factors governing true development are concerned, and on the planning and locating of the production of certain crop plants on the basis of this knowledge. The breeding of new varieties and strains after an analysis has been made of their respective environmental requirements is discussed in the following chapter.

Adaptation of Plants to the Environment

The broad aspects of this particular subject cover many problems such as the relation of plants to soil fertility and moisture, length of frost-free season, and similar environmental factors, that generally do not have a direct effect upon the development to maturity as understood in this book. The most important factors as regards true development of crop plants are, of course, the seasonal and daily trends in temperature and the length of the daily periods of light and darkness.

It is now fairly certain that every plant variety has its own definite optimal requirements of temperature and light without which it cannot proceed at an economically desirable rate to flower formation, flowering and the production of seeds. It is equally obvious that the natural range of most plants that reproduce themselves in a normal sexual manner is to be found within conditions which provide that combination of temperature and light conditions which is required for their development. There are numerous examples among economic plants, in which different

varieties exhibit quite considerable differences as regards their individual requirements of thermal and photoperiodic conditions. These differences are probably inherent in the varieties concerned, and the extension of the area of cultivation of the crop as a whole may be made by the selection from the general plant material available of types and strains capable of growing and producing an economic yield under, say, more northerly conditions in the northern hemisphere. In the terminology of the school of phasic development, this would mean the selection of types with a longer thermo-phase and a photo-phase adapted to long days.

Flowering and Length of Day

It is doubtful, however, whether plants can adjust themselves to different environments, as might be understood from the following statement of Allard and Garner (see United States, Dept. Agric., 1940): 'Wild plants in their wanderings have always been forced to adjust themselves to length of day, and every successful wild plant represents an adjustment to this factor as much as to any other factor of the environment. It is a factor that comes into operation along lines of latitude and not in eastward or westward trends.' Actually the examples quoted by Allard and Garner do not support the idea of adjustment, but suggest rather that it is possible to find and isolate strains with a different critical daylength suitable for growing under the new conditions.

A plant population growing in a particular environment (say short day) may contain a range of day-neutral or even potentially long-day types which may make it adaptable to a more northerly environment (in the northern hemisphere). Stapledon (1943), remarking on the striking character of cocksfoot plants grown from seeds collected by Gwilym Evans in the Atlas Mountains, states that similar types are obtained among segregating material produced by repeated selfing of certain British plants. 'The outward and visible form that a plant assumes on any particular habitat cannot necessarily be taken as a complete mirror of that plant's internal and ultimate genetical constitution.'

The plants quoted as examples by Allard and Garner are *Poinsettia* and *Cosmos*. The daylength requirements for *Poinsettia* are rather rigidly fixed, with a critical point near 12 to 12·5 hours as necessary for flowering and bract colouration. The plant is a native of the American Tropics, and thrives out of doors in tropical and subtropical regions. At Washington, D.C., it flowers only during the shortest winter days, for a seasonal swing towards longer days in June of only one-half hour is sufficient to provide a length of day unfavourable for flowering. The behaviour of *Poinsettia* is the same on the Equator in Brazil and northward, so that even under these higher temperatures the plant has a

seasonal flowering associated with the winter months. The horticulturist in northern latitudes is therefore compelled to treat *Poinsettia* as a greenhouse plant, as the period of 12-hour days, occurring 'simultaneously over all the earth around September 21st', is close to the date of the first frosts.

The first cultivated strains of *Cosmos sulphureus*, a native of Mexico, have rather low length-of-day requirements around 13 to 13·5 hours and cannot flower in northern latitudes before the frost, even in the vicinity of Washington. They have, therefore, become garden plants in eastern South Carolina and farther south, where the shorter midsummer days initiated earlier flowering, and the autumn frosts are later.

The same authors then refer to the fact that earlier strains of *Cosmos* have now been isolated, strains that are early flowering because they have a higher critical daylength for flowering; they can therefore flower early, even in the longer summer days of Washington or farther north. Selection in this case, 'though perhaps not consciously determined by a knowledge of the action of daylength', has actually been based upon this factor.

After discussing similar behaviour with regard to *Sedum*, *Perilla*, *Salvia* and *Guizotia*, Allard and Garner state that long-day plants having a critical photoperiod of 14 to 15 hours or longer should be tried in northern regions, for they could not well be adapted to southern culture. The more sharply a plant flowers around a certain length of day, the more important becomes the question whether this daylength corresponds to high or to low light-darkness ratios. Such plants have rather rigid daylength requirements and are adapted to particular latitudes only. Indeterminate plants that flower about equally well in response to all lengths of day are the most amenable to culture, since as a rule they can be grown from the tropics to the poles, at least in so far as their daylength requirements are concerned. Allard and Garner quote the tomato, pepper and tobacco as being among the many economic plants of this kind.

Behaviour in Relation to Latitude

Evans, Allard and McConkey (1935) made a study on the time of heading and flowering of early, medium and late strains of timothy at different latitudes, and noted the extent to which their results confirmed Hopkins' Bioclimatic Law (1918). This law states (as quoted by these authors) that, if other conditions such as those relating to longitude, altitude, distance to large bodies of water, and other factors that may have an effect on local climates are equal, then the time of flowering, or any other periodic event in the spring, should progress from south to north, in the northern hemisphere, over the entire range of latitude

where any species of plant under consideration may grow, at the uniform rate of one-fourth of a degree of latitude each day.

Before describing their experiments, Evans, Allard and McConkey refer to the fact that two of the strains used had also been grown in an earlier experiment, carried out at six stations, ranging from Savannah, Georgia, at 30° 6′, to Fairbanks, Alaska, at 64° 51′ N. Lat. The time when the first florets bloomed progressed from south to north, not at a uniform rate, but at a rate that was constantly accelerated as the season

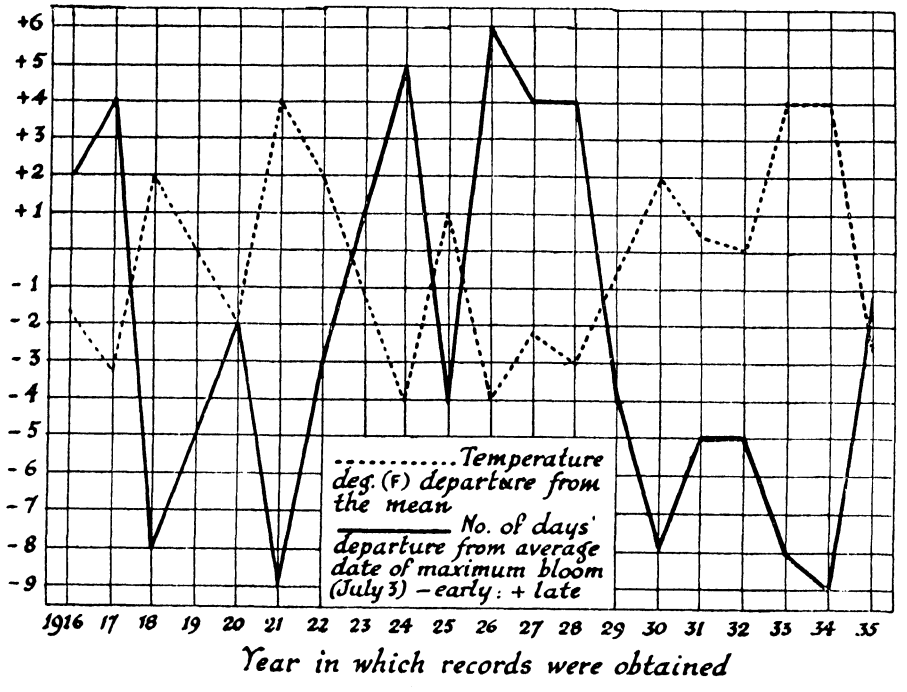


FIGURE 40

Latitude in relation to growth phases in timothy (*Phleum pratense*). Relation of mean temperature during April, May and June to the date at which the maximum percentage of plants are in full bloom (Evans, 1939)

advanced. This effect Evans (1931) attributed to the greater lengths of day occurring during late spring and early summer, at northern as compared with southern latitudes.

This earlier experiment indicated the desirability of conducting further investigations on the way in which the season for the appearance of the inflorescences or heads and the beginning of the flowering process progresses from one latitude to another. Thirteen strains of timothy were therefore chosen, showing fairly uniform gradations from very early to very late, and these were grown at three stations at different latitudes, as follows:

Washington, D.C.	38° 54′ N. Lat.	Altitude, 50 ft.
North Ridgeville, Ohio	41° 23′ N. Lat.	Altitude, 750 ft.
Guelph, Ontario	43° 33′ N. Lat.	Altitude, 1,120 ft.

The plants of each strain had been propagated vegetatively from the same original plant, so that there were no possible genetical differences between them as there would have been if they had been grown from seed. The dates when the first florets bloomed are shown in Table 24.

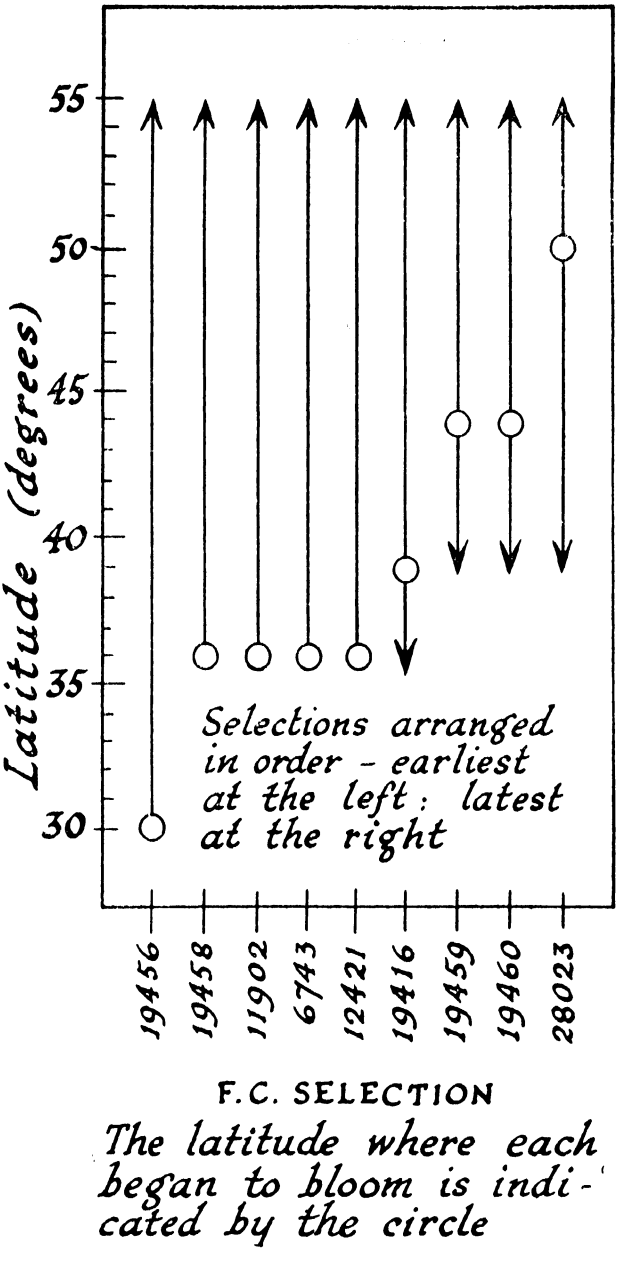
TABLE 24

Dates when the first florets bloomed on timothy plants grown at stations at three different latitudes (in 1933).

Strain number	*Washington, D.C.*	*North Ridgeville Ohio*	*Guelph, Ontario*
19456	May 27	June 5	June 20
19458	June 2	June 8	June 20
15092	June 6	June 10	June 22
11902	June 8	June 12	June 25
6127	June 13	June 16	June 25
6743	June 14	June 22	June 28
9220	June 23	June 27	June 28
12421	June 28	June 29	July 3
15485	July 3	July 4	July 8
19416	July 10	July 5	July 6
15445	July 13	July 10	July 7
19459	July 25	July 15	July 8
19460	July 31	July 22	July 15

It is considered possible that Hopkins' Bioclimatic Law may apply reasonably well to all but three of the strains, but this does not explain why the season for heading and flowering of the latest three selections should progress from north to south. The explanation suggested by Evans, Allard and McConkey is given in the following quotation from their paper: 'In very early strains heads develop and the flowering process occurs with days 10 to 12 hours long. In strains which are later under natural conditions, longer days are required for these processes, if the plants are grown under days artificially made of uniform lengths. At the southern station where this experiment was conducted, the lengths of day during late spring and early summer are not as great as at the stations farther north. For the earliest strains, the lengths of day at the southern station are sufficient for the development of heads to begin before the temperature becomes high enough for active growth at the stations farther north. In the case of very late strains of timothy, on the

FIGURE 41



Progress of the 1935 season for blooming of different selections of timothy. For the earliest strains, at the southern border of the timothy-growing area in the northern hemisphere, the days are sufficiently long for development of culms and inflorescences when or soon after the weather has become warm enough for spring growth. For these early strains, the season for heading, blooming and maturing progresses northward at a gradually accelerated rate as the season advances. A medium maturing strain such as 6743 shows at first a delay in the season for heading, blooming and maturing, after temperatures are suitable, until the days become of sufficient length; eventually the season begins at the southern border of the timothy area, progressing northwards, at first slowly and then at a constantly accelerating rate. The late strains are even more delayed. Plants begin to bloom not at the southern border of the area, but at a latitude where suitable temperatures and daylengths first occur. The season for blooming then progresses in both directions—towards the north as the temperatures become higher, towards the south as the days lengthen

(Evans, 1939)

other hand, length of day apparently is the limiting factor at the latitudes where this experiment was conducted. Since the minimum length of day in the spring is attained, in the northern hemisphere at stations which are relatively far north, sooner than at stations farther south, the season for heading and flowering of these very late strains of timothy consequently progresses, in the latitudes where this experiment was conducted, from north to south.'

These experiments on timothy and those on the cultivation of wheat varieties in England and Australia noted below (p. 228) were done on economic plants in which the original biological composition and behaviour of the species may have become masked by long domestication. This is not the case with the native range grasses belonging to the genus *Bouteloua*, upon which fundamental investigations as to their growth and development have been made by Olmsted at the University of Chicago. As this work has a wide application as far as the behaviour of plants in different latitudes and the origin of ecotypes are concerned, it is desirable to review it thoroughly, on the basis of Olmsted's most recent paper on the subject (1944); see also earlier work on p. 291.

Side-oats grama (*Bouteloua curtipendula*) occurs over much of the eastern, central and south-western United States, extending into Canada on the north (southern Saskatchewan), southward into Mexico, and in South America to Argentina. It is a valuable forage plant in the western part of the prairie region in U.S.A., and at certain altitudes in the south-west. Seeds of twelve strains were obtained from localities between San Antonio, Texas, to Cannonball, North Dakota, a latitudinal range of about 17°. The effective photoperiods at these two stations are probably near 15 and 17 hours. The rate of increase to and decrease from these maxima to or from the nearly equal period of slightly over 12 hours from sunrise to sunset at the equinoxes (effective photoperiod under 13 hours) is obviously greater at the northern stations. The strains were grown at Chicago, where a parallel study of *Bouteloua gracilis* has also been conducted. The following are Olmsted's conclusions with regard to *B. curtipendula*. They are given at length because of their probable value in grass breeding and selection work in other continents where certain species have a wide latitudinal range, for example, Africa or Australia.

Olmsted's study has confirmed earlier reports that plants of side-oats grama from different latitudes are morphologically and physiologically distinct when grown together under similar conditions. This diversity must therefore have a genetic basis. Each strain in turn shows considerable genetic differentiation, and this diversity involves adaptation to different photoperiods by the various strains. The three strains from southern Texas and southern Arizona, in photoperiodic experiments, show most nearly normal (nearest to that under field conditions)

vegetative and flowering behaviour on a photoperiod (13 hours) close to those of their native growing season. Most of them fail to flower but grow luxuriantly on photoperiods longer than 14 hours. Under nursery conditions in more northern latitudes, most of the individuals in these strains are thus delayed in flowering until the shorter days of autumn, when they are likely to be injured by frost which often occurs while they are still in a vigorous vegetative condition. In Olmsted's experiment these strains were also non-rhizomatous. In North Dakota and Kansas, southern strains are also liable to injury in winter and it is obvious that they are not genetically suited for acclimatization in latitudes very far north of their native environments, unless their vigorous erect vegetative habit would make it desirable to attempt the selection of cold-resistant individuals capable of flowering on long photoperiods.

A North Dakota strain, in contrast, consists of individuals showing normal vegetative and flowering behaviour only in photoperiods of 14 hours or longer (long-day plants). In their natural growing season they are not subjected to photoperiods of much lower value. When grown in shorter photoperiods, most do not flower nor do the internodes elongate, although they tiller abundantly and form rosettes. Rhizomes are formed in the shorter photoperiods, but not so abundantly as in the longer ones, and dry weight yields are lower. When grown in southern latitudes in the United States where photoperiods do not exceed 14 hours for more than a few weeks, such a strain could not compare favourably with those of more southerly origins, irrespective of the suitability of other environmental conditions.

Strains from central latitudes, especially from Oklahoma, show considerable variation within strains, although the photoperiodic responses tend to show a gradient among strains correlated with latitude. Strains from Nebraska and Kansas consist mostly of long-day plants, although the critical photoperiods are probably shorter than in those from North Dakota. Strains from Oklahoma and New Mexico include some long-day individuals and also probably some intermediate types. Vegetative growth of these central latitude strains is less adversely affected by short photoperiods with decrease in latitude of origin, while all exhibit luxuriant vegetative growth in long photoperiods. Olmsted considers that the strains from Oklahoma and New Mexico, because of their apparently greater genetic diversity, and their behaviour resembling that in the field over a wide range of photoperiodic conditions, would probably be best fitted for acclimatization to latitudes north or south of their own if they had other desirable characteristics. Within their own latitudes, they show most promise for the selection of 'early' and 'late' individuals, so far as this behaviour is correlated with photoperiod.

The different strains of side-oats grama have exhibited practically the

entire range of reported photoperiodic responses, and as a species it cannot be placed in any photoperiodic class except with reference to strains. This is striking evidence that it is unwise to attempt any generalizations at the species level until strains from a wide latitudinal range have been investigated.

These experiments also show that the habit of a strain in one environment is not predictable from its mode of growth in another, as has been conclusively demonstrated by Turesson (1922, 1925 and 1930) and Clausen, Keck, and Hiesey (see Washington, 1940). These investigators showed that genotypic differences not apparent in one environment were often revealed in another. The range of vegetative expression induced in one strain by the different photoperiods was greater in the northern than in the southern strains, and strain differences of a vegetative nature were accentuated by the shorter photoperiods. This is in contrast with the results of Werner (1942), who found that a simulated 'northern' environment (longer photoperiods as one factor) gave opportunity for manifestation of more varietal differences among several varieties of potatoes than did a 'southern' one. It also contrasts with the observations of Clausen *et al.* (see Washington, 1940), who found in their reciprocal transplant experiments that 'ecotypical differences may be accentuated at one station over another, and the most vivid impressions of these differences are obtained at that garden where the species (*Potentilla glandulosa*) as a whole does its best'. The first but not the latter part of their statement applies to the growth of side-oats grama in these experiments.

Olmsted considers that there is little doubt that side-oats grama originated in low latitudes, possibly in south-western United States or Mexico, and that it has spread north and south to higher latitudes in southern Canada and Argentina. The centre of distribution of the genus *Bouteloua* is in Mexico and south-western United States (Griffiths, 1912). Other species in the same subgenus are confined to low latitudes (under 35°), and plants in the genus with low chromosome numbers have been reported chiefly from this region (Fults, 1942). Most of the investigated individuals of side-oats grama are hexaploids ($2n = 42$), but Fults (1942) also reported chromosome numbers of 28, 35, 40, 45, 56, 70, and 98 in the species. The individual with $2n = 28$ was from Kansas, while the few plants with numbers higher than $2n = 42$ were from Oklahoma, Texas, Arizona, and Colorado. Fults stated that 'the production of new types through various chromosomal aberrations is probably still a dynamic process in this region', and that 'it is likely that the diploid type of $2n = 14$ will be found by further search especially in the south-western biotypes'. Fults' first statement may help to explain in part the genetic variability of Olmsted's material from Oklahoma and New

Mexico, although no chromosome counts have been made upon it. His data thus suggest, although they do not confirm, an origin and the continuing evolution of side-oats grama in low latitudes, but apparently the hexaploid complex has been most involved in the spread to higher latitudes in the United States.

Finally Olmsted considers that the present photoperiodic differentiation which he has noted within the species *Bouteloua curtipendula* is of interest in connection with the probable origin and evolution of the species. The typical short-day response of the three southern strains could represent the original adaptation to the short photoperiods of low latitudes in which the species originated and in which these strains persist. Within these strains, however, a few individuals (possibly day-neutral, although clonal studies on different photoperiods are not completed) are able to flower on longer photoperiods. While of little importance in adjustment of these strains to their present environments, they suggest that races with similar ability, however it originated, would have been perpetuated through natural selection in a migration to higher latitudes in which flowering must necessarily occur in the long days of the frost-free season. Even with the development of the rhizomatous habit, it is probable that plants capable of flowering only on short photoperiods would have been eliminated or very restricted in their rate of migration if they persisted through vegetative propagation. The populations spreading north thus would have come to consist largely of day-neutral plants, or of intermediate or short-day plants with a very long critical photoperiod. Some of the 'late' plants from Oklahoma and New Mexico may be of the latter type, but it is doubtful whether many individuals in these strains are day-neutral. The mode of evolution of the typical long-day response of the more northern strains is obscure. The ability to flower on a 20-hour photoperiod is not of survival value at present, and it is doubtful whether the species has ever ranged to latitudes where such photoperiods are encountered. Any complete evolutionary history of the species must also account for a loss of ability to flower on short photoperiods by the northern strains and their tendency to limited growth and dormancy as photoperiods decrease below a certain level. But whatever the mechanism of the evolutionary process behind such diversity, it has certainly resulted in a high degree of adjustment by the respective strains to the range of photoperiods encountered in their native environments during the season of the year otherwise favourable for growth. The ability of some individuals in most of the strains to grow and flower well over a wider range of photoperiods, while of no importance in their native environments, has undoubtedly been of evolutionary significance and of survival value in the migration of the species to different latitudes. Such variants hold most promise for acclimatization

to areas north or south of their native ones and possibly for the ultimate segregation of desirable day-neutral types.

Before proceeding to discuss the practical significance of temperature, both alone and in combination with light, in relation to the development of crop plants, reference may be made to experiments on the intensity of light in relation to the growth and flowering of range grasses. Benedict (1941) carried out an experiment to discover whether the high sunlight intensities characteristic of western localities such as Cheyenne, Wyoming, which are so much higher than in some other parts of the United States, might not be too high for the best growth of some of the range grasses. Crested wheatgrass (*Agropyron cristatum*), bluestem (*A. smithii*) and blue grama (*Bouteloua gracilis*) were therefore grown in full sunlight and under shades transmitting various percentages of full sunlight but not changing the daylength. Height, dry weight, and number of plants that flowered were recorded.

Plants grown in the shade were taller than those in full sunlight, but had a smaller dry weight. Reduction of light intensity caused an increase of flowering plants of the *Agropyron* spp., but a decrease in *Bouteloua*. Using dry weight as a measure of growth, the results are taken to indicate that these species make their best growth in full sunlight, but that full sunlight, while favouring flowering of *B. gracilis*, is so intense as to retard it in the *Agropyron* spp.

Flowering and Temperature

Research appears to indicate that there is a wide variation in the degree and amount of temperature that different crop plants and varieties require before they can flower. Some require a long duration at low temperatures; different species and even different varieties of the same species may require only a small amount of low temperature. In describing these types, it is frequently stated that they have a long or a short thermophase. Some plants would appear to be able to flower without low temperature at one phase in their life, and yet are not thermophilous in character, as are cotton, soybean and millet. Naylor (1941) states that dill (*Anethum graveolens*) does not require low temperature at any phase of its life, and that the variety of *Beta vulgaris* used in his experiments differs from most varieties in not having a definite thermo-phase.

Crop plants that do require a certain amount of low temperature before they can flower at a normal economic date require to be sown at such a time as will allow for the natural acquisition of the required dose of temperature. Postponement of the sowing time beyond a given date will mean that no fruiting will take place in that season. This type of behaviour and the similar well-known behaviour of biennial and peren-

nial plants which have to pass through a winter before they can flower, are important factors in locating crop production in regions where sufficient natural vernalization will take place.

Reference has already been made in Chapter V to the work of Kostjučenko and Zarubaïlo, and Gregory and Purvis on vernalization of embryos while still developing in the ears of the mother plant. While not attempting to formulate generalizations that would apply to all crops (other than their original experimental plant, wheat), and to all conditions, the Russian authors do consider that this phenomenon is of considerable practical significance. They state that the facts established are of great importance in the first place for varietal tests, as in future only seeds of local reproduction can safely be used. If imported seeds must be used, the conditions under which they ripened must be ascertained. Similar data on conditions of ripening of local reproductions would also help to explain strange behaviour of varieties from year to year.

Several authors have noted the fall in winter hardiness that occurs with advance in development; if this is actually so, evaluations of the winter hardiness of individual varieties may show quite considerable variations from year to year, depending upon the degree of pre-dormancy development.

Kostjučenko and Zarubaïlo also refer to the location of seed-producing areas in this connection, and the latitudinal transference of seeds. It is regarded as being too risky to import seeds of winter crops from more northerly regions, where temperatures below 15° C. occur for some considerable time during ripening, into other regions with a severe winter, as the plants derived from these seeds, although of a reputed winter-hardy variety, might prove to be insufficiently winter hardy.

Care is also recommended in importing seeds of those spring crops with a relatively long thermo-phase requiring lower temperatures into more northerly regions where the vegetative season is short and there are lower temperatures during crop ripening, as there may be a danger of obtaining from these seeds plants which will be too late, and will consequently give lower yields than plants of the same variety grown from seed reproduced locally. On the contrary, the importation of seed of spring forms from the north to the south, as well as of winter forms from a relatively southerly region with a severe winter into the north, is not only free from any risk, but may even in some cases produce a conspicuous result. It is considered that a similar statement might be made about the introduction from southern into more northerly regions of seeds of those spring crops that are known to require relatively higher temperatures for passing through the thermo-phase.

Accordingly, when spring forms requiring low temperature at the

thermo-phase are being transferred northwards, their seed should, according to these authors, be reproduced at the place of their destination or as far north as possible. The reverse is probably the case with spring crops requiring a high temperature for the thermo-phase, when they are to be transferred northwards. If one takes as a boundary the limits north of which spring crops of that type fail when reproduced locally, it might be expected that in some cases these crops could advance beyond that boundary by the annual importation of seeds reproduced in southerly regions with appropriate temperatures during the ripening season. This statement is considered to be still more true of winter crops, and particularly of wheat.

Kostjučenko and Zarubaĭlo then refer to the fact that the northern limits for the cultivation of a winter crop lie to the south of those of spring forms, a phenomenon which they consider to be due to the fact that there are low summer temperatures. When these varieties are cultivated north of their present limits, they can endure the first winter well only if seeds reproduced in some more southerly regions are used in sowings. In subsequent years, the failure of seed reproduced locally at these northern latitudes can, according to these authors, be predicted, since these seeds would have been vernalized during ripening and would thus have lost their winter habit and their winter hardiness to such an extent that they are unable to endure even a mild winter.

It is suggested that natural vernalization during seed ripening might be artificially induced by varying the sowing date or locating seed production areas at different altitudes, where temperatures during seed ripening would be at a suitable level. It is not claimed that natural vernalization during ripening is a universal means of solving all difficulties; it is only one of many factors, but it is one that deserves consideration in studying the behaviour of crop plants.

The behaviour of *Iris tingitana* (var. Wedgwood) and *Amaryllis belladonna* in their original habitats and in the Netherlands has been investigated by workers at the Laboratorium voor Plantenphysiologisch Onderzoek, Wageningen (Luyten, 1942 and Hartsema and Leupen, 1942). These plants originate in Morocco and Cape Province, S. Africa, respectively. The earlier formation of the flower of *Iris* in Morocco is thought to be due to soil temperature at that latitude, which is 17° C. compared with 23° C. which they receive from August to October in the Netherlands. Bulbs of *Amaryllis belladonna* were placed (unplanted) in eight different temperatures. In some temperatures (9°, 13° and 31° C.) no flower formation occurred, at 17° C. only in three bulbs. The best and most rapid flower formation occurred at 23° C.; it is presumed that flowers will also be formed in *planted* bulbs at other temperatures. In the Netherlands, the foliage on the perennial bulbs of *Amaryllis* appears

in spring and dies off at the end of July; the flower stalks appear in September or October. In S. Africa also the plant flowers after warm summer months, in February–April, but it is not known when the formation of the new inflorescence begins in that country. An interesting comparison is made between *Amaryllis belladonna* and *Hippeastrum hybridum*. In *Amaryllis* flowers are formed only once a year, while in *Hippeastrum* they are formed more frequently and regularly, every time four foliage leaves (minimum leaf number?) have been formed.

Behaviour in Relation to Altitude

Alpine plants exhibit different growth forms and behaviours as compared with plants of the same species growing at lower elevations at the same latitude and therefore the same length of day. This is a special aspect of plant physiological research to which it is possible to refer only briefly with a few examples from different parts of the world.

Scientists on the staff of the Carnegie Institution of Washington have been using the air-conditioned greenhouses at the California Institute of Technology, Pasadena, to study the physiological differences between climatic races, in particular of *Achillea millefolium*. This plant has developed a complete series of ecotypes for altitudes between sea level and 12,000 ft., and for latitudes from warm temperate to arctic; the species has the further advantage for experimental use in its ease of propagation, both vegetatively and by seed (Clausen, Keck and Hiesey, 1944). In the experiments at Pasadena, representative plants have been used from a transect across California at 38° N. latitude, from elevations from sea level to 10,000 ft., and from Alaska, Denmark and Lapland.

Extreme and intermediate artificial environments have been used by Hiesey. In the extreme environments the greatest differences in reaction are seen, thus beginning to indicate the mode of operation of natural selection. Races from high altitudes in the Sierra Nevada reacted very differently from those of lower elevations. Alpine and subalpine races from 10,000 and 8,200 feet elevation remained dormant throughout the 4-month period of the experiment at 17° day and 7° C. night temperatures, while the coastal forms grew vigorously and flowered. The alpine races did become active with a day temperature of 26° and a night at 7° C., suggesting the existence in the alpines 'of a sensitive physiological mechanism governing dormancy, that is determined by temperature'.

For flowering, alpine and subalpine races appear to require more

light than races from lower altitudes, which flower even with an 8-hour day. None of the plants from high altitudes flowered or even thrived under such short periods of illumination, but their growth was accelerated and flowering stimulated in natural daylight for 8 hours at 26°, supplemented by fluorescent light of 450 candlepower intensity for the remaining 16 hours at 17° C. In their native high-altitude environments of high light intensity, these races flower when the days are long, whereas the plants from lower altitudes flower earlier when the days are somewhat shorter.

It is suggested by Hiesey that this method might be applied to the breeding of range grasses also being conducted by the Carnegie Institution. The relation between altitude and latitude and behaviour is being studied in a number of *Poa* species, in which great differences in periodicity (summer and winter dormancy) are evident. *Poa secunda* from the dry ranges east of the Cascade Mountains and the Sierra Nevada has the most rigid periodicity; even the young seedlings go completely dormant in May without having flowered, irrespective of the amount of soil moisture. *Poa nervosa* from the high Sierra Nevada has a very unusual behaviour for an alpine species, since it flourishes under the lowland conditions, remaining green all winter and developing many tall culms in spring, but, unlike *P. pratensis*, going dormant during the summer.

Disease resistance is linked with altitude and latitude. Races native to higher altitudes and latitudes usually become badly attacked by rusts and mildew at low elevations in California, while forms native to the Coast Ranges are relatively resistant. Markedly resistant forms have, however, been found among races native to high altitudes, and two completely resistant forms of *P. pratensis* found have originated in high latitudes.

Russian investigators have also been interested in high-altitude plants, but with reference to their vitamin content and enzyme activity. Grebinskiĭ (1941) has studied the question in the region of the University of Alma-Ata at altitudes ranging from 800 to 3,100 metres, and finds that in this environment the vitamin C content in the leaves and the activity of catalase and peroxidase are increased in direct proportion to the deterioration in the environment and the consequent retardation of growth which occurs. The increase in vitamin C content is especially marked on dry, well-lit southern mountain slopes. Data of this type are of importance in connection with the cultivation of vegetables and the use of the natural herbage of the region as animal fodder.

The flowering behaviour of species of *Taraxacum* (dandelion) in relation to altitude has been observed in Scandinavia (Christiansen, 1941). The following observations were made on 24th June:

Metres above sea level	*Behaviour*
200	Fruit dispersal completed.
400	Flowering completed in some plants, others flowering.
800	All plants in flower.
2,000	No plants in flower.

The times of flowering at heights from 400 to 1,200 m. are near one another. *Taraxacum* flowers in the lowlands about the middle of May, and is therefore a month later at 400 m.

Location of Sugar Beet Seed Production in U.S.A.

Possibly one of the most striking examples of the practical application of research on plant development in relation to the environment is in the location of the new production of sugar beet seed in the United States. In changing from a position of complete dependence for seed supplies upon European sources to one in which the American sugar beet industry is now virtually self-supporting in this respect, full use has been made of new agronomic practices, the breeding of new varieties and the knowledge obtained of the nature of the vegetative and reproductive phases in the life of this crop plant. The following notes on this last aspect are taken from a recent review of the whole situation as regards sugar beet production and supplies by Coons (1943).

The close alliance of basic research to practical objectives has been shown by the studies on the factors which determine whether the sugar beet growth is to be of vegetative or reproductive phase. It has long been recognized that the sugar beet, as many other plants, requires a period of cold exposure to induce seed stalk formation to take place. The problems involved in this whole matter were strongly brought to attention with curly top resistant varieties because of the tendency of U.S. 1, U.S. 33 and other curly top resistant varieties to bolt in relatively high percentage when used for winter plantings in California. Some notion of the practical problem in these winter plantings is given by the report that, in one large field in which a root crop of 16 tons was harvested, 9 tons of seed stalks had to be cut and removed before the roots could be harvested. Investigations indicated that the curly top resistant varieties were of such genetic composition that relatively slight cold exposure was adequate to induce a considerable percentage of the population to go to seed. Earlier work had indicated that frank annualism in sugar beets may be due to a simple genetic factor of Mendelian nature (Abegg, 1936). Such types may be readily eliminated by the plant breeder. But, in the complex represented by the mass-selected curly top varieties, a whole

series of intermediate responses was involved, seed stalk formation (bolting) manifesting itself in large or small amount, depending upon the type and duration of cold exposure.

What might be termed the converse of these problems when sugar beets were grown for the factory was encountered in seed-growing districts, such as Arizona, and also in southern California where relatively warm winter weather in certain seasons did not give adequate cold exposure to bring all the plants in the field population to seed. Varieties grown under very mild winter conditions frequently had only a limited percentage of plants forming seed stalks, only those with strongest bolting tendencies participating in seed production. Thus, a drift in the populations took place so that, when the seed was used in the commercial fields to produce roots for the factory, if spring conditions were cold or backward, heavy bolting occurred in the fields.

Study of this situation (Owen, Carsner, and Stout, 1940) has led to very important developments in the sugar beet seed enterprise. On the basis of an analysis of the important factors controlling reproduction in sugar beets, progress has been made in classifying varieties as to the conditions required in order that full and efficient reproduction may take place. On the other hand, the experience in different sugar beet seed-growing districts, together with meteorological data, have permitted determinations concerning the varieties which should be grown in the respective places. An important development from these and other studies was the suggestion that the Pacific Northwest, because of the long, cool winters which favoured induction of the reproductive phase of sugar beet growth, offered an excellent place for the sugar beet seed enterprise. As a result, many locations in northern California, Oregon, and Washington have become important for production of seed. (The early history of the exploratory work by George T. Scott is reported in Stoker and Tolman, 1941.)

Coupled with thermal effects in inducing the fruiting phase are light effects. The sugar beet is a long-day plant, short days favouring vegetative growth. The interrelations of light and temperature are not well understood, but they act together in promoting the reproductive cycle. In nature, the normal timing of operations automatically brings the crop to the period of fruiting when daylength is increasing. In experimental work, both factors are employed, lessening the period from seed to seed.

Production of commercial seed may safely be continued in seed-growing areas with warm winter climates if precautions are taken to produce the *stock seed* under conditions of full reproduction and other steps are taken to increase the percentage of plants going to seed. An added safety factor in such productions of commercial seed, since the fructification is chiefly related to cold exposure, has come from the deduction by Carsner

in which the quantity of foliage was related to this matter of cold exposure. It had been noticed that early plantings in Arizona or southern Utah gave higher percentages of plants going to seed than were found with later plantings. Similarly, sparse stands not only suffered more from curly top but, irrespective of this factor, gave relatively low percentages of plants producing seed stalks. Favourable effects from early plantings and heavy stands have been related to the shading effect of heavy foliage as contrasted to warmer conditions in fields with sparse foliage (Owen, Carsner and Stout, 1940). These conditions have also been confirmed by temperature measurements on defoliated beets and on late planted beets as compared with plants in full foliage and in early planted sugar beets. Similar direct experimental proof was adduced in artificial shading experiments. Thus, by application of the physiological principles involved, the important seed areas in Arizona, southern Utah, and southern California have been saved as areas of production in the face of what appeared to be an almost insuperable climatic obstacle.

Subsequent work on the same general lines was reported to the Pacific Section of the Botanical Society of America in June 1942. Carsner and Tolman (1942) showed that initiation of the seed stalk and flowering in sugar beets is brought about mainly by the cumulative effect of prolonged low temperature exposure followed or accompanied by the action of long photoperiods. In a seed-growing area it is impossible to control air temperatures during the over-wintering period, but it is possible to modify soil temperatures and in a measure control the thermal environment of the beet crowns. This modification of soil and crown temperature is brought about mainly by control of foliar growth, which may be done by controlling planting date, fertilizer practices and spacing of plants. In southern Utah, the development and maintenance of an extensive growth of leaves to shade the soil and help to create the most effective temperature range for thermal induction have proved to be beneficial.

Another related piece of research is that reported by Stout (1942) to the same conference; measurements of the relative extent of thermal induction during storage at different temperatures were made by conducting bolting tests in a warm environment under long photoperiods (comparable to the Soviet phasic analysis described in the next chapter). It was found that the beets bolted more rapidly and completely after storage at 6° to 8° C. than after storage at lower temperatures. There was little increase in the bolting tendency of beets as taken from the field in midwinter, after storage at temperatures near 0° C. The bolting tendency of beets which had been taken from the field in midwinter was greatly reduced by a comparatively short period of storage at a temperature of 23° to 24° C. Stout considers that this indicates that the biochemical

processes associated with thermal induction are reversible and that the rate of change is greatly influenced by temperature.

These examples of the application of the findings on plant development refer only to one crop, but it is obvious that similar phenomena are likely to be observed in all economic crops, although the variations in reactions would be very wide. Where crop cultivation extends over a wide latitudinal range, therefore, it may be expected that a study and complete analysis of the developmental processes and their relation to the environment would be of great value.

Behaviour of Wheat Varieties in Great Britain and Australia

A series of experiments that may ultimately be explained on the basis of developmental physiology are those reported by Forster, Tincker, Vasey and Wadham (1932), and continued by Forster and Vasey (1935). It has been known for some time that varieties of wheat which make satisfactory growth in Australia are failures in England, showing only poor development and giving low yields, but, most important as far as the present discussion is concerned, appearing usually as very early varieties. When English varieties are transferred to Australia, they tend to produce too many tillers and to develop their heads too late in the season to avoid the hot dry summer of the wheat belt in the southern part of Australia. In 1928, Professor Engledow transmitted to Australia six varieties raised as hybrids at the Cambridge Plant Breeding Station; three of these were stated to be earlier than any of the English commercial varieties. However, even though these varieties had in Australia a longer growing period than that experienced by a spring wheat in England, they were later in heading than the normal Australian varieties.

The locations of these experiments were Surrey, England (Lat. 51° 19′ N.), Aberystwyth, Wales (Lat. 52° 25′ N.), and Werribee, Victoria, Australia (Lat. 37° 54′ S.).

Forster and Vasey (1935) made experiments on similar lines at Werribee in a subsequent year, using seedlings of spring and winter types of wheat; the seedlings were sown in two sections at 7 to 10-day intervals throughout the year and were subjected to normal daylight and a 16-hour day. It was found that both length of day and temperature played an important part in the development through the rosette and jointing stages, recognized as two important stages in the development of wheat plants before heading. Germination and the ripening of the heads were controlled by temperature only. Significant differences were noted in the behaviour of spring and winter wheats at the rosette stage. The winter types showed a cessation in development at this stage after the soil tem-

perature had risen above 15° C. No such feature was observed in the spring varieties.

With regard to the acclimatization of imported plants, Forster and Vasey make the following statement: 'The acclimatization of imported varieties of wheat has been taken more or less for granted for some time without the realization of the fundamental changes that are taking place. The present trial has served to demonstrate the rapid changes that may take place in the reproductive phase of the plant's growth. When one remembers that important changes are also probably taking place in the vegetative growth phases of tillering and ear production, a better appreciation of the importance of acclimatization will probably follow. Not only do these remarks apply to importations from distant countries such as England, but they must apply, in some degree also, to introductions from States with climatic conditions different from those in Victoria.'

It might be considered, in the light of the evidence that is accumulating on developmental physiology, whether behaviour such as that of Australian varieties in England, and English varieties in Australia, might not now be easier to explain if new experiments were to be initiated. Such experiments would presumably have to contain one or more series of seeds, the developmental environment of which would be fully recorded from the moment of fertilization of the ovules on the mother plants. 'Phasic analyses' of these mother plants would also be necessary.

Many plant breeders and others have reported that varietal trials of strains and varieties introduced from other latitudes and environments have been disappointing. Jenkin (1930) has reported on the behaviour of exotic strains of perennial ryegrass in trials at Aberystwyth; in some cases at least, this behaviour may be due to the resolving or breaking up of a strain which was apparently reasonably uniform in its original environment into a wide range of types released by the new environment.

The outlook of the New Zealand herbage plant breeders is expressed by Hamilton (1942-3) as follows: 'The improvements made so far have been mainly a process of taking up the slack—using the best naturally occurring ecotypes to replace inferior strains. The potentialities of this method will in due course be exhausted, and it seems probable that, before further progress can then be made, additional fundamental knowledge of the breeding material will be necessary. To date we have little other than empirical knowledge of the response of the pasture plant to its environment. It is rather striking that the best selected European strains of ryegrass and white clover do not compare favourably under our conditions with local selections. There is a suspicion also that the reverse may be true when our selections are grown in northern Europe. A knowledge of how our strains respond to variations in length of day, temperature, level of fertility, etc., may be exceedingly important if we

desire to increase our export of pasture seeds to conditions other than those in which they were selected, and a lack of such knowledge may eventually hamper further development of superior strains for our own conditions. The solution of the facial-eczema problem might also be expedited by a fuller knowledge of the physiology as well as the biochemistry of our pasture species, and the development of research in plant physiology would seem to be a logical extension of present breeding-work.'

CHAPTER XV

BREEDING AND ANALYSES OF ENVIRONMENTAL REQUIREMENTS

Developmental Physiology in Relation to Formal Genetics

This is the section of the whole problem of developmental physiology that has caused most disagreement and controversy between the various schools of thought and interpretation. One chapter is completely inadequate to deal with the many fundamental issues that arise in the discussions and, in addition, the subject awaits detailed and unbiased consideration by a specialist in all respects of plant genetics and the theories of evolution. The forthcoming review by the Imperial Bureau of Plant Breeding and Genetics is awaited with great interest.

The basic criticism levelled by the supporters of phasic development at what they call the Mendelism-Morganism school of formal genetics would appear to be that the geneticists belonging to the latter have, in the very large number of experiments that have been carried out, concerned themselves with a study of many purely morphological and growth-type characters, with little or no regard to the physiological characters of a plant. The claim is put forward that it is the physiological inheritance of a plant that is important, both genetically and economically, and that many if not all of the morphological characters that have been the subject of economic plant breeding for many years are merely the expression of the type of inheritance of the physiological (developmental) characters under the environment of the experiment. The natural sequence in this argument is to say that many if not all the pure lines that have been developed are not true pure lines at all, as they are thoroughly heterozygous for the physiological characters and segregate out for these as soon as the environmental or other conditions permit.

In place of the conventional methods of plant breeding based upon factorial analysis, cytogenetics, the gene theory and similar methods that have been the foundation of genetical research for so long, it is argued that plant breeding should now be based upon a thorough knowledge of the developmental period and phases (or environmental requirement), obtained by phasic analysis, and that intelligent crossing of parents with

the required developmental phases will provide a progeny with the requisite seasonal behaviour, growth type, morphological characters, yield, etc.

Another outcome of this research on the developmental period of plants is the emphasis on the method of vegetative hybridization in the Soviet Union. It is claimed that these graft-hybrids are true hybrids in that they show segregation, and this is used as an argument disproving the theory 'that the heredity of an organism is due to a special discrete object located in the chromosomes' (Lysenko). The connection between this result and the research on grafting in relation to hormonal exchange between plants noted in Chapters X and XI is obvious, and indicates how immediately applicable in crop production will be the results of this most specialized branch of developmental research.

The fact that it is possible to change a plant, even by the loosest form of contact-grafting, from a short-day to a long-day type or vice versa, from a 'late' to an 'early' type, and so on, seems to cast some doubt on the ability to regard these expressions of reaction to the environment as themselves based directly upon genetical factors and genes. It appears to be a question whether breeders who regard earliness and lateness, spring and winter habit, length of the thermo-phase or photo-phase as inheritable characters are not all talking about the same thing, namely the individual requirement of a plant or a variety as regards the individual factors of the environment, without a sufficiency of which its progress to maturity (development) would be impossible.

While fully realizing the scope and complexity of this whole question, some examples will now be discussed to indicate how the 'formal' geneticists and the 'developmental' geneticists might both regard and interpret the same phenomena. Reference will be made first to a study made at the Research Institute of Plant Physiology, London.

Inheritance of Spring and Winter (or Annual and Biennial) Habit

In the report by Purvis (1939) on this research, it is stated that vernalization would appear to convert a winter rye into a spring rye within one generation as far as physiological behaviour is concerned, that is it induces in winter rye a physiological condition leading to early flowering that is already inherent in spring rye.

Purvis states that a review of the literature would support the dominance of the spring habit, but varying results have been reported. Tschermak (1923) found winter habit dominant in wheat, but not in barley or rye; Spillman (see Washington, 1909) obtained an intermediate type in the F_1 generation of a wheat cross and a 1:2:1 segregation in the F_2,

and similar results were obtained in various wheat and barley hybrids by Ollson, Schafer, McCall and Hull (see Washington, 1920).

Dominance of spring habit, with a 3:1 segregation or an approximation thereto in the F_2 generation is reported by the following (references from Purvis, 1939): Nihlson Ehle (1917), Takahasi (1924), Fruwirth (1923), Tschermak (1906). Purvis also refers to examples of dominance of spring habit associated with less simple ratios. Cooper (1923) crossed two spring wheats with three winter varieties, and found the spring habit dominant in the F_1 generation in all six cases. In the F_2 generation, however, the segregation ratio was 13:3 with Marquis as the spring wheat parent, and 3:1 with Manitoba 169 as the spring parent. Cooper postulates that a dominant winter gene is present, but that its operation is suppressed by an inhibiting gene present in both the spring forms. It is suggested that the winter gene is present in one spring variety but absent in the other. Gaines (see Washington, 1917) offers a similar explanation of his results from crossing two spring barleys, when he obtained three winter-type plants in every sixteen plants of the F_2 generation.

Purvis continues: 'The assumption that the winter gene is dominant but can be inhibited provides an explanation of the different types of inheritance described above. If *W* represents the winter gene and *I* the inhibitor, then the gametes of winter forms would have the genetic constitution *Wi* while those of spring forms might be *Wi*, *WI*, or *wI*, and these, crossed with the winter forms, would give (*a*) 3:1 winter dominance, (*b*) 3:1 spring dominance, and (*c*) 13:3 spring dominance respectively. This does not, however, justify the statement that the winter *habit* is dominant. If the inhibiting gene has the effect of curtailing the long vegetative period associated with the "winter" gene, then it is not clear on what grounds one may discriminate between such a gene and one carrying the spring habit.'

Again Purvis notes that this relatively simple inheritance in which one gene delays flowering beyond the minimum period, while a second gene may render the first inoperative, 'thus restoring the status quo', may possibly apply in a number of cases. Much more complex ratios have, however, also been recorded, which Purvis considers indicate the possible operation of multiple factors. Reference is made to the work of Vavilov and Kuznečova (1921) and of Aamodt (1923).

The following summary of Aamodt's results of a cross between Marquis and Kanred wheats is taken from Purvis' paper, in order that it may fit in properly with her own discussion and her experimental results. The F_1 generation seed from this cross was sown in autumn, so that its earliness could not be assessed. The plants were harvested individually and 5,250 plants were sown in the spring of the following year. Of these 4,808 eared before autumn and 442 remained vegetative. Purvis notes

that the apparently anomalous ratio of 10·8:1 resembles that of 9·6:1 recorded by Vavilov and Kuznečova (1921). Heading of the 4,808 annual plants was spread over a period of 8 weeks, the earliest flowering at the same time as the spring parent. Selected families were harvested from the groups heading in each week, and F_3 plants were grown separately from their seed. This revealed that the earliest group in the F_2 generation was homozygous, all giving spring plants, and the proportion of heterozygotes increased as the heading dates of the F_2 parent became later. In addition, some plants were homozygous for much later flowering dates than the spring parent, and the later groups included plants that were homozygous for the winter habit. Aamodt regarded his results as a demonstration of partial dominance of the spring habit, and considered that the operation of multiple factors is responsible for the varied inheritance of the spring and winter habit in wheat.

After quoting the conclusion of Kajanus (1927) that the genetic basis of the spring and winter types is by no means clear, Purvis states her own conclusions that there is clearly no generalization which can be applied to all cereals, although most of the evidence points to complete or partial dominance of the spring habit. It is suggested that possibly in the diploid genus, rye, a single pair of factors is concerned, while in the tetraploid genera, wheat and barley, two or many pairs may operate. 'Since, so far as is known, no qualitative differences appear in the response of the temperate cereals to external physiological factors controlling flower production, it would appear probable that the genetic factors controlling flower formation are throughout identical, and therefore a general agreement in dominance might reasonably be expected. Until more is known of the actual physiological processes concerned in flowering and their relationship to genes, any attempt at explanation must be largely speculative.'

The above paragraphs are from the introductory discussion on the inheritance of spring and winter habit in Purvis' paper (1939), after which is given a description of her own experiment, in which reciprocal crosses were made between Petkus winter rye and Petkus spring rye. In the F_1 generation, the spring habit was completely dominant, while in the F_2 generation, 'spring' and 'winter' plants (quotes inserted by Purvis) occur in approximately the ratio of 3:1. There is a dispersion of flowering dates similar to that observed by Aamodt (1923), but very much less marked. This is tentatively explained on the basis of independent segregation of factors for early and late ripening as distinct from spring and winter habit. In this, Purvis is agreeing with Tschermak (1923), who lists early and late ripening as a pair of factors distinct from the annual or biennial habit.

Another relevant study discussed by Purvis should be quoted here.

Melchers (1936-7) confirmed the work of Correns (1904) in finding in the species *Hyoscyamus niger* the existence of two races which are annual and biennial in their flowering behaviour. The biennial race itself includes two forms, one of which may be vernalized. After being sown in spring, the type that can be vernalized flowers during the summer, while the other forms a rosette of leaves and a tuber, and flowers only after a winter rest. Purvis quotes Correns as finding that hybrid plants formed rosettes and yet began to shoot late in autumn.

It is obvious from this abridged version of the discussion and results from Purvis' paper that the attempt to explain the particular phenomena at issue on a genetical basis, using simple multiple or inhibitory factors, has not been markedly successful. What would appear to be desirable now would be a series of experiments to prove whether or not the views of the phasic development school could contribute anything to a final and satisfactory explanation.

Criticism Based upon Developmental Physiology

This alternative Russian view, while not necessarily denying the existence of genetics as a subject, states that research on genetics and plant breeding has up till recently been based upon the theories of Mendel and Morgan, theories the soundness of which are regarded with great suspicion, to state the situation mildly. It is stated that what is inheritable is not a time of flowering or an annual or biennial habit, but a developmental period of a given type, individual and distinct types for every plant or at least for every variety. By 'developmental period' is understood that period characterized by a succession of requirements of environmental factors under the influence of which a plant can proceed to sexual reproduction and the formation of mature fruit.

There can be little or no objection to this statement that every plant has a developmental period, and that to complete it every plant has its own environmental requirements, varying in degree, intensity, period of reaction and so forth. This would not necessarily mean the acceptance of a strict succession of discrete phases, one dependent upon low or high temperature, another on daylength or other variation in the supply of light.

The phasic development theory, however, upon which the criticism of formal genetics is based, does assume a definite and unchangeable succession of phases in the progress of a plant towards sexual maturity. It is also stated that these phases are inherited independently. Thus it is argued that, although plants may have been selected or bred for a definite *total length* of the vegetative period, such as the number of days from sowing to flowering or seed maturity, rarely if ever have pure lines been

based upon the inheritance of the individual phases. For this reason, lines that may be 'pure' for total length of the vegetative period frequently show degeneration or resolution into a series of hitherto masked types when cultivated under conditions differing from those in which they were created.

Again, it is not necessary to accept the phasic development theory *in toto*, as the term 'requirement of low temperature' may be used in place of 'thermo-phase', and 'requirement of daylength' in place of photo-phase. The argument is that these 'requirements' are heritable characters in the constitution of a plant; as they have been ignored in most genetical studies, they have remained frequently in a heterozygous condition. Upon this basis would be explained the puzzling behaviour of crosses made to study earliness or lateness, or the annual and biennial habit, as well as the degeneration of pure lines noted above.

It would appear to be desirable to make what the Russian biologists call phasic analyses, or what might here be called, less controversially, analyses of environmental requirements for development. This would provide the data necessary to support or contradict the alternative interpretations of the results of experiment noted in the early paragraphs of this chapter. If, as the Russians state, the requirements of a plant for temperature (so many hours below a certain temperature for wheat, for example) or for light (so many long days or short days, or short days followed by long days) are inheritable characters, then all the material of wheat, barley, rye and other plants already studied for inheritance of spring or winter habit, or earliness and lateness, would require to be re-investigated on this basis. The filial generations would also have to be grown in a series of controlled environments or at different latitudes, in order that the potentialities of all plants for full development would be fully expressed.

From the Russian point of view, the segregation ratios noted in experiments such as those of Aamodt (1923) and Purvis (1939) ought to differ according to the environment in which they are grown, and the extent to which that environment was attuned to the individual developmental requirements of the plants. It is possible that the inexplicable behaviour of the Australian and English wheats described on p. 228 may also be due to the heterozygous condition of the developmental characters of the plants concerned, and to the fact that some particular component of the environment was inhibiting the normal expression of the developmental period at one or other of the latitudes at which the experiments were made.

By adopting this outlook, it may also be possible to explain the behaviour of improved 'pasture' strains of herbage plants under conditions different from those obtaining at the centre at which they were produced.

It may also be possible to plan the breeding of pasture grasses on the basis of analysis of phases (or environmental requirements). A 'pasture' type of grass is necessarily a 'late' type, continuing to provide vegetative tillers throughout the grazing season. It is difficult to obtain high seed yields from them, the strains being known as 'shy seeders'. In multiplying seed of these strains, everything is done to maintain this late quality, by deferring the date of cutting as far as possible, for example. In selecting pasture types, the herbage breeder is actually selecting types upon the basis of the developmental physiology, although probably in no case has an analysis of the environmental requirements and reactions of the original material been made. Further, the selection of pasture types on the basis of their developmental physiology has been made only under one set of environmental conditions; it is not known whether that particular environment may be preventing the full expression of the plant's potentialities, and its true nature may not be revealed until the so-called 'pure' strain or combination of strains is grown in a different environment, whether natural or artificial.

Inheritance Studies on Duration of Developmental Stages

One example will be taken of what may be regarded as an intermediate stage between those geneticists who concern themselves with total developmental period and those who base their genetical work on a theory of the existence of individual developmental phases of a qualitative nature.

Powers and Lyon (1941) studied the inheritance of the duration of three stages of development in certain crosses involving varieties of tomato (*Lycopersicon esculentum* and *L. pimpinellifolium*). The three stages recognized by these workers were: (1) number of days from sowing to first bloom; (2) number of days from first bloom to first fruit set; and (3) number of days from first fruit set to first complete change of colour of any fruit. The sum of these three stages is regarded as a measure of the earliness-of-maturity character.

The purposes of the investigation were to determine whether these natural biological periods in the development of the tomato plant are definite sub-characters and to ascertain the efficiency of the fit between obtained and theoretical means, based upon certain formulae, as a method of determining whether the effects of the genes differentiating the quantitative characters are arithmetically or geometrically cumulative. Throughout the study and interpretation of the data, an attempt was made to keep in mind the probability that the genes bring about the differentiation of a character by initiating, either directly or indirectly, developmental processes which no doubt in many cases interact among themselves.

From the experimental data it was found that the earliness-of-maturity character, as measured by number of days from sowing to first complete change of colour of any fruit, is composed of at least the 'three stages of development' noted at the beginning of this section. This fact is regarded as having considerable importance in breeding early varieties of tomatoes. The cross Danmark × Johannisfeuer is used as an example. Danmark has a short period of development from planting of the seed to first bloom but a long period of development from first fruit set to first complete change of colour of any fruit, whereas Johannisfeuer has a long period of development from planting of the seed to first bloom, but a short one from first fruit set to first complete change of colour of any fruit.

As the F_1 generations of the crosses between the tomato varieties Danmark × Red Currant and Johannisfeuer × Red Currant have short periods for both these stages of development, it would appear that a variety could be produced re-combining the genes for short duration of the stage from sowing to first bloom, characteristic of Danmark, with the genes for short duration of the stage from first fruit set to first complete change of colour of fruit, characteristic of Johannisfeuer. 'Adverse linkage relationships would complicate the problem. Also, the nature of the interactions of the re-combined genes would determine whether a strain could be developed that possessed a short period for both of these stages of development. At the present time neither the linkage relationships nor the nature of the interactions of the genes are known.'

Solidago sempervirens is a short-day species. Goodwin (1944) working at the University of Rochester, New York, has isolated three strains from natural populations; these can be distinguished from one another by their dates of floral initiation, which are controlled primarily by the length of the photoperiod, and by their rates of bud development. From an analysis of F_1 and F_2 hybrid populations, it is estimated that the minimal number of gene substitutions which must determine the above physiological difference between strains approximates the haploid number of chromosomes, which is nine; it is considered probable that these genes are located in many if not all the linkage groups.

Before proceeding to a description of a Russian experiment conducted on the basis of the phasic development theory, passing reference may be made to the work of Baranov (1939), which produces evidence to prove the formative role of the environment, which is the basis of Lysenko's method of 'training' of plants to change their genotype.

Varieties of barley were tested in the Pamir, at an elevation of 3,860 m.; the forty-five varieties that had been reproduced in the Leningrad region (Pushkin) failed to attain full ripeness, and only twelve of these reached wax ripeness. Plants from seed of the same varieties that had

been reproduced near Tashkent ripened fully. In subsequent years it was noted that in all cases the plants from seeds obtained under dry southern conditions ripened earlier and more completely; the shortening of the total vegetative period was due to shortening of the period from earing to ripening (the generative phase), as it was found that the period from seed germination to earing was in most cases longer than that in plants from seeds reproduced in northern latitudes. Subsequent reproduction of their progeny in the Pamir still further accentuated the initial differences. The conclusion drawn is that the environmental conditions of the place of reproduction may, in 2 or 3 years, induce profound changes not only in the phenotype, but also in the genotype of plants.

Breeding Based upon Analysis of Environmental Requirements

Two papers by Reimers on analysis of the respective environmental requirements of different species of lettuce (*Lactuca sativa* var. *capitata*) and the use of this information in breeding work will be used to exemplify the outlook of the phasic development school. In the first (1938) Reimers refers to earlier research by other authors in which it was established that both shooting and flowering in lettuce can be accelerated by keeping the germinating seeds at low temperature and cultivating the plant under conditions of prolonged day; shortening the duration of day retards development. Reference is also made to the attempts of Bremer to apply the variation in daylength to the study of genetic differences between winter, spring and summer forms of lettuce.

Reimer himself approached the same question of the cause of differences in time of shooting from the viewpoint of the theory of phasic development, and paid particular attention to the thermo- and photophases. Several varieties of lettuce were selected which differ sharply in earliness and are typical representatives of the various biological groups within the sub-species. The vernalization experiments were made on the varieties Ideal, Eier Gelber, Steinkopf and Trotzkopf. The photo-phase was studied in the same varieties with the exception that Steinkopf was replaced by Gr. Blonde Paresseuse. Ideal is regarded as a typical spring variety, Gr. Blonde Paresseuse as a typical summer variety, and the others as intermediate in type.

The purpose of the experiment, carried out at the Laboratory of Physiology of the U.S.S.R. Research Institute of Vegetable Production, Moscow, is stated by Reimer as follows:

1. To determine the duration of the thermo- and photo-phases in the representatives of the different groups.

2. To discover whether it would be possible to split the lettuce varieties into biological strains by the method of phasic analysis.

3. To ascertain the response to vernalization of varieties differing in length of vegetative period, when germinated seeds and green plants were used [this variant was introduced because some vegetables (cabbage, turnips) give a better response to vernalization when the treatment is applied to green plants rather than germinated seed].

Analysis of Temperature Requirement

Seeds were germinated until about 5 per cent showed the first appearance of rootlets; the seeds were then transferred to a room with a temperature kept within the range of 2·5 to 5° C., for periods of 10, 20 and 30 days respectively. Vernalized and control seeds were sown on May 5th. Growth became visible on May 11th to 12th. Different variants did not indicate varietal differences in appearance of 1st, 3rd and 5th leaf. The total number of leaves formed until the formation of the flower shoot was equal in all variants. Shooting began on June 10th.

Vernalization for 10 days caused an acceleration of shooting in the variety Ideal of from 3 to 5 days, but none of the other varieties were able to complete their thermo-phase in this time. It is concluded that the thermo-phase in the variety Ideal is passed in 10 days, but that in the other varieties it is longer, taking about 20 days.

Experiments on green plants indicated that, although the optimal temperature for completion of the thermo-phase by seeds is from +2 to +5° C., the same temperature has a deleterious effect upon green plants, inhibiting their growth and development. A comparison is made with other vegetables. As already noted, cabbage and turnips cannot be vernalized in the form of germinated seeds; radish can be vernalized both as green plants and as germinated seeds, while lettuce can be vernalized only in the form of germinated seeds.

Analysis of Light Requirement

Experiments to discover the conditions under which the photo-phase proceeds and also its duration were made on the lettuce varieties Ideal, Eier Gelber, Trotzkopf and Gr. Blonde Paresseuse. The plants were sown in plots in the open, and were exposed to daylight from the appearance of young growth to the end of vegetation: (*a*) for 10 hours; (*b*) for 14 hours; (*c*) from sunrise to sunset; and (*d*) during the whole day plus continuous illumination during the night. Shortening of the day greatly retarded shooting in the early (winter) varieties, but had little effect on the late (summer) varieties. The biological difference between

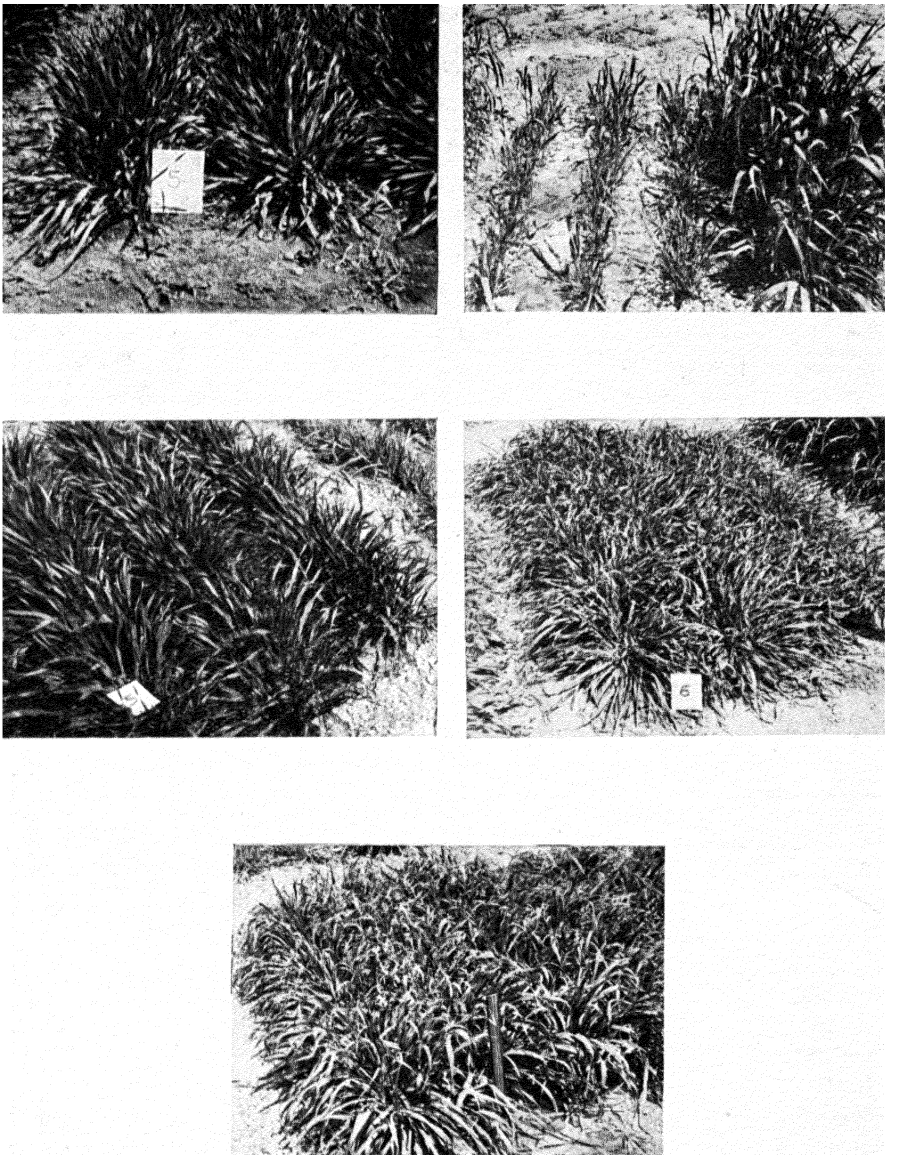


PLATE 21. The use of cereals in Canada to produce herbage of high nutritive value for conversion into dried grass pellets for poultry feed (see p. 254). Photos: J. M. Appleton.

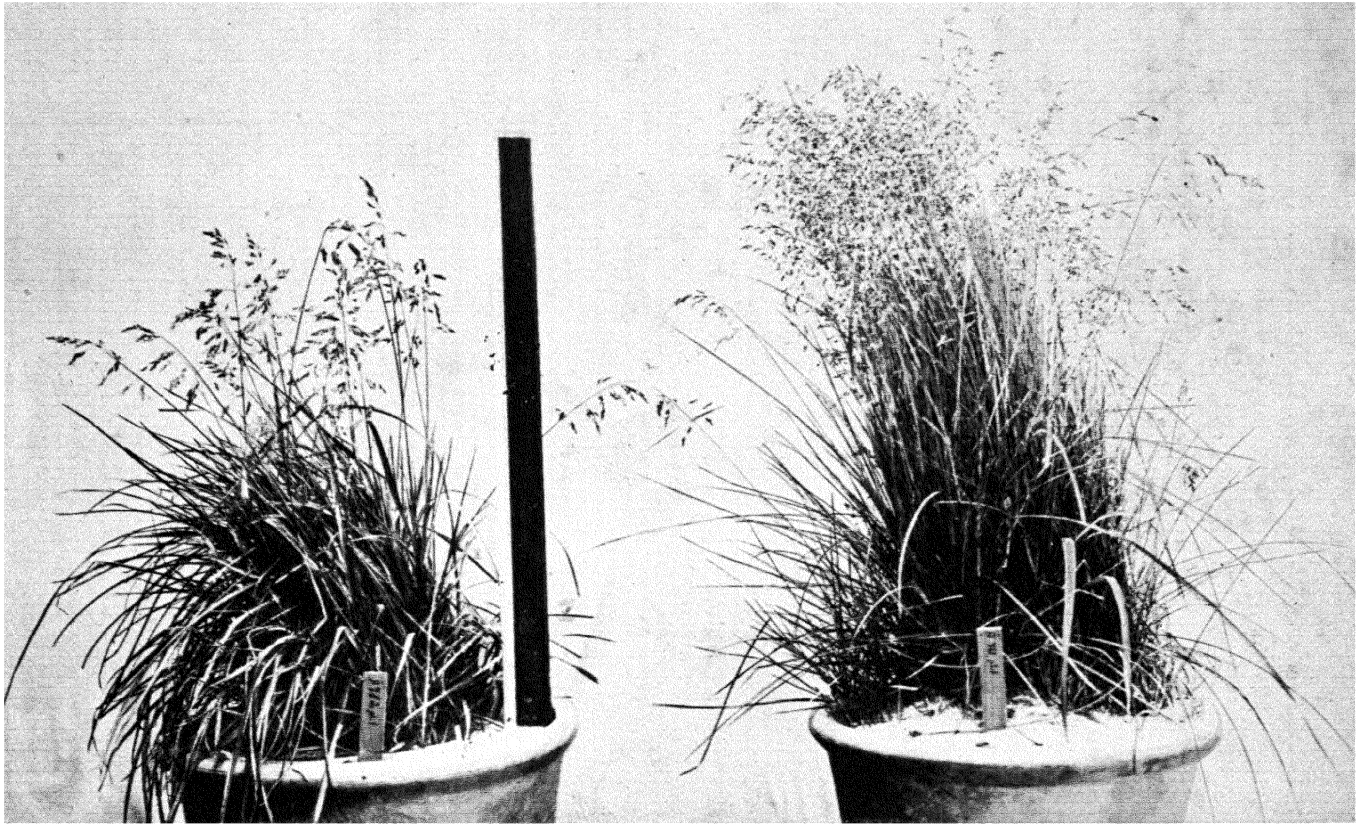


PLATE 22. Types of *Poa pratensis* grown at Weibullsholm, S. Sweden. That on left (few panicles) brought from N. Sweden, and therefore out of optimal environment for flowering. Photo: E. Åkerberg, 1938.

the winter and summer varieties of lettuce is that the former have a short thermo-phase and a long photo-phase, while the latter have a long thermo-phase and a short photo-phase.

Cultivation of lettuce plants at different daylengths had a marked effect upon the morphological characters and behaviour of different plants within a variety. Under a natural daylength as well as in a 24-hour day, plants of all varieties remained uniform in all respects; when grown under a 14-hour day, and even more so under a 10-hour day, their behaviour and appearance were very diverse. Plants belonging to one and the same variety now differed markedly in general shape and other morphological characters, as well as in time of shooting. Thus a variety that has been carefully selected under a normal daylength in one region is nevertheless a population or mixture composed of biological races differing with regard to their physiological properties. In other words, they are heterozygous for the phases of development but this heterozygosity is not manifested so long as the strain is cultivated under the same conditions as those in which it was produced.

Selection Following Phasic Analysis

The experiments described above were continued (Reimer, 1939) to establish whether the length of the photo-phase (or the daylength requirement) observed in a given lettuce plant when it was grown in a reduced daylength would prove to be a hereditary character under the same conditions of development. If this was so, it was regarded as possible to breed for a new variety differing in its behaviour from the initial one, with a character such as absence of bolting. It was concluded that the simplest method to avoid early formation of floriferous shoots would be to select plants after the length of their photo-phase had been determined by phasic analysis. Two different sets of the varieties Ideal and Eier Gelber were selected on the following basis.

Ideal

No. 1. Various plants grown in natural daylength ('initial variety').

No. 2. The plant which had been the first to form a floriferous shoot in a 14-hour day (short-phase plant).

No. 3. The plant which had been the last to start stem formation in a 14-hour day (long-phase plant).

Eier Gelber

No. 4. Initial variety (as No. 1).

No. 5. Short-phase plant (as No. 2).

The seeds were sown in two prepared beds, and the plants grown in one of the beds received the natural daylength, the others 14-hour day. The plants grown in normal day were distinctive in form and size, no morphological differences between the plants of the initial variety and the other strains being observed. Again there were striking differences within the initial variety when grown in a 14-hour day, but within the progeny of the strains selected for short photo-phase and long photo-phase respectively there were no differences, irrespective of the day-length they received.

These results are only preliminary, but are regarded as proving the possibility and even the necessity of applying the method of phasic analysis to selection of lettuce plants, as has been done by Lysenko in the case of cereals (ref. No. 1 in Reimer, 1939, and Imperial Agricultural Bureaux, 1935).

Breeding Based upon Photoperiodic Reaction and Temperature Relations

The inheritance of the photoperiodic reaction has been studied by Lang and Melchers for *Hyoscyamus niger* (1943), Driver for potatoes (see Cambridge, 1944) and Sylvén for forest trees (see p. 324) to mention only a few cases. Driver states that a large number of genes are involved, but the short-day determining genes seem to be dominant over the long-day ones. There is a great variation in the gene make-up of varieties. Whereas earlier varieties on selfing give a large percentage of long-day types, later varieties give a greater percentage of short-day types, while some South American varieties appear to be almost pure short-day forms. It is possible that some of the short-day types from South America may be of value in breeding potatoes for tropical countries, while breeding for the higher latitudes may be more successful if based upon the long-day or day-neutral types. Breeding for the warmer tropical climates may have to be based upon heat-resisting species, as the majority of the most promising Andean species are accustomed to temperatures no higher than those of the best northern potato-growing areas, and will probably be adversely affected by high temperatures.

Bell (1945) is using the reactions of sugar beet to light and temperature in his study of bolting in that crop. This is in two parts as follows:

(*a*) The isolation of strains showing extreme resistance to bolting.

Suitable adjustment of the length of the time for which seedlings are exposed to continuous light treatment while growing slowly under low temperature conditions during the winter results in a physiological resolution of the material. Under such conditions, a certain proportion of the plants will show no tendency to bolt after the young plants are trans-

planted into the field in the spring. Such non-bolting plants have been selected, grown for seed in the normal way the following year under strict isolation, but allowing the plants to interpollinate. The seed from each plant is harvested separately, for analysis of cluster characters, and the best lines retained for observation of bolting properties and root characters in the following year.

Very early sowing in the field of material obtained in this way has shown great reductions in the number of bolters. In one experiment in which sowing took place on February 8th, the average number of bolters in 42 lines obtained from non-bolting plants was just over 8 per cent, while the original material from which the non-bolters had been selected showed over 70 per cent of bolters. Re-selection on root characters is then practised within the lines most resistant to bolting.

(*b*) The study of the developmental physiology of selected lines in breeding material.

The physiology of the biennial habit in sugar beet is very significant in breeding work. The rate of development of the root with the consequent seasonal increment in root weight and sugar percentage is obviously of basic importance in attempting to increase the sugar production by selection. Plants pass into the reproductive stage, i.e. bolt, when they have reached a certain physiological stage when growing under field conditions, and this stage is determined by the developmental balance in relation to the biennial habit. In Great Britain early maturation of the roots is most desirable, but it is necessary to ensure that early root maturation does not accompany a tendency to bolt.

All selected lines are subjected to continuous light treatment in the seedling stage and are then transplanted into the field. Detailed observations are made on each line with regard to earliness, time spread, and total number of bolters. Periodic counts are made for dates of anthesis of individual plants within each line, and by this means a reasonably accurate assessment is obtained of the developmental physiology of the material. This study is conducted at the same time that the lines are being tested in normal field sowings for assessment of the root and general vegetative characters, and the scheme enables a valuable comparison to be made, in the same year and under the same conditions, of the two phases of growth and development. It has been found that individual lines show very characteristic behaviour in relation to bolting after the continuous light treatment.

It is well known that plant breeders use the photoperiodic behaviour of plants in breeding types with different flowering dates. One or other of the parents used in a cross is grown in an environment differing to some extent from normal in order that the pollen of the male parent is produced at the same time as the ovule is ready for fertilization, or

vice versa. A somewhat unusual variant of this method is used by Fennell (1945) in his grape breeding programme at the Inter-American Institute of Agricultural Sciences, Costa Rica. Since grape pollen retains its potency for a very short time, one of the greatest problems of the plant breeder is to ensure a supply of fresh, viable pollen on the date when the seed parent is in flower. This is particularly the case in the humid tropics, an environment alien to most cultivated varieties; frequently it is practically impossible to grow to flowering size certain varieties of North American and European grapes most desirable for breeding. The prolonged dormancy resulting from insufficient low temperature in the warmer climates often retards the flowering of most varieties of the *labrusca* and *vinifera* species until a date too late for breeding purposes. This difficulty is overcome by a combination of the grafting technique with a knowledge of the varietal differences in the growth and flowering habits of both proposed parent vines, and a careful selection of stock vines especially as to whether they are early, medium or late in budding out.

The Russian workers, Vinogradova and Novoderižkina (1941), base their breeding work on herbage grasses on the environmental requirements of the species used. The whole breeding procedure can be much hastened by means of the glasshouse which enables a second generation to be raised, additional to that grown out in the field. Perennial grasses before being put in the glasshouse must have passed through the vernalization stage. Plants to be transferred to the glasshouse are usually put in pots or boxes at the end of August or beginning of September in order that they may be hardened and begin vegetative growth. Under the conditions described, the plants were left in the open until the end of November or beginning of December after which they were transferred to a glasshouse having a temperature of 3° to 6° C. where they were left long enough for the soil to thaw. Then the temperature was raised to between 12° and 15° C. From the end of December to the beginning of January the period of daylight was supplemented by electric light, ensuring a period of illumination amounting to 16 or 17 hours, for which purpose 230-watt lamps were used. The plants flowered early in March. It is advisable to raise the temperature to between 20° and 25° C. during the emergence of the spikes. The seeds ripen by the end of April or beginning of May.

This discussion of the relationship between developmental physiology and plant breeding merely touches the fringes of a large and complex subject, which may lead to problems such as the existence of different kinds of genes (Darlington, 1944) and related subjects.

CHAPTER XVI

MANIPULATION OF DEVELOPMENTAL PHYSIOLOGY OF CROPS

The literature on the application of this research on the developmental behaviour of plants to the production of economic crops is already very extensive and awaits a detailed and critical review. New experiments will in many cases be required, as many of the early ones were made with incorrect technique or were not submitted to adequate statistical analysis. Accurate experimental observations are essential when one of the chief objects of the work is the recording of such an indefinite plant character as time of flowering. The possibility of error due to individual bias is quite considerable and the general reader is not to know whether an advance of up to 7 days in time of flowering of, say, a grass plant is the result of the previous treatment of the seed or plant or not.

In reading the following sections on the developmental periods of economic crops and their adjustment in one direction or another by artificial means, the crop botanist should understand that these are only a few papers taken at random from a considerable literature on the subject as examples to indicate the general trend and application of the work. Those who are specialists in some particular crop will themselves know whether the claims for earlier flowering appear to be reasonable, and will await accurate experiments based on probable error and spread of flowering dates before forming final conclusions.

Chief Treatments and Objectives

Agronomists and horticulturists have a number of methods of inducing vegetative growth or reproductive activity, according to the nature of the economic crop with which they are working. Adjustments in type of nutrients supplied and the time of their application, time and method of sowing, hot water treatment of bulbs, raising of seedlings in a greenhouse and planting out later in the open, cutting of roots or planting with bent roots and similar methods have been used. All probably may be ultimately expressed as having an influence on the developmental physiology of the plant in question, causing the directing substance or substances to operate in such a way that the plant exhibits vegetative growth or reproduction.

Suggestions have also been made, but not by any means put into

practice, regarding the possibility ultimately of isolating the flower-promoting substance and injecting it or its chemical equivalent into a plant that it is desired to bring into flower. Experiments have also been reported on the effect of injection of sugars and other solutions into a plant on its reproductive behaviour.

Possibly these various manipulative methods may acquire some significance in the practical operations of the future, but the chief interest at the moment is centred on the possible use of treatments in which are applied those environmental factors that are known to be decisive as far as reproduction under natural conditions is concerned. Their application under a wide range of conditions is therefore directly dependent upon the results of the many physiological studies examined in earlier chapters.

The chief factors are, of course, temperature and light. If the required amounts of these factors and the optimal times and conditions for their application can be found, it would then be possible to introduce the related secondary factors of type of nutrition, water supply and so on that are necessary for the highest economic return to be obtained from the growth and/or reproductive activities of the plant in question. Thus, the extent to which a cereal plant may produce grain will depend upon the extent to which its environmental requirements for reproduction have been met, but the actual 1,000-grain weight of the crop will depend upon the presence of other factors in optimal amount at the appropriate time.

In applying these chief environmental factors, temperature and light, use is made of the phenomenon of the after-effect that can be obtained from treatments with those factors. It has already been indicated (pp. 61 and 117) how the effect of a suitable period of treatment with temperature or light may be manifested in the behaviour of the treated plant at a much later period in its life-history. Particularly as regards temperature, the Russian physiologists and agronomists who were concerned in the development of the method of pre-treatment of seed with low temperature thoroughly disapprove of the use of the term 'stimulation' to describe their method. It may be argued, however, that whether or not there is a definite thermo-phase in the life of all plants at which they require a certain temperature for a certain period, the plant of winter wheat sown in the open in the autumn still requires the 'stimulus' of the low temperature of the winter months before it can come into ear. The method of vernalization is merely the provision of this thermal stimulus in the barn or the laboratory.

Attempts at the manipulation of plant development have been made with a number of objectives, and are conceivably suitable for a number of others. The chief aims of the work in Russia were to avoid either the

severe winter months or the periods of excessive summer drought. In the one case vernalization has made possible the sowing of winter varieties in the spring, in the other it is stated to cause earlier ripening, thus ensuring the harvesting of a crop before severe droughts begin, in the southern Ukraine, for example. In Germany and other parts of Europe, vernalization has not been introduced into general farming practice, although a considerable amount of research has been done, and the method has been considered as possibly suitable for extending the cultivation northwards of such introduced and somewhat non-adapted crops as soybeans.

There is a considerable literature in Russia on the use of vernalization in connection with the cultivation of catch crops in regions where the combined lengths of the vegetative periods of the main crop and the catch crop are longer than the possible growing season. Apparently, if one or both of these crops are sown with seed that has been vernalized, they may both be grown to the desired stage of maturity, for example a grain crop followed by a forage or green manure crop. In Germany, however, where the practice of growing catch crops is so widespread, the use of vernalization does not appear to have been recommended by any authority.

The extension of cultivation northwards is also a problem in Canada, where crop cultivation in Northern Alberta is difficult due to the short growing season. Vernalization has not been regarded as a useful weapon in this development, nor has it been applied in North America generally to the extension of the northern limits of cultivation of such comparatively new crops as the soybean. The location of seed production areas for sugar beet in order to provide for what is equivalent to the natural vernalization of the young plants has been noted on p. 225.

In countries where climatic conditions are not a factor hindering normal development of varieties selected as being those most suitable for the environment, the chief interest has been in obtaining earlier crops of economic plants of the high cash value class, such as tomatoes and other market garden crops. Under ordinary commercial conditions when prices are not controlled, an advance of a week in time of maturity of such crops may mean quite a considerable additional financial return.

There has also been a considerable interest in the application of vernalization to biennial and perennial plants that do not form seeds in the first year. These include a number of root crops, vegetables and herbage and forage plants, that require to grow through a winter before they develop seed heads. Little advance has, however, been made or thought necessary in this particular direction. Experiments on plants of this type are discussed in later sections.

The Technique of Treatment with Temperature and Light

The pre-treatment of seed with temperature has been described fully in earlier publications (Pasture Bull. 9 and Joint Publ. No. 1), and in earlier chapters of this book, and need not occupy much space at this stage. The principles are as follows.

Germination is induced by soaking the seed or grain in adequate amounts of water, but must not be allowed to proceed as far as the formation of seedlings that will be difficult to handle in the subsequent parts of the technique. By reducing the proportion of water to seed, growth is arrested just as the radicle is about to pierce the seed coat. From a biological point of view, the non-reactive period of dormancy has been broken, and the new organism is exhibiting that minimum amount of growth which permits the application of those external factors that are known to influence development. On the assumption that growth may proceed very slowly, while in the same young organism development may proceed quite rapidly, the object of the method of vernalization is to induce rapid development towards a physiologically older or more advanced condition while growth is held at a minimum.

The correct degree and duration of treatment with low temperature (assuming one is working with winter rye, for example) should already have been found for the same variety under controlled experimental conditions, and are now applied by various methods. In countries with low winter temperatures, the natural low temperatures may be used by 'sowing in the barn', keeping the seed at the required moisture for an appropriate period. In milder winter conditions, cold chambers or refrigerators are required.

For vernalization of crops requiring high temperatures, such as soybeans, it is possible that an apparatus such as that evolved by Rudorf, Stelzner and Hartisch (1937) might be of value. This apparatus contains a series of flasks arranged along a rotating axis, and facilitates the maintenance of temperature and moisture at the desired level.

It is stated that the grain may be dried and stored after being vernalized, and may thus be sown when circumstances permit. Some adjustments may be necessary in the rate of seeding, since the treated grain may be larger and heavier than the untreated. If vernalization by temperature is to become a normal agricultural practice, it is probable that it will be advisable to form special centres where the seed can be so treated and distributed to growers. The practice in the early years of the method in Russia was to bring farmers to special training courses at selected centres, after which they were capable of vernalizing grain on their own farms, using the low temperatures of the Russian winter. This

arrangement would be suitable where the natural winter temperatures are sufficiently low, but probably not so convenient where these temperatures have to be created artificially.

According to data collected by Oljhovikov, the following acreages in the U.S.S.R. were sown with vernalized seed in the years 1932-7 inclusive:

1932	43,000
1933	200,000
1934	600,000
1935	2,100,000
1936	7,000,000
1937	10,000,000

It is not known to what extent Russian farmers have been using the method of vernalization in recent years, and whether any centres for treatment and distribution of seed have been operating. In Great Britain at least one seed merchant has advertised vernalized seeds of tomatoes at a high price, but otherwise no developments in the wide use of the method have been noted.

A special study of the application of the method under wartime conditions in Great Britain was begun in 1942 by Professor F. G. Gregory of the Research Institute in Plant Physiology, South Kensington, London, under the auspices of the Agricultural Research Council, but the results of this work have not yet been published. Experiments were made with various cereals, vegetables and herbage plants. Plate 20b shows the plots of rye, vernalized and unvernalized. Results of the experiments on cereals are given on p. 258.

It may be of interest at this stage to describe the detailed technique used by Sen and Chakravarti (1942) in the vernalization of mustard; their results are described elsewhere. Having already developed a technique for vernalizing small samples of seeds (1938), necessary modifications have been introduced for larger samples, with particular reference to containers for seeds, and provision for absorption of CO_2 from the respiring seeds. The seeds to be chilled are first soaked in excess water until they absorb about 60 per cent of their weight of water; this generally requires about 6 to 8 hours according to the room temperature. After removal of excess water by spreading the seeds over several layers of absorbent cloth, they are placed in muslin bags or unglazed porcelain pots and placed inside the moist chamber of the chilling cabinet. Any watertight box of required dimensions with removable lid can be used for a moist chamber. Boxes of thin wood require to be asphalted inside and out. The inside of the box is lined with blotting paper and sufficient water placed at the bottom of the box to keep the absorbent lining moist. For absorption of CO_2, a concentrated solution of KOH is kept at the

bottom of the box in a large flat porcelain dish, the rim of which is paraffined to prevent creeping of the KOH solution. A removable thick wire-net frame is placed over this dish to protect the seeds from accidental contact. Seeds in bags are suspended from hooks in the lid of the box; the bags must not touch the wire-net guard or the moist blotting paper. The chilling cabinet may be of the Frigidaire electrically operated type or, as in these experiments in the United Provinces, India, a kerosene-operated Electrolux. An ordinary ice-box or even a thermos flask may be used. After the required periods of chilling the sprouted mustard seeds are discarded (see p. 331) and the unsplit seeds washed and dried at room temperature until they reach a constant weight (from 3 to 5 days according to season). The seeds are then packed in a sealed container and stored inside the Electrolux.

Before proceeding to consider the developmental periods and behaviour of different economic plants, it may therefore be concluded that, although the research on the physiology of plant growth and development is beginning to provide a basis for the understanding and interpretation of a number of problems of crop production, it has not yet provided any revolutionary methods of wide application for the manipulation of growth and development by artificial means, according to the wishes of the cultivator.

In certain restricted fields of production, adjustments in the light environment can be made with considerable ease and success. This may be done by using houses of the special type used by Garner and Allard in their classic research on photoperiodism, in which plants on trolleys may be run on rails between open-air conditions, and a special dark chamber for shortening the daily exposure to light; or by the more modern greenhouse used by Went (Fig. 13). This method, and the converse one of providing long day or continuous day by artificial illumination, are possibly of some economic value, in addition to having some value in making breeding material flower at the same time, or in reproducing seeds of valuable lines more rapidly than would be possible under natural conditions. The shading of tobacco and analogous treatments should also be considered in this connection.

Manipulation of Growth and Development by Agronomic Means

The degree and method of application of a full knowledge of the developmental behaviour to the cultivation of any economic crop will depend upon the purpose for which that crop is being grown. The three chief classes that can be recognized are crops in which the seeds or grains are the economic product, those in which storage roots are the objective

and the numerous fodder, herbage and green manure plants, the economic value of which depends upon maximum vegetative growth combined with a certain amount of development. In addition to these three main classes based upon ultimate economic value of the production, there are the other major groups of annuals, biennials, and perennials, that require to be considered.

ANNUAL GRAIN OR SEED CROPS

The annual crops in which the ultimate economic product is the seed or grain present the simplest examples as regards the application of the knowledge of their developmental behaviour to their cultivation. The seeds or grains are the product at the end of the normal processes of reproduction and every practice or adjustment that will provide the most favourable conditions for the developmental processes leading to maturity will also ensure the maximum grain yield. The conditions of the environment that have to be considered are the decisive or directing factors that act primarily upon the developmental processes, and the incidental factors of nutrient supply and water relations which can have their maximum influence upon seed yield only in the presence of those essential conditions that favour optimal development towards seed maturity. By using dates of sowing that have been found most suitable by a long process of trial and error, the cultivator ensures that his crops receive adequate quotas of the decisive factors, and so adjusts his other agronomic measures relating to manuring, watering, etc., that the grains or seeds produced in the first place under the influence of the decisive factors will be nearest the quality he desires.

It should be noted that the factors that are decisive as regards the developmental processes in general may have quite a different effect upon the plant when present under different conditions and to a different degree. For example, a plant may require low temperature before it can proceed to maturity, but its tissues may nevertheless be seriously damaged or even killed by excessively low or excessively high temperatures. This is, however, purely a physical effect on the tissues concerned, and unaffected tissues on the same or related plants can proceed with their development normally, according to the degree to which the local environment meets their requirements.

ROOT CROPS AND VEGETABLES

The second type of economic product to be considered is the storage root that is used for the production of sugar, for animal fodder, or as a vegetable for human consumption. The agronomic practices, such as time of sowing, adopted for the production of roots or seeds of these crops are completely different. For the former purpose, the seed are

sown at a date that ensures that the growing plants will not be exposed to a temperature that will permit any marked progress in development. In some cases, when varieties have not been thoroughly selected for uniformity as regards environmental requirements, or when the season is particularly favourable to development, a number of plants will be enabled to change from vegetative growth to reproduction and will exhibit bolting. Such 'bolters' are 'rogued' from the standing crop in order that their presence will not contaminate the whole line by the production of an increasing number of off-types of this kind.

The main bulk of the crop of a superior variety will, however, be unable to advance towards maturity in the first year, and will, under the influence of the length-of-day conditions then prevailing, produce the storage roots which contain the reserves produced by optimal growth conditions and which are required as the economic crop. In most cases, superior plants from this crop are selected for seed production and are then planted and grown under conditions that will favour development and the ultimate production of a maximum seed yield. It has yet to be seen whether the new agronomic practices adopted in the production of seed of sugar beet in the United States (Coons, 1943) will be applicable to the production of seed of such related crops as carrots, parsnips, etc.

Similar remarks could be made to apply to vegetables such as the cabbage group and the lettuces, in which the primary economic objective is the production of green leaves in the form of a 'heart', the tendency to form seed heads being an undesirable attribute in the cultivation of crops and the selection of varieties for this particular purpose. By suitable adjustment of sowing dates and management, however, these crops again may be exposed to the type of environment that may favour the formation of seed heads rather than green mass, and seed production will follow automatically. Again, if varieties are not properly selected, or if they are accidentally exposed owing to seasonal variations to an excessive quota of the decisive environmental factors, those plants among the cabbages or lettuces being grown for marketing that have the lowest requirement as regards these factors will naturally form seed heads instead of proper marketable specimens.

HERBAGE AND FORAGE PLANTS

The position becomes more complicated when we turn to consider herbage and forage plants, due partly to the fact that so many of them are not one plant but many (members of the Gramineae), and partly because there are three different purposes (or combinations thereof) for which they may be grown. Let us first consider the nature and possible developmental behaviour of such a herbage plant as perennial ryegrass

(*Lolium perenne*), and then how the treatment of this plant under varying systems of management might affect the ultimate product, whether in the form of herbage grazed, or cut and removed as hay or silage, or in the form of seed.

Like the root crops and vegetables discussed above, the grasses of temperate latitudes do not flower to any great extent until they have been permitted to grow through a winter. If a seed is sown in one season it will during the remainder of that season and the beginning of the next give rise to a number of tillers, all of which will compose the new plant. It is probable that these tillers will be of a number of different physiological ages, according to the time when their new meristematic growing point was first formed and the environmental conditions that have been operative since that time.

Not all the tillers will flower in the next season (the first harvest year) as some will not have been exposed to the influence of environmental conditions for a sufficiently long period. This is probably the reason for the fertile and barren tillers noted generally on most members of the Gramineae, including the cereals and the herbage grasses. It must, however, also be considered whether some of the non-flowering tillers are not in many cases just as advanced in development as the flowering tillers, but are prevented from flowering by a shading effect, or because of competition for soil nutrients, or because of a bottleneck in the congested vascular system. Evidence in support of the possibility that not all barren tillers are backward in their development is provided by the fact that, in producing seed of 'shy seeders', it is often possible to increase the yield of seed considerably by suitable agronomic measures that reduce competition and improve the nutrient supply (cultivation in drills rather than broadcast).

Further anatomical investigations such as those discussed on p. 56 are necessary to show when flower primordia are formed in the most advanced tillers and to indicate in which tillers no primordia are formed owing to insufficient exposure to the appropriate conditions. This should provide an explanation of the increased seed yields noted in the foregoing paragraph, and also show to what extent the lavish formation of aftermath in some varieties is due merely to vegetative growth and to the further development of late reproductive heads that were not removed at the first cut, or had been exposed to the necessary conditions since the first cut was made.

In pasture management it is frequently the custom to graze fields early in the season, and then to close them for the purpose of taking a hay or seed crop. From the point of view of developmental physiology, this would appear to be rather a strange practice. For both hay and seed crops, it is the product of development rather than growth that is re-

to a greater extent than with annuals, on the research on the localization of response to environmental factors and on the transmission of that response in the form of a directing influence from one part of the plant to another.

Pending more definite information, it may be hypothetically assumed that when a shrub of temperate latitudes has passed through a winter and into a period of lengthening days, there will be transmitted a flowering stimulus from the leaves to the meristematic buds under their control, flowers will then be formed and flowering will take place under appropriate conditions of nutrition. Once these flowers have all been formed, no more will arise until the plant is exposed to another 'winter'. If the plant were transferred to a warm greenhouse or could be grown in warmer latitudes, it might remain in a vegetative condition until its full requirement of environmental conditions was met.

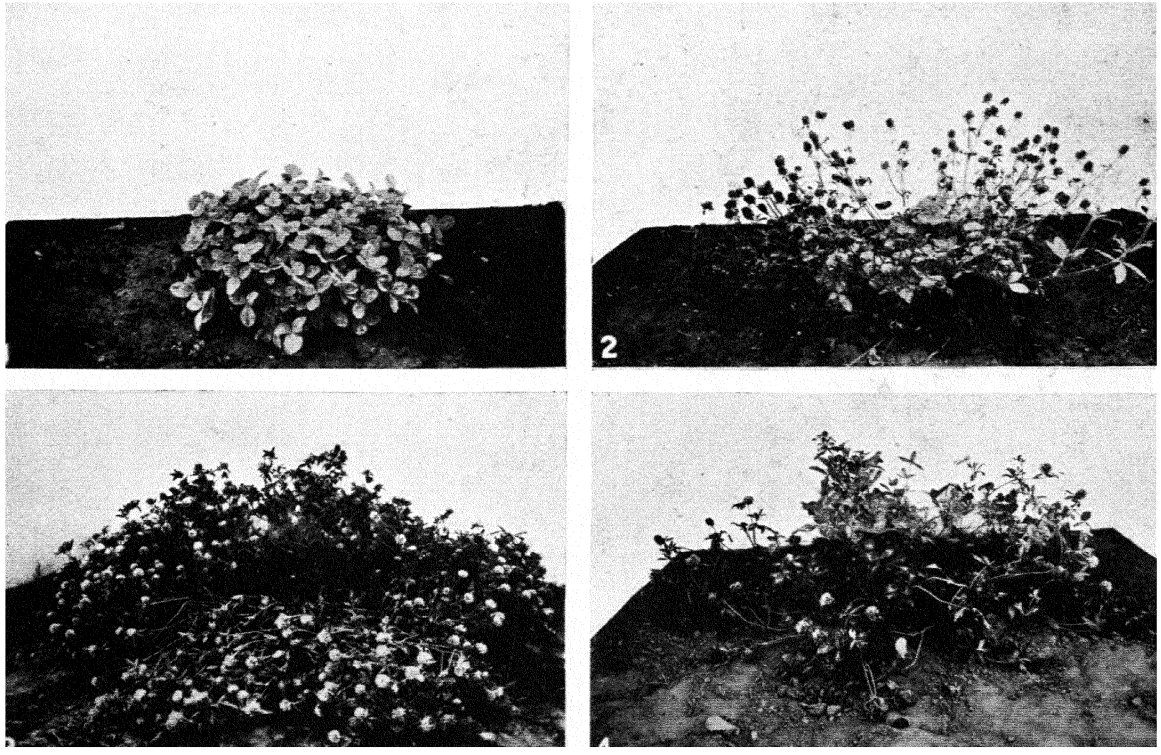


PLATE 23. Growth habit of red clover at Macdonald College, Montreal. In planting year (October). 1. Single-cut. 2. Double-cut. In second year (July). 3. Single-cut. 4. Double-cut. Photo : J. N. Bird, 1935.



(*a*) Silage cut.



(*b*) Seed stand.

PLATE 24. Production of silage and seed of white clover S100 in Breconshire (see p. 297). Photo : Breconshire War Agricultural Executive Committee.

CHAPTER XVII

DEVELOPMENTAL PHYSIOLOGY OF ECONOMIC CROPS

The objectives of the methods of artificial manipulation of growth and development and the technique that can be employed, with reference more particularly to temperature treatments, have been given in the foregoing chapter. Pending an up-to-date review of the position with regard to the pre-treatment of seed since the appearance of the Imperial Agricultural Bureaux' Joint Publication No. 1 in 1935, some results of experiments on the developmental physiology of various representative crops made since that date will now be given.

Cereals (Wheat, Oats, Barley)

These crops have been the subject of many of the scientific studies made upon the physiology of development. Lysenko's early experiments were made upon varieties of wheat, and Gregory and Purvis have made use of wheat and rye for their experiments on the effect of pre-treatment with temperature on time of maturity. References to literature will be found in Chapter IV and elsewhere. Experiments on the vernalization of wheat were described in I.A.B. Joint Publication No. 1 and there have not been any outstanding developments in Russia since that time as regards this crop, with the exception of the work of Kostjučenko and Zarubailo described in Chapter V. The following additional Russian papers on wheat have been selected at random.

Eremenko (1936) vernalized wheat grain in atmospheres containing low concentrations of various gaseous stimulators at temperatures of 0 to 1° C., 4 to 6° C., and 7 to 8° C. The period of vernalization was reduced from 35 days (under normal air conditions at the optimal temperatures of 4 to 6° C.) to 21 days when the grains were vernalized in an atmosphere containing 0·001 per cent ethylene chloride at a temperature of 7 to 8° C. The period of vernalization was reduced to 24 days in an atmosphere of pure oxygen at 0 to 1° C. Thus it appears that with a change in the atmosphere the optimal temperature also changes. Vernalization in closed jars progressed more slowly than in open jars, indicating the noxious effect of the products of respiration. Grains could be vernalized in a hydrogen atmosphere containing a small amount of oxygen. The author considers that free access of air is necessary not so much for increasing the oxygen content as for removing the CO_2 that

accumulates as a result of respiration. (Cf. the experiments of Gregory and Purvis, p. 69.)

Reference to degree of tillering has been made in the section on herbage plants (p. 252). Konovalov and Frolova (1939a) studied this aspect in connection with the vernalization of wheat. Lutescens 062 was vernalized for 4, 8 and 12 days and Hordeiforme 010 for 5, 10 and 15 days. The total number of fertile and sterile tillers decreased under the longer treatments. The largest number of tillers (20·8 fertile and 1·6 sterile in Lutescens, 22·8 and 2·0 in Hordeiforme) was found in plants grown from unvernalized seeds. It is therefore concluded that the number of tillers is inversely connected with the rate at which the plants reach sexual maturity.

The same authors (1939b) studied the effect of vernalization upon heading of the same wheat varieties and on the number of spikelets in a spike. It is stated that the largest number of normally developed spikes and of spikes bearing ten to fifteen spikelets as well as the largest total number of fertile spikelets, were obtained when plants of Lutescens 062 and Hordeiforme 010 were derived from seeds vernalized for 4 and 10 days respectively. Prolongation of the duration of vernalization caused a slight reduction, but the figures were still above those of the control series sown with dry and germinated seeds. In experiments with Lutescens 329 and Ukrainka winter wheats in high temperatures, the number of sterile spikelets was much reduced after vernalization.

Efeĭkin has made experiments on the reversibility of vernalization; in one experiment on this aspect (1939) seeds of winter wheat Durable were first vernalized at 0 to 2° C. for 40 to 45 days and then exposed for 6 days to high temperatures (27 to 33° C.) in electrically illuminated chambers. Devernalization is said to have been induced, the plants failing to shoot when grown in normal conditions, and the growing cones being morphologically similar to those on unvernalized plants in the control series. When wheat seedlings grown from vernalized seeds were exposed for 6 days to high temperatures at a later stage (2nd and 3rd leaf), the treatment was less effective, some plants being able to shoot when returned to normal conditions. Efeĭkin considers that the process of vernalization is reversible until a certain developmental phase is reached and can be nullified by high temperatures.

In the field experiment at East Malling already mentioned on p. 249, two each of the cereals wheat, barley and oats were used (Gregory, 1945). Vernalization treatments were adopted covering the range of temperatures recommended by the Soviet agronomists, and at each temperature two durations, one long and one short, were employed.

The varieties used and the vernalization treatments given are stated below:

	Variety
Wheat	Little Joss, April Bearded.
Barley	Plumage Archer, Spratt Archer.
Oats	Victory, Resistance

Temperature	*Duration of Vernalization in weeks*
37° F. (2·8° C.)	4 and 2
40° F. (4·4° C.)	3 and 2
45° F. (7·2° C.)	3 and 2
50° F. (10° C.)	2 and 1

Sowing dates (1) April 6—11; (2) May 4—9.

There were thus, in all, six varieties with four vernalization temperatures each with two durations of treatment and in addition two controls. The whole experiment was carried out with two sowing occasions. Each treatment was replicated eight times giving in all ($6 \times 10 \times 2 \times 8$) 960 plots. A factorial design was used for the experiment which covered an area of approximately 0·6 acres. As the results are shortly to be published in full, only a brief summary is given here.

The variety, Little Joss wheat, was found to behave like a winter wheat and showed a very large response to vernalization as seen from Table 25.

TABLE 25

Yield of Grain and Straw for Little Joss Wheat in cwt. per acre

Temperature of Vernalization	*Duration of Treatment*		*Duration of Treatment*	
	Long	*Short*	*Long*	*Short*
	Grain		*Straw*	
37° F.	17·5	10·7	33·2	28·2
40° F.	17·0	11·6	35·1	28·0
45° F.	13·1	12·0	30·2	27·0
50° F.	6·9	6·1	22·9	22·9
Control (unvernalized)	3·5		22·7	

The effect in the true spring varieties of the vernalization treatments on grain yields are given in Table 26.

TABLE 26

Effect of Treatment on Grain Yield in cwt. per acre in True Spring Cereals

Variety	*Vernalized*	*Control*	*Difference*
April Bearded	21·5	21·1	+0.4±0·73
Plumage Archer	28·2	25·8	+2.4±0·90
Spratt Archer	24·8	22·3	+2.5±1·19
Victory	19·9	18·9	+1.0±0.86
Resistance	23·6	23·1	+0.5±0·97
Mean of all varieties	23·6	22·2	+1·4±0·42

With each variety vernalization has led to an increase in grain yield, but only in the case of the two barley varieties are these increases statistically significant. The mean effect of vernalization on all varieties combined is about 5 per cent and is significant. The mean effects of temperature of vernalization on grain yield combining all varieties used were:

37° F. 23·5 cwt.; 40° F. 24·0; 45° F. 23·3; 50° F. 23·6.

There is no suggestion of an optimal temperature of vernalization, and consequently no support can be found in this experiment for the view that spring cereals require higher temperature than winter cereals during vernalization, as Lysenko recommended. Nor is there any evidence that shorter durations are more effective; the mean grain yield for long duration being 23·2 cwt. and short duration 23·8 cwt.

Observations were made during the course of the experiment on ear emergence in the true spring cereals; only a small effect of vernalization was recorded, ranging from less than 1 day above the controls in Plumage Archer barley to 4 days in Resistance oats. This acceleration in ear emergence, although statistically significant, is too small to be of practical importance in the climate of Great Britain. A small effect of vernalization was noted on the total number of ears produced, but this was not consistent among the varieties used, some giving an increase others a decrease, so that the mean overall effect was not significant.

This experiment, in which a high order of accuracy was attained (S.E. of mean yield per acre less than 2 per cent of the mean) showed an effect of vernalization on grain yield not exceeding 10 per cent in the barley varieties, 5 per cent in the oats, and no effect on spring wheat, and of these results only those with spring barley attained statistical significance.

The experiments of the German investigator, Voss, have already been mentioned in Chapter IV, where it was noted that short days alone (at high temperatures) can induce earing in German winter wheats, and that, given a very long period of growth, winter wheat may ultimately achieve flowering even under continuous illumination and high temperatures (1938). Voss objects to the use of the word 'jarovization' and suggests in its place the German word 'Entwicklungsbeschleunigung' (acceleration of development), a term which would not be accepted by the Russians, who state that there is no acceleration concerned in the process. Voss divides the winter wheat varieties into three groups, according as to whether it is easy, moderately difficult, or difficult to induce shooting by the application of artificial environments.

Voss defines a winter wheat as a variety which, under a constant high temperature (approximately +20° C.), constant illumination by natural or artificial light, as far as possible not $<$ 1500 luxes, and otherwise favourable conditions in a hothouse, does not exhibit the beginning of shooting within 4 to 6 weeks. A winter wheat can pass from the vegetative to the reproductive condition under the influence of different external factors, in particular low temperature and short day, acting alone or in combination at different stages of development. A sufficiently long period of low temperature and short day must again be followed by long-day conditions, that is winter wheat is first a short-day and then a long-day type.

The Canadian investigator, Wort, working at the Department of Botany of the University of Chicago, made a number of experiments on vernalization and related topics. The effects of vernalization were observed on Hannchen and O.A.C. barleys, Banner and Victory oats, Prolific rye, and in greater detail on Marquis spring wheat (1939). After being germinated, the seeds were vernalized for a varying number of days at different temperatures and several moisture conditions; some 125 combinations or vernalizing formulae were tested on Marquis wheat in 1939. The response to vernalization and also the optimal formulae varied in different varieties. The best results in experiments with Marquis wheat were obtained when the seeds were vernalized for 8 days at 3° C. with 60 per cent water, the plants flowering 21 days earlier and producing a much larger grain yield than the controls.

The response to vernalization varied also according to the conditions obtaining after sowing, being less pronounced under field conditions than in the greenhouse. To a certain extent, deviations of temperature during vernalization could be counteracted by adjustments in the moisture supply. The drying of seeds after they had been vernalized caused a reduction in germination; the percentage germination was 94·75 before vernalization, 95·0 after vernalization, and 86·0 after drying. The rela-

tive response to vernalization was less pronounced if the treated seeds were sown in long photoperiods than if they were in short days; prolongation of the daylength to 24 hours had a greater effect in reducing the length of the vegetative period in unvernalized plants (11 to 23 days) than in vernalized plants (7 to 19 days).

This work was extended to a number of other varieties of spring wheat in North America (Wort, 1940), as little information was available as to which of these respond to pre-treatment. Samples from Illinois, North Dakota and South Dakota were vernalized in an attempt to determine which varieties do respond, and whether the conditions of ripening in the place of origin have any effect on this response. Twenty-seven varieties showed a reduction in the period from sowing to flowering after vernalization, nine a retardation of flowering. Some varieties responded differently according to the locality in which the seed had been produced, others responded similarly regardless of origin. The samples that gave the greatest response had been produced in areas with relatively high temperatures during the flowering and ripening of the parent plant.

In view of the fact that many suitable spring varieties of wheat are available for use in Canada, it is not considered desirable that vernalized seed of winter varieties be sown, as is the practice in Russia. One series of experiments on the vernalization of winter wheat in Canada has been reported (Gfeller and Fraser, 1940). Vernalized and spring-sown winter wheats were significantly higher in yield than spring varieties (in two out of four tests) but matured somewhat later. The milling qualities of grains from vernalized crops were quite satisfactory. With the late maturing winter varieties, Turkey Red and Kanred, a distinct vernalizing effect of low temperature during seed ripening was noted.

Oats have also been the subject of experiment in North America. Taylor and Coffman (1938) studied the value of vernalization as a method of increasing the yields of spring-sown oats to the level of those attained from autumn sowings. The oats belonged to the groups, *Avena sativa* and *A. byzantina*. Data were obtained regarding the effect of vernalization on date of heading, yield, and smut infection for winter and spring varieties, and for varieties intermediate in growth habit. Vernalization reduced the period from sowing to heading for those varieties that had a definite requirement for low temperature, but spring varieties were generally unaffected. The treated lots of the varieties, Frazier, Nortez and Fulghum (C.I. 2499) gave higher yields on the average than untreated lots, but Lee, Fulghum (C.I. 708) and the spring variety, Iogold, gave lower yields after vernalization. Spring oats sown early were superior in yield to all the vernalized oats, while the oats sown in the normal way in the autumn gave 20 per cent more grain than the best of the vernalized lots. Smut attacks were greatly reduced as a result of vernalization.

Canada is the fourth ranking producer of oats in the world, and Ontario produces nearly 25 per cent of the total for the Dominion. This crop has therefore been taken by Zacks (1945) as the object of an attempt at zonation of crops in Ontario, which at present lacks a climatic-agricultural atlas. Climate, 'the longer phase of weather', is regarded as the dominant factor in limiting the yield of oats, while soil fertility, methods of cultivation, and varieties of seed used have less effect upon year to year variation in yields. Although agreeing that production in any year is the result of the interaction of many factors of nature, Zacks takes rainfall and temperature as the factors for her geographical survey of oat yields in relation to climate. July temperatures and June rainfalls are most significant in affecting yields; a requirement of low temperatures in July is similar to that found in Great Britain for earlier periods of the year. Time of seeding is recognized as having an important effect on productivity, but lack of phenological data makes it impossible to draw definite conclusions as to the cause. This survey is a study of the wider aspects of the relation of crop production and the environment, extending the field from the narrow understanding of the term environment adopted in this book to cover complex relationships and effects of weather and climate.

Reports of some experiments by Oleĭnikova were given in Joint Publication No. 1. This worker has now made a study of phasic development in a world collection of barleys at the U.S.S.R. Institute of Plant Industry, Leningrad (1939). It is claimed that a relation has been established between the rapidity and character of phasic development and the geographical origin of the particular variety. For instance, the thermo-phase was found to be much longer in the southern forms than in northern forms, while, conversely, the photo-phase was longer in the northern forms. Within each geographical region there were differences in the length of developmental phases.

Oleĭnikova found it possible to divide barleys into five groups, according to the length of the thermo-phase. Vernalization of the thermo-phase in the first group may be effected at 0 to 2° C. for 35 to 40 days with moisture in the treated seed at 55 per cent; the duration of vernalization could be reduced to 20 to 30 days for the second group, and to 15 to 20 days for the third group; the fourth and fifth groups could be fully vernalized at 5 to 10° C. for 5 to 10 days with moisture of seed at 50 per cent.

Plants with long thermo-phases could be vernalized in much shorter ranges of temperatures than those with shorter thermo-phases; a rise in temperature up to 8° C. would greatly retard vernalization of long phases but would have little effect on the rapidity of vernalization of shorter thermo-phases. In semi-winter strains the thermo-phase could be ver-

nalized almost normally under alternation of temperatures (periods of 10 to 12 hours), but earing of winter forms was much delayed by this treatment. With a frequent (hourly) alternation of high and low temperatures, vernalization of the thermo-phase could not be effected. No differences other than sensitiveness to temperature and the length of the thermo-phase were observed in a comparison between typical 'winter' and typical 'spring' forms.

Again, according to Oleĭnikova, barleys can be divided into four groups as regards length of the photo-phase. Tests of the length of this phase were made by sowing vernalized seeds in a greenhouse or in the open and growing the young plants under different photoperiods (24-hour and 14-hour). The length of the photo-phase was judged by the degree of retardation of earing in shortened photoperiods. At temperatures of 18 to 20° C. the rate of progress of the photo-phase was accelerated in all varieties. A reduction in temperature retarded the rate of progress through the photo-phase more markedly in southern than in northern forms.

Other investigators examined the efficacy of vernalization of barley at different latitudes, namely, beyond the Arctic Circle, at Detskoe Selo (Leningrad), and in the Crimea (Banteev, Kalinin and Gorjunov, 1936). As regards a reduction in the vegetative period, vernalization had a greater effect in the south than in the north. The lesser effect of vernalization in the north is regarded as due to the different natural conditions, which favour the more rapid progress of natural vernalization, as a result of which the majority of spring forms, both in the control and in the vernalized sowings, were similar as regards their vegetative period.

Many of the barleys of southern origin, for example, those from Egypt, Arabia, Cyprus, Abyssinia, Iran, India and Afghanistan showed no reaction to vernalization at any of the points of trial. The majority of the strains from Scandinavia and northern provinces of U.S.S.R. showed a greater sensitiveness in the south than in the more northerly latitudes. Barleys from the higher regions of Abyssinia, Asia Minor, Central Asia, India and Transcaucasia, as well as half-winter and winter forms everywhere showed a reduction in the vegetative period to a greater or less extent. Vernalization of barleys may also cause an increase in yield; this is most commonly noted in northern regions where the insufficient or complete absence of reduction in the vegetative period frequently leads to false conclusions regarding the economic significance of vernalization.

Two papers on Lysenko's method of 'training' as applied to barley are discussed below, one describing the conversion of winter barley into a spring form, the other the conversion of a spring barley into a winter form. This is one of the more controversial and less widely accepted aspects of the Russian theory of plant development and its manipulation.

Hitrinskiĭ (1939) attempted to 'alter the type of the thermo-phase' by this method, in experiments made with four winter Pallidum varieties and a winter Nigrum variety. Seeds vernalized for a varying number of days under optimal conditions were sown on March 26th and April 20th 1938 at Odessa. The seeds collected from all plants that produced ears in that year were sown unvernalized on 9th April 1939. Although the behaviour of plants in 1939 was very diverse, it was possible to observe that the progeny of plants vernalized fully in 1938 and that of plants vernalized for 1 to 4 days failed to ear in 1939. Only the progeny of plants vernalized in 1938 for 5 to 17 days eared more or less fully and rapidly in 1939, that is they behaved as spring forms. Morphological study of the ears revealed a series of intermediate types between the many-rowed (winter) and two-rowed (spring) types.

The converse experiment was made by Soloveĭ (1939). Beginning in 1936 and for three generations, seeds of a spring Pallidum variety were sown in the autumn as well as the spring (control series). The plants obtained after the first winter, which eared 10 to 15 days earlier than those sown in the spring, showed a number of morphological distinctions which were retained in their progeny. When sown in the following autumn, they also showed differences in winter hardiness. All plants from seeds from the control series perished; the percentage survival was 1·5 among the progeny from August-sown seeds, and 3 from September-sown seeds; the figures for the progeny of the October sowings was 55 (without intravarietal crossing) and 68 (after intravarietal crossing).

The progeny of the 1937 plants gave seventeen morphologically distinct forms in 1938. Their winter hardiness was considerably increased, reaching 96 or 100 per cent survival in some cases after autumn sowings. The winter habit which was now regarded as having been acquired by 'training' was tested by sowing in summer; when sown at this time, the 'altered' forms failed to ear, whereas the control (the initial variety) eared fully and rapidly. Some plants also showed a tendency to perenniality, giving a second seed crop in 1939. The conclusion drawn from both these experiments is that the hereditary nature of plants may be changed in a desired direction during their individual development.

The method of identifying winter and summer varieties, and the definition of the terms 'winter form' and 'summer form' proposed by Voss for wheat (see p. 68) are also considered to apply to barley, rye and oats (1939). Low temperature (+ 3° C. and + 10° C.) and short day were employed to group different winter barleys in accordance with their varietal manner of shooting; it was found that, as in the case of winter wheats, the lower temperature +3° C. had a greater effect than +10° C. in accelerating development.

A study by Grebennikov and Hohlovskiĭ (1939) on the relation

between the application of artificial fertilizers and the method of vernalization is related to the work on nutrition in relation to reproductive phases noted in Chapter XII. Varieties of millet were sown in the field, vernalized and unvernalized, and grown under different conditions of mineral nutrition. The general conclusion was that the greatest effect of basic plus supplementary nutrition could be obtained after the seed had been vernalized. This is expressed in terms of plant height, seed yield, 1,000-grain weight and chemical composition of the grain.

The outstanding fact in this work on controlling the developmental behaviour of cereals is that there appear to be widely divergent views regarding the effect of vernalization on winter and spring varieties. It is unlikely that these will be cleared up until an analysis of environmental requirements has been made of the varieties being tested; this is what the Russian physiological agronomists call 'phasic analysis'. When the varieties with a high requirement of low temperature, such as the Swedish winter rye Stålråg (Åberg, 1940), have been separated from those with low or medium requirements, it should then be possible to postulate the results to be expected from vernalization. In some of the more 'spring' varieties (small requirement of low temperature), development is even inhibited by vernalization at low temperature, possibly because the plants are at that stage of their development when they require a higher temperature (or thermoperiod) in combination with appropriate length of day.

The results of phasic analyses are valuable not only in forecasting whether winter, semi-winter and spring varieties will respond to pre-treatment with low temperature, but also in guiding farmers in the choice of suitable varieties to sow in their locality for grain or forage, and in the adoption of appropriate agronomic measures such as time of sowing, grazing, manuring, etc. An example may be quoted from Switzerland.

Experiments on variation in sowing dates were conducted (Buchli, 1943) from 1936-9 on spring wheats comprising one Swiss strain bred from Manitoba wheat, five Canadian and three German strains. Sowings began on February 2nd and continued at intervals of 7 days up to the end of April. Harvesting was graded similarly in order to harvest the different varieties as far as possible at the same stage of maturity. Results expressed in grain yield, straw yield, hectolitre grain weight, 1,000-grain weight, and gluten quantity and quality confirm the reports of other workers (including Voss, 1938 and Klitsch, 1935) that spring wheats (or as they are called in Europe 'summer wheats'), and especially varieties such as 'Strube's Red Schlanstedt', require a certain amount of cold before they can shoot or develop ears; their development may be greatly accelerated by exposure to low temperature at germination. Under Swiss conditions, the time of sowing spring wheat is of great importance for

yield (grain, hectolitre weight, 1,000-grain weight) and quality. Varietal differences can be seen, as the 'early' varieties such as the Canadian were less seriously affected by late sowing than the 'late' Strube variety mentioned above. Swiss farmers are therefore recommended to sow spring wheat as early as is practicable. (A similar study on variation of sowing dates of wheat in India is discussed on p. 330.)

The converse is probably true when cereals are sown for grazing, hay, silage, or the production of dried grass (see p. 254). Varieties slightly out of tune with their environment as far as their development is concerned might be expected to supply more herbage of a higher nutritive value, provided development could proceed to that stage preceding shooting when the nutritive value of the leaves is at its highest, just before the transference of nutrients to the developing ear.

Sugar Cane

Experiments with this crop are naturally concerned more with the effect of daylength than of temperature. Two papers, one from the United States of America, one from India, may be taken as examples of the type of problems that arise in inducing the varieties to flower. This problem does not arise in normal production, as the crop is generally reproduced vegetatively.

Sartoris (1938) has found that the apparently capricious behaviour of the sugar-cane plant with regard to flowering makes it very difficult to carry on a definite breeding programme. Regulation of time of flowering is a matter of great importance in this work, and it is recognized that length of day is one of the decisive factors influencing the change from a vegetative to a reproductive state.

There have been several attempts to control the time of flowering in sugar cane, some partially successful. For several years, at the U.S. Sugar Plant Field Station, Canal Point, Louisiana, the range in time of flowering of certain varieties has been extended a month or more by varying the type of soil. Venkatraman (1936) subjected strain Co 290 to a 6-hour day, and the plants flowered 26 days earlier than the controls. The pollen, however, gave only 1 per cent germination. Sartoris notes that a 6-hour day is very near the minimum for survival, that it is not comparable to any natural daylength, and that it is hardly to be expected that plants would produce fertile flowers under such conditions.

Although the light period is the factor that stimulates the change from vegetative to reproductive growth, the other factors upon which the growth of the plant is dependent, namely temperature, moisture and soil fertility, also play an important preliminary part. The plant must reach a certain stage of vegetative growth before it is capable of responding to

the influence of a daylength favourable to flowering. The minimum requirement of vegetative growth for sugar cane is not known, but Sartoris suggests that the stalk must have several mature nodes before it can be induced to flower. This requirement of a minimum amount of vegetative growth is apparently common to all species, but is particularly noticeable in the variety of *Saccharum spontaneum* from Central Asia.

The interpretation as regards this Russian variety is that the first year's growth is concerned with the establishment of the plant, the development of roots and shoots. Not many mature nodes are formed and the stalk attains a height of only 2·5 to 3 ft. An occasional stalk may flower in the first year, but the tassels are small or they may not emerge. In the following year, the stalks attain a height of 5 or 6 ft. and flowering is profuse (not stated at which latitude in U.S.A.).

Since sugar cane flowers in the northern hemisphere during the autumn and winter months, and in the southern hemisphere during a short-day period, which corresponds to the late spring and summer months in the United States, the critical light period for inducing the change from vegetative growth to reproduction would appear to be somewhat longer than the days at the time of actual flowering, as the flower is differentiated a month or two before emergence. This daylength is stated to be in the vicinity of 12 hours, but somewhat longer for *Saccharum spontaneum*, because varieties of this species usually flower earlier than the other species of sugar cane.

General field observations show that the natural change in daylength is not a dominating influence, because these changes are constant from year to year, while the flowering dates of sugar cane are not constant. Some varieties flower every year, some seldom flower, many are irregular in their flowering. Even when a variety flowers profusely, not all the stalks flower, although the flowering and non-flowering stalks may be the same size and age. Some stools have flowering stalks while others in the same plot have none. Large stalks flower first, slender stalks later in the season.

Sartoris quotes the behaviour of sugar cane in Colombia, South America, where cane tassels throughout the year. The location of these observations is Palmira, 4° north of the equator, where the length of day does not deviate markedly from 12 hours. It is stated, however, that sugar cane does not behave in this manner in all places similarly located with respect to the equator, and it is concluded that there must be factors other than length of day that influence flowering in the sugar cane.

It will ultimately be interesting to compare sugar cane with its gramineous relatives, the cereals and the herbage grasses, as what is discovered regarding flowering behaviour, degree and nature of tillering, the importance of carbohydrates and reserve materials in general in one

will apply at least to some extent in the others. Although there is no direct evidence on the point, the behaviour of sugar cane as regards flowering, and particularly the example of the Russian variety noted above, seems to suggest that temperature as well as light may be a decisive factor in controlling the change from vegetative growth to reproduction.

Sartoris, however, concludes his article by stressing the need for evolving a technique in which light and nutrition might both be controlled. It is stated that plant containers of sufficient size are necessary to support normal growth, and also to provide the growth conditions (presumably temperature and moisture) that will help the plants to reach a stage of vegetative growth in which they may be influenced by a favourable light treatment. For some varieties this requirement can be readily attained, with others it is thought that it may be more difficult to provide the conditions for adequate vegetative growth than it would be to provide the correct light period. This state of readiness which must be acquired in sugar cane before it can be treated with photoperiods may be compared with the ripe-to-flower conditions observed by Klebs (p. 23).

Similar problems with regard to flowering of sugar cane have arisen at the Imperial Sugar Cane Breeding Station, Coimbatore, India, where a large world collection is being maintained for breeding purposes. Some varieties have not flowered once in 30 years, others flower quite regularly but their flowering dates do not synchronize with those of other varieties with which they have to be crossed; the difference may be of the order of 4 to 5 weeks. Several devices have been adopted to delay the flowering of some and hasten that of others. Dutt (1943) describes two of these methods, artificial regulation of daylight, and 'topping'. Work with the variety Co 290 has been mentioned above. When this late variety was submitted to 6 hours' daylight, the treated cones flowered 26 days earlier than the control; other varieties were a fortnight earlier. A very early variety such as Co 285 could conversely be delayed in flowering by exposure to long days. By these methods, and by delaying flowering by decapitating the plants above the growing point, it was found to be possible to make adequate adjustments in order to synchronize time of flowering of desirable parents in a breeding programme.

Grain and Fodder Legumes (other than Herbage Plants)

Experiments on the vernalization of this group of economic plants have been made with lupins, vetches, lentils, soybean and groundnuts, among others. Like all other experiments and recommendations connected with vernalization, it should again be noted that the data refer

only to the varieties tested and only under the conditions of the actual experiment.

Several authors have reported trials with lupins in Russia and Germany. Savvičev (1936) vernalized seeds of *Lupinus luteus* by chilling sprouted lots in snow for 15 and 30 days. The vegetative period (from sowing to flowering) was reduced by 7 to 18 days in one year, and by 0 to 30 days in another, the average being 20 days. A direct correlation was noted between the length of the vegetative period of the control plants and the response of the treated plants to vernalization. Sowing date also affected relative earliness; the vegetative period was reduced by 0 to 3 days after early sowing (April 15th) and by 4 to 13 days after late sowing (April 29th). The unvernalized control plants flowered 4 to 8 days earlier after the earlier sowing than after the later.

Krasulina (1937 and 1939) vernalized various forms of *Lupinus angustifolius* and *L. luteus* at temperatures of 5, 10, 15 and 20° C. for 15 days. After the lower temperatures, the vegetative period was shortened (particularly in the 10° C. series), and the seed yield increased (particularly in the 5° C. series). Plants vernalized at higher temperatures differed little in flowering behaviour from the control, but their forage yield was much increased. These and other species of *Lupinus* were later vernalized at 8 to 10° C. for a varying number of days. There was a wide variation in response, the optimal duration of pre-treatment varying with species and varieties from 7 to 28 days, with *L. angustifolius* and *L. luteus* being fully vernalized in 21 days.

Sapožnikova (1937a and b) was interested in the possibility of ensuring a yield of seed from lupins in Western Siberia. Seeds vernalized at 6 to 7° C. for 15 days were planted in late May and early June; the difference in time of flowering between vernalized and unvernalized plants sown on the same dates varied between 6 and 27 days. Seeds ripened in all the sowings of vernalized plants, but only in the earliest sowings of the unvernalized. The seed yield and percentage of matured plants both fell with delay of sowing. The height of vernalized plants was uniformly less than that of unvernalized plants.

Axelrod (1939) vernalized lupin seed at 8 to 10° C. and 100 per cent moisture for 13 days, and sowed the seed after inoculation on mineral and peaty soils. In both cases, the vernalized plants flowered 11 days earlier than the control, and on the mineral soil they ripened seed 23 days before the control. On the peaty soil the vernalized plants flowered 4 days and ripened 8 days later than on mineral soil; the unvernalized plants did not ripen on the peat.

In Germany, Hartisch (1939) subjected several cultivated varieties of lupin to different conditions of length of day and temperature; results are compared with those obtained from graduated sowings at Leipzig

and Müncheberg. Lupins were found to be plants of a neutral to long-day type, experiencing a slight inhibition of development under short-day conditions. Vernalization at temperatures below 10° C. hastens development, pre-treatment at higher temperatures inhibits it. After vernalization at a low temperature, the acceleration of development may be so great as to be discernible even after allowance has been made for the duration of the treatment.

As sowings in the graduated series become later, grain yield and the proportion of grain in the total plant bulk become less, but straw yield increases. Under favourable precipitation, however, late sowings may still produce optimal grain yield. Vernalization at low temperature causes a limitation of the growth of the plant in length, together with a reduction of its capacity for branching. The formation of levels, a hindrance to uniform pod ripening, is thus eliminated.

According to Vasiljev (1939a and b), the areas of lupin, vetch and lentil sown with vernalized seeds in Russia rose from 285,000 ha. in 1937 to 400,000 ha. in 1938 and to over 500,000 ha. in 1939. This investigator, of the Institute of Northern Grain Husbandry and Grain Legumes, Moscow, has published a pamphlet giving the technique to be adopted under farming conditions. All these crops, and particularly late forms thereof, gave a good response to vernalization, flowering 15 to 20 days earlier, but the response varied widely according to time and place of sowing.

The recommendations for lupins are that the seeds should be given 90 kg. of water per 100 kg. of seed and germinated for a day or two at 10° C. When there are 5 to 10 per cent of germinating seeds, the lots are transferred to a temperature not below 5° C. for 18 days, or to 7 to 10° C. for 12 days. Vetch seeds are given 72 kg. water per 100 kg. of seed; when germination has begun (within 2 or 3 days), *Vicia villosa* and winter and late forms of *V. sativa* are transferred to 0 to 2° C. for 35 days, and the earlier forms to 5 to 7° C. for 18 days. If growth of vetch seed during treatment is too rapid, 3 to 5 per cent of oats is added and the moisture reduced. Lentils are given 78 kg. water for 100 kg. seed, and vernalized at 6 to 8° C. for 12 days.

Kalantyrj (1939a and b) makes similar recommendations for vetch and compares the effect on forage and seed yield. After vernalizing lentils at 8° C. for 12 days, Tulaïkova (1939) found that the response varied from 1 to 14 days according to the variety, while among extra-early forms some flowered later after vernalization. Late forms showed the greatest response, flowering 9 to 14 days earlier. Early flowering was generally followed by early ripening, although simultaneous flowering of vernalized and control plants might be followed by earlier ripening of the vernalized.

The story of the introduction of the soybean from its home in the Far East into many countries where the crop is grown for many different purposes is one of the more dramatic of modern agriculture. Dies (1943) describes its introduction into the United States of America where the area now (1941) under cultivation has reached a total of 5,855,000 acres (for beans only). As will have been noted in the earlier chapters of the present work, the soybean has been widely used in experiments on developmental physiology, largely due to its ease of handling. There are a great many varieties of this crop varying widely in the length of their vegetative periods (days to mature). The list of varieties given by Dies gives a range of from 90 to 170 days. This variability has obviously had much to do with the wide adaptability of the crop.

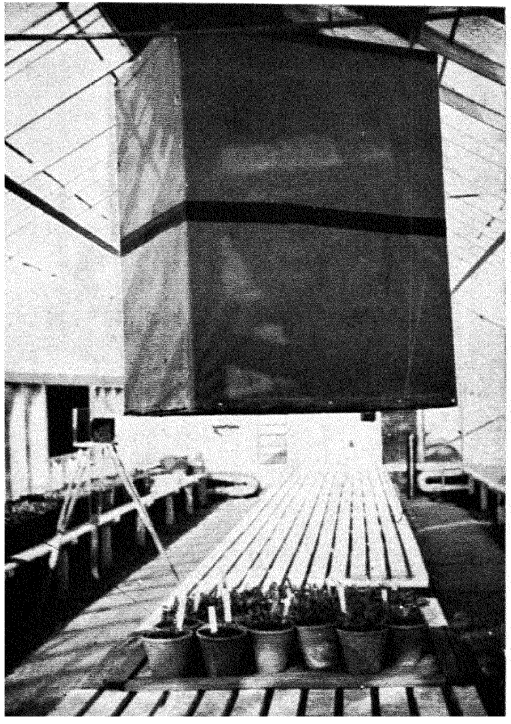
The soybean has not become an important crop in British agriculture, probably due to the fact that the summer does not provide the degree of warmth necessary for growth and development. Only on the Ford Estates in Essex is it known to have been cultivated on any scale. Germany is another border-line country for the cultivation of soybeans, and experiments have therefore been made in the manipulation of development of the crop.

Experiments on vernalization of soybeans have been made in Germany by Rosenbaum (1937a and b); although it is agreed that the conditions of treatment laid down by Lysenko are practically correct, it is considered that similar effects may be attained with other temperatures, and that by the suitable arrangement of conditions of growth and development during the early stages of the plant's life, the vernalization treatment may be dispensed with altogether. The environmental conditions following sowing govern the course and rate of development more than does previous vernalization, for which reason it is considered to be difficult to make reliable comparisons of the results of vernalizing different varieties. A reduction in the time taken to flower may be more readily obtained by means of the photoperiodic after-effect, although this is said to entail a reduction in yield. The advantages attributed to the practice of vernalization and the after-effects of light treatment are not recommended by Rosenbaum as far as soybeans are concerned, either to the practical farmer or to the plant breeder in Germany.

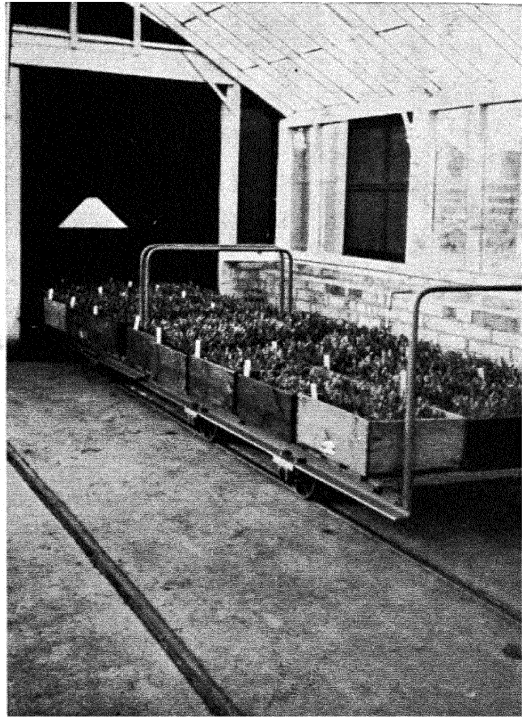
The following points from Rosenbaum's articles may be noted. Germination and shooting capacity are not diminished in treated seeds. Hand-sowing of vernalized seeds is necessary; drilling can be used only for large quantities. Treated seed cannot be dried, as germination capacity is almost entirely lost. Habit is affected, in that species characterized by branching mostly lose this character after vernalization. The increased capacity to produce flowers in plants from vernalized seed may be clearly recognized by the fact that they form flowers at internodes which on the



PLATE 25. Sugar beets ready for overwintering in the field prior to taking seed in the following season. Saanichton, British Columbia (see p. 225). Photo: T. M. Stevenson and R. M. MacVicar.



(*a*) Equipment for controlling light exposure pot experiments.



(*b*) Equipment for field sowing.

PLATE 26. Effect of daylength on sugar beet (see pp. 242 and 280). Photos: G. D. H. Bell.

control plants exhibit no flowers. Flowering may begin 0 to 15 days earlier, but the differences at maturity are not so marked, nor are there any differences in yield or quality. This is said to be due to the fact that the flowering intervals within a variety are in general very considerable. The response to treatment depends upon the individual requirement of high temperature of the variety concerned.

The difficulties experienced in early work on the vernalization of soybeans, for example, mould formation during treatment, reduction of germination capacity, and the stunted form and lack of vigour of resulting plants, were overcome by adopting the technique evolved by Rudorf (1935). This includes disinfection of seed in a 0·25 per cent solution of 'Abavit' for 30 minutes; seed kept carefully and shaken continuously during disinfection to remove air bubbles; swelling to follow immediately after disinfection, water dose being 75 to 80 per cent of the air-dry seed; after absorption of all the water, generally within 24 hours, seed is mixed with some neutral substance such as pulverized charcoal and kept in motion for the remainder of the treatment (15 days at 25° C.).

The response of soybeans to photoperiods has been discussed in earlier chapters. A recent experiment made by Almeida (1941) in Portugal may be quoted as an example of what may be done to shorten the vegetative periods of the late varieties, Nanking 8401 and Biloxi 8402. These varieties require 150 days to reach maturity at the National Station of Agronomy, Sacavém, where the experiment was made. When the plants were 15 days old, two series were shaded periodically so that one received a 9-hour day (9 a.m. to 6 p.m.), and the other a 12-hour day (9 a.m. to 9 p.m.), while the control plants grew in what is at Sacavém approximately a 15-hour day. The methods and times of shading were chosen so as to eliminate as far as possible any increase of temperature in the shaded species, while at the same time the plants at 15 days old should have passed the stage when vernalization would be possible. The shading treatment was continued for 21 days.

The effect was to reduce the number of days from germination to flowering, as compared with the control series, as follows:

TABLE 27

Variety	*Daylength*	*Per cent reduction in vegetative period*
Nanking	9-hour	53·57
	12-hour	48·21
Biloxi	9-hour	47·83
	12-hour	43·48

The morphology of the plants was also affected to some extent, shading producing a diminution in size, which became more marked with longer treatments.

Working with culinary peas, Fuchs (1943) found that temperature during the growth of the crop played a decisive part and is not merely a reinforcement of the effect of daylength. Under Central European conditions (Halle, Germany), this may be attributable either to the existence among the peas of forms neutral to daylength, or to the fact that, even with very early or very late sowings, the daylength does not fall below that critical for the variety. This result is compared with the published and unpublished work of Kopetz (see p. 46) and Pesola, who worked in Finland (1935). Days are longer in Finland, but nevertheless under the warmer environment at Halle peas are found to flower earlier.

Masjuk (1940 a and b) has made a number of experiments on *Arachis hypogaea*, using 10-hour day, or high temperatures (35 to 40° C.), or treatment with blastanin (hormonization). No conspicuous differences were noted in time of flowering, but in total weight, number of nuts and total yield of nuts the control plants were inferior to the treated plants, particularly those grown in short photoperiods or from seeds that had been treated with high temperature. In a separate experiment, vernalization of seeds at 22 to 25° C. for 20 days caused flowering to be 5 days earlier. Total yields of pods per plant and number of pods per plant were increased from 32·1 grm. and 29, to 54·1 grm. and 39 respectively. The number of unripe pods was reduced from 20·2 to 14·6 per cent.

Since the capacity of legumes to produce good growth and high yields depends to a great extent on their root nodules, and since the symbiotic relationship between leguminous plants and nodule bacteria is affected by the carbohydrate content of the plant, it may be postulated that a more active formation of nodules should occur on the roots of plants grown under long day than in those grown in short day. Čaĭlahjan (1945) investigated this supposition in the short-day plants, *Phaseolus vulgaris* and soybean, and the long-day plants, *Ervum lens*, *Vicia sativa* and *Phaseolus aureus*. The formation of root nodules (total weight) is more intense in long day in all plants irrespective of class. The internal agent responsible is thought to be the high carbohydrate content in plants in long-day conditions, and the high content of growth hormones also present.

CHAPTER XVIII

DEVELOPMENTAL PHYSIOLOGY OF ECONOMIC CROPS (*cont.*)

Sugar Beet

The literature on the developmental behaviour of this crop, or 'the duration of the beet cycle', as Munerati (1942) has called it, is very extensive. Munerati's review contains a long list of literature, and refers to other reviews of the subject and of the literature by specialists such as Günther (1900), Montemartini (1917-18), Shaw (1917), De Vilmorin (1923), Fruwirth (1923), Lippmann (1925 and 1935), Schneider (1926), Römer (1927), Parisi (1929), Chroboczek (see Cornell, 1934), Hollrung (1936) and Voss (1940 a and b). The most recent work in Great Britain is that by Bell (pp. 242 and 280), and the developments in American research and practice have been brought up to date in the review by Coons (1943).

The value of sugar beet as an economic crop depends upon those physiological functions and processes that lead to a maximum sugar content, while the production of seed for multiplication of the crop requires to be carried out under conditions that will ensure the correct quota of temperature and daylength at the appropriate time in the life of the plant. This latter question has already been discussed to some extent (p. 225), but it is now necessary to consider which environment provides the most suitable conditions for the production of sugar from the sugar beet plant, the source of one-third of the world's supply of sugar.

According to Brandes and Coons (1941), whereas sugar cane requires 8 to 9 months to attain adequate tonnage and satisfactory quality (for which suitable conditions are found only in tropical and subtropical latitudes), the sugar beet is a relatively cold-hardy plant, grown for sugar production as an annual which in 160 to 200 days is capable of producing a large tonnage of roots of high sucrose percentage. In the northern hemisphere, sugar beet is grown from an extreme southern limit of about 35° N. to an extreme northern latitude of about 60°.

The Russian workers (Vavilov, 1935) place the centre of origin of the genus *Beta* in the Near East, possibly Asia Minor or the Caucasus. From this general area its distribution has been westward along the Mediterranean, northwards and eastward in the arid steppe regions, and as a littoral plant northward along the Atlantic and North Sea coasts. The

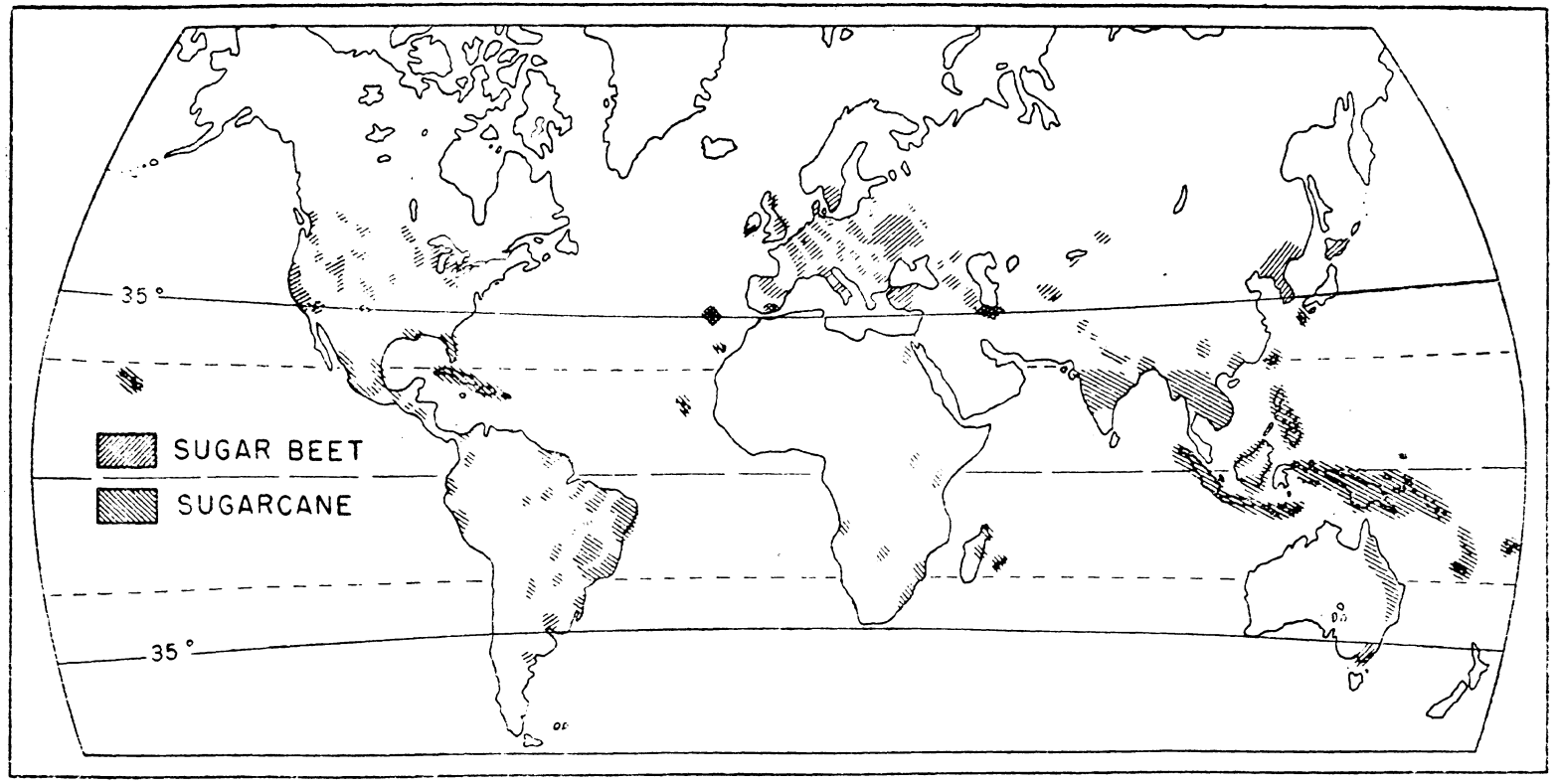


FIGURE 42

World distribution of sugar cane and sugar beet. Potential areas of production are shown without reference to quantities of sugar produced (Brandes and Coons, 1941)

wild relatives of the sugar beet, particularly *Beta maritima*, are winter hardy, extremely resistant to drought, tolerant of high salt concentrations in maritime regions, and adapted to a wide range of soil conditions. There are among the ecotypes of *B. maritima* annuals, winter annuals, biennials and perennials. Thus the genus *Beta* possesses a genetic composition that makes possible its cultivation as a crop plant from Spain to Iran in the south of the northern hemisphere, and as far north at least as central Sweden.

Taking the United States of America as an example, it may be said that sugar beet makes its best and most efficient growth as a crop plant

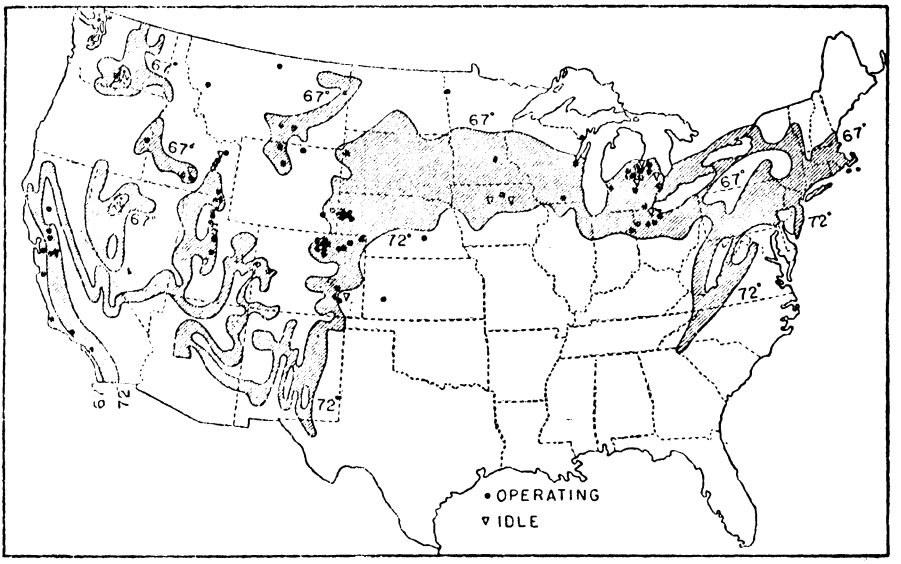


FIGURE 43

Location of beet-sugar factories in the United States of America. The zone between the mean summer isotherms of 67° and 72° F. is shaded (Brandes and Coons, 1941)

within a zone lying between the summer-temperature isotherms of 67° and 72° F. This potential belt was forecast by Wiley (see United States, Dept. Agric., 1901), and the sugar beet industry has become localized here, subject to controlling factors such as water supply and plant diseases (Fig. 43).

The major areas for the production of sugar beet in Europe lie slightly north of the July 70° F. isotherm, cultivation of the crop meeting more difficulties in countries south of that line, for example, Spain, Italy, the Balkans, Turkey and Iran; the districts in the last two countries are nearer the July 80° F. isotherm. The cultivation of the crop in the

southern hemisphere is confined largely to areas crossed by the corresponding January 70° F. isotherm.

Summer temperatures probably affect the yield and quality of a sugar-beet crop less than does the water supply, but autumn temperatures have a marked effect on the storage of sugar and therefore on the ultimate economic value of the crop. In the humid area and in general in irrigated areas in U.S.A., a plant that has made luxuriant root and top growth has usually attained a sucrose percentage of about 12 by September 1st. With the cool days and frosty nights of late September or October, growth is checked but there is an increase in photosynthetic activity and the storage of sugar (Tottingham, 1926). Sucrose percentages rise, reaching averages of 15 or more by mid-October, and as high as 18 or more in November, if severe frosts do not occur. On the other hand, in southern areas (Wiley, see United States Dept. Agric., 1901) it has been noted that sucrose percentages may reach 12 in later August or early September, but may fall in subsequent months due to the vigorous growth produced under the influence of the relatively high temperatures.

An exception to this is noted in the case of California. Here sugar beets are planted in December, January or February, and harvested and processed in late July and onwards. The highest sucrose percentages are achieved in the hottest months, and sucrose accumulation takes place at day temperatures frequently greatly in excess of 100° F. The common practice in these areas is to withhold irrigation water as the harvest period approaches. Coons suggests that the high temperatures and decreased water supply operate to check further growth while intensive photosynthetic activity continues; the storage of sugar increases in proportion to the reduction in growth, the continuance of which would consume the food stocks of the plant.

The economic production of the sugar-beet crop therefore depends upon the adjustment of agronomic practices such as choice of time of sowing, manuring and irrigation methods in such a way as to ensure first a maximum degree of vegetative growth under conditions that do not meet the plant's requirements for reproduction, with a subsequent retardation of growth due to lower temperature or reduced water supply, whereby a maximum amount of sugar is stored in the roots due to continued photosynthetic activity.

The environmental conditions under which sugar-beet plants will produce seed have a marked effect on the seed yield and also on the bolting characteristics of the progeny. Initiation of seed stalks and flowering of biennial beets is brought about mainly by the cumulative effect of low-temperature exposure followed or accompanied by the effect of long photoperiods (Owen, Carsner and Stout, 1940). The selection carried on by plant breeders away from the bolting tendency that reduces the

economic return from a sugar-beet crop makes it more difficult to provide the requisite conditions for seed production. Within varieties selected for non-bolting, there still remains a small proportion of individual

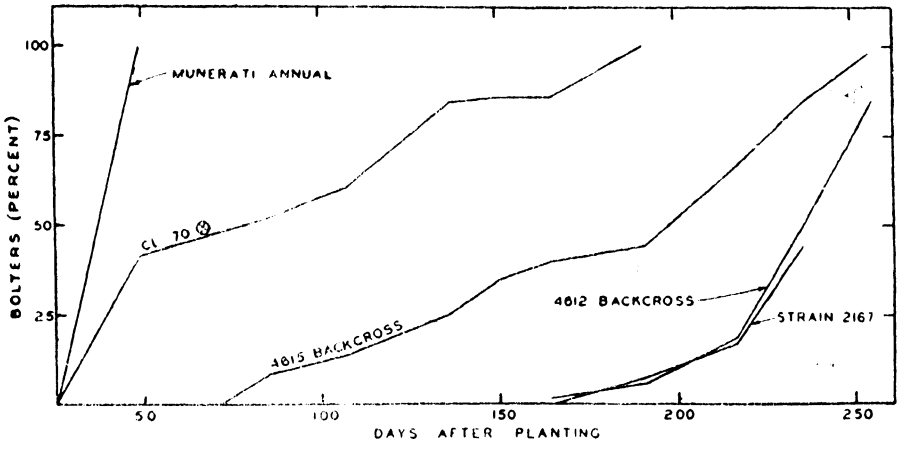


FIGURE 44

Inheritance of bolting in beet, and the isolation of a new genetic factor for bolting. This graph summarizes results obtained with non-vernalized seeds and shows a gradation of types from strong annual to strongly vegetative biennial habit (Owen, Carsner and Stout, 1940)

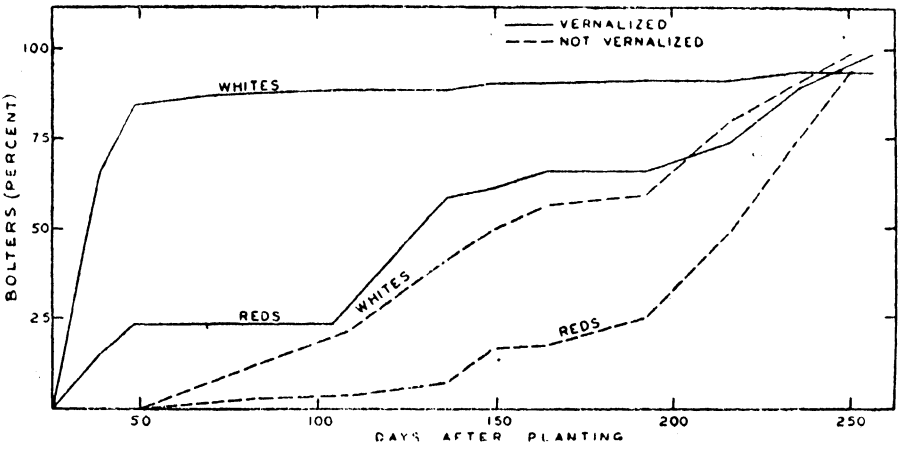


FIGURE 45

Bolting reaction of colour types in backcross progeny 4615 (see Fig. 44) (Owen, Carsner and Stout, 1940)

plants which will go to seed readily even when exposed to mild conditions. In a mild winter, the individuals with a tendency to bolt go to seed, those that have greater requirements of low temperature do not. Thus, if seed production is carried on in regions with mild winters, there

will be a tendency for the variety to show an increased percentage of 'bolters' in subsequent years, since only those individuals with a low requirement of low temperature hours will perpetuate themselves.

The production of sugar-beet seed may thus be best carried on in regions that provide a long exposure to prevailingly cool weather, not necessarily below freezing, followed by the appropriate length of day required for this long-day plant to produce flowers and seed. These conditions may be supplied naturally by selection of appropriate regions and the adoption of suitable agronomic practices, as has been done for the development of the American sugar-beet seed industry, or may be provided partially artificially and partially by natural means, as found by Bell and Bauer (1942).

In the work conducted at Cambridge during the last 3 years (Bell, 1945), the technique of continuous light and low temperature treatment has been used in three quite distinct ways, two in direct application to the breeding work, already discussed on p. 242, and one in a study of the physiological basis of the bolting tendency. These three problems, and details of the third, are given below:

A. The isolation of strains showing extreme resistance to bolting.

B. The study of the developmental physiology of selected lines in breeding material.

C. The environmental factors affecting bolting.

Small-scale pot work in the greenhouse has been used to test various methods of inducing bolting. Exposure of soaked clusters or of young plants to low temperature in a refrigerator, followed by growth in long or short days, have been studied. So far it has been possible to observe only the stimulating effect on the early stages of bolting by refrigeration at 3° C., whether of soaked clusters or young plants. The experiments have shown very clearly the inhibitive effect of growth at high temperatures, all plants failing to produce flowers in the greenhouse, regardless of previous treatment or of growth in long or short days, when the temperature of the greenhouse rose above 65° F. or thereabouts.

Bell states that the most interesting results of these experiments have been:

(*a*) plants can be induced to start bolting in the four-leaf stage, and they have flowered and set seed in the greenhouse provided the temperature is not too high;

(*b*) refrigeration of soaked clusters appeared to have a similar effect on early growth as growing in continuous light, namely the young plants were more erect in habit, and the leaves were paler green with longer petioles and laminas than the control plants.

Plates 26, 27 and 28 illustrate Bell's experiments at Cambridge. 26a shows the equipment for controlling light exposure for pot experi-

ments. Continuous light exposure is obtained by lighting the black-out cage internally with electric light. The control, in 8-hour day, had a blacked out (but lighted) bulb in order to ensure similar temperatures. 26b shows equipment for field sowings. Each box contains a single plant culture. Material is grown in 24-hour illumination before being transplanted out of doors.

Plate 27a shows plants exposed to 8-hour day from the open cotyledon stage onwards to 1st March; no bolting has occurred. 27b shows plants exposed to 8-hour day plus electric light for the remainder of the 24 hours; photo taken on 1st March indicates bolting in each pot.

Plate 28 shows two treatments. The plants in flower were grown in continuous light, daylight plus electric, from 1st January (when they were 38-day-old seedlings) to 12th April; flowering started on 20th March. The other plants still in the rosette stage were grown in normal daylight throughout.

In addition to a German paper on bolting in beets and swede turnips (Voss, 1940b), there are a great many Russian papers that deal with vernalization by temperature and the light relationships of sugar-beet plants. This literature must await a detailed review elsewhere; it may be noted here that little success has been obtained in the vernalization of sugar-beet seed, although a response may be obtained by the exposure of one-month-old seedlings to temperatures of, for example, 3 to 5° C. for between 30 to 59 days, the longer treatments producing the highest percentage of seeding plants. The need to use seedlings rather than seed in the vernalization treatment also applies to certain other crops, for example turnips and kale.

Potatoes

The extensive literature on the environmental relationships of this crop has been fully reviewed by Driver (see Cambridge, 1943) and the photoperiodic reactions of South American potatoes described by Hawkes in the same publication (see Cambridge, 1943). (See also Werner, 1942 and Moreau, 1944.)

Driver concludes that the most favourable conditions for maximum vegetative activity are long, warm days of moderate light intensity. Flowering would seem to be favoured by long days and moderate temperatures and to be greatly depressed by short days. A long day does not markedly increase the number of flower primordia differentiated, but rather increases the number of flowers that attain maturity. Pollen from flowers of equal maturity grown under long- or short-day conditions appears to be equally fertile and capable of effecting a similar percentage of successful pollinations. The photoperiod has a lower effect once the berries have been formed, although they tend to grow faster and to have

a higher percentage of seeds under long days. Southern mountainous regions of the U.S.S.R. and the Andes region of South America are stated by Driver to be in some way especially favourable for flower production, in spite of their short days.

The economic value of the potato depends upon its production of tubers, and this is dependent upon stolon growth and the production of reserve materials. Driver finds that stolon growth is favoured by long days; under these conditions, stolons are long and there are numerous lateral and branched ones. They frequently turn their ends above the soil surface and may form leafy shoots. Stolons under short-day conditions are shorter and limited to those required for tuber formation. Very short-day types may have difficulty in producing stolons under long-day conditions and may produce a greater number under short-day conditions.

As the daylength decreases, the ability of the plant to utilize the products of photosynthesis for vegetative growth decreases more rapidly than the decrease in photosynthetic activity. There is thus a larger surplus of available carbohydrates, and tuber formation is consequently much increased. Total yield, however, depends upon total available carbohydrate; it may happen that highest yields are obtained under long-day conditions in which, although the proportion of available carbohydrate is low, the plants are so large that the total carbohydrate available may be greater than from the smaller though more efficient short-day plants. Driver concludes that the conditions most suitable for maximum tuber yields appear to be long days to stimulate vegetative growth followed by short days to turn the plant activity towards efficient tuberization, that is the conditions under which potatoes are grown in temperate latitudes where the highest yields are obtained. No explanation has been found for the fact that the commercial varieties of higher latitudes do not grow well under the conditions of low temperature and short daylength of the Andes; it is suggested that some other factor may be operating to reduce yield.

Driver's final conclusions are as follows: 'The exact cause or mode of action of the photoperiodic effect have still to be fully worked out. However, a number of relationships have been established, particularly between the carbohydrate-nitrogen ratio of the plant at different stages of development. The inability of the plant to utilize the surplus carbohydrate for growth results from an inhibition of the assimilation of nitrogen which may occur under short days, at low temperatures or under a nitrogen deficiency. All the carbohydrate may not play a part in altering the carbohydrate-nitrogen ratio, but only that which is mobile. Delayed translocation when the nights are short may lock up a large amount of carbohydrate in the leaves of short-day plants. It has been shown that there is an increase in soluble carbohydrate on flowering or

tuber formation. . . . A number of other characteristics of the plant such as cell turgor and cell acidity seem to be affected by the photoperiodic stimulus, but exactly what part they play in producing the photoperiodic effect is not clear.'

The experiments on the photoperiodic reactions of South American potatoes described by Hawkes (see Cambridge, 1943) were carried out on part of the Empire Potato Collection made by an expedition sent to the South American Andes by the Imperial Agricultural Bureaux. The clones studied came from the department of Puno in the Lake Titicaca region of Peru, and also (in the case of *Solanum demissum* only) from Mexico. The Peruvian material belonged to several distinct species. Assessments are made on the basis of tuber weight, tuber number, stolon production, time of maturity, height of plants, and flowering. The following are the conclusions reached by Hawkes.

Results for tuber weight are in general agreement with those of Russian and German workers on the South American potatoes and quite different from those of Dennis (1939). Most species give a short-day reaction, some clones appear to be day-neutral, while two clones only gave a long-day reaction. Results for tuber number do not support Hackbarths' statement (1935) that short days exert their beneficial effect on short-day plants by increasing the number of tubers rather than their average weight. In general there is no agreement between photoperiodic index for tuber weight and tuber number.

The material used can be classified into four groups on the basis of stolon production in relation to daylength:

(*a*) short stolons in short day, none in long day;

(*b*) short stolons in both short and long day;

(*c*) short stolons in short day, long stolons in long day;

(*d*) long stolons in both short and long days.

The clones examined take on the average about one and a half times as long to mature under long day as they do under short day, but the height of the plant is two and a half times as great. Short days have a depressing influence on flowering, although flowering is extremely abundant in the high Andes under short-day conditions. Hawkes considers this to be due to the fact that flowering in the potato is not dependent on a photoperiodic mechanism but rather on the quantity of light received. A 12-hour day is sufficient in the intense light of tropical mountains but not in temperate regions, where a full summer day of 15 to 18 hours is required before flowering can take place.

Hawkes compares the potato with other tropical plants such as tobacco or soybean, where flowering does depend upon a photoperiodic stimulus. It is suggested that the photoperiodic mechanism applies only to the dominant method of reproduction. In potatoes reproduction is almost

entirely vegetative and tuber production is controlled by a photoperiodic response. With soybeans and tobacco reproduction is by flowers and seed, and these are produced only in an appropriate light period. Hawkes suggests that a comparison is desirable between the potato and other tuber-bearing tropical plants.

As far as the terminology and distinction between growth and development adopted in this book are concerned, this statement would appear to be rather confusing the issue. Even though the potato may reproduce itself by tubers, these nevertheless remain a manifestation of growth rather than of development or sexual reproduction. Many other plants, for example, many herbage grasses and legumes will reproduce themselves vegetatively for an indefinite period under conditions of temperature or daylength opposite to those required for sexual reproduction. If a plant requires a long day for reproduction by seed, it is more than likely that it requires a short, or at least a shorter day for vegetative reproduction by means of tubers, stolons, tillers, rhizomes, etc.

Herbage Plants

Some of the problems that arise concerning the relationship between growth and development and the production of fodder have already been discussed in the introductory crop chapter (p. 252). The herbage value of a species depends upon the maintenance or attaining of a maximum growth peak, with as little inhibition of tillering or branch formation as possible. This maximum growth is generally attained, however, just before the plant is about to change or in the process of changing from a vegetative to a reproductive state. If the change does take place, the plants will still have value for hay up to a certain stage of development; the time of cutting in ordinary agronomic practice is chosen in such a way that the hay may be of maximum nutritive value and may yet be dried in the field without any great difficulty. If left too late before cutting, all or most of the nutrients will have been transferred to the seed.

Research on the developmental physiology of herbage plants is still in a preliminary stage. The work on timothy and ryegrass in relation to latitude (pp. 212 and 229), on the effect of light intensity upon western range grasses in U.S.A. (p. 220), and the production of highly nutritive dried grass (p. 254) has already been discussed. It is noted that one of the research projects of the U.S. Regional Pasture Research Laboratory is an environmental study of pasture plants; for this purpose it is suggested that some regional experiments should be conducted to correlate climatic data with growth, before attempting a detailed analysis and summary of the weather records in the north-eastern States. In this way it is

hoped to ascertain what part of the voluminous weather data is likely to be of direct application. In this connection, reference may again be made to the study of phenology already mentioned on p. 19, where it was indicated that the usual weather records are unlikely to provide an accurate picture of the climate to which a plant responds. Plant growth and development are dependent more upon the total number of hours at or above or below a given critical temperature than upon averages for months or other periods, and upon the length of day and/or night in direct or indirect relation to that temperature.

The early work on vernalization of herbage plants described in Joint Publication No. 1 indicated a reduction in vegetative period as a result of treatment, and also the existence of an after-effect in subsequent years. The evidence now available would not appear to support the latter claim. The behaviour of a perennial herbage plant in the third or fourth season would not depend upon the initial vernalization of the seed before they were sown, but upon the conditions under which those particular plants had been growing since the previous season, and more especially during the preceding winter. The only reasons why an after-effect might be observed are that (1) the vigour or growth rate of a plant in one season is dependent upon the severity of its treatment under grazing or cutting conditions in the previous season, and (2) an earlier flowering due to vernalization in one season may lead to increased tillering later in the same season, and to the longer exposure of those tillers to those conditions of the environment that are decisive as regards development towards maturity.

A more recent review of Russian experiments on vernalization of herbage plants has appeared in *Herbage Reviews*, 8, 199-214 (1940), covering the work of Sevčenko (1939), Lubenec (1939), and Tužihin (1939). The reviewer points out that, if vernalized and unvernalized plants of *Vicia villosa* are cut at the time of flowering of the unvernalized, these latter will be superior in forage yield. This is regarded as due to the fact that the vernalized plants had reached their maximum growth at an earlier date and that, compared on the basis of forage production per unit of time, the vernalized are superior. Such a result would be of possible value in the production of fodder from annual crops which are required to be in the ground for a minimum period, but not so desirable in pasture plants, where slower progress towards peak growth and developmental maturity would presumably increase the potential period of high production of nutritive fodder for grazing.

Tincker (1925, 1928) has studied the effect of length of day upon the growth and chemical composition of the tissues of certain economic plants with special reference in the second paper to herbage plants grown at Aberystwyth. The rate of elongation of the stem of red clover is con-

trolled by short days. Plants that possessed tall stems and flower buds before being placed under short days flowered in a 10-hour day. Several species including sweet vernal, cocksfoot, timothy and red clover, which were prevented from flowering in one season by short days, flowered earlier in the subsequent season when placed under natural conditions than did the control plants. Cocksfoot and timothy produced less dry weight of top growth under shortened days, and the leaves of these plants were rich in protein. The leaf-sheaths did not develop as did the controls, and had a lower fibre content.

Cairns has made a number of experiments on the effect of vernalization and photoperiodic induction on *Lolium perenne* (1940), *Trifolium repens* (1941) and *T. pratense* (1941a). In each case records were made of growth, forage yield, maturity, vegetative period and seed yield. The tabulated data quoted in Tables 28 to 33 indicate the type of results obtained with *Lolium perenne*. The papers on the clovers contain a similar series of tables.

Observations on the initiation of flower primordia in herbage grasses are being made at the Welsh Plant Breeding Station (Griffiths, 1945); from these it appears that, although grasses such as cocksfoot and ryegrass may be ripe-to-flower during the winter months (with no external evidence of this condition), the flower primordia are not laid down until March of the flowering year. Studies of this type have a direct application to the management of grass stands for seed production, and to the more general questions of management for grazing or hay production. They provide the physiological basis for such practices as closing fields for hay or seed at a date which will permit full reproduction and maximum yields. With the British herbage grasses, a seed production stand of grasses will generally not be grazed after Christmas. If flower primordia are not formed until late March or early April, possibly a little early spring grazing might be permissible without danger of damage to the tender primordia caused by the bite or hoof of the grazing animal. When wheat is grazed in the Southern Great Plains of U.S.A., the stock have to be removed by April 1st in order to ensure ultimate development of grain in the same season. In the south-eastern United States, it is noted that barley will provide more autumn grazing, rye more winter grazing and wheat more spring grazing, a distinction probably connected with differences in the growth and developmental behaviour of these crops.

Another relevant study is that being conducted by Crespin (1945a and b) at the Botany School, Cambridge. Crespin is concerned with the effect of cold winter temperatures on subsequent panicle emergence in *Dactylis glomerata* (cocksfoot), and on the age, morphological position, etc., of the panicle-bearing tillers. The results of this investigation being conducted on Aberystwyth S204 cocksfoot should be of interest. Tincker

TABLE 28. Perennial ryegrass: growth comparisons after chilling.

Number of days in soil	*Number of days of chilling*				*Control Plants*
	Five	*Ten*	*Fifteen*	*Thirty*	
15	Cotyledon just sprouted	Cotyledon only Average height $\frac{3}{4}''$	Cotyledon only Average height $1\frac{1}{4}''$	First leaf fully developed	Cotyledon only Average height $2\frac{1}{2}''$
20	Cotyledon only Average height $\frac{1}{2}''$	Cotyledon only Average height $1\frac{1}{4}''$	First leaf just shooting	Second leaf developed	First leaf fully developed
25	Cotyledon only Average height $1\frac{3}{4}''$	First leaf just appeared	First and second leaf fully developed	Five to seven leaves per plant	Fourth and fifth leaves developed
30	First leaf well formed	Second leaf developed	Third leaf developing	Nine to eleven leaves per plant	Seven to eight leaves per plant
35	Second and third leaf developing	Third leaf developing	Third and fourth leaves fully developed	Fourteen to sixteen leaves developed	Ten to twelve leaves developed
40	Fourth leaf developing	Third and fourth leaves fully developed	Six and seventh leaves developed	Eighteen to twenty leaves developed	Thirteen to fifteen leaves
45	Fourth and fifth leaves fully developed	Sixth and seventh leaves developed	Fifteen to sixteen leaves per plant	Twenty-five to twenty-eight leaves per plant	Seventeen to nineteen leaves per plant
50	Eighth leaf developed	Fifteen to eighteen leaves per plant	Twenty-three to twenty-four leaves per plant	Thirty-five to thirty-eight leaves per plant	Twenty-five to twenty-nine leaves per plant
55	Fifteen to twenty leaves per plant	Twenty-four to twenty-six leaves per plant	Twenty-eight to thirty leaves per plant	Vegetative growth prolific	Vegetative growth prolific
60	Twenty-eight to thirty-three leaves per plant	Vegetative growth prolific	Vegetative growth prolific	—	—
65	Vegetative growth too prolific to record as above	—	—	—	—

TABLE 29

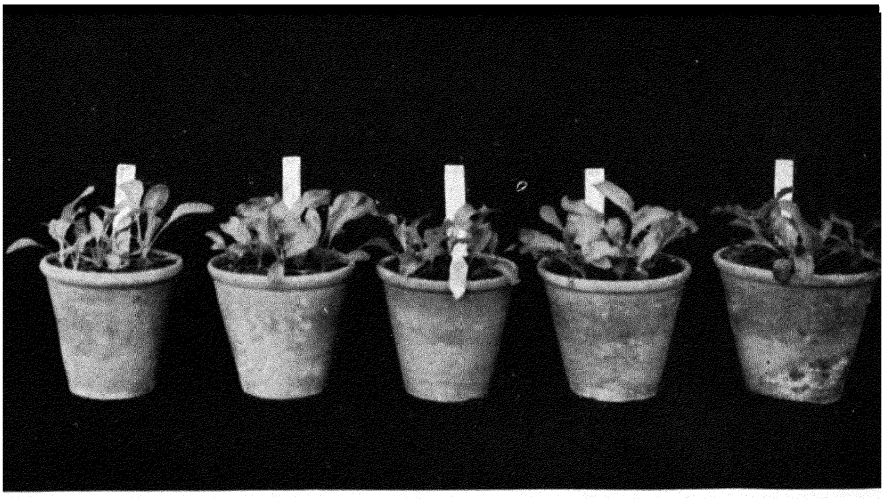
Perennial ryegrass: weight of forage after chilling

	Weight of forage, in grams	*Average weight*	*Percentage increase over controls*
Number of days of chilling:			
5	45·6, 35·0, 27·5, 46·5, 35·3, 38·2, 37·6, 36·4, 37·3, 38·5, 39·8, 40·2, 35·6, 34·7, 37·5	37·7	—12·5
10	92·0, 68·1, 86·2, 60·8, 51·7, 72·9, 52·4, 82·3, 69·0, 71·5, 75·4, 70·4, 72·3, 65·6, 68·1	70·6	+63·8
15	36·0, 33·1, 25·8, 38·7, 37·8, 35·8, 39·6, 26·2, 37·1, 33·8, 27·2, 36·5, 32·4, 34·6, 30·5	33·7	—21·8
30	75·5, 61·5, 54·0, 64·8, 55·9, 63·8, 63·1, 60·5, 60·0, 62·1, 64·3, 62·5, 72·5, 58·4, 56·3	62·3	+44·5
Control Plants	46·1, 42·8, 36·7, 39·4, 56·0, 37·8, 49·2, 52·0, 29·1, 44.4, 43.6, 46·5, 40·0, 38·2, 45·9	43·1	—

TABLE 30

Perennial ryegrass: vegetative period after chilling

	Length of vegetative period, in days	*Average*	*Days earlier than control*
Number of days of chilling:			
5	110, 128, 139, 140, 151, 153, 137, 135, 130, 142	136	—11
10	105, 134, 136, 116, 126, 143, 131	127	— 2
15	118, 114, 126, 110, 123	118	+ 7
30	119, 121	120	+ 5
Control Plants	99, 127, 100, 119, 135, 123, 134, 125, 136, 121, 138, 142	125	—



(*a*) Plants exposed to 8-hour day from open cotyledon stage to March 1; no bolting.



(*b*) Plants exposed to 8-hour day plus electric light for the remainder of the 24 hours; photo taken March 1 indicates bolting in each pot.

PLATE 27. Effect of daylength on sugar beet (see pp. 242 and 280). Photos: G. D. H. Bell.

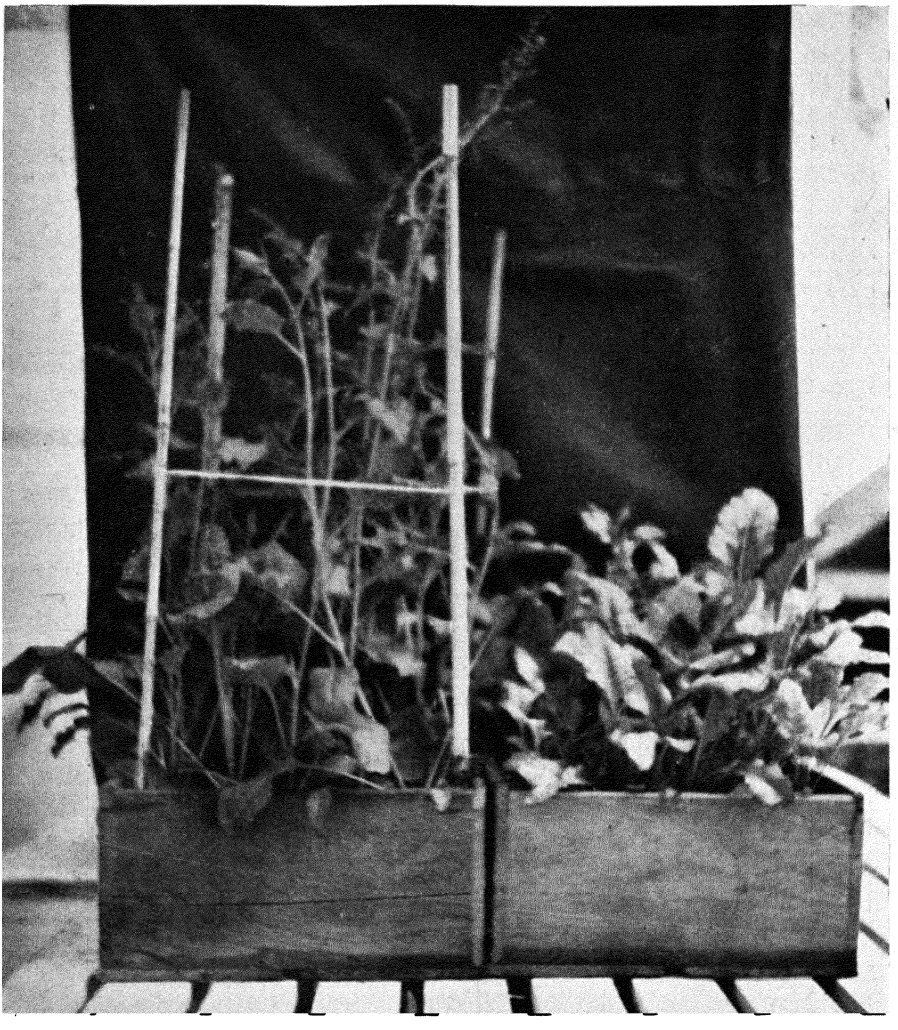


PLATE 28. Effect of daylength on sugar beet (see pp. 242 and 280). Photo: G. D. H. Bell. Left: Plants in flower grown in continuous light from January 1 to April 12; flowering began on March 20. Right: Plants still in rosette stage grown in normal daylight throughout.

TABLE 31

Perennial ryegrass: growth comparisons after photoperiodic induction

Number of days in soil	*Number of days of short photoperiod*			*Fifteen days complete darkness*	*Control plants*
	Five	*Ten*	*Fifteen*		
15	—	Cotyledon only Average height ¾″	Cotyledon only Average height 1½″	First leaf, ½″ long	Cotyledon only Average height 1½″
20	Cotyledon only Average height ½″	Cotyledon only Average height 1¾″	First leaf half developed	First leaf developed	First leaf developed
25	Cotyledon only Average height 2″	First leaf half developed	First and second leaves developed	Second leaf developing	Fourth and fifth leaves developed
30	First leaf developed	Second and third leaves developed	Second and third leaves developed	Third leaf developed	Seventh and eighth leaves developed
35	Second and third leaves developed	Third and fourth leaves developed	Fourth and fifth leaves developed	Sixth and eighth leaves developed	Ten to twelve leaves per plant
40	Fourth and fifth leaves developing	Fourth and fifth leaves developed	Seven to nine leaves developed	Twelve to fifteen leaves developed	Thirteen to fifteen leaves per plant
45	Sixth and ninth leaves developing	Fifth and sixth leaves on all plants	Thirteen to fifteen leaves per plant	Twenty-one to twenty-three leaves per plant	Seventeen to nineteen leaves per plant
50	Sixteenth and seventeenth leaves developed	Fifteen to seventeen leaves per plant	Twenty-eight to thirty-one leaves per plant	Thirty to thirty-five leaves per plant	Twenty-eight to thirty leaves per plant
55	Twenty-eight to thirty leaves per plant	Thirty to thirty-three leaves per plant	Vegetative growth prolific	Vegetative growth prolific	Vegetative growth prolific
60	Forty to forty-five leaves per plant	Vegetative growth prolific	—	—	—
65	Vegetative growth too prolific to record as above	—	—	—	—

TABLE 32

Perennial ryegrass: weights of forage after photoperiods

	Weight of forage, in grams	*Average weight*	*Percentage increase over controls*
Number of days of short photoperiod:			
5	38·7, 38·1, 29·8, 36·1, 42·5, 40·0, 44·4, 36·2, 38·5, 38·8, 39·2, 45·5, 40·5, 31·0, 37·4	38·4	—10·9
10	20·0, 36·2, 25·7, 41·9, 24·5, 20·1, 27·9, 28·0, 28·4, 30·4, 32·4, 24·5, 26·5, 27·0, 29·2	28·1	—34·8
15	34·7, 45·5, 27·5, 36·0, 35·6, 36·5, 40·1, 31·0, 35·2, 40·5, 35·8, 31·2, 36·2, 34·2, 37·4	35·8	—16·9
Fifteen days of complete darkness	49·1, 32·1, 37·7, 35·4, 38·4, 46·9, 37·5, 30·2, 39·7, 34·4, 41·7, 42·6, 35·4, 43·8, 33·2	38·5	—10·7
Control plants	46·1, 36·7, 42·8, 39·4, 56·0, 37·8, 49·2, 52·0, 29·1, 44·4, 43·6, 46·5, 40·0, 38·2, 45·9	43·1	—

TABLE 33

Perennial ryegrass: vegetative period after photoperiod

	Length of vegetative period, in days	*Average*	*Days earlier than controls*
Number of days of short photoperiod:			
5	110, 132, 140, 124, 154	132	—7
10	117, 120, 119, 129, 139	125	0
15	No plants flowered	–	–
Fifteen days of complete darkness	No plants flowered	–	–
Control plants	142, 99, 127, 119, 121, 123, 125, 134, 138, 136, 100, 135	125	–

(1925 and 1928) subjected year-old plants of various strains of cocksfoot to 12, 9 and 6-hour days from February onwards; the plants were examined after the summer and no signs of panicle primordia were found on those subjected to a 9- or 6-hour day. As many of Crespin's plants have numerous primordia by February, it should be considered whether Tincker removed some of the primordia in cutting the plants to 1·5 to 2 cm. above the ground. Some American results indicate that no heading occurred in cocksfoot plants grown for 6 months under a 16-hour photoperiod in a greenhouse; when pre-conditioned by being grown in short days and low temperature in winter for 2 to 3 months, heads were produced after removal to the 16-hour day in the greenhouse. This behaviour is analogous to that utilized by the Russians in their breeding work with herbage grasses (see p. 244), and to the flowering of a late strain of perennial ryegrass at the Welsh Plant Breeding Station 3 months ahead of schedule, after exposure to the natural conditions of the Welsh winter followed by transference to continuous light plus the temperature of a centrally heated room.

The work at the U.S. Regional Pasture Research Laboratory has already been noted. Sprague (1943) has reported on a study of the effects of temperature and daylength on seedling emergence and early growth of Sudan grass, brome grass, cocksfoot, meadow fescue, timothy, Kentucky bluegrass, browntop and Ladino white clover. This study is comparable with that already reported by Brown (see Missouri Agric. Exp. Sta., 1939) who observed the temperatures at which certain herbage plants would grow. Sprague, however, combined daily alternating temperatures of 40 to 55°, 55 to 70°, 70 to 85°, and 85 to 100° F. with daylengths of 9 and 16 hours. Temperatures between 55° and 85° F. were generally favourable for germination and increase in dry matter. Sudan grass alone maintained its emergence and growth at 85 to 100° F. and lost weight at 40 to 55° F. In all species the dry matter produced, the height of the tallest leaf on each plant, and the ratio of root to top were lower under a 9-hour day as compared with a 16-hour day. This study is concerned only with the relation of growth to the environment, and does not show the type of conditions required for development.

A study of the biochemical processes in herbage grasses, including timothy, from the first leaf to flowering, and taking catalase as an index, has shown the shifting of the centres of life processes from one organ of a plant to another during the process of development. There were indications of a very definite localization of oxidation-reduction processes in the leaves in the early part of their development, and in the stems and especially in the reproductive organs in the later periods (Čepikova, 1941).

Text Figs. 46 to 48 are reproduced from a paper by Olmsted (1943) on

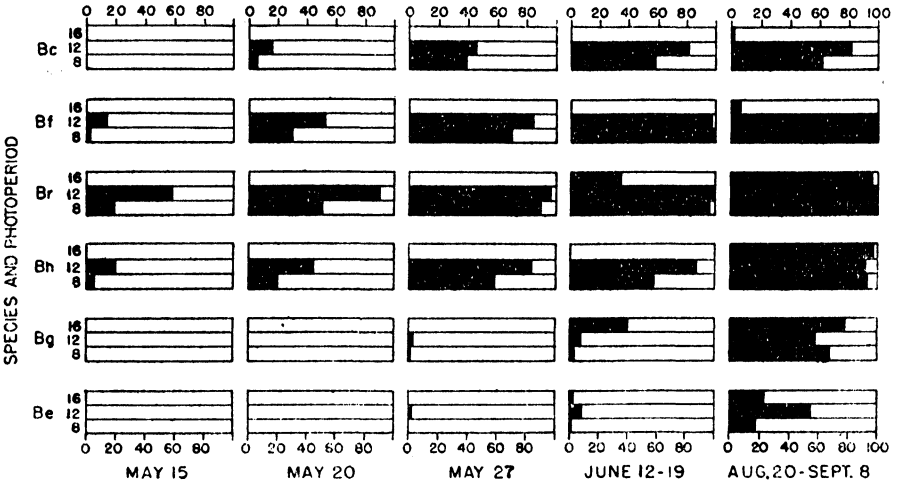


FIGURE 46

Photoperiodic responses in the range grass genus, *Bouteloua* (Olmsted, 1943). Percentages (shaded) of plants in flower (inflorescence emergent above surrounding leaf sheath) of six species, subjected to photoperiods of 16, 12 and 8 hours per day after germination on 6th April. Bc = *B. curtipendula*; Bf = *B. filiformis*; Br = *B. rothrockii*; Bh = *B. hirsuta*; Bg = *B. gracilis*; Be = *B. eriopoda*

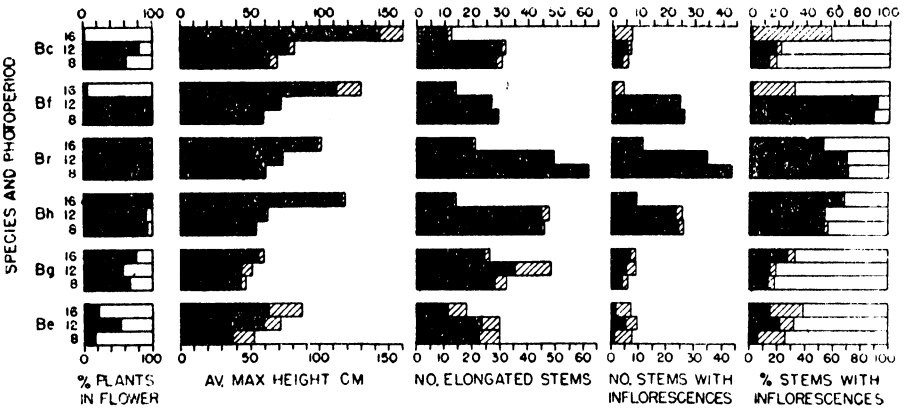


FIGURE 47

Growth and flowering of six species of *Bouteloua*, subjected to photoperiods of 16, 12 and 8 hours per day after germination, and harvested when 4½ to 5 months old. Solid black bars are averages of 60 plants (100 for *B. eriopoda*) for each species on each treatment; solid black bars plus hatching are averages of all plants which flowered on each treatment. Species as in Fig. 46 (Olmsted, 1943)

the photoperiodic responses in six species of *Bouteloua*, a genus of great economic importance in the western United States, where several of its species contribute largely to the forage supply on many native ranges, and where some of them show great promise in artificial reseeding of denuded range lands. The characters for which data are given in the diagrams are therefore of considerable economic value. The results are also of interest in connection with the spread of a species from one latitude into another and the adjustment in photoperiodic reaction that then becomes necessary (see also p. 216).

Plants grown from seed collected in Southern Arizona (with the exception of *Bouteloua gracilis* from Montana, 13° in latitude north of the

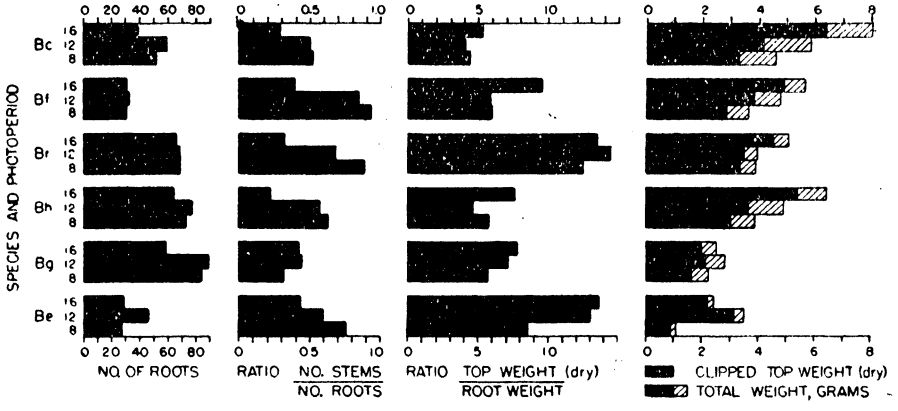


FIGURE 48

Growth of six species of *Bouteloua*, subjected to photoperiods of 16, 12 and 8 hours per day after germination and harvested when 4½ to 5 months old. Species as in Fig. 46 (Olmsted, 1943)

others) were grown for 4·5 to 5 months after germination on April 6th in photoperiods of 16, 12 and 8 hours in a greenhouse. Reciprocal transfers were then made among treatments, with or without simultaneous clipping of the tops, and the plants were allowed to grow for another 4 to 6 months. The strains of *B. filiformis* and *B. curtipendula* are 'typical' short-day plants, most individuals failing to flower in a 16-hour photoperiod; their critical photoperiod is between 14 and 14·5 hours. The other four species made less decisive flowering responses. Those with strains from Arizona were considerably delayed in flowering in the longest photoperiod and should probably be regarded as short-day plants. The strain from Montana was more or less indeterminate, with some long-day tendencies.

The strains from Arizona exhibited more or less typical short-day vegetative behaviour; the total number of tillers, of tillers bearing in-

florescences, and of crown roots was inversely correlated with length of photoperiod in most species; while average maximum height, average dry weight of roots and tops, and vigour of individual inflorescences were correlated positively with length of photoperiod. Olmsted concludes that the genus *Bouteloua* is certainly sensitive to photoperiod, and that its effect should be considered in interpreting growth habits of the species in nature, and in selection and breeding programmes designed to develop strains more desirable for forage production or for use in artificial revegetation of overgrazed or denuded areas.

Another comment on the adaptability of grass species within the wide latitudinal range of the Great Plains of U.S.A. is made by Rogler (1945, quoting Newell and Keim, 1943). It is recommended that only strains of southern origin should be used in Nebraska. These produce more vigorous seedlings under the short days of autumn and early spring, are more tolerant of drought and heat, possess greater vegetative vigour, and are more productive than strains of northern type. Apparently these differences between northern and southern types of range grasses are not so pronounced farther north, at Mandan, North Dakota; southern types are winter-hardy and can be used successfully in the Northern Great Plains.

As information accumulates on the developmental physiology of herbage grasses, it may become possible better to locate the latitudes or other environmental conditions optimal for growth on the one hand (for grazing, silage, soil conservation or the production of roots for crop rotation purposes) and reproduction on the other (hay, seed production). It would then be possible to breed strains even more 'pasture' in type than Aberystwyth ryegrass S23, and then to grow the pasture mixtures under one set of environmental conditions (temperature, photoperiod, etc.) and to produce the seed in another.

This double problem need not arise when pastures are established vegetatively, as with many African and other tropical grasses, or with Bermuda grass in the south-eastern United States. Coastal Bermuda grass is a new strain developed for these conditions. It has very few seed heads, and those that are produced have few viable seed (Lovvorn, 1945). This is an advantage as the grass is reproduced vegetatively and the seeds are not distributed in the manure. Finding the environment more suited to growth than to reproduction, this strain produces a larger vegetative yield than common Bermuda grass, and is used for grazing and hay.

The developmental physiology of the pasture and fodder legumes has not yet received intensive study. Much of the agronomic literature is concerned with the type and intensity of utilization that can be adopted without affecting adversely the persistence of the stand from year to year. The capacity to withstand severe grazing or defoliation depends on

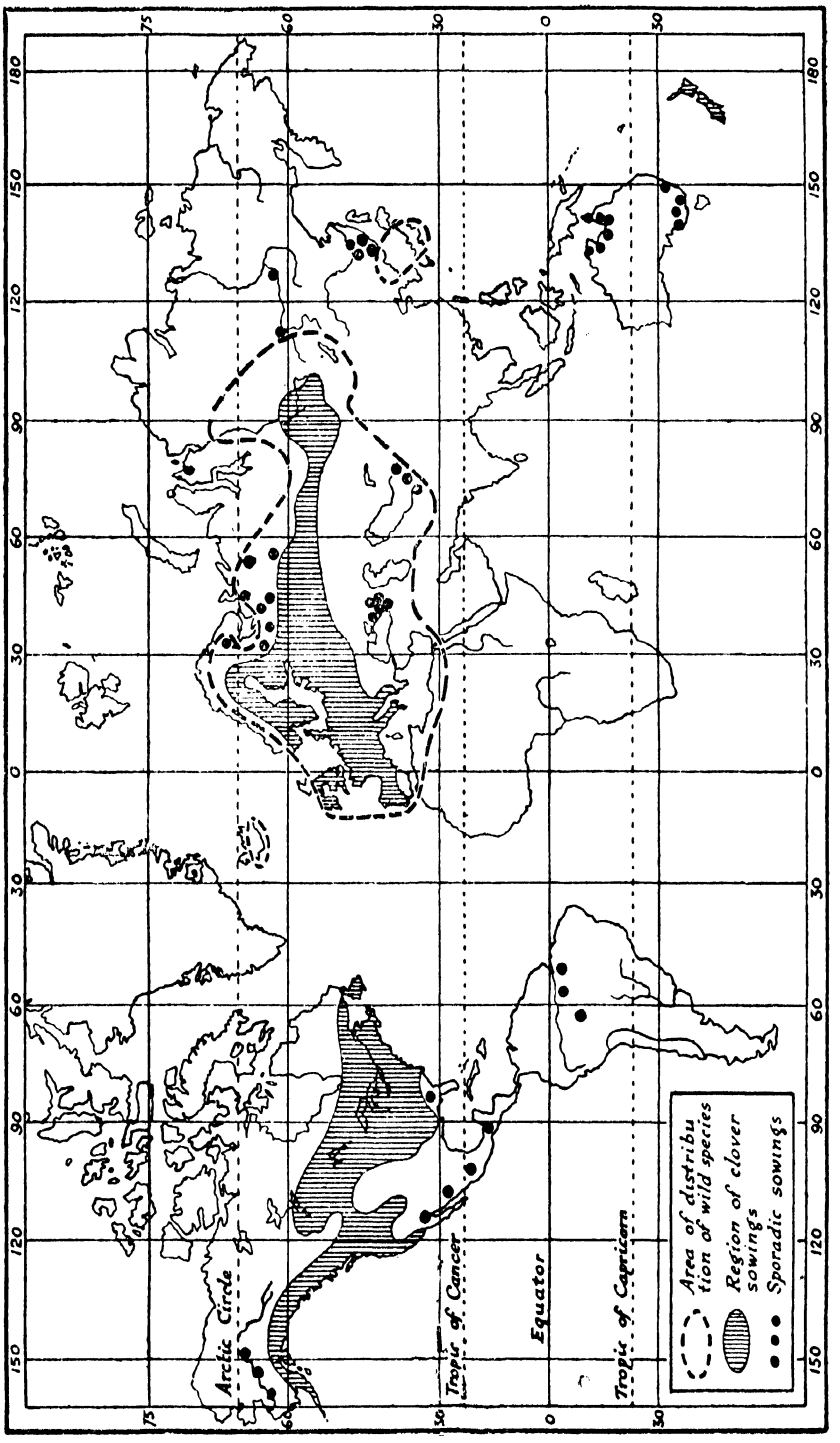


FIGURE 49

Regions of red clover (*Trifolium pratense*) sowings (Travin and Ščerbačeva, 1941)

growth habit, the ability to revive from buds placed below the cutter knife or out of reach of the grazing animal, and on the ability to accumulate stores of root reserves before the winter to meet the needs of the following spring. For maximum economic return a balance must be struck between growth and development.

The distinction between early and late flowering red clovers (the single and double-cut, or spring and winter types of European literature) is

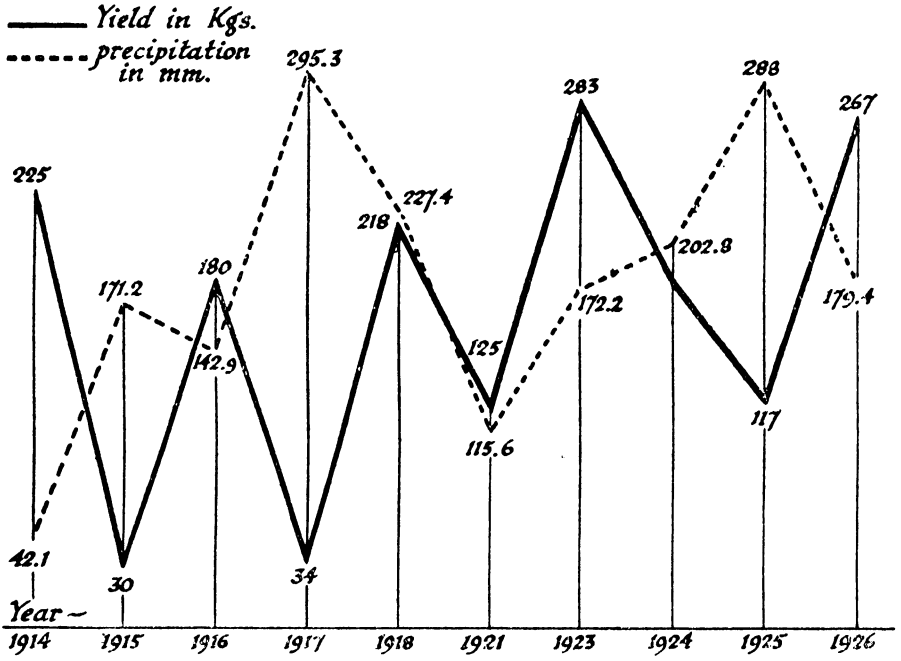


FIGURE 50

Effect of precipitation during the period of flowering on the seed yield of red clover. The weather during the vegetative period of a crop is an accessory factor of the environment which may have a considerable inhibitory effect on the yield of crops already brought into a reproductive state by the decisive factors of the environment (Travin and Ščerbačeva, 1941)

based on their developmental physiology, but an exact interpretation has not yet been given (Plate 23). An early type may produce a considerable percentage of flowers in the seeding year, and two cuts in the first harvest year. It would be desirable to know the age of the buds that produce the second cut; are they buds that have over-wintered and thus received their cold requirement, or has the type only a slight need for preliminary low temperature, in which case even physiologically young buds might be able to develop and reach maturity between the first and second cuts. It is interesting to note that it is possible to cut white clover as late as May and yet obtain a seed yield in the same season.

Plate 24 shows an area in Breconshire, Wales, used for the production of seed from the bred strain of white clover, S 100, produced by the late R. D. Williams at the Welsh Plant Breeding Station. This particular field was sown under oats in 1942 and grazed periodically. The upper photograph shows the stand before a cut was taken for ensiling in May 1943. The field was then closed for the production of seed. The lower photograph shows a portion of the flowering stand before being taken for seed in the same season. The interest from the physiological point of view is that most of the growth, and of the leaves which were capable of directing the behaviour of the growing points, was removed in the silage cut and yet a good seed yield was obtained. Were these flowers produced from basal buds which had missed the knife at the silage cut, and had already reached the necessary stage of development through overwintering?

As with grasses, so with clovers it is desirable to consider their natural distribution in relation to their area of cultivation. Fig. 49, taken from Travin and Ščerbačeva's monograph on 'Red Clover' (1941), gives their interpretation of the position with regard to red clover. It would be interesting to know whether the northern single-cut and the southern double-cut forms acquire optimal economic value to the south and north respectively of the habitat which is optimal for full reproduction.

Important work in this connection is that carried out by the late R. D. Williams at Aberystwyth, and recently reviewed by his successor, Watkin Williams (1945). A map is given in this publication indicating how the cultivated strains of red clover are distributed in Europe. The cultivated early-flowering types are found south of a line which roughly corresponds to the 50° N. latitude and are therefore more adapted to warm southerly latitudes. Countries south of this line, that is France, Spain, Italy, Switzerland, Hungary and Czechoslovakia, rely mainly on early-flowering types, and, except at high altitudes in Alpine and sub-Alpine regions, few late-flowering types appear to be cultivated. North of about 60° N. the late-flowering types prevail, while between 50° and 60° N., for example, the British Isles, both early and late-flowering red clovers are grown. These facts are of great importance in the production of strains suited to a particular environment or type of use.

CHAPTER XIX

DEVELOPMENTAL PHYSIOLOGY OF ECONOMIC CROPS (*cont.*)

Vegetables

Reports of experiments upon vegetables and related crops are accumulating rapidly. A review by Milthorpe and Horowitz (1943) attempts to define the environmental conditions that determine whether plants such as onions, beetroot, cabbages and lettuces produce the vegetative organs required for marketing, or premature seed heads in a vegetative crop, or a crop of seed for reproduction of the line. There is, of course, a close resemblance between sugar beet and the vegetable and fodder root crops such as carrots, parsnips and mangolds as far as the manifestation of growth and/or development is concerned. In making their summary, reference is made to work on carrots (Barnes, see Cornell, 1936, see also Sakr and Thompson, 1942), cabbage (Boswell, see Maryland, 1929, Miller, see Cornell, 1929b), beet (Chroboczek, see Cornell, 1934), onions (Jones and Emsweller, see California, 1939, Magruder and Allard, 1937, Thompson, 1934, Thompson and Smith, see Cornell, 1938), tomato (Kraus and Kraybill, see Oregon, 1918, Nightingale, Schermerhorn and Robbins, see New Jersey, 1928, Watts, see United States Dept. Agric., 1931), spinach (Knott, see Cornell, 1939), celery (Thompson, see Cornell, 1929a) and lettuce (Thompson and Knott, 1933).

Milthorpe and Horowitz conclude that the most favourable conditions for the initiation of seed stalks in beet are temperatures of 40 to 50° F. and long days; temperature is the more important factor. The most satisfactory results are obtained by growing beet for 2 to 3 months before exposure to cold, or by storing the roots at temperatures of 40 to 50° F. for 2 months before planting, if the temperature after planting is likely to be high.

Seeding in cabbage is influenced chiefly by exposure to low temperature; the length of day is stated to have no effect. Carrots require exposure to low temperatures (40 to 60° F.) for about 2 months for the initiation of seed stalks, their temperature and photoperiodic requirements being very like beet. A serious check in growth of celery, produced by freezing temperatures, crowding or soil drought, delays or entirely prevents the formation of seed stalks. If seed are required, it is recommended that, in mild districts, the crop should be planted so that it will

mature before winter; after experiencing the low winter temperatures, it will run readily to seed in the following spring.

Milthorpe and Horowitz state that there are differences in the behaviour of varieties of lettuce as regards seed and head formation (see also p. 239 and Rudorf and Stelzner, 1934). Exposure to low temperature for 10 to 20 days at 40° F. during germination and early growth stimulates seed stalk-production, if such conditions are followed by high temperatures and long photoperiods. Germination at 70 to 80° F. followed by low temperature gives a marked increase in fresh weight and thus in marketing value. A similar result may apparently be obtained under short days, as these favour the development of rosettes of leaves and increase the head weights.

Gray (1942) found that plants obtained from seed that had been germinated and given 28, 42 and 56 days' exposure to 5° C. all produced flowering stalks 14 to 20 days earlier than the controls. Simpson (1943) found that when moistened seed were kept at 2 to 8° C. for 16 days, the plants from them formed flowering stalks 20 days earlier than the controls and were ready for harvesting for seed 26 days ahead of the controls. The date of hearting was not affected, but the plants from vernalized seeds remained in the hearted condition for only 4 to 5 days, compared with approximately 26 days for the control. Again we have an example of the need to adjust those environmental conditions that govern development or growth according to the economic product in view. Vernalization is of no value for market gardeners, but may be useful in the production of lettuce seed.

A somewhat neglected group of plants in photoperiodic studies are those that cannot be clearly classified as either long or short-day types. Danielson (1944) selected the commercial strain of *Cucumis sativa* known as the small gherkin as a plant of this indeterminate type, and grew plants in contrasted diurnal photoperiods of 8, 12 and 16 hours. Quantitative and qualitative determinations of growth and development were made at intervals on vines from which all lateral branches and flowers were removed as formed. Stem elongation was retarded by 16-hour day, and was maximal in 8-hour day. Contrasted vegetative responses became especially obvious with onset of flowering, suggesting that the photoperiodic reaction of the stem is in some manner physiologically related to, if not dependent upon the onset of flowering itself. Maximum number of staminate flowers was produced in the 8-hour day. Quantitative measurements of stem, leaf, and root growth as well as chemical composition showed that vegetative responses peculiar to each daylength occurred.

There is also a considerable amount of other literature on onions, tomatoes, and spinach awaiting a detailed review (Fry, 1942, Goodall

and Bolas, 1942, Litvinov and Lukjianov, 1938, Danielson, 1941, Filev, 1939, Withrow and others, 1943). It is desirable to give now, however, an account of the physiological investigation of the onion plant begun in 1940 in the Research Institute of Plant Physiology, Imperial College of Science and Technology; the work has been conducted at the Imperial College Laboratory, Rothamsted Experimental Station, and this account is based on that published by Heath (1945). This work on the onion is the most comprehensive study yet made of a bulbous type of plant; the technique of forcing bulbs for flower production developed by Blaauw, van Slogteren and their associates has been reviewed by Purvis (1937 and 1938).

Onions

The primary object was to discover the causes of 'bolting' (flowering) in onions grown from sets and the most satisfactory methods of control. As the work developed, investigations on the mode of production, storage and use of onion sets have been carried out. The practical recommendations are being dealt with by the investigators in another publication; the present account is concerned with the physiological effects of the factors of daylength and temperature, and their interactions, in controlling the developmental morphology of the onion plant—especially the processes of bulb formation, and flower initiation and development.

Onions are grown in practice from seed sown in the open, from transplanted seedlings, or from sets (small bulbs, produced from seed in one season, stored dry through the winter and planted out in a second season to give a crop of large onions). Before the war considerable quantities were imported, mainly from southern Europe. Their chief disadvantage is their marked tendency to bolt; the bulb produced is then generally small and of little value. The chief practical interest has therefore been the preventing of flowering. Bolting may be prevented in a number of ways but there is little doubt that the most practical method lies in the use of suitable varieties (Cornell, 1938, and Holdsworth, 1945) and sets of suitable size (Heath, 1943a). Selection of low bolting strains has been carried out and re-selection work is being continued.

A brief description will first be given of the normal life history of an onion plant, covering growth and development from seed to mature harvested bulb, through two growing seasons and the intervening storage period. The development of the seedling (before bulb development) has also been described by Hoffman (1933) and that of the flower by Jones and Emsweller (1936).

Plates 2 and 3 reproduced from Heath (1945) and Heath and Mathur (1944) illustrate the growing points of the onion in the early stages. Plate 2a is a longitudinal median section of a four-leaved onion seedling

before bulb development. Note the sheaths of the first three emerged leaves surrounding the neck and, in the upper part of the figure, the blade of the fourth forming a solid core. Three unemerged leaf initials can be seen in the centre, each with the tip of its blade in the pore of the preceding leaf; two adventitious root initials can be seen on the left.

Plate 2b is a longitudinal median section of an onion set in the vegetative condition. Counting from the left, the following parts may be seen: lower portions of (i) the shrivelled base of one emerged leaf, (ii) the swollen base of another, (iii) the swollen bases of two unemerged initials now bulb scales, (iv) the unswollen bases of two others also bulb scales; then the sheathing base and pore of the oldest leaf initial which would form a leaf blade on sprouting; finally the four youngest leaf initials and the terminal growing point. In the stem can be seen the vascular bundles from the leaves, surrounding the central pith.

Plate 3a is an enlargement of the central portion of 2b, showing again the growing point in the vegetative state. Plate 3b is a longitudinal section of an onion set after initiation of an inflorescence, showing the terminal growing point raised on an elongation of the axis (the scape) and surrounded by the spathe within which a bract has developed; also the lateral bud, in the axil of the innermost leaf initial surrounding the inflorescence.

DEVELOPMENT FROM SEED TO SET

At germination, the cylindrical cotyledon emerges, and through a pore near the bottom the first foliage leaf later protrudes. Each foliage leaf in turn emerges through a similar pore in its predecessor; the pore thus marks in each leaf the junction of the cylindrical leaf 'blade' and the cylindrical sheathing leaf base. During development, the first formed portion of the leaf initial gives rise to the pointed embryonic leaf blade. This expands both longitudinally and centripetally, over-arching the axis; at the same time the embryonic leaf base extends round the growing point and completely surrounds it at a very early stage. The pore is thus left on the side of the axis opposite to the tip of the leaf blade, and as the phyllotaxy is alternate is thus in the correct position for the emergence through it of the next leaf in succession (Plate 2a). The leaf blade is at first solid, and becomes hollow only after emergence by the formation of a lysigenous cavity.

Before the onset of bulbing, new leaves emerge about once a fortnight, at ordinary summer temperatures, and there are generally three unemerged leaf initials to be seen at the growing point on dissection (Fig. 1). Under short-day conditions (less than about 12 hours) the plant can apparently continue growing and producing new leaves indefinitely in this way without bulb formation. The older leaves die off; the pseudostem or neck, formed of thin concentric leaf bases enclosing a practically

solid core of growing leaf blade, becomes gradually thicker and longer; the short basal stem tends to rot away below but grows gradually at the upper end, where new adventitious roots emerge. After a time (18 months of artificially shortened days in one experiment) an inflorescence emerges; further leaf production is then carried on by an axillary bud: this mode of growth without bulb formation can continue for more than 3 years.

Under natural conditions, however, the daylength ultimately attains a critical value at which a bulb begins to form; that this is a response to the stimulus of long days is well established (Cornell, 1938, McClelland, 1928, Magruder and Allard, 1937, Heath, 1943b, Heath and Holdsworth, 1943). The critical daylength varies for different strains of onion between about 12 hours and 16 hours (Magruder and Allard, 1937) at ordinary temperatures. The effect of temperature on the photoperiodic requirements of seedlings is similar to that described below for plants grown from sets. With the onset of bulbing the sheathing bases of one or more of the *innermost of the emerged leaves* begin to swell, and this is either accompanied or followed by the swelling of the sheaths of usually three of the *outermost unemerged leaf initials*. This swelling occurs by increase in cell size and development of intercellular spaces, and without cell division.

When these unemerged initials swell to form bulb scales, they apparently suffer some irreversible change, for they lose the capacity ever to develop a leaf blade, and this also applies to one or two of the adjacent unswollen initials. Furthermore, when definite bulb development occurs, the emergence of further leaves normally ceases, immediately or soon according to the temperature (Heath, 1943a and b). This observation has proved of the greatest value in accounting for the behaviour of the onion plant under various conditions (Heath, 1943b, Heath and Holdsworth, 1945).

Although no more leaves emerge after onset of bulbing the production of leaf initials at the growing point goes on very rapidly until there are about 9 unemerged leaves of which the outermost two to four are swollen (Plate 2). Some four to six of the unswollen leaf initials are available to produce foliage leaves in the next growing season; this number varies but little with set size (Heath and Mathur, 1944) and hence the higher yields obtained with large sets, in the absence of bolting (Cornell, 1938, Holdsworth, 1945) is due to large size of parts rather than to a greater number of leaf initials ready for emergence (Heath and Mathur, 1944).

In this condition the neck of the onion plant collapses, the leaf blades falling over on to the ground while several of them are still green and turgid. This collapse can occur with abundant soil moisture, though

hastened by drought, and is due to the cessation of emergence of new leaves at bulbing. When the blade of the last leaf has fully emerged, the neck no longer has a solid core (as in Plate 2a) and thus becomes a thin-walled hollow tube formed of concentric leaf bases. This tube readily buckles under the weight of the green leaf blades, especially in wind or drought (Holdsworth and Heath, 1945).

Following the collapse of the neck the leaves die and the bulb enters upon a dormant period, which can also occur with plentiful soil moisture; if the bulb has been kept small by late sowing and close spacing it now constitutes an onion set, which is normally lifted and stored dry through the winter.

The processes of bulb development and ripening normally follow the course outlined above, once bulbing has begun. But if plants that have recently begun to form bulbs are again subjected to short days, although some individuals complete their bulb development and ripen satisfactorily, in others the process of bulbing is arrested and the emergence of new leaves begins again, some of these leaves then showing transitional forms between true foliage leaves and bulb scales; lowering the temperature may have similar effect. There thus appears to be a critical stage in bulbing beyond which the process becomes irreversible. The practical interest lies in the similar reversal of the bulbing process which sometimes occurs, under field conditions during August or September, in onion plants which have bulbed late owing to very late sowing or low temperature. The longer the harvest of such plants is delayed the worse they become.

DEVELOPMENT DURING THE DORMANT PERIOD

With ripening, activity at the growing point almost ceases; during storage at ordinary temperatures only one to two more leaf initials are formed and these mainly during the latter part of the winter (Heath and Mathur, 1944). Then, in March or April, the central axis bearing the terminal growing point begins to elongate, as the first stage in the development of a scape. At the same time, a spathe develops, and a lateral bud appears in the axil of the last leaf initial (Plate 3b). This stage of inflorescence development seems to be reached rapidly, but no further development occurs until after the set has been planted out.

Inflorescence initiation only occurs in bulbs above a certain size which varies with the variety of onion, but is of the order of 2 grm. weight or 1·5 cm. diameter. Inflorescence initials have only been found where a total of at least thirteen leaf initials has been formed at the growing point (Heath and Mathur, 1944) and this may represent the stage of 'ripeness-to-flower' (Gregory, 1936). The mode of operation of this 'size effect' is under investigation.

When inflorescence initiation occurs in a bulb as described above, the plant has necessarily been exposed to long days to enable a bulb to form. The flowering of plants kept in short days throughout, described earlier, shows that at no stage of ontogeny are long days (>12 hours) *essential* either for initiation or emergence of inflorescences. Short days (<16·5 hours) have similarly been found to be non-essential.

DEVELOPMENT FROM SET TO MATURE ONION

When the set is planted out, the eight or nine unswollen leaf initials begin to elongate, all except the outermost one or two having leaf blades; the swollen scales shrivel and later rot away. During a period of about a month at ordinary temperatures three or four leaf blades emerge in rapid succession. Thereafter the leaves emerge in serial order about once a fortnight. In due course, in the absence of bulbing and if the set was large enough to have formed an inflorescence initial, the inflorescence emerges from the sheathing base of the last leaf.

Under long-day conditions, however, renewed bulb development occurs. The critical daylength for plants grown from sets is almost certainly lower than for seedlings (Heath, 1943b), which perhaps accounts for the earlier crops from sets (Illinois, 1914). For a given daylength, bulbing is accelerated by high temperature and greatly delayed or prevented by low temperature (Cornell, 1938, Heath, 1943b, Heath and Holdsworth, 1943); thus at lower temperatures longer days are needed. There appears to be a minimum time lag of about 3 weeks between the first application of the long-day stimulus and the first external appearance of bulb development (21° to 27° C. and 16·5 hours).

If conditions are such as to produce early and rapid bulbing, inflorescence *emergence* is suppressed (Heath and Mathur, 1944). This appears to be a consequence of the stimulus to bulb formation, for at temperatures low enough to prevent or greatly delay bulbing, long days actually accelerate inflorescence emergence (Heath and Holdsworth, 1943). The acceleration is thought to be brought about mainly by a great increase in the rate of scape elongation, associated with more rapid emergence of the surrounding leaves; inflorescence initiation is apparently independent of daylength (Heath and Holdsworth, 1943). This effect of long days on elongation of the scape resembles their effect on the 'shooting' of spring cereals (Purvis, 1934). It would appear that long days always promote cell extension in the onion plant. At moderate and high temperatures, long days promote radial extension (bulbing) and limit longitudinal extension (emergence of new leaves and inflorescences); at lower temperatures such longitudinal extension is enhanced and radial extension inhibited.

Since long days combined with high temperatures prevent inflores-



ASTER (BALLS' LATE WHITE)

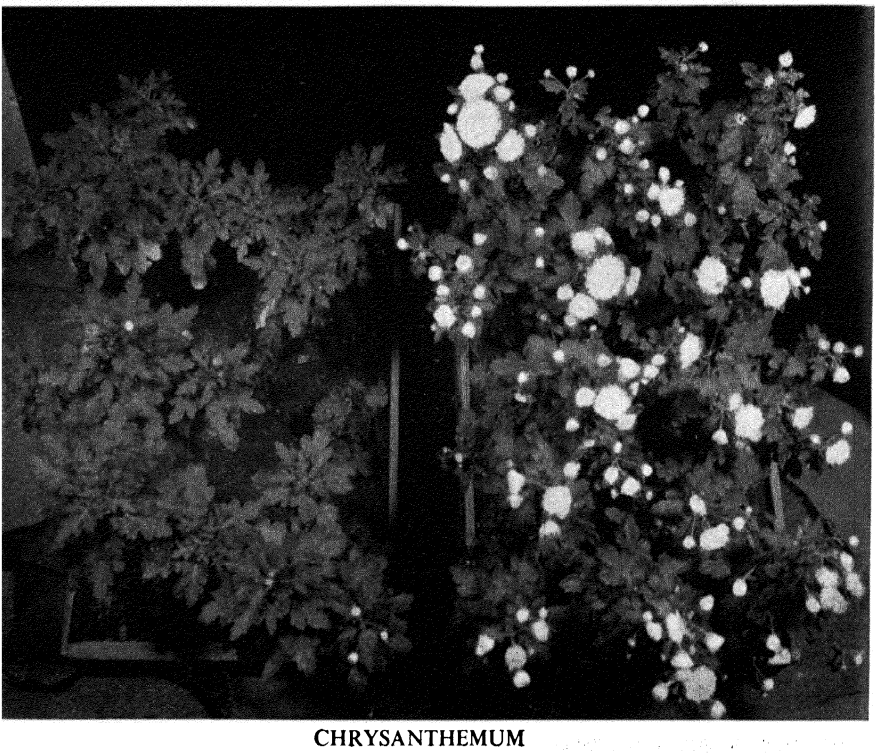


BEGONIA (LADY MAC)

PLATE 29. Effect of daylength and temperature on florist crops (see p. 318). Photos: Cornell University Agricultural Experiment Station.



CINERARIA



CHRYSANTHEMUM

PLATE 30. Effect of daylength and temperature on florist crops (see p. 319). Photos: Cornell University Agricultural Experiment Station.

cence emergence, late planting of sets in the field should and actually does reduce bolting (Holdsworth, 1945). Unfortunately this advantage of late planting is more than offset by the great reduction in yield, which is probably mainly due to the reduced leaf area caused by the cessation of leaf emergence with rapid bulbing. The small yields often given in warm seasons in Great Britain by 'early' strains of American origin, which are likely to have a low photoperiod for bulbing, may be similarly explained. Conversely, the large bulbs commonly produced by autumn sowing or spring sowing under glass may be attributed to the large leaf area produced before bulbing puts an end to the emergence of further leaves. The effects of daylength (Magruder and Allard, 1937, Heath, 1943b) and temperature (Heath, 1943b) upon ripening intensify those upon bulbing onset.

Very high temperature (21° to 27° C.) during the second season's growth not only prevents flowering by accelerating bulb development, but also exerts a direct influence even in the absence of bulbing (short days), suppressing both inflorescence initiation (Heath and Holdsworth, 1943) and the emergence of initials already present (Heath and Mathur, 1944). Such suppression without bulb development is unlikely to be of importance under field conditions in Great Britain, since high temperatures seldom occur except during the long days of summer.

FURTHER TEMPERATURE EFFECTS

Attempts to vernalize onion seed have so far given negative results, but the exposure of the seedlings to relatively high temperatures (mean about 21° C.) throughout the first season's growth results in sets which do not form inflorescence initials in the following spring (Heath and Mathur, 1944) and fail to flower when planted (Heath, 1943a and b). In the data so far obtained this effect is, however, inseparable from a size effect, for owing to more rapid bulbing such sets are smaller than those produced at lower temperatures out of doors (Heath, 1943a).

The effects of high or low temperature, during the whole or part of the storage period have proved somewhat complex. High temperature (30° C.) throughout the storage period (22 weeks) not only inhibits inflorescence initiation during storage but exerts a remarkable after-effect in preventing such initiation during the following season's growth (Heath and Mathur, 1944). Bolting may thus be almost completely controlled (Heath, 1943a). High temperature for the first 8 weeks of the storage period also exerts an after-effect in delaying and greatly reducing inflorescence initiation and flowering; high temperature for the last 8 weeks of storage, although it does delay initiation and flowering to some extent, is much less effective (Heath, 1943a, Heath and Mathur, 1944).

Subsequent work has indicated that this difference is an effect upon

emergence rather than on initiation of inflorescences: late high temperature storage by delaying bulbing allows of the emergence of inflorescences formed after planting, but with early heat treatment some of these are prevented from emerging by the relatively rapid bulbing.

It was deduced from indirect evidence (Heath, 1943b) that these effects of high temperatures were not in the main brought about by the drying of the sets, and this has been confirmed by subsequent experimentation with controlled humidities. Cold storage (0° C.) for the first 8 weeks exerts an after-effect in somewhat reducing inflorescence initiation and bolting; when given for the whole 22 weeks or the last 8 weeks only, initiation is prevented during treatment, but whereas in the former case subsequent initiation and flowering are reduced, in the latter they appear to be actually increased on return of the sets to normal temperature (Heath, 1943a, Heath and Mathur, 1944). This suggests that the onion plant is adapted to climatic conditions in which a cold spell in January-February is frequent. Greater survival in the field of sets from the late cold storage treatment points in the same direction. The greater effectiveness of early low temperature treatment in preventing inflorescence initiation is of theoretical interest in view of the fact that such initiation does not begin before March.

The formation of new leaf initials during storage is also affected by the temperature but these effects are mainly direct; the only after-effect found was a tendency for sets from treatments preventing initiation to produce initials more rapidly on return to normal temperatures (Heath and Mathur, 1944), thus resembling the effect of late cold storage on inflorescence initiation noted above.

High temperature storage not only affects initiation of inflorescence and leaves, but also exerts remarkable after-effects in delaying bulbing and ripening (Heath, 1943a, Heath and Mathur, 1944). Such delay of bulbing allows of the emergence of more leaves (Heath, 1943b), the delay of ripening gives a longer growing season, and doubled or even quadrupled yields may result (Heath, 1943). As in the case of flower initiation, the effects of early and late high temperature storage (8 weeks) differ greatly, but here the difference is in the opposite sense: early heat treatment is almost without effect on bulbing and ripening, but the effect of late heat treatment is considerable; heat treatment throughout the whole 22 weeks period has a still greater effect. The increase in yield due to delay of bulbing and ripening is greater when drying of the sets in store is prevented by combining high humidity with the high temperature. The earlier deduction (Heath, 1943b) that these effects of heat treatment were not due to drying is thus confirmed. The disadvantage of high temperature storage in that it causes shrivelling may apparently be overcome by the use of high humidities, but the delay of ripening which

causes the increased yield may itself be a disadvantage in some seasons, especially in Scotland and northern England.

The effects of the factors on flowering in the onion may be summarized as follows:

First, a direct effect of high temperature on flowering may be distinguished. Inflorescence initiation *and* emergence are inhibited, partially or completely, by exposure of the plants to temperatures above about 21° C., either during the whole period of growth from seed to set, during the whole storage period (October-March) or the earlier part, or throughout the second season of growth from replanted set to mature onion. The effect from seed to set *may* be solely due to the reduction of set size consequent on earlier bulb development; the effect in the second season is independent of daylength and hence of bulbing. When high temperature is applied during the last part of the storage period it delays but may not ultimately reduce flowering. The effects of high storage temperature are not in the main due to drying of the sets.

Very low temperature (0° C.) throughout the storage period or for the first part only reduces flowering, but low temperature for the last part only results in a sudden flush of inflorescence initiation on return to normal temperature and appears actually to increase flowering. Medium temperatures (10 to 15° C.) at any time during the life history are apparently the most favourable to flowering, except for the accelerating effect of late cold storage.

On flowering, length of day has an indirect effect associated with bulbing as well as a direct effect. At temperatures high enough to encourage rapid bulbing in plants grown from sets, long days suppress inflorescence emergence; at temperatures low enough to prevent or delay bulb formation, long days accelerate the emergence of inflorescences by increasing the rate of scape elongation. The former effect of long days may thus be considered as indirect and due to the promotion of bulb development. Daylength is apparently without effect on flower initiation, and affects only the further development and emergence of the initials.

The more important effects on bulbing and ripening are: The onset of bulbing is a response to the stimulus of long days and there is an interaction with temperature such that at lower temperatures longer days are needed. Seedlings apparently need a longer photoperiod for bulbing than do plants grown from sets. At high temperatures bulb development is rapid and the emergence of new leaves ceases abruptly with its onset; at lower temperatures one or occasionally several more leaves may emerge. With a return to short days and/or low temperature, bulbing may be arrested and leaf emergence recommence without the usual dormant period. Long days and high growth temperatures not only stimulate rapid bulbing onset and development but also expedite ripening. Bulbing

onset and ripening are delayed in plants grown from sets stored at high temperature, either throughout the winter (October-March) or for the last part only; heat treatment for the first part only of the storage period has little or no such effect. Such delay is increased if drying of the sets in store is prevented by high humidity.

Further work is now being directed towards a more rigorous analysis of the internal rather than the external factors involved in bulb development and inflorescence initiation. The importance of such factors is indicated by the striking effect of size of set; large size is the outstanding characteristic leading to bolting, and the experimental fact that artificial reduction in size by the removal of swollen leaf bases prevents or delays bolting points the way to further progress in the analysis.

Tomato

Went's experiments with the tomato have already been noted (p. 84). This plant is photoperiodically indifferent since under properly controlled temperatures (air-conditioning), the daily length of illumination

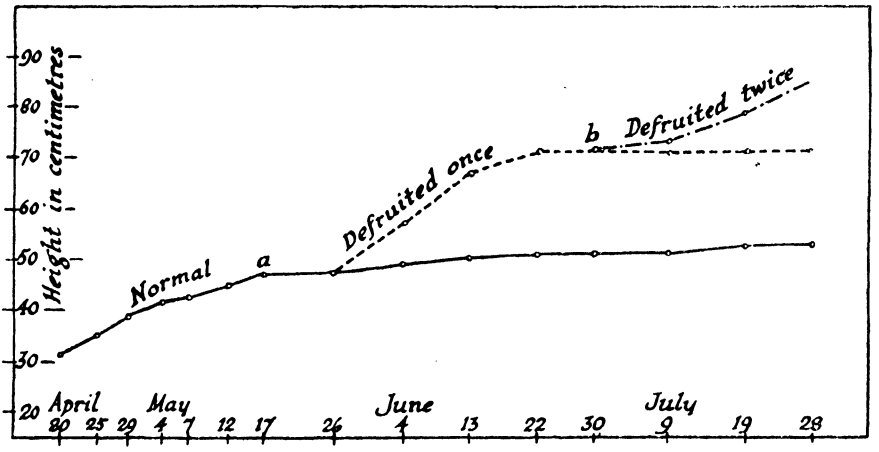


FIGURE 51

The inhibitory effects of seeds and fruits on growth. With extremely low amounts of nitrogen present in tomato plant and none coming from an external source, further growth of the stem is inhibited even by a single fruit. The terminal growing point is finally obliterated, the fruit becoming the main developing organ. Removal results in recovery of vegetative growth. First defruiting at *a*, second at *b* (Murneek, 1939)

has practically no effect on its development. For best growth and fruit set, the day temperature should be 26° C. and the night 15 to 18° C. (thermoperiodicity). The cool period for optimal development is effective only in darkness or at least greatly reduced light. Since no fruit set

possible above 22° C. and below 10° C. night temperature, tomatoes ɔ not bear fruit in winter or spring nor during hot spells in summer, ⁄en though day temperatures are within the rather wide range of pos- ble growth (15 to 35° C.). Each day sugar production by assimilation tomato leaves continues only until early afternoon, when a maximum ıgar content is reached (Went, 1945a).

In Southern California, winter and early spring night temperatures are ıually below 10°, but the afternoon temperatures range between 15° and)°, optimal for growth and fruit set. Therefore, if part of the afternoon ere changed into a functional night, by daily covering tomatoes from p.m. (war-time) onwards, no loss of photosynthesis would occur, and ı optimal night temperature would exist for a few hours.

To discover whether by these means tomato plants growing outside ıuld thus be made to produce fruits out of season, some were planted the field in the middle of November 1943. Each afternoon at 3 p.m., ılf of the plants were covered with tar paper, and uncovered next orning between 7 and 8 a.m. The first ripe fruits were harvested from e covered plants on 1st April 1944, and from then onwards they con- ıued to produce. The non-covered plants did not produce any fruits.

A more extensive experiment was started on 17th March 1944. Eight ots 9 ft. × 9 ft. were each planted to tomatoes, beets and a few other ;getables. Two plots served as controls, and were not covered, but the her plots were covered at different hours in the afternoon. On July 6th, ter an exceptionally cool spring, the plants were harvested; some re- lts are shown in Table 34.

From these data, it appears that the development of tomato plants is ɔt limited by photosynthesis, but that the use of the photosynthates is gulated by processes occurring in darkness at temperatures between ;° and 20°. This is not true for all plants, since the covering of beets ·oduced only a slight and insignificant increase in weight.

TABLE 34

Effects of Shading (fresh weight in grm. per plant)

	Stone Tomato		*Earliana tomato*		*Beets*	
	Whole plant	*Fruit only*	*Whole plant*	*Fruit only*	*Whole plant*	*Root only*
ɔntrol, not covered	304	10	420	37	126	61
ɔvered 2 p.m.–8 a.m.	433	0	545	7	62	9
ɔvered 3 p.m.–8 a.m.	1264	256	1054	272	122	37
ɔvered 4 p.m.–8 a.m.	719	101	677	121	149	67

Under certain conditions by proper treatment, the apparent efficiency of photosynthesis can be increased considerably in tomatoes. The effects of the covering were not due to photoperiodicity, but to thermoperiodicity (simulating photoperiodicity).

A gradual shift in optimal night temperatures has been noted (Went, 1945b), from 30° C. in small plants to 18° C. for the San José Canner and 13° C. for the Illinois T 19 in the early fruiting stage. A similar response has been found in fourteen other varieties, but they each have slightly different temperature characteristics. In general, the English and Greenhouse varieties grow fastest and have the lowest optimal night temperatures. Western varieties have the highest optimal night temperatures; Eastern varieties are intermediate as far as night temperature is concerned, but have the lowest absolute growth rates. When tomatoes are grown in full sunlight, their optimal night temperature is higher than on cloudy days, provided they are shaded by other plants. Incidence of virus diseases is greatly modified by both day and night temperatures.

Florist Crops

In their various papers, Garner and Allard described experiments on the response of a number of these crops to variations in daylength, and more particularly in their most recent publication described their behaviour and classified them into one of the main daylength groups adopted by them (United States Dept. Agric., 1940). As examples of practical results emanating from their work, they referred to certain practices in the cultivation of chrysanthemums and asters. Growers of chrysanthemums have forced their crops into earlier flowering by the use of black cloth to exclude light for a certain period each day, whereby the natural daylight period is shortened at a time when this is above the critical limit for flowering. Electric light has been used to supplement the shortened days for the China aster (*Callistephus*), thus forcing the plants into earlier and more vigorous flowering. These are examples of responses of short-day and long-day plants respectively. It would also appear that flowering may be artificially induced in *Calceolaria hybrida*, *Gaillardia lorenziana*, *Salpiglossis* and *Schizanthus* by increasing the daily light periods by weak artificial light.

Post (see Cornell, 1942) considers that Garner and Allard's classification is entirely inadequate unless the other conditions essential to flowering are clearly stated and understood. Daylength and temperature are regarded as decisive factors, while other incidental factors include time of propagation, supply of moisture and nutrients in the soil, humidity of the air, amount of sunshine, and supply of carbon dioxide in the air. Temperature affects the reactions of many plants to length of day and

TABLE 34

Optimal treatment of florist crops at New York latitude

Plant	*Temperature, night (F.)*		*When to use artificial light*	*Effects of long days*	*When to darken*	*Effects of short days*
	For growing	*For budding*				
Asters	50°–60°	Any temperature in long days, 75° any day-length	On seedlings, before May 1	Elongate stems, delay bud opening	First colour on buds	Cause rosetting of young plants, hasten bud opening, reduce flower size and stem length
Azaleas	Force 55°–80°	70°–90°, buds mature at 40°–55°	Never	Hasten bud opening	Never	None
Begonia semperflorens	55°–65°	Below 70°	Never	Increase growth	Never	Decrease growth
Begonia (winter-flowering)	55°–65°	Not specific	October 1	Prevent budding	Before Oct. 10	Induce budding
Bougainvillea	60°–70°	Not specific	Never	Reduce bud production	Before Sept. 20	Increase bud production
Bouvardia humboldtii	60°–75°	60°–75°	Winter	Cause budding at 60°–75°	August	Hasten bud development at 70°–75°
Browallia	60°–70°	Not specific	Never	None	Never	None
Buddleia	50°–60°	50°–65°	Never	None	Never	None
Bulbs, hardy	(Not classifiable here)					
Calceolaria	45°–60°	45°–65°	After buds show	Hasten bud development, weaken stems	Never	Delay bud development

TABLE 34 (*cont.*)

Plant	*Temperature, night (F.)*		*When to use artificial light*	*Effects of long days*	*When to darken*	*Effects of short days*
	For growing	*For budding*				
Calendula	45°–50°	Not specific	Never	Lengthen stem	Never	Reduce stem length
Calla, yellow	60°–70°	Not specific	Never		Never	
Carnations	45°–55°	Above 45°	Never	Weaken stem: hasten bud opening, reduce flower size	Never	
Centaurea	50°–60°	Not specific	At two months	Induce budding, elongate stems	Never	Prevent budding, cause rosetting
Christmas cactus	55°–75°	55°–65°	Never	None	September	Induce budding at 63°–65°
Chrysanthemums (annual)	50°–55°	Not specific	At two months	Induce budding	Never	Prevent budding, cause coarse growth
Chrysanthemum frutescens	50°–60°	Not specific	Nov. to April	Induce budding	Summer	Stimulate vegetative growth
Chrysanthemums (fall)	45°–65°	60° or above	Start August 15	Prevent budding	Before Aug. 20	Induce bud formation
Cineraria	45°–60°	Below 65°	After buds show	Hasten bud development, weaken stems	Never	Delay bud development
Clarkia	60°–70°	Above 60°	October to May	Hasten maturity, reduce production	Never	Delay maturity, increase production

TABLE 34 (*cont.*)

Plant	*Temperature, night (F.)*		*When to use artificial light*	*Effects of long days*	*When to darken*	*Effects of short days*
	For growing	*For budding*				
Cosmos	55°–65°	55°–65°	Seedlings before April	Prevent budding	Before Oct. 1	Induce budding
Cyclamen:						
Seedlings	55°–65°					
Mature plants	50°–60°	(?)	Never	(?)	Never	(?)
Delphinium (annual)	50°–60° three months, 60° 70° to mature	Above 60°	After three months	Hasten maturity, reduce production	Never	Delay maturity, increase production
Dianthus barbatus	55°–65°	55°–65°	Never	Make flowering more profuse	Never	Reduce flowering
Didiscus	50°–60° two months, 60°–70° to mature	Above 60°	October to May	Hasten maturity, reduce production	Never	Delay maturity, increase production
Digitalis	40°–70°	41°	After four months at 41°	Stimulate bud development	Never	Delay bud development
Eupatorium	60°–70°	Not specific	After August 5	Prevent budding	Before August 5	Induce budding
Euphorbia	55°–70°	58°–65°	Dec. to Jan. 20	Cause vegetative growth and bud drop	March 10 to October 10	Induce budding, prevent bud drop
Feverfew	50°–60°	Not specific	After two months	Induce budding and stem elongation	Never	Prevent budding, cause rosetting

TABLE 34 (*cont.*)

Plant	*Temperature, night (F.)*		*When to use artificial light*	*Effects of long days*	*When to darken*	*Effects of short days*
	For growing	*For budding*				
Freesia	45°–55°	Not specific	Never	Reduce flowering	Never	Increase flowering
Fuchsia	60°–70°	Not specific	Never	Stimulate flowering	Never	Reduce flowering
Gardenias	62°–65°	Below 65°	Perhaps Dec. and January	Stimulate bud maturity	Never	Delay bud development
Genista	45°–60°	Below 65°	Never	(?)	Never	(?)
Geranium	50°–60°	Not specific	Never	Weaken plants	Never	Give stocky plants
Gladiolus	55°–65°	Not specific	Before March	Prevent bud blasting	Never	Induce bud blasting
Godetia	55°–65°	Not specific	At two months	Hasten bud development	Never	Delay growth
Heather	40° up	Not specific	In summer	Induce budding	Never	Prevent budding
Hunnemannia	60°–80°	Above 60°	During winter	Stimulate growth	Never	Reduce growth
Hydrangeas	55°–65°	Below 65°	Never	Stimulate growth weaken stem	Never	No effect
Iceland poppy (*see* Poppy, Iceland)						
Iris, bulbous	45°–55°	(?)	Never	Hasten maturity	Never	Delay maturity
Kalanchoë	50°–70°	Not specific	Before Sept. 25	Induce budding	Start Sept. 25	Delay budding
Lilies	60°–70°	(?)	Below 60°	Hasten maturity below 60°	Never	
Lupine, annual	50°–60°	Not specific	Never	None	Never	None

TABLE 34 (*cont.*)

Plant	*Temperature, night (F.)*		*When to use artificial light*	*Effects of long days*	*When to darken*	*Effects of short days*
	For growing	*For budding*				
Marguerite (*see* Chrysanthemum frutescens)						
Marigold	55°–65°	Not specific	October to April	Stimulate vegetative growth	Never	Hasten flower development
Mignonette	45°–55°	Not specific	Never	Weaken stem	Never	Strengthen stem
Morning-glory	55°–65°	63°–65°, any daylength	For flowering at 55°	Induce budding at 55°	At 70°–75°	Induce budding at 70°–75°
Nasturtium	50°–70°	50°–65°	October to April at 63°–65°	Induce budding at 63°–65°	Never	Prevent budding at 63°–65°
Nemesia	45°–55°	Not specific	Never	Cause spindling	Never	Dwarf plant
Orchids	55°–70°	(?)	Never	Hasten flowering	Never	Delay flowering
Pansies	45°–55°	Not specific	When plants are flowering	Reduce flower size and stem length, increase production	Never	Strengthen stem
Pelargonium domesticum	50°–60°	Below 60°	Never		Never	
Perennials, hardy (forced)	50°–65°	Not known	At forcing to May	Stimulate flowering	Never	Delay flowering
Petunia	55°–75°	55°–60° and 68°–75°	October to April at 63°–65°	Induce budding at 63°–65°	Never	Prevent budding at 63°–65°
Phlox, annual	55°–60°	Not specific	At two months	Induce budding, stimulate development	Never	Prevent budding, increase growth

TABLE 34 (*cont.*)

Plant	*Temperature, night (F.)*		*When to use artificial light*	*Effects of long days*	*When to darken*	*Effects of short days*
	For growing	*For budding*				
Poinsettia	55°–65°	58°–65°	October 10 and later	Prevent budding	Before Oct. 10	Induce budding
Poppy, Iceland	45°–50°	Not specific	Never	Increase production, weaken stem, reduce flower size	Never	Decrease production, strengthen stem, increase flower stem
Primula malacoides	50°–60°	Below 60° if days long	Start September	Prevent budding above 60°	Before Sept.	Induce budding regardless of temperature
Rochea	50°–60°	Below 60°				
Roses	58°–65°	Not specific	Never	Increase growth and weaken stems	Never	Delay growth
Saintpaulia	60°–70°	Not specific	Never	Increase growth	Never	Decrease growth
Salpiglossis	55°–65°	Not specific	At two months	Hasten bud development	Never	Delay growth
Salvia splendens	55°–75°	55°–60°	Never	Prevent budding above 60°	Above 60°	Induce budding above 60°
Scabiosa	50°–60°	Not specific	To May 1	Cause elongation and flowering	Never	Prevent elongation
Schizanthus	45°–55°	Not specific	Never	Induce budding, weaken growth	Never	Prevent budding, cause compact growth

TABLE 34 (*cont.*)

Plant	*Temperature, night (F.)*		*When to use artificial light*	*Effects of long days*	*When to darken*	*Effects of short days*
	For growing	*For budding*				
Snapdragons	45°–55°	Not specific	Never	Shorten and weaken stem	Never	Lengthen and strengthen stem
Stevia	40°–65°	Not specific	Never	Prevent budding	Before Sept. 25	Induce budding
Stock	45°–60°	Below 65°	When temperature is 50°–60°	Hasten bud development, weaken stem		
Sweet peas, winter-flowering	45°–60°	Not specific	Never	Increase growth, stimulate vine maturity	Never	Reduce growth, delay vine maturity
Violets	35°–50°	Not specific	Never	Produce cleistogamous flowers and vegetative growth	Before Oct. 1	Produce petaliferous flowers
Zinnias	Above 60°	Not specific	Never	Delay bud development	Never	Hasten bud development

daylength affects reactions to temperatures. Some plants do not form flower buds until the temperature is generally below 65° F. (stocks, *Calceolaria*, *Cineraria* and *Genista*); others such as chrysanthemums fail to form flower buds when the night temperature is below 60° F.

Post's recommendations for the treatment of the many florist crops discussed in his bulletin are quoted in Table 34. These are intended to apply under the conditions obtaining at Ithaca, New York; the approximate amount of artificial light necessary to give a 15-hour day at that latitude is indicated in Table 35.

TABLE 35

Approximate amount of Artificial Light necessary to give a Fifteen-hour Day at Ithaca, New York

August 15 to 30	30 minutes
September 1 to 14	1 hour 30 minutes
September 15 to 30	2 hours 30 minutes
October 1 to 14	3 hours
October 15 to November 5	4 hours
November 6 to February 1	5 hours
February 1 to 14	4 hours 30 minutes
February 15 to March 1	4 hours
March 1 to 14	3 hours
March 15 to April 1	2 hours
April 1 to 14	1 hour 30 minutes
April 15 to May 1	30 minutes

The following notes refer to Plates 29 to 31, which are reproduced from the Cornell University Bull. 787, and serve to explain the treatments given and the results obtained.

Aster, Plate 29a. The response of China asters to daylength and temperature treatments has already been discussed by Post (1934). The illustration shows how earlier flowers may be obtained by darkening the plants at any time after they are 4 or more inches high. The earlier the darkening is started, with respect to size of plant, the earlier will the plants flower, the shorter will be the stems, and the smaller the flowers. Darkening hastens the development of lateral buds if it is done when the terminal bud shows colour. A grower can darken without greatly reducing the quality of the flowers, and can obtain the maximum cut in a 10-day period. Post considers that it is the most satisfactory method of applying the short-day treatment to asters, particularly Royal and late varieties.

Plate 29a shows the aster variety, Ball's Late White, grown in a cloth house. The plant at the left received short-day treatment beginning 20th June, that on the right was in normal day (photo, 28th July).

Begonia, Plate 29b. On varieties such as Melior, Lady Mac, and Marjorie Gibbs, flower buds are started between October 10th and 20th (Post,

1936a). Longer days from October 1st did not delay flowering, probably owing to the low light intensity (10-foot candles) used. Darkening before October 10th hastened flowering in proportion to the time when treatment began before October 10th. Leaf cuttings of begonias produce small crowns and fail to develop a top rapidly until after March, probably because of the short-day period. Post suggests that the plants might develop much more rapidly if propagation were delayed until April, and time and greenhouse space might be saved thereby.

Plate 29b shows the effect of daylight on young *Begonia* plants of the variety Lady Mac. Left: leaves treated with 4 hours of artificial light in sand and after potting; centre: plant grown in normal day (New York State); right: plant grown in normal day, but 2 months older. Photos were taken March 27th.

Cineraria. Cineraria and *Calceolaria* form flower buds from December to April but only at temperatures below 60° F. (Post, 1936b). After buds are formed, the flowers develop faster when the days are longer than from December to April. Temperatures above 60° F. delay flowering if given before buds are visible. Additional light during January hastened flowering, but the long stems raised the flowers far above the foliage, a condition undesirable economically. If lights are used, they should be discontinued when the first flowers show colour. The temperature can be at 60° F. after the buds have formed, to hasten flowering. The bronze, red and pink pigments in the flowers of *Calceolaria* develop very poorly under the low light intensities and high temperatures of an ordinary home. The plant on the left in Plate 30a was grown at 50° F., that on the right at 60° F.

Chrysanthemum morifolium (*hortorum*), Plate 30b. Flower-bud formation is prevented or greatly retarded when the night temperature is 50° or lower (Post, 1940). The night temperature should be kept above 60° in the autumn until the flower buds are well developed, to obtain the maximum number of buds per stem and to prevent blindness of the vegetative shoots. High temperature reduces the intensity of colour in pink and bronze varieties. This colour intensity appears to be determined before the bud actually shows colour and is associated with the carbohydrate supply to the developing buds. High night temperatures or low light intensity produces a decrease in the reserve food and a paler colour.

Plate 30b illustrates the relation between temperature and blindness in *Chrysanthemum*. The plant on left was grown at a night temperature of 50° F., that on right at a night temperature of 80° F.

Didiscus (*Trachymene coerulea*). *Didiscus* and *Clarkia* normally flower in the greenhouse in April, May and June. When grown below 55° F. they produce thick succulent stems and large leaves and grow unusually tall, but produce no flower buds. Above 60° F. they produce

a small amount of vegetative growth and flower, and the flower stems are shorter but firmer. The left and right plants in Plate 31a were grown at 60° and 50° F. respectively.

TABLE 36

Effects of Additional Light (5 hours) and Temperature on *Didiscus*

Treatment	*One-half of flowers cut before*	*Average number of flowers per plant (15 plants)*
50° + light	May 22	15·5
50°	June 6	23·8
55° + light	May 7	33·5
55°	May 29	43·4
60° + light	April 12	29·1
60°	May 13	44·8

Genista. Plants flower in March from buds laid down in November or December. Buds are formed when the temperature is kept between 50° and 60° F. Plants in full flower placed at a minimum temperature of 65° dropped their buds and flowers within 3 to 6 days (Plate 31b). Plants kept at high temperatures during February, in order to cause buds to drop, formed a second crop of buds and flowered in May when placed in the lower temperature immediately after the first crop of buds had dropped. Growers having difficulty in holding genistas back for Easter or later may be able to do so by keeping the night temperature above 60° until 4 to 4·5 months before flowers are desired and then reducing the temperature to 50° F.

Shrubs and Trees

Ornamental shrubs, small fruits, orchard and plantation trees, and the trees grown for timber fall into one class as regards their developmental behaviour, although the ultimate economic return may depend on development or growth. Like herbage plants and other perennials, the degree to which their various parts are able to express outwardly their true physiological age and state of development towards reproductive maturity is governed largely by location of the bud on the shrub or tree; true development may be masked by factors connected with competition for nutrients, shading, and so on.

In a review of the physiological factors concerned in growth and reproduction of trees (primarily fruit trees, but applicable also to forest trees), Murneek (1940) states that a tree is a colony of more or less independent units, the branches, with varied ecological relationships in



DIDISCUS



GENISTA

PLATE 31. Effect of daylength and temperature on florist crops (see pp. 319 and 320). Photos: Cornell University Agricultural Experiment Station.

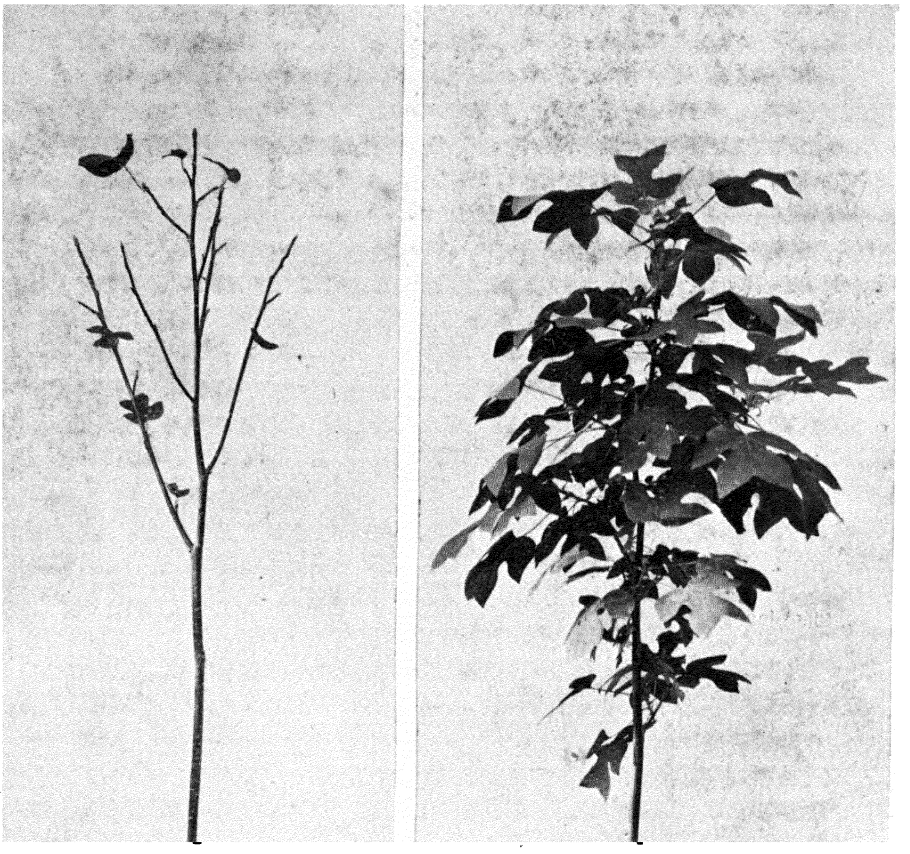


PLATE 32. Leaf fall of the tuliptree and many others may be delayed when the photoperiod is long. Photo: Bureau of Plant Industry, Soils and Agricultural Engineering, U.S.D.A.

their competition for moisture, soil nutrients, light, heat, food reserves, hormones, etc. Although this association of parts is complex, it is possible to recognize the following salient features:

(*a*) The terminal portion of a branch is usually most favourably located, is in a more juvenile and more vigorous state; it has the primary call on soil nutrients and available food reserves; it carries, and its own growth and development are directed by the largest number of best developed and most efficient leaves;

(*b*) from tip to base of a branch there is usually decreasing vigour, an increasing and then decreasing capacity for reproduction, and more senescent tissue;

(*c*) branches at the base or in the centre of the tree are starved largely because of lack of light (hence pruning to reduce the undesirable effects of excessive competition, and also to reduce the differences in physiology which exist between different parts of a tree or within the same branch).

The general physiology of a tree from early spring until late autumn resembles that of an annual plant (Murneek, *loc. cit.*). Rapid growth and development are usually followed by autumnal maturing of wood, dropping of leaves, and beginning of dormancy. Most fruit trees in the temperate zone have a biennial developmental cycle interlinked with the annual one. Flower buds are initiated in one season, and develop into flowers and fruits in the next. This overlapping of two periods of sexual reproduction and their superposition on the annual growth cycles makes the study of the nutrient requirements and the metabolism of fruit trees very complex.

The carbohydrate-nitrogen relationship plays an important part in the reproduction of trees, and the management of the land beneath the trees is therefore significant (see below). Murneek considers that nitrogen is predominant in the early stages of fruit development, hence the present practice of applying nitrogenous fertilizers early in the spring. Growth of fruit later becomes subject largely to the carbohydrate supply; most of it is currently synthesized by the leaves, thus explaining the almost direct relationship between leaf area number and fruit size.

The main aspects of sexual reproduction of trees, as far as they can be seen at present, are stated by Murneek (1937) as follows:

(*a*) There are genetically determined loci or terminal meristems where the specific (flower-inducing) hormone (tentatively named 'florigen') is concentrated and the condition of 'ripeness-to-flower' established physiologically. Frequently there may be more meristems than there is available hormone.

(*b*) With a relatively large number of meristems made 'ripe-to-flower' and having formed floral primordia, many of them undoubtedly are eliminated because of lack of essential substances for their continuous

development. Organic nitrogen compounds most likely play an important role here.

(*c*) Further elimination of a large proportion of the developing flowers takes place due to competition for available food. Far more floral primordia are usually formed than can possibly develop into functional flowers.

(*d*) Not all flowers, although reaching anthesis, will form gametes or participate successfully in fertilization for diverse reasons. If fertilization does not take place and the zygote is not present, the fruit will grow but slightly and usually will absciss promptly. That fruit development is stimulated by the embryo is a well-known fact. At least a part of this effect apparently is due to production of growth hormones in the ovule (Gustafson, 1938).

(*e*) Though the beneficial effects from fertilization and growth of the zygote are obtained chiefly by the tissues that become the fruit, other parts of the mother sporophyte may receive likewise at least a transitory stimulation (Missouri, 1926).

(*f*) In the presence of a relatively large set of fruit there is an extensive competition for available food supply and those less favourably situated or with weaker or fewer embryos absciss. Why this dropping of fruit is wave-like in some species of trees is not yet clear (Missouri, 1933).

Ringing of branches of trees in full bloom usually will increase the fruit set due possibly to an augmented supply of growth hormones. It will increase also fruit size because of the damming up above the ring of carbohydrates and other synthesized substances. Under certain circumstances the draft by the fruit on the available food resources, and possibly also accessory substances, may be so great that inhibition and even destruction of certain tissues of the parent organism may take place. Thus cyclic sterility, periodic flower development and discontinuous growth may be brought about. Cyclic flowering and fruiting of many fruit trees is a well-known phenomenon. Some tropical trees die promptly after sexual reproduction, whether this happens after a few or several years of vegetative growth.

Murneek (see Missouri, 1942) has continued his studies of the quantitative distribution and autumnal changes of nitrogen and carbohydrates of vigorous apple trees in a bearing year and draws attention to the following salient features:

(*a*) Migration of nitrogen and carbohydrates proceeds from the leaves into the twigs and then into older wood and the root system.

(*b*) Roots are the chief storage organs for carbohydrates and to a large extent also for nitrogen.

(*c*) Starch is the most important reserve carbohydrate of the apple tree. A large proportion is hydrolized into sugar with the onset of cold

weather. Hemicellulose and sugar are of secondary importance as food reserves although quantities present are considerable.

The accumulation and translocation of food reserves in the autumn have a bearing on certain orchard practices. Because of the relatively late movement of nitrogen from the peripheral regions to the main limbs and roots, Murneek recommends that pruning of dormant trees should be delayed until the latter part of winter or early spring. In this way, the nitrogen reserves of a tree will be conserved and its vitality maintained. On the contrary, summer pruning, which has now been largely discredited, will tend to dissipate nitrogen and also interfere seriously with carbohydrate synthesis.

When for one reason or another a tree is to be removed, this too should be done during the latter part of the dormant period, when one-third to a half of the nitrogen and large quantities of other reserves are in the roots. In felling a tree most of the roots are usually left in the ground, where they will decay in 2 to 3 years, releasing a considerable supply of nutrients for the benefit of adjoining or succeeding trees or other crop plants.

An interesting example of the effect of orchard floor management on the fruiting of trees has been brought to notice by Ashby (1944). The cultivators of apple orchards in the Hood River Valley, Oregon, were troubled by lack of fruiting or unreliable cropping. Kraus (of Kraus and Kraybill, see p. 23) explained this on the basis of the carbohydrate-nitrogen relationship as dependent upon the type of utilization of the orchard floor. This was treated in the following five different ways: grazing pigs, cultivation of legume, potatoes, grass, and heavy applications of N-fertilizers. In addition, heavy pruning was practised.

Fig. 52 is a diagrammatic representation of the analysis of the condition of these orchards under the different types of management. Pigs, legumes, heavy nitrogen and pruning would all shift a tree from the right hand column to the left. If a tree was not flowering because of excess carbohydrate, a slight dose of pigs, legumes or nitrogen might bring it into a flowering condition, but the movement might easily carry it too far and into the excess nitrogen column, where flowering would not occur. The converse would be true when potatoes or grass were grown.

The significance of photoperiodic response in forest tree breeding has only recently been recognized; the literature is reviewed in Imp. Agric. Bur. Joint Publ. No. 8 (1945), with reference to pines, birch and poplars. Photoperiodic response is particularly important when selecting northern genotypes for cold resistance. On transplanting these long-day forms to the short day of southern latitudes, a serious disturbance of the growth of the plant results and the trees usually become stunted and of little value. In order to correct this, long-day illumination may be supplied

artificially or long-day trees may be crossed with short-day forms in the hope of obtaining a hybrid combining the desirable qualities of the northern genotype with the short-day photoperiodicity of the southern plants.

The photoperiodic response of poplar species may be of considerable importance to breeders as the maximum rate in any type will only be achieved when it is grown under the conditions of illumination to which it is adapted. Detailed studies of photoperiodism appear to have been

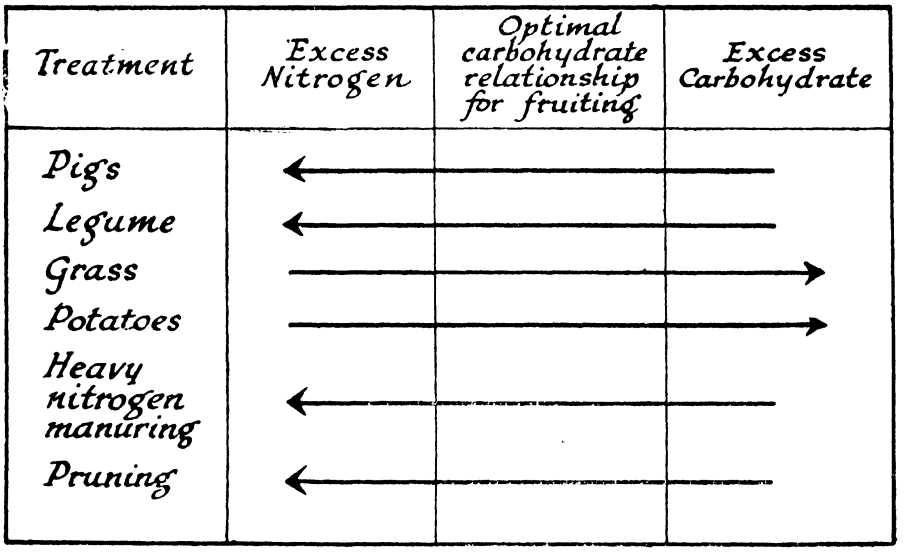


FIGURE 52

The effect of management of the land under apple trees on the carbohydrate/nitrogen relationship within the trees and therefore on fruiting. Trees in a non-flowering condition due to excess carbohydrate may still remain non-flowering even after provision of too much nitrogen in one form or another, owing to passage through the optimal range into an excess-nitrogen state

confined almost entirely to *P. tremula*; in Sweden, at least, the genotypes from northern provenances are characterized by adaptation to long-day illumination while southern races are characterized by adaptation to short days. Sylvén (1940) found that trees from Norbotten were homozygous for long-day response while those from Småland and Scania were homozygous for short-day reaction. Types from the geographically intermediate stations at Vasterbotten and Medelpad were heterozygous in respect of photoperiodic characters.

Genetical studies on the mode of inheritance of long-day response have been made. Short and long-day types were crossed and the progenies grown under the short-day conditions of southern Sweden. The F_1 hybrids were dwarfs and subsequent investigation showed that these

plants had inherited that adaptation to long-day illumination of the northern races as a dominant character. These studies demonstrate that photoperiodism must be considered when breeding programmes involving the utilization of northern aspens are undertaken. Such types often possess desirable economic characters but before they can be utilized in the production of new forms suitable for southern zones, the elimination of the undesirable long-day reaction must be effected.

CHAPTER XX

TROPICAL AND SUBTROPICAL CROPS

The environment in which tropical and subtropical crops are cultivated differs in several important respects from that of more northerly or southerly latitudes. The days are short and seasonal variations in daylight are small. There is an abrupt transition from light to darkness without a twilight of the northern type possibly suitable for development if not for growth. The temperatures of day and night are in general high, except in high altitudes or on desert fringes, and resistance to drought is a desirable character in crops growing over many regions of the tropics and subtropics.

The developmental physiology of tropical crops and natural vegetation does not yet present a complete picture. References have already been made in earlier chapters to research and experience with crops of tropical latitudes such as sugar cane. Much of the work described in this chapter has been done by Professor B. N. Singh and his colleagues or students at the Benares Hindu University, and should in the meantime be taken as applying primarily to Indian crops and Indian conditions.

There is again an absence of adequate phenological data, a point already stressed by Champion, who stated that there is a need for the study in India of the effect of climatic conditions on the average dates when plants of the same species and race enter on their various phases of growth and reproduction. Champion suggested that trees have a relative advantage over low herbs for this purpose, but noted that the planting and flowering of certain grasses, notably species of *Saccharum*, might be of value. In this connection, the work on microclimates in relation to crop production conducted by Ramdas will probably provide useful data which can be correlated with the developmental physiology. Probably under hot tropical conditions even more than under humid temperate conditions, the micro-climate in which a crop plant actually grows, and in which its growing points and active leaves are situated, differs quite considerably from that recorded by ordinary meteorological stations. Such factors as density of stand, presence or absence of irrigation, and other agronomic details have a profound effect on the climate at the plant level. Ramdas (1942) has presented a co-ordinated plan for a crop-weather observation scheme to be carried on at selected experimental farms in India, evolved as a result of a meeting of the Crop and Soils Wing of the Board of Agriculture and Animal Husbandry held at New Delhi on 20th February 1942.

Only a few isolated statements on the developmental physiology of tropical crops in general have been noted. For example, Bünning (1940), writing on his work in Java and Sumatra, states that it appears that many tropical plants are much more sensitive to photoperiodic stimuli than the plants of more northerly latitudes. Bünning notes the work of Kuilman, which indicates that the slight annual periodic variations in the length of day in the tropics are sufficient to produce strange photoperiodic reactions in rice, which have to be taken into account when selecting seed for growing in different regions. Singh and Kapoor (1939) consider that the photoperiodic classification into long-day, short-day and other types of plants suggested by Garner and Allard is, as far as tropical plants are concerned, quite empirical and inapplicable to the tropics. Many so-called short-day plants were more successful when grown in long days. The cultivation of maize, for example, in winter short days resulted in a poor yield and in some profound anomalies for which photoperiodism failed to provide an adequate explanation.

Discussing the possible application of vernalization by temperature of those Indian crops known to respond to the treatment, Sen (1940) has reviewed some technical aspects which will require to be considered before the method can become part of the routine agronomic practice of India. It is not expected that Indian cultivators will master vernalization on their own, and Sen suggests that a central station for vernalization should be opened, as most seeds can be dried, stored and distributed after vernalization without suffering damage.

With tropical as with other plants, the developmental physiology of a crop has to be related to the end product for which that crop is being grown, and above all to whether that end product is the result of growth or development, or a combination of the two. The yield of rice and the other cereals depends upon the existence of an environment promoting optimal development; the same applies to the seed production of vegetables visualized for all latitudes in the British African Colonies (I.A.B., 1943). Green manure crops such as *Crotalaria* require maximal growth, although the production of fibre from this and other fibre crops probably needs a certain amount of development.

The work of Singh, Kapoor and Choudhri (1938) may be mentioned as an example of a quantitative determination of the growth behaviour of certain crops in relation to alterations in the duration of light. The photoperiod was varied in the different sets from plants growing in complete darkness on the one hand to continuous illumination on the other. Plants of the crops used (wheat, barley, cotton, *Crotalaria*, etc.) failed to grow normally in durations of light exposure shorter than 12 hours. The occurrence of sexual reproduction is confined only to certain specific limits; below these they tend to become sterile; above them giant

growth sets in. The need for light among the different competing members of a plant society differs widely from crop to crop. Those having simpler end-products appear, according to Singh and his associates, to need less light than the more complex ones. Frequent failure of catch and subsidiary crops, as also the absence of weeds in densely growing fields, are in part attributed to after-effects of unfavourable light conditions. It was found that the superior quality of grains of cereals depends to a not inconsiderable extent on an improved light environment. Plants of more or less similar constitutions growing in different seasons of the year differ markedly in their light requirements due perhaps to seasonal adaptations.

None of the examples described below of experiments on the developmental physiology of tropical crops and crop varieties yet provide an adequate picture of relation between growth, development, and the environment for any one crop, but the general trend of the results can be seen for comparison with the non-tropical plants discussed in the preceding chapters.

Rice

The Russian physiologist, V. Skripčinskiĭ (1940a) made an attempt to interpret in terms of the phasic development theory the behaviour of rice plants in the experiments of Ramiah (1933), and more especially those of Lord and de Silva (1931) and Haigh (1935) in which changes in seeding date caused conspicuous but regular variations in the time of flowering. Using the reports of the Meteorological Station at Kandy, it is argued that the limiting factor lies in the special features of the photoperiodic response of certain native plants at the photo-phase to the seasonal variation of daylength in the tropics. It has already been noted that varieties of rice are thought to be very sensitive to slight changes in daylength.

Skripčinskiĭ considers that varieties of the so-called maha type (usually sown in August) have become adapted to gradually but persistently decreasing photoperiods in contrast to varieties of the so-called yala type (sown usually in March) which must have become adapted to gradually but persistently increasing daylength. It is therefore assumed that if sown in December and/or January the maha types will come into bloom rapidly only when the natural photoperiods are reduced to 11 hours 40 minutes or less. Skripčinskiĭ links this behaviour with that of the short-day Biloxi soybean and of late and early *Sesamum* in Rhind's experiments (1935).

The results of Japanese and other workers in the developmental physiology of rice are discussed by Beachell (1943) in an article reviewing his own experiments on the effect of photoperiod on ten out of the hundreds of varieties of rice introduced into the United States. When

varieties introduced from the tropics are grown in the Southern States, they often fail to head or head so late that they do not set seed or mature before being killed by cold.

Many tropical varieties when grown under long natural daylight periods in temperate regions make a rather vigorous vegetative growth and have a tendency to continue growth until the short days of late autumn (in southern U.S.A.). They may then head slowly and unevenly, set a few seed on comparatively long panicles, but fail to mature normally. Conversely, some late varieties from temperate regions, when grown in the tropics under a relatively short day, produce rather small plants with few tillers, bearing short panicles which set seed and mature much earlier than in temperate climates.

Certain varieties from the tropics do, however, head early enough to mature seed in the southern States and these or selections from them have proved to be well adapted for growing there. In addition, the known photoperiodic response of rice varieties can be used to control the time of heading of varieties to be used in hybridization. Information as to varietal reactions to early and late sowing can also be obtained by tests of photoperiodic response.

The varieties used by Beachell have been divided into 'sensitive' and 'less sensitive' groups according to their reactions to the covering periods. The sensitive varieties, when subjected to a daily 10-hour photoperiod at the earliest covering dates, showed a marked decrease in number of days from seeding to first heading, number of tillers and panicles, length of panicle, height of plant, and grain and straw weights. According as the date of covering was delayed, the effects became gradually less marked. The less sensitive varieties showed little or no effect on these characters for the earliest covering periods, followed by a gradual intensification of the effects for later covering dates.

Indian and Russian workers write about vernalization of rice by temperature or short day. Using the latter treatment on varieties in Bengal, Sircar and Parija (1945) obtained results of agricultural importance with a winter variety, 'Rupsail'. The flowering duration of this variety has been reduced from 133 to 47 days by 'vernalization by short days'. This is thought to be the shortest period yet reported within which winter varieties of rice will flower. Alam (1940-1) had already concluded that all varieties require a minimum period of 30 days for vegetative growth, and a subsequent period of about 30 days of short-day treatment for flowering. This acceleration noted by Sircar and Parija is applicable to the cultivation of rice in Bengal. A variety of fine rice could be grown in a much shorter time; by inducing early maturity it could escape flood; early harvesting would leave sufficient time for preparation of fields for subsequent crops in the rotation.

Two experiments on vernalization by temperature may be noted. Parthasarathy (1940) vernalized sterilized seeds in darkness or continuous light at 10 to 20° C. for 3 weeks. Those vernalized in darkness flowered 4 to 5 days earlier than the control. Skripčinskiĭ (1940b) obtained a distinct response from one variety only, British India 1220, in tests made for 3 years at the Rice Testing Station, Krasnodar. This variety eared 10 days earlier after vernalization at 6 to 8° C., and 8 days earlier after vernalization at 15 to 17° C., than the control plants grown in short day.

In addition to experiments on the relation between light and temperature and the course of development, Indian workers have also adopted a special pre-sowing treatment for inducing or increasing drought resistance. Chinoy (1942) developed the technique for wheat, and Parija (1943) has applied it to rice; water requirements for the treated plants were significantly less than for the control plants and the yield of grain significantly greater when the interval of watering was 8 days. Similar experiments have been made with jute, the effects of alternate moistening and drying and after-sowing light conditions being observed on drought resistance and earliness of flowering (Kar, 1944). There was an increased resistance to drought after treatment, but the earliness observed was due to the photoperiods following sowing.

Wheat

As this crop has already been discussed fully (pp. 257-62), it is necessary to give only references to experiments on tropical and subtropical varieties and conditions. Wheat was one of the crops used in the experiments of Singh and others on light already noted (p. 327); the variety Pusa 4 was used, and the optimal light period found to be 15 hours. The effect of agronomic practices such as variations in dates and times of sowing, different depths of sowing, different spacing and soil type on the growth and flowering time and behaviour of wheats (Punjab 8A, Pusa 52 and Pusa 165) has been studied by Singh and Alam at Lyallpur (1944). The number of days from October sowings to ripening and emergence of ears were 192 and 131, while the corresponding figures for January sowing were 125 and 83. Length of ear depends on spacing distance. The number of fertile spikelets decreases with delay in sowing (20·8 in October, 7·8 in January); spacing again affects number of spikelets. Sterility in wheat is due to thick stands, late and especially deep sowings, and later formation of tillers in individual plants. Date of sowing affects number of grains per ear to a great extent (October, 45 to 50; January, 11 to 21).

Pal and Murty (1941) state that although low temperature at the time

of germination may be indispensable for the normal development of English winter wheat, Indian wheats come into ear (without chilling) even at high summer temperatures, indicating that low temperature is not indispensable. A further indication that Indian varieties have little if any requirement of low temperature, but that response to light can be readily obtained is also seen in the experiments of Kar (1940).

Mustard

It has been noted elsewhere that a certain minimum amount of germination (growth) is essential before vernalization can be effective. This period requires to be watched very carefully in mustard, as only unsplit vernalized seeds can have any practical value. Sprouted chilled seeds have to be sown very carefully as drying is fatal for them; unsplit seeds can be dried and stored without losing their subsequent germinating capacity. Having found that chilled seeds of mustard produce plants which flower significantly earlier (Sen and Chakravarti, 1938), these workers in the United Provinces of India made experiments for 4 years to discover (*a*) the optimal conditions and period of chilling necessary to induce maximum vernalization in unsplit chilled seeds, (*b*) response of different strains, (*c*) effect on progeny, (*d*) period for which unsplit chilled seeds can be dried and stored without reversal of vernalization, and (*e*) the effect of after-sowing temperature and daylength on the developmental physiology of plants from control and vernalized seeds. The technique adopted for this vernalization has already been described (p. 250).

All five strains tested responded, the degree of response varying with variety. Seeds which sprout as well as those which remain unsplit during the period of chilling are vernalized, but for the same dose of chilling, plants from sprouted chilled seeds are earlier. The vernalization effect is not transmitted to progeny. When growth of the embryo is confined within the elastic limits of the seed coat, the chilled seeds can be dried and stored for long periods (at least 863 days) without any resultant devernalization. Under all after-sowing temperatures and photoperiods, plants from vernalized unsplit seeds flower earlier. Mustard Type 27 used in these experiments has no obligatory low-temperature requirement for the thermo-phase, plants from untreated seeds flowering even when the minimum night temperature is 20° C. or more. Partial natural vernalization can, however, be induced in Type 27 when the embryo develops under low temperature, and artificial vernalization has its maximal effect in 6 weeks. Type 27 is neither a short-day nor a long-day plant as it flowers under photoperiods of 10 or 16 hours; it is, however, not indifferent to photoperiods. Thirteen hours is thought to be the

optimal photoperiod for mustard; the optimal temperature for the photo-phase is 30° C.

Following the detailed experiments by Sen and Chakravarti outlined briefly above, Sen Gupta and Sen (1944) of the Botany Department, Presidency College, Calcutta, made observations on the effects of times of sowing, photoperiods and vernalization on the growth and development of the two varieties of mustard, Tori No. 7 and Rai No. 5. Finding no response to vernalization, these workers stated that their results did not confirm those of Sen and Chakravarti, who replied as follows (1944).

The results of the latters' experiments apply only to the five strains tested. At the discussion on vernalization held by the Imperial Council of Agricultural Research in December 1939 it was emphasized that (*a*) experimental data must be obtained to discover whether particular strains of a selected crop will or will not respond to vernalization, (*b*) to obtain this information, experiments with different strains should be undertaken in different regions, and (*c*) the study of the effect of prevailing after-sowing environmental factors of given regions on the life cycle of both vernalized and untreated seeds is essential to evaluate the practical possibilities of vernalization for Indian agriculture. With regard to the actual results of Sen Gupta and Sen, Sen and Chakravarti consider that no definite conclusions are warranted because the maximum period of chilling used was only 30 days; the fact that unsprouted soaked seeds were chilled at 2 to 4° C. for different periods does not in itself ensure that they were properly vernalized; the technique or conditions after chilling have not been described; the conclusions are based on data obtained from a single sowing of Rai No. 5 and Tori No. 7.

Gram

Low temperature applied to gram (*Cicer arietinum*) at the time of germination accelerates subsequent inception of the reproductive phase while high temperature definitely retards it. The degree of response in both cases is a varietal character (Pal and Murty, 1941).

Pillay (1944) has reported a preliminary experiment to determine whether pre-sowing low temperature treatment would induce earlier flowering and high yield in gram under the conditions of Orissa. Seeds of uniform size of the variety, Sabour Type 4, were soaked in water for 22 hours at room temperature. The smaller seeds were then placed in a kelvinator at 0 to 2° C., one lot for 7 days and another lot for 14 days. The latter seeds produced plants which flowered only 3 days earlier than the controls, and there was no significant difference in dry weight of pods and of stems.

Crotalaria

Purely physiological studies of the response of *Crotalaria juncea* to light and particularly photoperiods have been made by Singh, Kapoor and Choudhri (1938) and Singh and Singh (1939). The present interest is in the work of B. N. Singh and his associates which affects the value of this plant as a green manure or as a source of fibre.

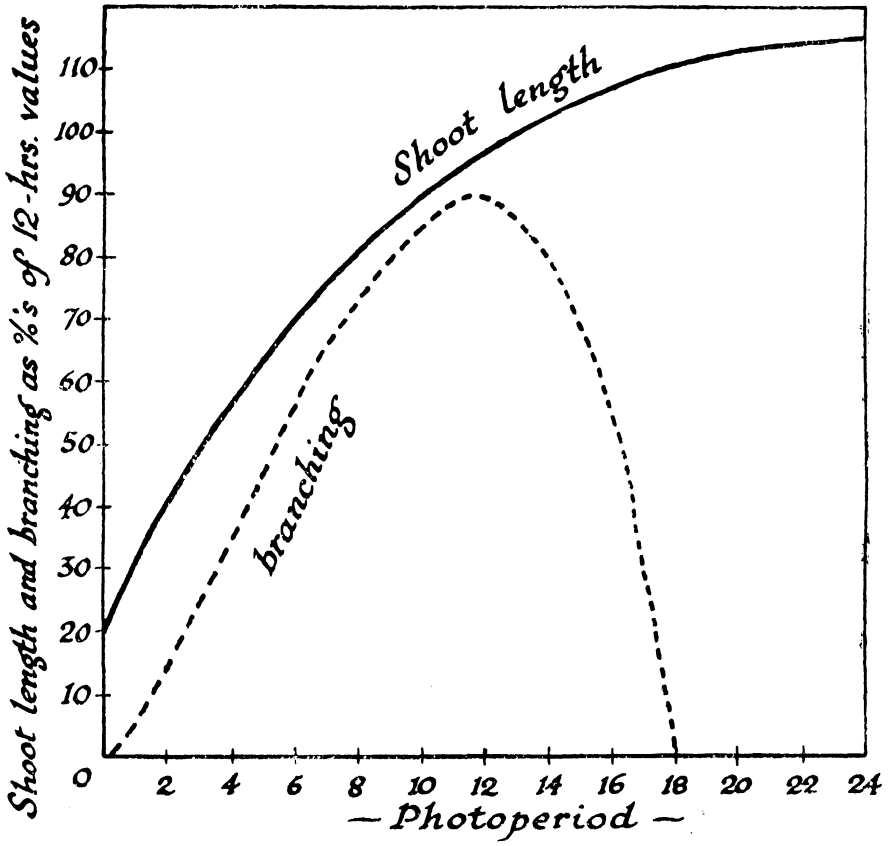


FIGURE 53

Effect of photoperiod on shoot growth and branching on the fibre plant, *Crotalaria juncea* (Singh and Choudhri, 1938)

Crotalaria is used as a green manure plant in different parts of the world. Presumably optimal growth conditions provide the greatest amount of green mass for ploughing under. The best photoperiods for growth vary from 6 to 20 hours, the best for reproduction between 11 and 16 hours. On this basis, and providing other environmental factors do not interfere, Singh, Singh and Srivastava (1937) suggest that it may

with advantage be introduced as a green manure crop in regions with long days of 16 to 20 hours (provided the crop would not then become exposed to frost injury). As the light requirements are low during the first half of its life cycle, and since the plant seems incapable of utilizing all the energy at its disposal during this early period, it is suggested that it may be suitable to sow it in mixtures with early maturing crops.

The application of the results described by Singh, Kapoor and Choudhri (1938) to the use of *Crotalaria* as a fibre plant is discussed by Singh and Choudhri (1938). Fibre length is a characteristic of great technical importance. In the studies made at the Benares Hindu University relating to this character, plants were divided into fifteen groups, each under a different photoperiod ranging from zero to continuous light. Fig. 53 gives smoothed curves for 14-week-old plants, one representing length of shoot and the other the number of branches under different daily periods of illumination. Each is expressed as a percentage of the value for 12 hours, as plants in this photoperiod most closely resembled normal plants.

Increasing illumination caused a rapid increase in shoot length until a photoperiod similar to normal daylight was reached; photoperiods above this value caused much smaller increases. Increasing illumination up to normality caused plants to form more branches, but with longer daily periods, there was a rapid decline in the number, so that with 18 hours' daily illumination no branches at all were formed.

With photoperiods less than 12 hours, both elongation and branching are retarded because the duration of light is not sufficient for optimal growth. In longer days there is a pronounced specific effect on branching. The small further elongation as the photoperiod is increased beyond 12 hours is thought to be related to the suppression of branching, probably because the materials for growth are no longer diverted to branches, but remain in the main stem. The production of high-class fibre from this crop would appear to be favoured by long days, and therefore latitude and seasonal characteristics should be taken into consideration when the cultivation of *Crotalaria* for fibre purposes is projected.

Conclusion

It will be seen that the Indian workers are playing an important part in the modern research on the developmental physiology of plants, and that they fully appreciate its potential application in Indian agriculture, where critical periods caused by drought, floods and other natural phenomena frequently make crop production a risky enterprise. India is probably the only country outside the U.S.S.R. where vernalization of crop plants has received anything approaching full and repeated trial,

and where the use of the method as part of regular agronomic practice has apparently been seriously considered. Just as from the Research Institute in South Kensington, London, we may expect further advances in our knowledge of the fundamental biological processes concerned in vernalization, so also from India it is hoped the methods of pre-treatment of crops by temperature or light will be given full trial, in order that their practical application under the extreme conditions of that country can be fully assessed.

BIBLIOGRAPHY

CHAPTER II

Aberystwyth, Imperial Bureau of Pastures and Forage Crops, 1934, Bull. 16.

ASAMI, Y., and ITO, H., 1937, *J. Hort. Assoc. Japan*, **8**, 337.

BISSONETTE, T. H., 1931, *J. expt. Zool.*, **58**, 281–319.

GARNER, W. W., and ALLARD, H. A., 1920, *J. agric. Res.*, **18**, 553–606.

GASSNER, G., 1918, *Zeitschr. Bot.*, **10**, 417–30.

GREGORY, F. G., 1936, *Sci. Hort.*, **4**, 143–54.

GREULACH, V. A., 1945, *Science*, **101**, 353–4.

KIDD, F., and WEST, C., 1918, *Ann. appl. Biol.*, **5**, 1–10, 112–42.

KIDD, F., and WEST, C., 1919, *Ann. appl. Biol.*, **5**, 157–70, 220–51; **6**, 1–26.

KLEBS, G., 1918, *Flora*, **111–12**, 128–51.

KNODEL, H., 1936, *Zeitschr. Bot.*, **29**, 449.

LANG, A., and MELCHERS, G., 1943, *Planta*, **33**, 653–702.

MARCOVITCH, S., 1923, *Science*, **58**, 537.

MELCHERS, G., 1937, *Biol. Zbl.*, **57**, 568–614.

MELCHERS, G., 1943, *Planta*, **33**, 653–703.

Missouri, Agricultural Experiment Station, 1937, Bull. 268.

MURNEEK, A. E., 1939, *Growth*, **3**, 295–315.

Oregon, Agricultural Experiment Station, 1918, Bull. 149.

PURVIS, O. N., 1934, *Ann. Bot., Lond.*, **48**, 919–55.

PURVIS, O. N., and GREGORY, F. G., 1937, *Ann. Bot., Lond.*, N.S. **1**, 569–91.

TINCKER, M. A. H., 1924, *Ann. appl. Biol.*, **12**, 440–71.

VON DENFFER, D., 1939, *Jahrb. wiss. Bot.*, **88**, 759–815.

CHAPTER III

Aberystwyth, Imperial Bureau of Pastures and Forage Crops, 1934, Bull. 16.

Aberystwyth, Imperial Bureau of Pastures and Forage Crops, and Cambridge, Imperial Bureau of Plant Breeding and Genetics, 1933, Bull. 9.

Aberystwyth, Imperial Bureau of Pastures and Forage Crops, and Cambridge, Imperial Bureau of Plant Breeding and Genetics, 1935, Joint Publ. 1.

ADLER, R., 1940, *Forschungsdienst*, **9**, 332–67.

ALMEIDA, J. M. de, 1942, *Agron. Lusitana*, **4**, 223–30.

BENNETT, O. T., 1935, *J. agric. Res.*, **51**, 451–7.
BENNETT, O. T., 1936, *J. agric. Res.*, **53**, 445–51.
BRIGGS, G. E., KIDD, F., and WEST, C., 1920, *Ann. appl. Biol.*, **7**, 103–23.
DOLGUŠIN, D. A., and LYSENKO, T. D., 1929, *Trudy Vsesojuz. S'ezda Genet., Selek., Semenovod. plemennomu Život.*, **3**, 189–99.
EVANS, M. W., and GROVER, F. O., 1940, *J. agric. Res.*, **61**, 481–520.
HARDER, R., and STÖRMER, L., 1936, *Landw. Jb.*, **83**, 401–15.
KOPETZ, L. M., 1936, *Gartenbauwiss.*, No. 3.
KOPETZ, L. M., 1937a, *Pflanzenbau*, **13**, 386–91, 417–38.
KOPETZ, L. M., 1937b, *Züchter*, **9**, 181–4.
KOPETZ, L. M., 1943, *Gartenbauwiss.*, **17**, 255–62.
KREIER, G. K., 1941, *Sovet. Bot.*, Nos. **1–2**, 39–50.
KRENKE, N. P., 1940, [The theory of the cycle of senescence and rejuvenation of plants and its practical application]. Moscow, Seljhozgiz, pp. 135.
KREUSLER, U., PREHN, A., and HORNBERGER, R., 1878–9, *Landw. Jb.*, **7**, 536–64 and **8**, 617–22.
LAIBACH, F., 1943, *Naturwissenschaften*, **31**, 246.
LAIBACH, F., and MEYER, F., 1935, *Senckenbergiana*, **17**, 73–86.
LYSENKO, T. D., 1935, Theoretical basis of vernalization. Moscow.
MCKINNEY, H. H., 1940, *Bot. Rev.*, **6**, 25–47.
MAXIMOV, N. A., and KROTKINA, M. A., 1930, *Trudy Prikl. Bot., Genet. i Selek.*, **23**, 427–78.
Missouri, Agricultural Experiment Station, 1926, Res. Bull. 90.
Missouri, Agricultural Experiment Station, 1943, Res. Bull. 371.
MURNEEK, A. E., 1924, *Proc. Amer. Soc. hort. Sci.*, **21**, 274–6.
MURNEEK, A. E., 1926, *Plant Physiol.*, **1**, 3–56.
MURNEEK, A. E., 1937, *Science*, **86**, 43–7.
MURNEEK, A. E., 1939, *Growth*, **3**, 295–315.
NOGUCHI, Y., 1929, *Tokyo Imp. Univ., Coll. Agric. J.*, **10**, 247–304.
PURVIS, O. N., 1934, *Ann. Bot., Lond.*, **48**, 919–55.
SAPEGIN, A. A., 1940, *Izv. Akad. Nauk S.S.S.R.* Ser. biol., No. 4, 451–62.
SAPEGIN, A. A., 1941, *C. R. (Doklady) Acad. Sci. U.R.S.S.*, **30**, 754–6.
SHARMAN, B. C., 1942, *Nature, Lond.*, **149**, 82.
SHARMAN, B. C., 1943, *Naturalist*, No. 807, 101–2.
SHARMAN, B. C., 1945a, Personal communication, Feb. 25.
SHARMAN, B. C., 1945b, *Bot. Gaz.*, **106**, 269–89.
SIVORI, E., and WENT, F. W., 1944, *Bot. Gaz.*, **105**, 321–9.
THUT, H. F., and LOOMIS, W. E., 1944, *Plant Physiol.* **19**, 177–30.
TOLMAČEV, M. A., 1929, *Trudy Vsesojuz. S'ezda Genet., Selek., Semenovod. plemennomu Život.*, **3**, 539–53.
VON DENFFER, D., 1939, *Jahrb. wiss. Bot.*, **88**, 759–815.
WENT, F. W., 1943, *Amer. J. Bot.*, **30**, 157–63.

WENT, F. W., 1944, Personal communication, Aug. 9.
WENT, F. W., 1945b, *Amer. J. Bot.*, **32**, 469–79.
WHYTE, R. O., 1939, *Biol. Rev.*, **14**, 51–87.

CHAPTER IV

Aberystwyth, Imperial Bureau of Pastures and Forage Crops, 1933, Bull. 9.
Aberystwyth, Imperial Bureau of Pastures and Forage Crops, 1934, Bull. 16.
AVAKJAN, A. A., and TAGI-ZADE, A. H., 1935, *Jarovizacija*, No. 1, 65–107.
BASSARSKAJA, M. A., and GROSSMAN, V. JU., 1941, *Herb. Abstr.*, **11**, S11–S17.
BONNER, G., 1890, *Rev. gén. de Botanique*, **2**, 513–46.
BONNER, G., 1895, *Ann. Sci. Nat. Bot.*, 7th series, **20**, 217–358.
BONNER, G., 1920, *Rev. gén. de Botanique*, **32**, 305–26.
BORTHWICK, H. A., PARKER, M. W., and HEINZE, P. H., 1941–2, *Bot. Gaz.*, **103**, 326–41.
BORTHWICK, H. A., PARKER, M. W., and SCULLY, N. J., 1943, *Bot. Gaz.*, **105**, 100–7.
DENNISON, R. A., 1945, *Plant Physiol.*, **20**, 183–99.
DE ROPP, R. S., 1939, *Ann. Bot., Lond.*, **3**, 243–52.
DOLGUŠIN, D. A., and LYSENKO, T. D., 1929, *Trudy Vsesojuz. S'ezda Genet., Selek., Semenovod. plemennomu Život.*, **3**, 189–99.
EFEĬKIN, A. K., 1939, *Doklady Akad. Nauk S.S.S.R.*, **25**, 308–10.
FILIPPENKO, I. A., 1940, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **28**, 167–9.
GREGORY, F. G., and DE ROPP, R. S., 1938, *Nature, Lond.*, **142**, 481–2.
GREGORY, F. G., and PURVIS, O. N., 1936, *Nature, Lond.*, **138**, 1013–14.
GREGORY, F. G., and PURVIS, O. N., 1938a, *Ann. Bot., Lond.*, N.S. **2**, 237–51.
GREGORY, F. G., and PURVIS, O. N., 1938b, *Ann. Bot., Lond.*, N.S. **2**, 753–64.
HALL, H. M., 1932, *Sci. Monthly*, **35**, 289–302.
HAMNER, K. C., 1938, *Bot. Gaz.*, **99**, 615–29.
HAMNER, K. C., 1942, *Cold Spring Harbor Symposia Quant. Biol.*, **10**, 49–60.
Imperial Agricultural Bureaux, 1935, Joint Publ., No. 1.
LEWIS, H., and WENT, F. W., 1945, *Amer. J. Bot.*, **32**, 1–12.
LOJKIN, M., 1936, *Contr. Boyce Thompson Inst.*, **8**, 237–61.
LYSENKO, T. D., 1928, *Trudy Azerbaidžan Op. Sta.*, No. 3, 168.
MARSDEN-JONES, E. M., and TURRILL, W. B., 1935, *J. Ecol.*, **23**, 443–69.
MARSDEN-JONES, E. M., and TURRILL, W. B., 1937, *J. Ecol.*, **25**, 189–212.

MARSDEN-JONES, E. M., and TURRILL, W. B., 1938, *J. Ecol.*, **26**, 359–79, 380–9.
MURNEEK, A. E., 1940, *Bot. Gaz.*, **102**, 269–79.
NAYLOR, A. W., 1941, *Bot. Gaz.*, **102**, 557–75.
OLJHOVIKOV, M. A., 1940, *Herb. Rev.*, **8**, 83–94.
PARKER, M. W., and BORTHWICK, H. A., 1943, *Bot. Gaz.*, **104**, 612–19.
PURVIS, O. N., 1934, *Ann. Bot., Lond.*, **48**, 919–55.
PURVIS, O. N., 1940, *Nature, Lond.*, **145**, 462.
PURVIS, O. N., 1944, *Ann. Bot., Lond.*, **8**, 285–314.
PURVIS, O. N., and GREGORY, F. G., 1937, *Ann. Bot., Lond.*, N.S., **1**, 569–91.
PURVIS, O. N., and GREGORY, F. G., 1945, *Nature, Lond.*, **155**, 113–14.
RUDORF, W., and SCHROECK, O., 1941, *Z. Pflanzenz.*, **24**, 108–33.
SAKR, EL SAYD, 1944, *Proc. Amer. Soc. hort. Sci.*, **44**, 473–8.
SIVORI, E., and WENT, F. W., 1944. *Bot. Gaz.*, **105**, 321–9.
TETJUREV, V. A., 1940, *Bot. Ž. S.S.S.R.*, **25**, 503–13.
TETJUREV, V. A., 1941, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **30**, 189–90.
THOMPSON, H. C., 1939, *Proc. Amer. Soc. hort. Sci.*, **37**, 672–9.
TURESSON, G., 1922, *Hereditas, Lund*, **3**, 211–350.
TURESSON, G., 1925, *Hereditas, Lund*, **6**, 147–236.
TURESSON, G., 1930, *Hereditas, Lund*, **14**, 99–152.
VASILJEV, I. M., 1934a, *Doklady Akad. Nauk S.S.S.R.*, **3**, 333–9.
VASILJEV, I. M., 1934b, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **3**, 533–9.
VOSS, J., 1938, *Pflanzenbau*, **15**, 1–35.
Washington, Carnegie Institution, 1940, Pub. No. 520.
WENT, F. W., 1943, *Amer. J. Bot.*, **30**, 157–63.
WENT, F. W., 1944a, Personal communication, Aug. 9.
WENT, F. W., 1944b, *Amer. J. Bot.*, **31**, 135–50.
WENT, F. W., 1944c, *Amer. J. Bot.*, **31**, 597–618.
WENT, F. W., 1945, *Science*, **101**, 97–8.
WHITE, P. R., 1937, *Plant Physiol.*, **12**, 183–90.
WHYTE, R. O., 1939, *Biol. Rev.*, **14**, 51–87.

CHAPTER V

GREGORY, F. G., and PURVIS, O. N., 1936, *Nature, Lond.*, **138**, 973.
GREGORY, F. G., and PURVIS, O. N., 1938, *Ann. Bot., Lond.*, N.S., **2**, 237–51.
HARLAN, H. V., and POPE, M. N., 1922, *J. Hered*, **13**, 72–5.
HARLAN, H. V., and POPE, M. N., 1926, *J. agric. Res.*, **32**, 669–78.
KOSTJUČENKO, I. A., and ZARUBAĬLO, T. JA., 1935, *Selek i Semenovod.*, Nos. 3–11, 49–53.

KOSTJUČENKO, I. A., and ZARUBAĬLO, T. JA., 1936, *Trudy Prikl. Bot.*, Ser. A., No. 17, 17–23.

KOSTJUČENKO, I. A., and ZARUBAĬLO, T. JA., 1937, *Herb. Rev.*, **5**, 146–57.

NUTMAN, P. S., 1939, *Ann. Bot., Lond.*, N.S., **3**, 731–57.

NUTMAN, P. S., 1941, *Ann. Bot., Lond.*, N.S., **5**, 353–74.

CHAPTER VI

ADLER, F., 1940, *Forschungsdienst*, **9**, 332–67.

ALLARD, H. A., 1943, *Rhodora*, **45**, 169–70.

ALLARD, H. A., and GARNER, W. W., 1940, see United States, Dept. Agric., Tech. Bull. 727.

AVAKJAN, A. A. and TAGI-ZADE, A. H., 1935, *Jarovizacija*, No. 1, 65–107.

BODE, O., 1942, *Planta*, **33**, 278–89.

BORTHWICK, H. A., and PARKER, M. W., 1938, *Bot. Gaz.*, **99**, 825–39.

BRIGGS, G. E., 1941, *Proc. Roy. Soc., Lond.*, Ser. B, **130**, 24–31.

BURKHOLDER, P. R., 1936, *Bot. Rev.*, **2**, 1–52 and 97–172.

ČAĬLAHJAN, M. H., 1937, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **16**, 227–230.

DUGGAR, B. M., 1936, Biological effects of radiation, 2 vols., McGraw-Hill Book Co., New York and London.

EGIZ, S. A., 1928, *Mém. Inst. Agron. Leningrad*, **5**, 5–32.

EGUCHI, T., 1937, *Proc. Imp. Acad. Tokyo*, **13**, 332–3.

FABIAN, I., 1939, *Z. Bot.*, **33**, 305–57.

FRANCK, J., and GAFFRON, H., 1941, *Advances in Enzymology*, **1**, 199–262.

GAERTNER, T. v., and BRAUNROTH, E., 1935, *Beih. bot. Zbl.*, **53**, A., 554–63.

GARNER, W. W., 1936, Biological effects of radiation, edited by B. M. Duggar, Chapter 19, 677–713, McGraw-Hill Book Co., New York and London.

GARNER, W. W., 1937, *Bot. Rev.*, **3**, 259–75.

GARNER, W. W., and ALLARD, H. A., 1920, *J. agric. Res.*, **18**, 553–606.

GARNER, W. W., and ALLARD, H. A., 1923, *J. agric. Res.*, **23**, 871–920.

GREGORY, F. G., 1936, *Sci. Hort.*, **4**, 143–54.

HAMNER, K. C., 1940, *Bot. Gaz.*, **101**, 658–87.

HAMNER, K. C., 1944, *Ann. Rev. Biochem.*, **13**, 575–90.

HAMNER, K. C., and BONNER, J., 1938, *Bot. Gaz.*, **100**, 388–431.

HARDER, R., and WITSCH, H. v., 1941, *Naturwissenschaften*, **29**, 770.

HARDER, R., WITSCH, H. v., and BODE, O., 1942, *Jb. Bot.*, **90**, 546.

Imperial Agricultural Bureaux, 1935, Joint Publ., No. 1.

JOHNSSON, H., 1944, *Hereditas, Lund*, **30**, 469–566.

KATUNSKIĬ, V. M., 1937, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **15**, 500–4.

KLEBS, G., 1913, *S.B. Akad. Wiss. Wien, math.-naturw. Kl.*, Abt. B., Abh., **5**, 1–47.
KLEBS, G., 1918, *Flora*, **111–12**, 128–51.
LANG, A., 1942, *Naturwissenschaften*, **30**, 590–1.
LANG, A., and MELCHERS, G., 1943, *Planta*, **33**, 653–702.
LOEHWING, W. F., 1939, *Science*, **90**, 552–5.
MANN, L. K., 1940, *Bot. Gaz.*, **102**, 339–56.
MAXIMOV, N. A., 1938, Plant physiology, 2nd edn., McGraw-Hill Publishing Co., London.
MOŠKOV, B. S., 1941, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **31**, 699–701.
SNYDER, W. E., 1940, *Bot. Gaz.*, **102**, 302–22.
United States, Department of Agriculture, 1940, Tech. Bull. 727.

CHAPTER VII

BORTHWICK, H. A., and PARKER, M. W., 1938, *Bot. Gaz.*, **100**, 374–87.
EMSWELLER, S. L., STUART, N. W., and BYRNES, J. W., 1941, *Proc. Amer. Soc. hort. Sci.*, **39**, 39–42.
HAMNER, K. C., 1940, *Bot. Gaz.*, **101**, 658–87.
HAMNER, K. C., 1942, *Cold Spring Harbor Symposia Quant. Biol.*, **10**, 49–60.
HAMNER, K. C., and BONNER, J., 1938, *Bot. Gaz.*, **100**, 388–431.
HARDER, R., and BODE, O., 1943, *Planta*, **33**, 469–504.
MANN, L. K., 1940, *Bot. Gaz.*, **102**, 339–56.
MELCHERS, G., and CLAES, H., 1943, *Naturwiss.*, **31**, 249.
MOŠKOV, B. S., 1939, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **22**, 456–9.
PARKER, M. W., HENDRICKS, S. B., BORTHWICK, H. A., and SCULLY, N. J., 1945, *Science*, **102**, 152–5.
RASUMOV, V. I., 1941, *Sborn. Rabot. Fiziol. Rast.*, 283–98.
SNYDER, W. E., 1940, *Bot. Gaz.*, **102**, 302–22.
WITHROW, R. B., and WITHROW, ALICE P., 1944, *Plant Physiol.*, **19**, 6–18.

CHAPTER VIII

BORTHWICK, H. A., and PARKER, M. W., 1938, *Bot. Gaz.*, **100**, 374–87.
CULPEPPER, C. W., and MOON, H. H., 1941, *J. agric. Res.*, **63**, 335–43.
EREMENKO, V. T., 1936, *Zbirn. Prac. (Rob.) Agrofiziol.*, **2**, 3–21.
EREMENKO, V. T., 1938, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **18**, 603–6.
HARLAN, H. V., and POPE, M. N., 1922, *J. Hered.*, **13**, 72–5.
KRAEVOĬ, S. J., and KIRIČENKO, F. G., 1935, *Doklady Akad. Nauk, S.S.S.R.*, **1**, 171–6.
MODILEVSKIĬ, J. A. S., 1943, *Uspehi Sovrem. Biol.*, **16**, 335–46.
NIELSEN, C. S., 1942, *Bot. Gaz.*, **104**, 99–106.

NOGUCHI, Y., 1929, *Jap. J. Bot.*, **4**, 385.
NUTMAN, P. S., 1939, *Ann. Bot., Lond.*, N.S., **3**, 731–57.
NUTMAN, P. S., 1941, *Ann. Bot., Lond.*, N.S., **5**, 353–74.
POOLE, C. F., 1932, *Genetics*, **17**, 125–36.
SAMOHINA, Z. F., and ZIHERMAN, H. JA., 1941, *Doklady Vsesojuz. Akad. S.-H. Nauk*, No. 9, 7–11.
SEXSMITH, J. J., and FRYER, J. R., 1943, *Sci. Agric.*, **24**, 95–100.
WANSER, H. M., 1922, *Science*, N.S., **56**, 313–15.
WHYTE, R. O., and OLJHOVIKOV, M. A., 1939, *Nature, Lond.*, **143**, 301–2.
WORT, D. J., 1941, *Bot. Gaz.*, **102**, 725–36.

CHAPTER IX

BORTHWICK, H. A., and PARKER, M. W., 1938, *Bot. Gaz.*, **100**, 374–87.
ČAĬLAHJAN, M. H., 1945, *C. R. (Doklady) Acad. Sci. U.R.S.S.*, **47**, 220–4.
ERMOLAEVA, E. JA, 1938, *Sovet. Bot.*, No. 1, 92–7.
GREGORY, F. G., and PURVIS, O. N., 1938, *Ann. Bot., Lond.*, N.S., **2**, 237–51.
HAMNER, K. C., 1939, *Bot. Gaz.*, **100**, 853–61.
HAMNER, K. C., and BONNER, J., 1938, *Bot. Gaz.*, **100**, 388–431.
Imperial Agricultural Bureaux, 1935, Joint Publ., No. 1.
KNOTT, J. E., 1934, *Proc. Amer. Soc. hort. Sci.*, **31**, 152–4.
LANG, A., and MELCHERS, G., 1941, *Naturwiss.*, **29**, 82–3.
LITVINOV, L. S., 1934, *Izvest. Biol. Nauč. Issledovat. Inst. Permsk. Gosudarstv. Univ.*, **9**, 59–70.
LOEHWING, W. F., 1938, *Proc. Soc. exp. Biol., N.Y.*, **37**, 631–4.
PARKER, M. W., and BORTHWICK, H. A., 1940, *Bot. Gaz.*, **102**, 256–68.
PSAREV, G. M., 1937, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **17**, 435–7.
ROBBINS, W. J., 1922, *Bot. Gaz.*, **73**, 376–90.
WITHROW, ALICE P., WITHROW, R. B., and BIEBEL, J.P., 1943, *Plant Physiol.*, **18**, 294–8.

CHAPTER X

AVERY, G. S., JR., 1942, *Cold Spring Harbor Symposia Quant. Biol.*, **10**, 1–6.
AVERY, G. S., JR., BERGER, J., and SHALUCHA, BARBARA, 1941, *Amer. J. Bot.*, **28**, 596–607.
AVERY, G. S., JR., BERGER, J., and SHALUCHA, BARBARA, 1942, *Amer. J. Bot.*, **29**, 765–72.
BURGER, J., and AVERY, G. S., Jr., 1944, *Amer. J. Bot.*, **31**, 199–203.
ČAĬLAHJAN, M. H., 1937, [Hormonal theory of plant development]. Publ. Acad. Sci. U.S.S.R., Moscow.

ČAĬLAHJAN, M. H., and ŽDANOVA, L., 1938, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **19**, 303–6.

CHOLODNY, N. G., 1935, *Planta*, **23**, 289–312.

CHOLODNY, N. G., 1936, *Doklady Akad. Nauk, S.S.S.R.*, **3**, 391–4.

CHOLODNY, N. G., 1939, *Herb. Rev.*, **7**, 223–47.

DOSTAL, R., and HOŠEK, M., 1937, *Flora*, **31**, 263–86.

East Malling, Imperial Bureau of Horticulture and Plantation Crops, 1939, T.C., 12.

GREGORY, F. G., and PURVIS, O. N., 1936, *Nature, Lond.*, **138**, 249.

GREGORY, F. G., and PURVIS, O. N., 1938, *Ann. Bot., Lond.*, N.S., **2**, 237–51.

HAAGEN-SMITH, A. J., LEECH, W. D., and BERGREN, W. R., 1942, *Amer. J. Bot.*, **29**, 500–6.

HAMNER, K. C., 1938, *Bot. Gaz.*, **99**, 615–29.

HAMNER, K. C., 1942, *Cold Spring Harbor Symposia Quant. Biol.*, **10**, 49–60.

HATCHER, E. S. J., 1943, *Nature, Lond.*, **151**, 278–9.

HATCHER, E. S. J., 1945, *Ann Bot., Lond.*, **9**, 235–66.

HATCHER, E. S. J., and GREGORY, F. G., 1941, *Nature, Lond.*, **148**, 623.

KONOVALOV, I. N., 1937, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **16**, 381–3.

PURVIS, O. N., 1934, *Ann. Bot., Lond.*, **48**, 919–55.

PURVIS, O. N., 1944, *Ann. Bot., Lond.*, N.S., **8**, 285–314.

PURVIS, O. N., and GREGORY, F. G., 1937, *Ann. Bot., Lond.*, **1**, 569–91.

SCHANDER, H., 1934, *Z. Bot.*, **27**, 433–515.

SEREĬSKIĬ, A., and SLUDSKAJA, M., 1937, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **17**, 55–8.

SNOW, R., see THIMANN, K. V., 1939, *Biol. Rev.*, **14**, 314–37.

STEWART, W. S., and HAMNER, C. L., 1942, *Bot. Gaz.*, **104**, 338–47.

TEMPLEMAN, W. G., 1939, *Emp. J. Exp. Agric.*, **7**, 76–88.

THIMANN, K. V., 1941, *Amer. Nat.*, **75**, 147–53.

THIMANN, K. V., and LANE, R. H., 1938, *Amer. J. Bot.*, **25**, 535–43.

THIMANN, K. V., and SKOOG, F., 1940, *Amer. J. Bot.*, **27**, 951–60.

VAN OVERBEEK, J., 1935, *Proc. nat. Acad. Sci. Wash.*, **21**, 292–9.

VAN OVERBEEK, J., 1942, *Cold Spring Harbor Symposia Quant. Biol.*, **10**, 126–34.

VAN OVERBEEK, J., 1944, *Ann. Rev. Biochem.*, **13**, 631–66.

WENT, F. A. F. C., 1928, *Rev. Trav. Bot. Néerland.*, **25**, 1.

ZIMMERMAN, P. W., 1942, *Cold Spring Harbor Symposia Quant. Biol.*, **10**, 152–9.

CHAPTER XI

ČAĬLAHJAN, M. H., 1937, [Hormonal theory of plant development]. Publ. Acad. Sci. U.S.S.R., Moscow.

ČAĬLAHJAN, M. H., 1940, *Doklady Akad. Nauk S.S.S.R.*, **27**, 159–62, 253–256 and 374–7.

CHOLODNY, N. G., 1936, *Doklady Akad. Nauk, S.S.S.R.*, **3**, 391–4.

CHOLODNY, N. G., 1939, *Herb. Rev.*, **7**, 223–47.

GREENE, L., 1943, *Proc. Amer. Soc. hort. Sci.*, **42**, 149–50.

HAMNER, K. C., 1942, *Cold Spring Harbor Symposia Quant. Biol.*, **10**, 49–60.

HAMNER, K. C., 1944, *Ann. Rev. Biochem.*, **13**, 575–90.

HAMNER, K. C., and BONNER, J., 1938, *Bot. Gaz.*, **100**, 388–431.

LJUBIMENKO, V. N., and BUSLOVA, E. D., 1937, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **14**, 149–52.

LYSENKO, T. D., 1932, *Bull. Jarov.*, Nos. 2–3, 16–34.

MELCHERS, G., 1939, *Ber. dtsch. bot. Ges.*, **57**, 29–48.

MOŠKOV, B. S., 1939, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **24**, 489–91.

MOŠKOV, B. S., 1940, *Sovet. Bot.*, No. 4, 32–45.

MURNEEK, A. E., WITTWER, S. H., and HEMPHILL, D. D., 1944, *Proc. Amer. Soc. hort. Sci.*, **44**, 428–32.

POMEROY, C. S., and ALDRICH, W. W., 1943, *Proc. Amer. Soc. hort. Sci.*, **42**, 146–8.

ROBERTS, R. H., and STRUCKMEYER, B. E., 1944, *Proc. Amer. Soc. hort. Sci.*, **44**, 417–27.

VAN OVERBEEK, J., 1944, *Ann. Rev. Biochem.*, **13**, 631–66.

WITHROW, ALICE P., and WITHROW, R. B., 1943, *Bot. Gaz.*, **104**, 409–15.

CHAPTER XII

BURKHOLDER, P. R., 1936, *Bot. Rev.*, **2**, 1–52, 97–172.

BUZOVIR, F., 1936, *Zbirn. Prac. (Rob.) Agrofiziol.*, **1**, 23–37.

ČAĬLAHJAN, M. H., 1944a, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **43**, 75–9.

ČAĬLAHJAN, M. H., 1944b, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **43**, 387–90.

ČAĬLAHJAN, M. H., 1945, *C. R. (Doklady) Acad. Sci. U.R.S.S.*, **47**, 146–9.

ČAĬLAHJAN, M. H., and LUKOVNIKOV, E. K., 1941, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **32**, 152–5.

CHOLODNY, N. G., 1939, *Herb. Rev.*, **7**, 223–47.

DEMIDENKO, T. T., 1945a, *C. R. (Doklady) Acad. Sci. U.R.S.S.*, **47**, 61-3.

DEMIDENKO, T. T., 1945b, *C. R. (Doklady) Acad. Sci. U.R.S.S.*, **47**, 215–7.

EREMENKO, V., 1936, *Zbirn. Prac. (Rob.) Agrofiziol.*, **1**, 84–109.

Imperial Agricultural Bureaux, 1935, Joint Publication, No. 1.

KATUNSKIĬ, V. M., 1939, *Izv. Akad. Nauk S.S.S.R.*, Ser. Biol., No. 1, 85–102.

KNOTT, J. E., 1926, *Proc. Amer. Soc. hort. Sci.*, **23**, 67–70.
KNOTT, J. E., 1932, *Plant Physiol.*, **7**, 125–30.
KONOVALOV, I. N., 1936, *Trudy prikl. Bot., Genet. i Selekcii*, Ser. A, No. **20**, 99–105.
KONOVALOV, I. N., 1938, *Trudy Inst. Fiziol. Timirjazev*, **2**, No. 2, 5–20.
KONOVALOV, I. N., 1944, *Sovet. Bot.*, No. 3, 21–36.
KONOVALOV, I. N., and POPOVA, T. M., 1941, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **31**, 58–60.
LOEHWING, W. F., 1940, *Science*, **92**, 517–20.
MAXIMOV, N. A., 1938, Plant physiology, 2nd edn., McGraw-Hill Publishing Co., London.
Missouri, Agricultural Experiment Station, 1937, Res. Bull., No. 268.
MURNEEK, A. E., 1939, *Growth*, **3**, 295–315.
OVEČKIN, S. K., and BEREZICKIJA, N. I., 1936, *Zbirn. Prac. (Rob.) Agrofiziol.*, **2**, 35–57.
OVEČKIN, S. K., BEREZICKIJA, N. I., BURJIAN, V. F., and ŠKURA, F. D., 1936, *Zbirn. Prac. (Rob.) Agrofiziol.*, **1**, 38–54.
PARKER, M. W., and BORTHWICK, H. A., 1939, *Bot. Gaz.*, **100**, 651–89.
PAŠEVIČ, V. JU., 1940, *Sci. Papers, Moscow State Univ.*, **36**, (Bot.), 43–8.
SAPEGIN, A. A., 1938, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **18**, 191–3.
SAPOŽNIKOVA, K. V., 1935, *Trudy Biol. Inst. Tomsk Univ.*, **1**, 238–53.
STANKOV, N. Z., 1938, *Himiz. Soc. Zemled.*, No. **5**, 74–81.
WITHROW, A. P., 1945, *Butler Univ. Bot. Stud.*, **7**, 40–64.
ZAĬCEVA, A. A., 1939, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **25**, 695–99.

CHAPTER XIII

BUĬLINA, E. S., 1935, *Semenovodstvo*, No. 8, 6–7.
DEXTER, S. T., 1935, *Plant Physiol.*, **10**, 149–58.
DEXTER, S. T., 1941, *Plant Physiol.*, **16**, 181–8.
HARVEY, R. B., 1935, An annotated bibliography of the low temperature relations of plants, Minneapolis, Burgess Publishing Co.
HARVEY, R. B., 1936, An annotated bibliography of the low temperature relations of plants, revised edn., Minneapolis, Burgess Publishing Co.
HENKEL, P. A., 1938, *Trudy Konfer. Pocvoved. Fiziol., Saratov*, **2**, 336–7.
HENKEL, P. A., and KOLOTOVA, S. S., 1938, *Zbirn. prisv. Pam. Ljubimenka*, 195–206.
ISIP, I. N., 1938, *Selek. Semenovod.*, No. 7, 35–8.
IVANOV, S. M., 1940, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **28**, 736–8.
KESSLER, W., 1935, *Planta*, **24**, 312–52.
KESSLER, W., and RUHLAND, W., 1938, *Planta*, **28**, 159–204.
KRASOVSKAJA, I. V., 1940, *Izv. Akad. Nauk S.S.S.R.*, Ser. Biol., No. **4**, 495–503.

KUPERMAN, F. M., 1936, *Ukr. Inst. Zern. Gospod.*, **4**, 147–80.

KUPERMAN, F. M., and ZADONCEV, A. I., 1935, *Trudy prikl. Bot., Genet. i Selekcii*, Ser. 3, No. 6, 97–120.

KUPERMAN, F. M., and ZADONCEV, A. I., 1936, *Kolh. Opyt.*, No. 10, 6–7.

LEVITT, J., 1941, Frost killing and hardiness of plants: a critical review. Minneapolis, Burgess Publishing Co.

LJUBINSKIĬ, N. A., 1940, *Sovet. Bot.*, Nos. 5–6, 60–4.

MAXIMOV, N. A., 1941, *Sborn. Rabot Fiziol. Rast.*, 299–309.

MOŠKOV, B. S., 1935, *Planta*, **23**, 774–803.

MOŠKOV, B. S., 1939, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **22**, 184–6.

MÜLLER-THURGAU, H., 1882, *Landw. Jb.*, **11**, 751–828.

NEWTON, R. 1924, *J. agric. Sci.*, **14**, 178–91.

OLJHOVIKOV, M. A., 1940, *Herb. Rev.*, **8**, 214–23.

PANTANELLI, E., 1919, *C.R. Accad. Lincei* (Cl. Sci. Fis. Mat. Nat.), **28**, 205–9 (*Bot. Abs.*, **6**, 1312, 1920).

PARIJA, P., and PILLAY, K. P., 1944, *Curr. Sci.* **13**, 183–5.

PASTUH, M. B., 1939, *Sborn. Rab. VNIS. Kiev-Harjkov*, 229–40.

RODENHISER, H. A., and TAYLOR, J. W., 1943, *Phytopathology*, **33**, 240–4.

RUDORF, W., 1938, *Züchter*, **10**, 238–46.

SALTYKOVSKIĬ, M. I., and SAPRYGINA, E. S., 1935, *Doklady Akad. Nauk, SSSR.* **4**, 92–6.

SALTYKOVSKIĬ, M. I., and SAPRYGINA, E. S., 1943, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **39**, 280–3.

SALTYKOVSKIĬ, M. I., and SAPRYGINA, E. S., 1944, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **44**, 201–4.

SAMPSON, KATHLEEN, and WESTERN, J. H., 1941, Diseases of British grasses and legumes, London, Cambridge University Press.

SCARTH, G. W., 1944, *New Phytol.*, **43**, 1–12.

ŠESTAKOV, V. E., 1936, *Selek. i Semenovod.*, No. 1, 14–16.

SKAZKIN, F. D., 1940, *Sovet. Bot.*, Nos. 5–6, 144–53.

TIMOFEEVA, M. T., 1935, see Tumanov, I. I., 1940.

TUMANOV, I. I., 1931. [Winter hardiness in plants]. Seljhozgiz, Moscow-Leningrad, 1–119.

TUMANOV, I. I., 1935, *Teoret. Osnovy. Selek.*, **1**, 753–82.

TUMANOV, I. I., 1936, see Tumanov, I. I., 1940.

TUMANOV, I. I., 1940. [The physiological bases of winter hardiness in cultivated plants]. Seljhozgiz, Leningrad, 336.

TUMANOV, I. I., and IVANOVA, 1935, see Tumanov, I. I., 1940.

VASILJEV, I. M., 1934, *Soc. Zern. Hoz.*, No. 6, 55–7.

VETUHOVA, A. A., 1936, *Zbirn. Prac. Agrofiziol.*, **2**, 83–102.

VOROBJEV, see HENKEL, 1938.

WILHELM, A. F., 1935a, *Phytopath. Z.*, **8**, 111–56.

WILHELM, A. F., 1935b, *Phytopath. Z.*, **8**, 337–62.

CHAPTER XIV

ABEGG, F. A., 1936, *J. agric. Res.*, **53**, 493–511.
BENEDICT, H. M., 1941, *Bot. Gaz.*, **102**, 582–9.
CARSNER, E., and TOLMAN, B., 1942, *Amer. J. Bot.*, **29**, 691–2.
CHRISTIANSEN, M. P., 1941, *Bot. Tidsskr.*, **45**, 429–30.
CLAUSEN, J., KECK, D. D., and HIESEY, W. M., 1944, Yearb. Carnegie Inst. Wash., No. 43, 69–81.
COONS, G. H., 1943, Imperial Agricultural Bureaux, Joint Publ., 5, 37–47.
EVANS, M. W., 1931, *Ecology*, **12**, 182–7.
EVANS, M. W., 1939, *Amer. J. Bot.*, **26**, 212–8.
EVANS, M. W., ALLARD, H. A., and MCCONKEY, O., 1935, *Sci. Agric.*, **15**, 573–9.
FORSTER, H. C., TINCKER, M. A. H., VASEY, A. J., and WADHAM, S. M., 1932, *Ann. appl. Biol.*, **19**, 378–412.
FORSTER, H. C., and VASEY, A. J., 1935, *J. Dept. Agric. Vict.*, **33**, 352–64.
FULTS, J. L., 1942, *Amer. J. Bot.*, **29**, 45–55.
GREBINSKIĬ, S. O., 1941, *Biohimija*, **6**, 253–60.
GRIFFITHS, D., 1912, *Contrib. U.S. Nat. Herb.*, **14**, 343–444.
HAMILTON, W. M., 1942–3, *N.Z.J. Sci. Tech.*, **23**, 257A–83A; **24**, 1A–35A, 157A–85A, 223A–63A, 273A–302A.
HARTSEMA, A. M., and LEUPEN, F. F., 1942, Mededeeling No. 69 Laboratorium voor Plantenphysiologisch Onderzoek, Wageningen-Nederland, 1–30.
HOPKINS, A. D., 1918, United States Dept. Agric., Weather Bull., Mon. Weather Rev., Suppl. No. 9, 1–42.
JENKIN, T. J., 1930, *Welsh J. Agric.*, **6**, 140–65.
LUYTEN, I., 1942, Mededeeling No. 67. Laboratorium voor Plantenphysiologisch Onderzoek, Wageningen–Nederland, 1–28.
NAYLOR, A. W., 1941, *Bot. Gaz.*, **102**, 557–75.
OLMSTED, C. E., 1944, *Bot. Gaz.*, **106**, 46–74.
OWEN, F. V., CARSNER, E., and STOUT, M., 1940, *J. agric. Res.*, **61**, 101–24.
STAPLEDON, R. G., 1943, The Way of the Land. London, Faber and Faber.
STOKER, G. L., and TOLMAN, B., 1941, *J. Amer. Soc. Agron.*, **33**, 657–65.
STOUT, M., 1942, *Amer. J. Bot.*, **29**, 692.
SUKAČEV, V. N., 1941, *C. R. (Doklady) Acad. Sci. U.R.S.S.*, **30**, 757–60.
TURESSON, G., 1922, *Hereditas, Lund*, **3**, 211–350.
TURESSON, G., 1925, *Hereditas, Lund*, **6**, 147–236.
TURESSON, G., 1930, *Hereditas, Lund*, **14**, 99–152.
United States Department of Agriculture, 1940, Tech. Bull., 727.

Washington, Carnegie Institution, 1940, Publ., 520.
WERNER, H. O., 1942, *Amer. Potato J.*, **19**, 30–40.

CHAPTER XV

AAMODT, O. S., 1923, *J. agric. Res.*, **24**, 457–68.
BARANOV, P. A., 1939, *Jarovizacija*, Nos. 5–6, 197–207.
BELL, G. D. H., 1945, Personal communication, Feb. 12.
BREMER, A. H., 1931, *Gartenbauwiss.*, **4**, 469–83.
BREMER, A. H., and GRANA, J., 1935, *Gartenbauwiss.*, **9**.
Cambridge, Imperial Bureau of Plant Breeding and Genetics, 1943, Occ. Publ. Photoperiodism in the potato.
COOPER, H. P., 1923, *J. Amer. Soc. Agron.*, **15**, 15–25.
CORRENS, C., 1904, *Ber. dtsch. bot. Ges.*, **22**, 517–24.
DARLINGTON, C. D., 1944, *Nature, Lond.* **154**, 164.
FENNELL, J. L., 1945, *J. Hered.*, **36**, 183–5.
FRUWIRTH, C., 1923, Handbuch der Landwirtschaftlichen Pflanzenzüchtung, Bd. 4.
GOODWIN, R. H., 1944, *Genetics*, **29**, 503–19.
Imperial Agricultural Bureaux, 1935, Joint Publ., 1.
KAJANUS, B., 1927, *Bibliogr. Genet.*, **3**, 141–240.
LANG, A., and MELCHERS, G., 1943, *Planta*, **33**, 653–702.
MAXIMOV, N. A., 1929, *Trudy Prikl. Bot., Genet. i Selek.*, **20**, 169–209.
MELCHERS, G., 1936, *Biol. Zentralbl.*, **56**, 567–70.
MELCHERS, G., 1937, *Biol. Zentralbl.*, **57**, 568–614.
NILSSON-EHLE, H., 1917, *Sverig. Utsädesfören. Tidskr.*, **28**, 51.
POWERS, L., and LYON, C. B., 1941, *J. agric. Res.*, **63**, 129–48.
PURVIS, O. N., 1939, *Ann. Bot., Lond.* N.S. **3**, 719–29.
REIMERS, F. E., 1938, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **20**, 603–8.
REIMERS, F. E., 1939, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **25**, 790–3.
TAKAHASI, N., 1924, *Jap. J. Genet.*, **3**, 22–8.
THOMPSON, H. C., 1933, *Proc. Amer. Soc. hort. Sci.*, **30**, 440–6.
THOMPSON, H. C., and KNOTT, J. E., 1933, *Proc. Amer. Soc. hort. Sci.*, **30**, 507–9.
TSCHERMAK, E., 1906, *Z. landw. VersWes. Öst.* **9**, 699–743.
TSCHERMAK, E., 1923, Handbuch der Landwirtschaftlichen Pflanzenzüchtung, Bd., 4.
VAVILOV, N. I., and KOUZNETZOVA, E. S., 1921, *Bull. Agr. Fac. Univ. Saratov*, **1**, 1–23.
VINOGRADOVA, N. M., and NOVODERIŽKINA, M. A., 1941, *Trudy Zonal. Inst. Zern. Hoz. Raion. Nečernozem. Pol.*, No. 10, 113–44.
Washington, Agricultural Experiment Station, 1909, Bull. 89.
Washington, Agricultural Experiment Station, 1917, Bull. 135.

Washington, Agricultural Experiment Station, 1920, Bull. 155 (29th Ann. Rpt.).

CHAPTER XVI

Aberystwyth, Imperial Bureau of Pastures and Forage Crops, 1933, Bull. 9.

APPLETON, J. M., 1943, Personal communication, Jan. 31.

APPLETON, J. M., 1944, Personal communication, July 15.

COONS, G. H., 1943, Imperial Agricultural Bureaux, Joint Publ., 5, 37–47.

GREGORY, F. G., 1942, Personal communication, Oct. 23.

Imperial Agricultural Bureaux, 1935, Joint Publ., 1.

KLAPP, E., 1942, *Pflanzenbau*, **18**, 347–52, 367–87.

RUDORF, W., STELZNER, G., and HARTISCH, J., 1937, *Angew. Bot.*, **19**, 491–505.

SEN, B., and CHAKRAVARTI, S. C., 1942, *Indian J. agric. Sci.*, **12**, 1–34.

CHAPTER XVII

ÅBERG, E., 1940, *Lantbrukshögsk. Ann.*, **8**, 71–86.

ALMEIDA, J. MARQUÉS DE, 1941, *Agron. Lusitana*, **3**, 183–8.

AXELROD, D. M., 1939, *Doklady Vsesojuz. Akad. S.-H. Nauk*, No. 8, 11.

BANTEEV, F., KALININ, P., and GORJUNOV, D., 1936, *Trudy Prikl. Bot.*, Ser. A, No. 19, 37–40.

BUCHLI, M., 1943, *Ber. Schweiz. bot. Ges.*, **53A**, 334–68.

ČAĬLAHJAN, M. H., and MEGRABJAN, A. A., 1945, *C. R. (Doklady) Acad. Sci. U.R.S.S.*, **47**, 439–43.

DIES, E. J., 1943, Soybeans, gold from the soil. New York, Macmillan.

DUTT, N. L., 1943, *Indian Fmg.*, **4**, 11–13.

EFEĬKIN, A. K., 1939, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **25**, 308–10.

EREMENKO, V., 1936, *Zbirn. Prac. (Rob.) Agrofiziol.*, **1**, 4–22.

FUCHS, W. H., 1943, *Pflanzenbau*, **19**, 216–20.

GFELLER, F., and FRASER, J. G. C., 1940, *Sci. Agric.*, **20**, 510–15.

GREBENNIKOV, P. E., and HOHLOVSKIĬ, A. P., 1939, *Trudy Beloruss. Seljskohoz. Inst.*, No. 10, 145–55.

GREGORY, F. G., 1945, Personal communication.

HARTISCH, J., 1939, *Pflanzenbau*, **15**, 256–88.

HITRINSKIĬ, V. F., 1939, *Jarovizacija*, No. **4**, 58–69.

KALANTYRJ, M. S., 1939a, *Trudy Inst. Severn. Zern. Hoz.*, No. 2, 29–37.

KALANTYRJ, M. S., 1939b, *Trudy Inst. Severn. Zern. Hoz.*, No. 2, 38–49.

KLITSCH, C., 1935, *Pflanzenbau*, **11**, 424–32, 473–80.

KONOVALOV, I. N., and FROLOVA, V. N., 1939a, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **25**, 311–13.

KONOVALOV, I. N., and FROLOVA, V. N., 1939b, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **25**, 314–16.

KRASULINA, M. I., 1937, *Selek. Semenovod.*, No. 4, 51–4.

KRASULINA, M. I., 1939, *Trudy Inst. Severn. Zern. Hoz.*, No. 2, 50–3.

MASJUK, P. D., 1940a, *Ž. Inst. Bot. Akad. Nauk U.R.S.R.*, No. 23, 185–9.

MASJUK, P. D., 1940b, *Praci. Inst. Biol. Kyiv. Univ.*, **3**, 147–50.

OLEĬNIKOVA, T. V., 1939, *Sovet. Bot.*, No. 5, 31–49.

PESOLA, V. A., 1935, *Valt. Maatalousk. Julk.*, No. 66, 1–83.

ROSENBAUM, H., 1937a, *Forschungsdienst*, **3**, 138–42.

ROSENBAUM, H., 1937b, *Angew. Bot.*, **19**, 441–91.

RUDORF, W., 1935, *Zeit. Züchtg.*, **20**, 251–67.

SAPOŽNIKOVA, K. V., 1937a, *Trudy biolog. Inst. Tomsk. Univ.*, Ser. E, **3**, 1–11.

SAPOŽNIKOVA, K. V., 1937b, *Trudy biolog. Inst. Tomsk. Univ.*, Ser. E, **3**, 60–8.

SARTORIS, G. B., 1938, *Proc. 6th. Congr. Sugarcane Tech.*, 796–802.

SAVVIČEV, K. I., 1936, *Selek. Semenovod.*, No. 3, 86–7.

SOLOVEĬ, G. T., 1939, *Jarovizacija*, No. 4, 70–5.

TAYLOR, J. W., and COFFMAN, F. A., 1938, *J. Amer. Soc. Agron.*, **30**, 1010–19.

TULAĬKOVA, K. P., 1939, *Trudy Inst. Severn. Zern. Hoz.*, No. 2, 54–60.

VASILJEV, I. M., 1939a, *Trudy Inst. Severn. Zern. Hoz.*, No. 2, 3–28.

VASILJEV, I. M., 1939b, [Vernalization of lupin, vetch and lentil]. Seljhozgiz, Moscow.

VENKATRAMAN, R. B. T. S., 1936, Scientific Reports on the Agricultural Research Institute, Pusa, Report of the Sugarcane Expert, 1933–4.

VOSS, J., 1938, *Pflanzenbau*, **15**, 1–35, 49–79.

VOSS, J., 1939, *Züchter*, **11**, 113–23.

WORT, D. J., 1939, *Bot. Gaz.*, **101**, 457–81.

WORT, D. J., 1940, *Plant Physiol.*, **15**, 137–41.

ZACKS, M. B., 1945, *Canad. J. Res.*, **23**, 45–75.

CHAPTER XVIII

BELL, G. D. H., 1945, Personal communication, Feb. 12.

BELL, G. D. H., and BAUER, A. B., 1942, *J. agric. Sci.*, **32**, 112–41.

BRANDES, E. W., and COONS, G. H., 1941, *Yearb. U.S. Dep. Agric*, 421–38.

CAIRNS, D., 1940, *N.Z.J. Sci. Tech.*, **22A**, 86–96.

CAIRNS, D., 1941, *N.Z.J. Sci. Tech.*, **22A**, 279–89.

CAIRNS, D., 1941a, *N.Z.J. Sci. Tech.*, **22A**, 359–68.

Cambridge, Imperial Bureau of Plant Breeding and Genetics, 1943, Occ. Publ. Photoperiodism in the potato.
ČEPIKOVA, A. R., 1941, *Doklady Akad. Nauk, SSSR.* **8**, 39–40.
COONS, G. H., 1943, Imperial Agricultural Bureaux, Joint Publ. 5, 37–47.
Cornell University, Agricultural Experiment Station, 1934, Mem., 154.
CRESPIN, J. F., 1945, Personal communications, Feb. 18 and March 2.
DENNIS, R. W. G., 1939, *Ann. appl. Biol.*, **26**, 87–101.
FRUWIRTH, C., 1923, Die Züchtung der vier Hauptgetreidearten und und Zuckerrübe, **4**, 449–55.
GRIFFITHS, D. J., 1945, Personal communication, March.
GÜNTHER, H. K., 1900, *Bl. Zuckerrüb.*, **7**, 57–61.
HACKBARTH, J., 1935, *Züchter*, **7**, 95–104.
HOLLRUNG, M., 1936, *Pflanzenbau*, **12**, 275–90, 303–18, 340–66.
LIPPMANN, E. O., 1925, Geschichte der Rübe (Beta) als Kulturpflanze. Berlin.
LIPPMANN, E. O., 1935, *Z. Ver. dtsch. Zuckerindustr.*, **84**, 15–67.
LOVVORN, R. N., 1945, Imperial Bureau of Pastures and Forage Crops, Bull. **34**, 128–38.
LUBENEC, P. A., 1939, *Mater. Soveš̌č. Korm. Trav.*, 91–114.
Missouri, Agricultural Experiment Station, 1939, Res. Bull., 299.
MONTEMARTINI, L., 1917, *Atti Ist. Bot. Univ. Pavia*, Ser. 2, **14**, 65–127.
MONTEMARTINI, L., 1918, *Atti Ist. Bot. Univ. Pavia*, Ser. 2, **15**, 1–42.
MOREAU, R. E., 1944, *E. Afr. Agric. J.*, **9**, 203–12.
MUNERATI, O., 1942, *Mon. Bull. agric. Sci. Pract.*, **33**, 177–214.
NEWELL, L. C., and KEIM, F. D., 1943, *J. Amer. Soc. Agron.*, **35**, 470–34.
OLMSTED, C. E., 1943, *Bot. Gaz.*, 105, 165–81.
OWEN, F. V., CARSNER, E., and STOUT, M., 1940, *J. agric. Res.*, **61**, 101–124.
PARISI, E., 1929, *Ital. agric.*, **66**, 13–21.
ROGLER, G. A., 1945, Imperial Bureau of Pasture and Forage Crops, Bull. 34, 169–79.
RÖMER, T., 1927, Handbuch des Zuckerrübenbaues. Berlin.
SCHNEIDER, F., 1926, *Dtsch. Zuckerindustr.*, **51**, 521–3.
ŠEVČENKO, A. JA, 1939, *Mater. Soveš̌č. Korm. Trav.*, 20–8.
SHAW, H. B., 1917, *Sugar*, **19**, 387–91, 431–4.
SPRAGUE, V. G., 1943, *Proc. Soil Sci. Soc. Amer.*, **8**, 287–94.
STUCKEY, IRENE N., 1942, *Amer. J. Bot.*, **29**, 92–7.
TINCKER, M. A. H., 1925, *Ann. Bot., Lond.*, **39**, 721–54.
TINCKER, M. A. H., 1928, *Ann. Bot., Lond.*, **42**, 101–40.
TOTTINGHAM, W. E., LEPKOSKY, S., SCHULZ, E. R., and LINK, K. P., 1926, *J. agric. Res.*, **33**, 59–76.
TRAVIN, I. S., and ŠČERBAČEVA, V. D., 1941, Red clover. Moscow, State Printers.

TUŽIHIN, G. A., 1939, *Sovet. Bot.*, No. 4, 111–26.
United States, Department of Agriculture, 1901, Farmers' Bull. 52 (2nd rev. edn.).
VAVILOV, N. I., 1935, Botanical-geographical bases of breeding.
VILMORIN, J. DE., 1923, L'hérédité chez la betterave cultivée, Paris.
VOSS, J., 1940a, *Landw. Jb.*, **90**, 245.
VOSS, J., 1940b, *Züchter*, **12**, 34–44, 73–7.
WERNER, H. O., 1942, *J. agric. Res.*, **64**, 257–74.
WILLIAMS, W., 1945, Welsh Plant Breeding Sta. Bull. Ser. H. No. 16–26.

CHAPTER XIX

ASHBY, E., 1944, Personal communication.
California, Agricultural Experiment Station, 1939, Bull. 628.
Cornell University, Agricultural Experiment Station, 1929a, Bull. 480.
Cornell University, Agricultural Experiment Station, 1929b, Bull. 488.
Cornell University, Agricultural Experiment Station, 1934, Mem. 154.
Cornell University, Agricultural Experiment Station, 1936, Mem. 186.
Cornell University, Agricultural Experiment Station, 1938, Bull. 708.
Cornell University, Agricultural Experiment Station, 1939, Mem. 218.
Cornell University, Agricultural Experiment Station, 1942, Bull. 878.
DANIELSON, L. L., 1941, *Proc. Iowa Acad. Sci.*, **47**, 157.
DANIELSON, L. L., 1944, *Plant Physiol.*, **19**, 638–9, 647.
FILOV, A. I., 1939, *Doklady Vsesojuz. Akad. Seljskohoz. Nauk*, No. 11, 14–18.
FRY, JEAN M., 1942, *Nature, Lond.*, **150**, 689.
GOODALL, D. W., and BOLAS, B. D., 1942, *Ann. appl. Biol.*, **29**, 1–10.
GRAY, S. G., 1942, *J. Coun. Sci. industr. Res. Aust.*, **15**, 211–12.
GREGORY, F. G., 1936, *Sci. Hort.*, **4**, 143–54.
GUSTAFSON, F. G., 1938, *Amer. J. Bot.*, **26**, 189–94.
HEATH, O. V. S., 1943a, *Ann. appl. Biol.*, **30**, 208–20.
HEATH, O. V. S., 1943b, *Ann. appl. Biol.*, **30**, 308–19.
HEATH, O. V. S., 1945, *Nature, Lond.*, **155**, 623–6.
HEATH, O. V. S., and HOLDSWORTH, M., 1943, *Nature, Lond.*, **152**, 334–5.
HEATH, O. V. S., and MATHUR, P. B., 1944, *Ann. appl. Biol.*, **31**, 173–86.
HOFFMAN, C. A., 1933, *Bot. Gaz.*, **95**, 279–99.
HOLDSWORTH, M., 1945, *Ann. appl. Biol.*, **32**, 22–34.
HOLDSWORTH, M., and HEATH, O. V. S., 1945, *Nature, Lond.*, **155**, 334.
Illinois, Agricultural Experiment Station, 1914, Bull. No. 175.
Imperial Agricultural Bureaux, 1945, Joint Publ., No. 8.
JONES, H. A., and EMSWELLER, S. L., 1936, *Hilgardia*, **10**, 415–23.
LITVINOV, L. S., and LUKJIANOV, N. I., 1938, *Zbirn. Prac. Pam. Ljubimenka*, 207–28.

McCLELLAND, T. B., 1928, *J. agric. Res.*, **37**, 603–28.
MAGRUDER, R., and ALLARD, H. A., 1937, *J. agric. Res.*, **54**, 719–52.
Maryland, Agricultural Experiment Station, 1929, Bull. 313.
MILTHORPE, F. L., and HOROWITZ, B., 1943, *Agric. Gaz. N.S.W.*, **54**, 53–7.
Missouri, Agricultural Experiment Station, 1926, Bull. 90.
Missouri, Agricultural Experiment Station, 1933, Bull. 201.
Missouri, Agricultural Experiment Station, 1942, Res. Bull. 348.
MURNEEK, A. E., 1937, *Science*, **86**, 43–7.
MURNEEK, A. E., 1939, *Growth*, **3**, 295–315.
MURNEEK, A. E., 1940, *Proc. Amer. Soc. hort. Sci.*, **37**, 666–71.
New Jersey, Agricultural Experiment Station, 1928, Bull. 461.
Oregon, Agricultural Experiment Station, 1918, Bull. 149.
POST, K., 1934, *Proc. Amer. Soc. hort. Sci.*, **32**, 626–30.
POST, K., 1936a, *Proc. Amer. Soc. hort. Sci.*, **34**, 618–20.
POST, K., 1936b, *Proc. Amer. Soc. hort. Sci.*, **34**, 627–9.
POST, K., 1940, *Proc. Amer. Soc. hort. Sci.*, **37**, 1003–6.
PURVIS, O. N., 1934, *Ann. Bot., Lond.*, **48**, 919–55.
PURVIS, O. N., 1937, *Sci. Hort.*, **5**, 127–40.
PURVIS, O. N., 1938, *Sci. Hort.*, **6**, 160–77.
RUDORF, W., and STELZNER, G., 1934, *Gartenbauwiss*, **9**, 142–53.
SAKR, EL SAYD, and THOMPSON, H. C., 1942, *Proc. Amer. Soc. hort. Sci.*, **41**, 343–6.
SIMPSON, A. C., 1943, *Nature, Lond.*, **151**, 279–80.
SYLVÉN, N., 1940, *Svensk PappTidn.*, **43**, 317–24, 332–42.
THOMPSON, H. C., 1934, *Proc. Amer. Soc. hort. Sci.*, **32**, 558–60.
THOMPSON, H. C., and KNOTT, J. E., 1933, *Proc. Amer. Soc. hort. Sci.*, **30**, 507–9.
United States, Department of Agriculture, 1931, Bull. 267.
United States, Department of Agriculture, 1940, Tech. Bull. 727.
WENT, F. W., 1945a, *Science*, **101**, 97–8.
WENT, F. W., 1945b, *Amer. J. Bot.*, **32**, 469–79.
WITHROW, ALICE P., WITHROW, R. B., and BIEBEL, J. P., 1943, *Plant Physiol*, **18**, 294–8.

CHAPTER XX

ALAM, N., 1940–41, Sci. Rep. Rice Res. Stat., Sabour, Bihar (India).
BEACHELL, H. M., 1943, *J. agric. Res.*, **66**, 325–40.
BÜNNING, E., 1940, *Forschungsdienst*, **10**, 550–3.
CHAMPION, H. G., 1937, *J. Indian Bot. Soc.*, **16**, 301–5.
CHINOY, J. J. 1942, *Curr. Sci.*, **11**, 400–2.
HAIGH, J. C., 1935, Personal communication to Imperial Bureau of Plant Breeding and Genetics, Cambridge.

Imperial Agricultural Bureaux, 1943, Joint Publ., 5.
KAR, B. K., 1940, *Curr. Sci.*, **9**, 233–5.
KAR, B. K., 1944, *Curr. Sci.*, **13**, 130–1.
LORD, L., and DE SILVA, J. S. T., 1931, *Trop. Agriculturist*, **76**, 332–3.
PAL, B. P., and MURTY, G. S., 1941, *Indian J. Genet. Pl. Breed.*, **1**, 61–86.
PARIJA, P., 1943, *Curr. Sci.*, **12**, 88–9.
PARTHASARATHY, S. V., 1940, *Madras agric. J.*, **28**, 133–7.
PILLAY, K. P., 1944, *Curr. Sci.*, **13**, 185–6.
RAMDAS, L. A., 1942, *Indian Farming*, **3**, 273–6.
RAMIAH, K., 1933, *Indian J. agric. Sci.*, **3**, 377–410.
RHIND, J. A. S., 1935, *Indian J. agric. Sci.*, **5**, 729–36.
SEN, B., 1940, *Indian Fmg.*, **1**, 55–9.
SEN, B., and CHAKRAVARTI, S. C., 1938, *Indian J. agric. Sci.*, **8**, 245–52.
SEN, B., and CHAKRAVARTI, S. C., 1944, *Curr. Sci.*, **13**, 234–5.
SEN GUPTA, J. C., and SEN, N. K., 1944, *Curr. Sci.*, **13**, 160–1.
SINGH, B. N., and CHOUDRI, R. S., 1938, *Trop. Agric. Trinidad*, **15**, 202.
SINGH, B. N., and KAPOOR, S. L., 1939, *Sci. Cult.*, **4**, 674–7.
SINGH, B. N., KAPOOR, G. P., and CHOUDHRI, R. S., 1938, *Proc. Ind. Acad. Sci.*, **7**, 143–60.
SINGH, B. N., and SINGH, S. N., 1939, *Proc. Ind. Acad. Sci.*, **9**, 323–30.
SINGH, B. N., SINGH, S. N., and SRIVASTAVA, M. B., 1937, *J. Amer. Soc. Agron.*, **29**, 123–33.
SINGH, S. S. L., and ALAM, N., 1944, *Proc. Ind. Acad. Sci.*, **19**, 29–64.
SIRCAR, S. M., and PARIJA, B., 1944, *Nature, Lond.*, **153**, 378.
SIRCAR, S. M., and PARIJA, B., 1945, *Nature, Lond.*, **155**, 395.
SKRIPČINSKIĬ, V., 1940a, *Trop. Agriculturist*, **95**, 205–11.
SKRIPČINSKIĬ, V., 1940b, *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **29**, 425–8.

GLOSSARY OF TERMS

(Based largely on Chambers' Technical Dictionary)

Abscission. The organized shedding of a part of a plant.

Aleurone layer. A special peripheral protein layer in most seeds, especially in grasses.

Anaerobic conditions. Without oxygen.

Anthesin. A hypothetical hormone controlling flowering.

Anthesis. Flowering.

Ascorbic acid. Pure vitamin C, deficiency of which in human diet causes scurvy.

Auxin. Hormone controlling growth.

Axil. The angle formed between the axis and any organ which arises from it, especially of a leaf.

Blastanin. Embryo extract.

Bract. The modified leaves intermediate between the calyx and the normal leaves.

Carotene (oid). A yellow pigment synthesized by plants; precursor of vitamin A.

Catalase. An enzyme present in animal and vegetable tissues, characterized by readiness to decompose hydrogen peroxide, while being slowly destroyed itself.

Catalyst. An agent which alters (usually accelerates) the speed of chemical reaction.

Catch crop. A rapidly-growing crop interpolated between two regular crops, or between a main crop and the end of the growing season.

Chlorophyll. The mixture of two green (chlorophyll *a* and *b*) and two yellow (carotene and xanthophyll) pigments, present in the chloroplasts of all plants which are able to synthesize carbohydrates from carbon dioxide and water.

Chloroplast. A plastid containing chlorophyll, with or without other pigments, embedded singly or in considerable numbers in the cytoplasm of a plant cell.

Chromosome. One of the deeply staining rod-like bodies, constant in number for any given species, into which the chromatin of the nucleus becomes condensed during cell division.

Chromosome conjugation. Pairing of chromosomes.

Clone. Any stock of plants raised vegetatively from one original parent.

Coleoptile. The first leaf to appear above the ground in the seedling of a grass.

Cotyledon. One of the first leaves (dicotyledon) or the first leaf (monocotyledon) of the embryo in flowering plants.

Cytogenetics. The study of genetics on the basis of cytology.

Cytology. The study of the structure, functions, and the reproduction of cells.

Deciduous. The falling off (of leaves).

Devernalization. The annulment of the vernalization response.

Dicotyledon. Plants in which the embryos have two primary leaves.

Drosophila. An insect used for mass production studies in animal genetics.

Ecology. The study of organisms in relation to their environment.

Ecotype. A category of variant individuals, based on genetical behaviour and ecological relationship.

Endosperm. A multicellular tissue formed inside a developing seed, serving in the nutrition of the embryo.

Enzyme. A catalyst produced by living organisms.

Facial eczema. A disease of animals caused apparently by the composition of the fodder.

Florigen. A hypothetical hormone controlling flowering.

Gametes. Reproductive cells which unite in pairs to produce zygotes.

Glucose. The grape sugar of plants and animals.

Glutathione. A sulphur-containing tri-peptide found in different tissues and capable of being alternately reduced and oxidized.

Hibernalism. Winter habit.

Hormones. Internal secretions with a specific physiological action.

Inflorescence. Arrangement of flowers on an axis.

Involucre. Bracts at base of chief branches of compound umbels.

Iso-electric point. The pH value at which the charge on a colloid is zero.

Meristem. A group of undifferentiated cells each of which is capable of division, giving rise to at least one daughter cell able to divide again, and so on.

Metabolism. The sum-total of the chemical and physical changes constantly taking place in living matter.

Microclimates. Climates over a limited area, as distinct from macroclimates (of continents or regions).

Micro-dissection. The dissection (of growing points) under magnification.

Microphotographs. Photographs taken at high magnifications.

Milk ripeness. A state of ripeness characterized by the milky consistency of the contents of a grain.

Monopodium. A branch system in which each or any branch continues to increase in length by apical extension and bears similar lateral branches in acropetal succession.

Morphogenesis. The origin and development of a part, organ, or organism.

Morphology. The study of structure and form of organisms, as opposed to a study of their functions.

Ontogeny. The history of development of an individual (see *phylogeny*).

Parenchyma. A tissue of thin-walled cells generally forming packing among conducting and mechanical tissues.

Parthenocarpy. The production of a fruit without previous fertilization, and without any development of seeds within the fruit.

Phenology. The study of organisms in relation to climate.

Photo-catalysis. A chemical reaction of a catalytic nature dependent on light.

Photoperiodism. Defined on pp. 109, 112, and 116.

Photosynthesis. A process of building up of simple carbohydrates in the green cells of a plant when the plant is sufficiently supplied with light.

Phyllody. The transformation of parts of a flower into leaves.

Phylogeny. The history of the development of a race.

Phyto-. Prefix meaning "relating to plants."

Polyploidy. The possession of multiple sets of chromosomes.

Precursor. A substance from which another substance originates.

Primordium. The earliest recognizable rudiment of an organ or structure in development.

Pubescence. Hairiness.

Rhizome. An underground stem with a superficial resemblance to a root.

Rosette. A cluster of leaves arising in close circles from a central axis.

Sporophyte. A plant or part of a plant bearing asexual spores.

Synapsis. Defined on p. 47.

Syngamy. Defined on p. 47.

Systematics. The study of the relationship of species and genera.

Taxonomy. Synonymous with 'Systematics'.

Thermoperiodism(icity). Defined on p. 82.

Tillering. The formation of tillers, i.e. branches produced from the base of the stem, especially in cereals and grasses.

Vacuolation. The formation of vacuoles, i.e. small spaces or cavities in cytoplasm, generally containing fluid.

Venation. The arrangement of veins in a leaf.

Vernalin. A hypothetical hormone controlling flowering.

Vernalization. Origin of term stated on p. 64.

Wax ripeness. The stage of ripeness in a grain when it has a waxy consistency.

Xanthophyll. One of the two yellow pigments present in the normal chlorophyll of green plants.

Zygote. The product of union of two gametes from which a new plant arises.

INDEX OF AUTHORS' NAMES

(Numbers indicate pages on which reference is made to their work)

Aamodt, O. S., 233, 234, 236
Abegg, F. A., 225
Åberg, E., 266
Adler, R., 42, 102, 112
Alam, N., 329, 330
Aldrich, W. W., 176
Allard, H. A., 13, 28, 29, 30, 77, 102, 108, 109, 111, 112, 116, 125, 126, 127, 132, 154, 203, 211, 212, 213, 214, 250, 298, 302, 305, 310, 327
Almeida, J. M. de, 57, 273
Appleton, J. M., 254, 255
Arthur, J. M., 102
Asami, Y., 23
Ashby, E., 323
Avakjan, A. A., 68, 124
Avery, G. S., 158, 161, 164
Axelrod, D. M., 270

Banteev, F., 350
Baranov, P. A., 238
Barnes, W. C., 298
Bassarskaja, M. A., 76
Bauer, A. B., 280
Beachell, H. M., 328, 329
Beljdenkova, A. F., 201
Bell, G. D. H., 242, 275, 280
Benedict, H. M., 220
Bennett, O. T., 57
Berger, J., 161, 164
Bergren, W. R., 161
Biebel, J. P., 154, 155
Bissonnette, T. H., 30
Blaauw, A. H., 300
Bode, O., 125, 126, 136
Bolas, B. D., 300
Bonner, G., 82, 89, 114, 129, 130, 131, 155, 165, 172, 173
Borthwick, H. A., 77, 78, 79, 114, 135, 147, 154, 155, 185
Boswell, V. R., 298
Brandes, E. W., 275, 276, 277
Briggs, G. E., 52, 53
Brown, E. M., 291
Buchli, M., 266
Buĭlina, E. S., 201
Bünning, E., 327
Burkholder, P. R., 122, 182
Buslova, E. D., 167
Buzovir, F., 181
Byrnes, J. W., 135

Čaĭlahjan, M. H., 122, 124, 156, 163, 167, 169, 170, 171, 172, 174, 188, 189, 274
Cairns, D., 286
Carsner, E., 226, 227, 278, 279
Cepikova, A. R., 291
Chakravarti, S. C., 331, 332
Champion, H. G., 326
Chinoy, J. J., 330
Cholodny, N. G., 75, 158, 159, 160, 161, 162, 163, 164, 169, 170, 171, 172, 173, 174, 179
Choudhri, R. S., 327, 333, 334
Christiansen, M. P., 224
Chroboczek, E., 275, 298
Claes, H., 137
Clausen, J., 89, 218, 223
Coffman, F. A., 262
Coons, G. H., 225, 252, 275, 276, 277, 278
Cooper, H. P., 233
Correns, C., 235
Crespin, J. F., 286, 291
Culpepper, C. W., 142

Danielson, L. L., 299, 300
Darlington, C. D., 244
Darwin, C., 54
Demidenko, T. T., 187
Demkovskiĭ, P. I., 179
Dennis, R. W. G., 283
Dennison, R. A., 112
De Ropp, R. S., 74, 75
De Vilmorin, *see* Vilmorin
Dexter, S. T., 195, 202
Dies, E. J., 272

Dolgušin, D. A., 33, 62, 63
Dorošenko, 113
Dostal, R., 165
Driver, C. M., 242, 281, 282
Duggar, B. M., 102
Dutt, N. L., 269

Efeĭkin, A. K., 70, 72, 258
Egiz, S. A., 117
Eguchi, T., 113, 114
Emsweller, S. L., 135, 298, 300
Engledow, F. L., 228
Eremenko, V. T., 143, 185, 257
Evans, G., 211
Evans, M. W., 57, 59, 212, 213, 214, 215

Fabian, I., 125
Fennell, J. L., 244
Filippenko, I. A., 71, 72
Filov, A. I., 300
Forster, H. C., 228, 229
Franck, J., 126
Fraser, J. G. C., 262
Frolova, V. N., 258
Fruwirth, C., 233, 275
Fry, Jean M., 299
Fryer, J. R., 147
Fuchs, W. H., 274
Fults, J. L., 218

Gaertner, T. v., 125
Gaffron, H., 126
Gaines, E. F., 233
Garner, W. W., 13, 28, 29, 30, 77, 102, 108, 109, 111, 112, 116, 122, 125, 132, 154, 203, 211, 212, 250, 310, 327
Gassner, G., 12, 13, 26, 27, 28, 29, 33, 62
Gavrilova, M. F., 179
Gfeller, F., 262
Goodall, D. W., 299
Goodwin, R. H., 238
Gorjunov, D., 264
Gray, S. G., 299
Grebennikov, P. E., 265
Greene, L., 176
Gregory, F. G., 30, 31, 44, 65, 66, 67, 68, 69, 70, 71, 72, 74, 75, 90, 95, 96, 97, 98, 99, 114, 124, 140, 143, 152, 153, 159, 161, 162, 163, 169, 221, 249, 257, 258, 303
Greulach, V. A., 30
Griffiths, D., 218
Griffiths, D. J., 286
Grover, F. O., 57, 59
Günther, H. K., 275
Gupta, J. C. Sen., 332
Gustafson, F. G., 322

Haagen-Smit, A. J., 161
Hackbarth, J., 283
Haigh, J. C., 328
Hall, H. M., 89
Hamilton, W. M., 229
Hamner, K. C., 77, 101, 114, 116, 119, 120, 121, 122, 128, 129, 130, 131, 154, 155, 156, 158, 163, 168, 169, 172, 173
Harder, R., 42, 43, 44, 125, 126, 136
Harlan, H. V., 99, 142
Hartisch, J., 248, 270
Hartsema, A. M., 222
Harvey, R. B., 194
Hatcher, E. S. J., 159, 161, 163
Hawkes, J. G., 281, 283
Heath, O. V. S., 300, 302, 303, 304, 305, 306
Heinze, P. H., 79
Hemphill, D. D., 176
Hendricks, S. B., 135
Henkel, P. A., 206
Hiesey, W. M., 89, 218, 223, 224
Hitrinskiĭ, V. F., 265
Hoffman, C. A., 300
Hohlovskiĭ, A. P., 265
Holdsworth, M., 300, 302, 303, 304, 305
Hollrung, M., 275
Hopkins, A. D., 212, 214
Hornberger, R., 51
Horowitz, B., 298, 299
Hošek, M., 165
Hudson, P. S., 34, 231
Hull, C. E., 233

Isip, I. N., 206
Ito, H., 23
Ivanov, S. M., 203
Ivanova, 198, 200

Jenkin, T. J., 229
Johnsson, H., 127
Jones, H. A., 298, 300
Jones, M., 210

Kajanus, B., 234
Kalantyrj, M. S., 271
Kalinin, P., 264
Kapoor, S. L., 327, 333, 334
Kar, B. K., 330, 331
Katunskiĭ, V. M., 125, 186
Keck, D. D., 89, 218, 223
Keim, F. D., 294
Kessler, W., 196
Kidd, F., 21, 52, 53
Kiričenko, F. G., 146
Klapp, E., 255
Klebs, G., 12, 13, 22, 23, 24, 25, 26, 27, 28, 29, 31, 39, 45, 56, 68, 101, 102, 103, 104, 105, 106, 107, 108, 113, 128, 269
Klitsch, C., 266
Knodel, H., 23
Knott, J. E., 155, 182, 298
Konovalov, I. N., 161, 180, 181, 258
Kopetz, L. M., 41, 44, 45, 46, 113, 274
Kostjučenko, I. A., 90, 91, 92, 94, 98, 99, 100, 221, 222, 257
Kraevoĭ, S. J., 146
Krasovskaja, I. V., 206
Krasulina, M. I., 270
Kraus, E. J., 23, 298, 323
Kraybill, H. R., 23, 298, 323
Kreier, G. K., 55
Krenke, N. P., 41
Kreusler, U., 51
Krotkina, M. A., 42
Kuilman, L. W., 327
Kuperman, F. M., 198, 200
Kuznecova, E. S., 113, 233, 234

Laibach, F., 52, 55, 160
Lamarck, J. B. de, 54
Lane, R. H., 162, 163, 164
Lang, A., 30, 114, 116, 117, 155, 242
Leech, W. D., 161
Leupen, F. F., 222
Levitt, J., 194, 195
Lewis, H., 87, 88, 89
Linnaeus, C., 54
Lippmann, E. O., 275
Litvinov, L. S., 151, 152, 300
Ljubimenko, V. N., 28, 167
Ljubinskiĭ, N. A., 206
Loehwing, W. F., 114, 154, 188
Lojkin, M., 67
Loomis, W. E., 44
Lord, L., 328
Lovvorn, R. N., 294
Lubenec, P. A., 285
Lukjianov, N. I., 300
Lukovnikov, E. K., 188
Luyten, I., 222
Lyon, C. B., 237
Lysenko, T. D., 13, 14, 21, 26, 33, 34, 35, 36, 37, 38, 39, 41, 42, 54, 55, 62, 63, 64, 65, 67, 117, 118, 121, 123, 128, 134, 140, 143, 150, 151, 153, 173, 232, 238, 257, 260, 264, 272

McCall, M. A., 233
McClelland, T. B., 302
McConkey, O., 212, 213, 214
McKinney, H. H., 34, 44
Magruder, R., 298, 302, 305
Mann, L. K., 114, 118, 119, 129
Marcovitch, S., 30
Marsden-Jones, E. M., 89
Masjuk, P. D., 274
Mathur, P. B., 300, 302, 303, 304, 305, 306
Maximov, N. A., 22, 33, 34, 35, 36, 42, 69, 102, 113, 187, 206
Melchers, G., 30, 32, 116, 117, 137, 155, 168, 171, 172, 235, 242
Mendel, G., 235
Meyer, F., 52
Miller, J. C., 298
Milthorpe, F. L., 298, 299
Modilevskiĭ, J. A. S., 142, 143
Montemartini, L., 275
Moon, H. H., 142
Moreau, R. E., 281
Morgan, T. H., 235
Moškov, B. S., 122, 123, 132, 134, 156, 167, 168, 169, 172, 173, 203, 206, 207, 208
Muller-Thurgau, H., 107 195
Munerati, O., 275
Murneek, A. E., 23, 46, 47, 77, 176, 177, 182, 183, 184, 308, 320, 321, 322, 323

Murty, G. S., 330, 332

Naylor, A. W., 78, 220
Newell, L. C., 294
Newton, R., 195
Nielsen, C. S., 146, 147
Nightingale, G. T., 298
Nihlson-Ehle, H., 233
Noguchi, Y., 57, 142
Novoderižkina, M. A., 244
Nutman, P. S., 99, 142

Oleĭnikova, T. V., 200, 263, 264
Oljhovikov, M. A., 69, 145, 196, 249
Ollson, G. A., 233
Olmsted, C. E., 127, 216, 217, 218, 291, 292, 293, 294
Ovečkin, S. K., 179
Owen, F. V., 226, 227, 278, 279

Pal, B. P., 330, 332
Pantanelli, E., 195
Parija, P., 208, 329, 330
Parisi, E., 275
Parker, M. W., 77, 78, 79, 114, 135, 147, 154, 155, 185
Parthasarathy, S. V., 330
Paševič, V. Ju., 180
Pastuh, M. B., 206
Pesola, V. A., 274
Pfeffer, W., 22
Pillay, K. P., 208, 332
Pinčuk, 206
Poole, C. F., 147
Pope, M. N., 99, 142
Popova, T. M., 180
Popp, H. W., 102
Post, K., 310, 318, 319
Powers, L., 237
Prehn, A., 51
Psarev, G. M., 156
Purvis, O. N., 31, 32, 43, 44, 56, 57, 65, 66, 67, 68, 69, 70, 71, 72, 74, 75, 76, 90, 95, 96, 97, 98, 99, 114, 124, 140, 143, 152, 153, 159, 161, 162, 169, 221, 232, 233, 234, 235, 236, 257, 258, 300, 304

Ramdas, L. A., 326
Ramiah, K., 328
Razumov, V. I., 113, 117, 128, 130, 134, 135
Reimers, F. E., 239, 241, 242
Rhind, J. A. S., 328
Richter, A. A., 179
Robbins, W. J., 152
Robbins, W. R., 298
Roberts, R. H., 176
Rodenhiser, H. A., 193
Rogler, G. A., 294
Römer, T., 275
Rosenbaum, H., 272
Rudorf, W., 42, 78, 113, 202, 203, 248, 273, 299
Ruhland, W., 196

Sachs, J., 30, 53
Sakr, El Sayd, 78, 298
Saltykovskiĭ, M. I., 198, 203, 204
Samohina, Z. F., 146
Sampson, Kathleen, 193
Sando, W. J., 44
Sapegin, A. A., 40, 41, 113, 190
Sapoznikova, K. V., 179, 270
Saprygina, E. S., 198, 203, 204
Sartoris, G. B., 267, 268, 269
Savvičev, K. I., 270
Scarth, G. W., 194, 196
Ščerbačeva, V. D., 295, 296, 297
Schafer, E. G., 233
Schander, H., 160
Schermerhorn, L. G., 298
Schneider, F., 275
Schroeck, O., 78
Scott, G. T., 226
Scully, N. J., 78, 135
Sen, B., 249, 327, 331, 332
Sereiskiĭ, A., 162
Šestakov, V. E., 201
Sevčenko, A. Ja., 285
Sexsmith, J. J., 147
Shalucha, Barbara, 161, 164
Sharman, B. C., 56, 59
Shaw, H. B., 275
Shirley, H. L., 102
Silva, J. S. T. de, 328
Simpson, A. C., 299
Singh, B. N., 326, 327, 328, 330, 333, 334
Singh, S. N., 333
Sircar, S. M., 329
Sivori, E., 58, 83

Skazkin, F. D., 205
Skoog, F., 161
Skripčinskiĭ, V., 328, 330
Sludskaja, M., 162
Šmelov (Šmelev in text), S. P., 201
Snow, R., 165
Snyder, W. E., 114, 129
Soloveĭ, G. T., 265
Sprague, V. G., 291
Spillman, W. J., 232
Srivastava, M. B., 333
Stankov, N. Z., 189, 190, 191
Stapledon, R. G., 211
Stelzner, G., 248, 298
Stewart, W. S., 158
Stoker, G. L., 226
Stout, M., 226, 227, 278, 279
Strömer, L., 42, 43
Struckmeyer, B. E., 176
Stuart, N. W., 135
Sukačev, V. N., 210
Sylvén, N., 242, 324

Tagi-Zade, A. H., 68, 124
Takahasi, N., 233
Taylor, J. W., 193, 262
Templeman, W. G., 158
Tetjurev, V. A., 70, 71, 79, 80
Thimann, K. V., 161, 162, 163, 164, 165, 166
Thompson, H. C., 77, 298
Thut, H. F., 44
Timofeeva, M. T., 198
Tincker, M. A. H., 21, 228, 285, 291
Tolmačev, M. A., 26, 33, 34
Tolman, B., 226, 227
Travin, I. S., 295, 296, 297
Tschermak, E., 232, 233, 234
Tschirch, 170
Tulaikova, K. P., 271
Tumanov, I. I., 196, 197, 198, 199, 200, 201, 202, 205
Turesson, G., 89, 218
Turrill, W. B., 89
Tužihin, G. A., 285

Van Overbeek, J., 158, 165, 175
Van Slogteren, 300
Vasey, A. J., 228, 229
Vasiljev, I. M., 67, 69, 198, 271
Vavilov, N. I., 233, 234, 275
Venkatraman, R. B. T. S., 267
Vetuhova, A. A., 202
Vilmorin, J. de, 275
Vinogradova, N. M., 244
Von Denffer, D., 32, 43
Vorobjev, 206
Voss, J., 68, 261, 265, 266, 275, 281

Wadham, S. M., 228
Wallrabe, 125
Wanser, H. M., 145
Watts, V. M., 298
Went, F. W., 44, 55, 58, 61, 80, 81, 82, 83, 84, 87, 88, 89, 163, 250, 308, 309, 310
Werner, H. O., 218, 281
West, C., 21, 52, 53
Western, J. H., 193
White, P. R., 85
Whyte, R. O., 34, 69, 145
Wiley, H. W., 277, 278
Wilhelm, A. F., 195
Williams, R. D., 297
Williams, W., 297
Withrow, Alice P., 137, 138, 154, 155, 168, 188
Withrow, R. B., 137, 138, 154, 155, 168
Witsch, H. v., 125, 126
Wittwer, S. H., 47, 48, 51, 52, 53, 176
Wort, D. J., 76, 145, 261, 262

Zacks, M. B., 263
Zadoncev, A. I., 198, 200
Zaĭceva, A. A., 181
Zarubaĭlo, T. Ja., 90, 91, 92, 94, 98, 99, 100, 221, 222, 257
Ždanova, L., 163
Ziherman, H. Ja., 14
Zimmerman, P. W., 158

INDEX OF GENERA AND SPECIES

Achillea, 82; *A. millefolium*, 223
Agropyron, 204, 220; *A. cristatum* see Crested wheatgrass; *A. repens* see Couch grass; *A. smithii* see Bluestem
Agrostemma githago, 42
Alopecurus myosuroides, 127
Amaryllis, 222, 223; *A. belladonna*, 222, 223
Anethum graveolens see Dill
Anthoxanthum odoratum see Sweet vernal
Apple, 176
Arabidopsis thaliana, 55
Arachis hypogaea see Groundnuts
Aster, 137, 311, 318
Avena, 163; *A. byzantina*, 262; *A. sativa* see Oats; *A. sativa* var. *byzantina*, 186
Azalea, 311

Baeria chrysostoma, 58, 83, 86, 87; *B. chrysostoma* var. *gracilis*, 82
Baileya multiradiata, 86
Barley, 19, 29, 41, 56, 57, 63, 79, 115, 142, 163, 186, 189, 190, 203, 232, 233, 234, 238, 254, 255, 258, 259, 260, 263, 264, 327
Beans, 176
Beet, 78, 206, 275, 277, 281, 298, 309
Beetroot, 298
Begonia, 311, 318; *B. semperflorens*, 311
Beta see Beet; *B. maritima*, 277; *B. vulgaris*, 220
Birch, 323
Blue grama, 216, 220, 292, 293
Blue lupin, 179, 188, 189
Bluestem, 220
Boltonia latisquama, 115
Bougainvillea, 311
Bouteloua, 19, 127, 216, 218, 220, 292, 293, 294; *B. curtipendula*, 216, 219, 292, 293; *B. eriopoda*, 292; *B. filiformis*, 292, 293; *B. gracilis* see Blue grama; *B. hirsuta*, 292; *B. rothrockii*, 292
Bouvardia humboldtii, 113
Brassica, 141
Brome grass, 291
Browallia, 311
Browntop, 291
Buckwheat, 188, 189

Cabbage, 141, 240, 252, 298
Calceolaria, 311, 318, 319; *C. hybrida*, 310
Calendula see Marigold
Calla, yellow, 312
Callistephus see China aster
Cannabis sativa, 186, 189
Capsicum annuum, 189; *C. frutescens*, 115
Carnations, 312
Carrots, 252, 298
Celery, 298
Centaurea, 312
China aster, 310, 318
Christmas cactus, 312
Chrysanthemum, 135, 167, 168, 173, 187, 312, 318, 319; *Ch. acticum*, 115; *Ch. frutescens*, 312; *Ch. indicum*, 189; *Ch. leucanthemum*, 115; *Ch. mepho*, 189; *Ch. morifolium* (*hortorum*), 319
Cicer arietinum see Gram
Cineraria, 312, 318, 319; *C. hybrida*, 115
Clarkia, 312, 319; *C. elegans*, 189
Clover, 55
Cocklebur, 55, 118, 119, 129, 130, 131, 136, 155, 156, 168, 173, 187, 189
Cocksfoot, 59, 211, 286, 291
Coreopsis californica, 86
Corn, see also Maize, 50, 51, 165, 187
Cosmos, 178, 182, 211, 212, 313; *C. bipinnatus*, 115; *C. sulphureus*, 212

Cotton, 35, 62, 150, 151, 189, 220, 327
Couch grass, 56, 59
Crested wheatgrass, 220
Crotalaria, 18, 135, 327, 333, 334
C. juncea, 333
Cucumber, 176, 187, 299
Cucumis sativa see Cucumber

Dactylis glomerata see Cocksfoot
Dandelion, 78, 224, 225
Delphinium, 313
Dianthus barbatus, 313
Didiscus, 313, 319, 320
Digitalis see Foxglove
Dill, 78, 137, 220
Drosophila, 55

Egg-plant, 176
Epilobium angustifolium see Rose-bay willow herb
Ervum lens, 274
Eschscholtzia californica, 86; *E. lobii*, 86
Euchlaena mexicana, 59
Eupatorium, 313
Euphorbia, 313

Feverfew, 313
Foxglove, 55, 313
Freesia, 314
Fuschia, 314

Gaillardia lorenziana, 310
Gardenia, 314
Genista, 314, 318, 320
Geranium, 314
Gilia tricolor, 86
Gladiolus, 314
Glycine max see Soybean
Godetia, 314; *G. quadrivulnera*, 86
Gram, 18, 332
Grape, 244
Grapefruit, 176
Groundnuts, 269, 274
Guayule, 82
Guizotia, 212

Heather, 314
Hemp, 189
Hippeastrum, 223; *H. hybridum*, 223
Hordeum pallidum, 64; *H. vulgare* see Barley
Hunnemannia, 314
Hydrangea, 314
Hyoscyamus, 32, 116, 138; *H. niger*, 30, 55, 117, 137, 155, 168, 171, 172, 235, 242

Iberis amara, 189
Iceland poppy see Poppy, Iceland
Iris, 222, 314; *I. tingitana*, 222
Italian ryegrass, 56

Jute, 18

Kalanchoe, 125, 314; *K. blossfeldiana*, 125, 136, 189
Kentucky bluegrass, 127, 224, 291

Lactuca sativa var. *capitata* see Lettuce
Lemon, 207, 208
Lentils, 180, 269, 271
Lettuce, 16, 141, 189, 191, 239, 240, 241, 252, 255, 298, 299
Ligustrum vulgare see Privet
Lilies, 314
Linanthus montanus, 86
Lolium multiflorum see Italian ryegrass
Lolium perenne see Perennial ryegrass
Lucerne, 189, 202, 255
Lupins, 180, 189, 269, 270, 271, 314
Lupinus see Lupins; *L. angustifolius* see Blue lupin; *L. luteus*, 270
Lycopersicon esculentum see Tomato; *L. pimpinellifolium*, 237

Madia elegans, 86
Maize, see also Corn, 29, 49, 50, 51, 52, 53, 75, 117, 142, 163, 164, 189
Mangolds, 298
Marguerite, 315
Marigold, 312, 315
Meadow fescue, 291
Medicago see Lucerne
Mentzelia Lindleyi, 86
Mignonette, 315
Millet, 29, 35, 59, 134, 135, 170, 181, 186, 188, 189, 220

Monardella lanceolata, 86
Morning glory, 315
Mustard, 18, 42, 43, 189, 331, 332

Nasturtium, 315
Nemesia, 315
Nicandra physaloides, 176

Oats, 29, 43, 44, 100, 163, 187, 188, 189, 254, 255, 258, 259, 260, 262, 263, 265
Oenothera deltoides, 86
Onions, 19, 298, 299, 300, 301, 302, 303, 304, 305, 306, 307
Orange, 176
Orchids, 315

Panicum, 186; *P. miliaceum* see Millet
Pansies, 315
Parsnips, 252, 298
Parthenium argentatum see Guayule
Pear, 49, 50
Peas, 46, 186, 187, 274
Pelargonium domesticum, 315; *P. hortorum*, 189
Pepper, 176
Perennial ryegrass, 59, 253, 286, 287, 288, 289, 290, 291
Perilla, 132, 133, 135, 156, 169, 174, 186, 189, 212; *P. nankinensis*, 156, 189; *P. ocymoides*, 132, 156, 167
Petunia, 315
Phacelia parryi, 83, 86, 88
Phalaenopsis amabilis, 82
Pharbitis nil, 115
Phaseolus, 186; *Ph. aureus*, 274; *Ph. coccineus*, 126, 127; *Ph. polystachios*, 126, 127; *Ph. vulgaris*, 126, 127, 186, 189, 274
Phleum pratense see Timothy
Phlox, 315; *Ph. paniculata*, 115
Physostegia virginiana, 115
Pineapple, 163
Pines, 323
Pisum see Peas
Poa, 224; *P. annua*, 55; *P. nervosa*, 224; *P. pratensis* see Kentucky bluegrass; *P. secunda*, 224
Poinsettia, 211, 212, 316
Poplar, 323, 324
Poppy, Iceland, 314
Populus tremula see Poplar
Potato, 19, 107, 112, 176, 187, 242, 281, 282, 283, 323
Potentilla, 82; *P. glandulosa*, 218
Primula malacoides, 115, 316
Privet, 56
Prunus besseyi, 207
Pumpkins, 176
Pyrethrum, 55

Radish, 240
Red clover, 210, 285, 286, 295, 296, 297
Rice, 18, 115, 142, 328, 329, 330
Robinia, 196; *R. pseudacacia*, 207
Rochea, 316
Rose-bay willow herb, 56
Roses, 316
Rudbeckia bicolor, 77; *R. speciosa*, 77
Rye, 26, 27, 29, 31, 32, 43, 44, 63, 65, 66, 67, 71, 72, 73, 74, 75, 96, 97, 98, 99, 142, 152, 153, 159, 160, 161, 162, 163, 164, 198, 199, 200, 201, 232, 234, 248, 249, 257, 265, 266
Ryegrass, 56, 59, 177, 229, 284, 286

Saccharum see Sugar cane; *S. spontaneum*, 268
Saintpaulia, 316
Salpiglossis, 310, 316
Salvia, 178, 212; *S. splendens*, 187, 189, 316
Scabiosa, 316; *S. atropurpurea*, 187
Schizanthus, 310, 316
Sedum, 212
Sempervivum, 23, 24, 25, 26, 106; *S. funkii*, 102, 103, 104, 107, 108
Sesamum, 328
Setaria italica, 189
Side oats grama, 216, 217, 218
Silene pendula, 115
Sinapis alba see White mustard
Snapdragons, 317
Soja see Soybean; *S. hispida* see Soybean; *S. max* see Soybean
Solanum demissum, 283
Solidago sempervirens, 238
Soybean, 18, 35, 55, 108, 110, 111, 115, 117, 120, 121, 135, 136, 146, 150, 151, 154, 155, 156, 178, 182,

Soybean (contd.)
183, 184, 185, 186, 187, 188, 189, 220, 269, 272, 273, 274, 284
Spinach, 47, 115, 137, 156, 157, 182, 187, 189, 255, 298, 299
Stevia, 317
Stock, 317, 318
Strawberries, 176
Sudan grass, 291
Sugar beet, 19, 34, 187, 225, 226, 227, 242, 243, 252, 275, 277, 278, 279, 280, 298, 326
Sugar cane, 267, 268, 269, 275, 276, 326
Sunflower, 189
Swede turnips, 281
Sweet peas, 317
Sweet vernal, 56, 59, 286

Tagetes erecta, 189
Tall oatgrass, 59
Taraxacum see Dandelion
Tea, 207, 208
Timothy, 57, 59, 193, 212, 213, 214, 215, 216, 284, 286, 291
Tinantia fugax, 189
Tithonia speciosa, 187
Tobacco, 108, 112, 168, 171, 172, 189, 284
Tomato, 44, 65, 81, 84, 85, 176, 191, 237, 238, 298, 299, 308, 309, 310
Trachymene coerulea, 319
Tradescantia, 56
Trifolium pratense see Red clover; *T. repens* see White clover
Trinia henningii, 210
Triticum, 54; *T. aestivum*, 54; *T. hibernum*, 54; *T. sativum*, 54; *T. vulgare* var. *erythroleucon*, 95; *T. vulgare* var. *erythrospermum*, 95; *T. vulgare* var. *erythrospermum rigidum*, 95; *T. vulgare* var. *ferrugineum*, 95; *T. vulgare* var. *pseudomeridionale*, 95
Turnip, 78, 240

Vetches, 269, 271
Vicia sativa, 271, 274; *V. villosa*, 271, 285
Violets, 317
Vitis labrusca, 244; *V. vinifera*, 244

Wheat, 18, 19, 29, 34, 39, 40, 41, 44, 54, 56, 63, 64, 65, 67, 68, 70, 72, 79, 90, 91, 92, 93, 95, 115, 123, 124, 142, 143, 144, 146, 163, 180, 181, 189, 190, 193, 198, 200, 201, 202, 203, 204, 221, 222, 228, 229, 232, 233, 234, 257, 258, 259, 260, 261, 262, 327, 330, 331
White clover, 189, 229, 286, 291, 297
White mustard, 42, 43, 44, 189

Xanthium pennsylvanicum see Cocklebur

Zinnia, 317

INDEX OF SUBJECTS

Aberystwyth: bred strains, 193; S23 ryegrass, 177, 294; S100 white clover, 297; S204 cocksfoot, 286; Welsh Plant Breeding Station, 228, 229, 285, 286, 291, 297
Abscission, 175
Acetylene, 163
Adaptation, physiological basis, 210
Age: and response, 98; of leaves, 156, 175
Agronomy, 11, 33, 137
Air-conditioning, greenhouses, 13, 54, 55, 80, 81, 223
Alaska, environment, 213
Alcohol content, 72
Aleurone layer, 160
Alpine plants, 223
Altitude: and development, 223; and photoperiodism, 113
Anaerobic conditions, 14, 69, 72
Analyses, environmental requirements, 231
Anatomy: and photoperiod, 187; grain, 99
Andes, expedition by Imperial Agricultural Bureaux, 19, 281
Animal, photoperiodism, 30
Annuals, 55, 232
Anthesin, 171
Arizona, environment, 225
Ascorbic acid content, 72
Assimilation, 52
Atlas Mts., Morocco, 211
Australia, environment, 216
Auxin: *see also* Hormone, growth, 172; synthetic, application, 165

Biennials, 55, 210, 232, 243
Biochemistry, 11; and vernalization, 179; herbage plants, 291
Bioclimatic Law, Hopkins', 212
Blastanin, 163, 274
Bolting: in onions, 300; in sugar beet, 225, 242, 280, 281
razil, environment, 211
Breeding: and development, 231; for winter hardiness, 203; herbage plants, 229, 236, 244, 254; range grasses, 224
Bud formation, 175; effect of auxin, 165
Bulbs, hot-water treatment, 245

Calcium, in plant nutrition, 187
California, environment, 225
Cambridge, Plant Breeding Station, 228
Canada: crop cultivation, 18; environment, 247
Carbohydrate: content, 113; nitrogen relationship, 11, 22, 165, 167, 182, 183, 185, 321, 323, 324; and vernalization, 75
Carbon dioxide, in air, 125, 154
Carnegie Institution of Washington, 223
Carotene, 177
Carotenoids, 136, 177
Catalase activity, 48, 49, 50, 51, 179, 182, 184
Catch crops, use of vernalization, 247
Cereals, 251, 257
Chicago, University, 19, 216, 261
Chilling, of seed or seedlings, 12
Chlorophyll content, 78, 181
Chloroplasts, 136
Chromosome number, and plant geography, 218
Coimbatore, Imperial Sugar Cane Breeding Station, 269
Cold Spring Harbor, 158
Coleoptile, test, 163
Colloids, and resistance, 195
Cotyledon: hormonal reserves, 160; character, 127
Costa Rica, Inter-American Institute of Agricultural Science, 244
Curly top, in sugar beet, 225
Cytogenetics, 231
Cytology, grains, 99

Dark chamber, 105
Darkness: and development, 14, 106, 119, 120, 121, 122, 128, 132, 133, 137, 145; and hormone manufacture, 173; and photosynthesis, 126; and respiration, 137
Deciduous character, 208
Defoliation: and photoperiodic reaction, 130, 155; in studies of hormones, 167
Development, 11, 21; effect on growth, 46
Devernalization, 14, 69, 70, 71
Disease(s), 16; (fungous or virus), 192; resistance, 224
Dormancy, 22, 90, 99
Drosophilas, botanical, 55, 87
Drought resistance, 16, 192, 205; and photoperiodism, 207
Drying, and vernalized grain, 71
Dry: matter content, 11, 78, 180, 182, 186, 188; weight, 54
Dwarf, grains, 99

Ear: emergence, 62; morphology, 40
East Malling, experiments, 258
Ecotypes, 19, 54; grasses, 216, 292, 293; physiological behaviour, 216; relation to altitude, 223
Elongation, stem, 48, 77, 85, 105, 164
Embryo: development, 142; excised, 95, 152, 162; extract, 163; vernalization, 74
Embryogenic phase, 190
Endosperm, 75; hormonal reserves, 160
England: environment, 216; market garden crops, 18
Environment, technique for controlling, 79
Enzyme(s): activity, 48, 224; and vernalization, 179; effect of hormones, 170
Evergreen character, 208

Facial eczema, 230
Fertilizers, 179, 227; and development, 187; and vernalization, 266
Flooding, resistance to, 208
Florigen, 16, 171
Florist crops, 310
Flowers: pistillate, 49, 51; staminate, 49, 51
Forest trees, 242
Formula, length of phase, 64
Frost resistance, 192
Fruit: set, 175; trees, 255

Gametes, and environment, 145
Gametogenic phase, 145, 190
Genetics, and development, 17, 231
Geographical distribution, crops, 209
Georgia, U.S.A., environment, 213
Germination, 22
Glucose, use in vernalization, 75
Graft hybrids, 232
Grafting, methods, 131, 154, 168, 175
Gramineae, 29
Grass, ecotypes, 216, 292, 293
Grazing, 157, 175, 210, 253
Green manure, 179
Growing points, 56, 57, 58
Growth: factors governing, 11, 21, 44; rate, 52, 53

Hardening, phases, 196
Heat, *see also* temperature, high, 72
Height, effect of photoperiod, 77
Herbage plants, 11, 12, 19, 127, 158, 177, 179, 229, 236, 244, 252, 284
Hibernalism, 62
Hibiny, experiments, 91
Hopkins' Bioclimatic Law, 212
Hormones: flower inducing, 30, 44, 78, 122, 125, 158, 164, 167, 170, 172, 182; growth, *see also* auxin, 50, 52, 85, 99, 158, 161, 164, 169, 175, 176; in reproduction, 15; translocation, 168, 174
Hot-water treatment, bulbs, 245
Hybridization, vegetative, 232

Imperial Agricultural Bureaux, 18, 19; Empire Potato Collection, 281
India, vernalization, 18
Indole-acetic acid, 163
Indole-3-acetic acid, 161, 164
Inheritance, 28; photoperiodic reaction, 324
Inhibition: growth, effect of auxin, 166; flower formation, 30, 42, 43, 47; flowering, 63, 106, 128, 175

Injection, hormone, 158, 246
Irradiation, 135, 138
Iso-electric point, 179

Juvenile plants, 87

Kirovobad, experiments, 91

Latitude: and development, 17, 61, 100, 145, 212, 215; and ecotypes, 54; and photoperiodism, 28, 113, 211, 323
Leaf (ves): morphology, 88; area, 54, 113, 164, 180; blades, effect of environment, 77; response of parts, 156
Legumes, grain, 269
Lens paper, use in grafting, 131, 168
Leys, management, 16, 19, 157
Light: and photosynthesis, 126; continuous, 103; decisive factor, 26, 41, 102, 137, 149, 154, 156, 246; intensity, 25, 83, 104, 108, 118, 119, 122, 125, 130; intermittent, 134, 137, 138; spectral composition, 108; wavelengths, 135
Location of response, 73, 149
London Imperial College of Science and Technology, 15, 18, 19, 65, 98, 159, 232, 249, 300
Louisiana, U.S. Sugar Plant Field Station, 267

Magnesium, in plant nutrition, 187
McGill University, Montreal, 194
Mendelism-Morganism, 231
Metabolism, 46; and photoperiodism, 182
Meteorology, recording, 19
Mexico, environment, 212
Microclimates, 19
Micro-dissection, 56, 57, 114, 140, 253, 286
Microphotographs, 59
Migration, 54, 211
Minimal leaf number, 31, 76
Moonlight, 125
Morphogenesis, 60
Morphology, indicator of development, 39, 189
Moscow, Research Institute of Vegetable Production, 239
Multidimensional models, 44

Narcotics, effect on transmission of response, 175
New York, environment, 311, 318
New Zealand, environment, 229
Nitrogen: and vernalization, 75; deficiency, 165; exposure to, 70; requirement, 187, 188
Nitrogenous substances, content, 180, 182
Nodules, and photoperiodism, 274
Number of leaves, 31, 44
Nutrition, 12; and development, 187, 188; and vernalization, 75
Nutritive value, 177

Ohio, environment, 214
Ontario, environment, 214
Orchard management, 323
Oregon, environment, 225

Pamir, environment, 238
Parthenocarpy, 51
Pasadena: air-conditioned greenhouses, 81, 87, 89; California Institute of Technology, 13, 223
Pelt cycles, 30
Pennsylvania, U.S. Regional Pasture Research Laboratory, 255, 284, 291
Perennials, 55, 210
Phases, in development, 13, 23
Phasic: analysis, 17, 19, 227, 229, 236, 240, 266; development, 36, 108, 117, 123, 140, 198, 234
Pests, 16
Phenology, 19
Phosphorus, in plant nutrition, 85, 187
Photochemical reactions, 138
Photoperiod, defined, 109
Photoperiodic: adaptation, 28; after-effect, 117, 122; classes, 77, 111, 112, 113, 115, 137, 203, 310; induction, 117, 129, 140; reaction, and defoliation, 130, 242

Photoperiodism, 12, 13, 28, 67, 86, 87, 88, 104, 108, 273; and altitude, 113; and latitude, 28, 113, 211; and metabolism, 182; and photosynthesis, 124; and respiration, 182; and taxonomy, 126; and temperature, 61, 76, 116, 117, 130; animal, 30; defined, 109, 112, 116; herbage plants, 285, 292, 293
Photophase, 13, 22, 40, 41, 119, 123, 190, 239
Photosynthesis, 44, 85, 136, 154, 180; and photoperiodism, 124; and respiration, 186
Phyllody, 136
Physiological: age, 29; predetermination, 21
Phytogeography, 137
Plumage cycles, 30
Pollen, formation, and environment, 146, 147
Polyploidy, and plant geography, 218
Potassium, in plant nutrition, 187
Poultry food, dried grass pellets, 254
Precursor, auxin, 164
Pre-treatment, 33, 63; by light, 117, 248; by temperature, 246, 248; hormonal, 163; inducing drought resistance, 206; inducing resistance to flooding, 208
Primordia, 31, 32, 56, 57, 59, 105, 106; flower, 13, 22, 26, 157
Protein content, 78, 177, 180
Puberty, in plants, 11
Pubescence, leaf, 88
Pure warmth sum, 46
Pushkin, experiments, 92

Radiation, biological effects, 102
Reactions (Purvis and Gregory), 67
Removal, reproductive organs, 48
Research Institute of Plant Physiology London, *see* London, Imperial College of Science and Technology
Respiration, 52, 179; and darkness, 137; and photoperiodism, 182; and photosynthesis, 186
Response, parts of leaves, 156
Resistance, mechanism, 194
Revernalization, 73
Reversibility (*see also* devernalization), 14, 38, 71, 122, 228, 258
Ripeness: (milk, wax or complete), 37, 62; to flower, 13, 22, 23, 26, 29, 31, 40, 45, 56, 68, 76, 102, 269, 286
Rochester, University, N.Y., 238
Root: crops, 251; growth, 113, 175
Rothamsted Experimental Station, 300
Rust, resistance to, 193

Salt, absorption, 53
Seed: production, 16, 19; prod., areas, location, 221, 225, 230, 280, 281; response to environment, 90
Segregation, of habit, 232
Shading, tomato plants, 309
Shooting, 19, 27, 37, 63, 67, 177
Short-day vernalization, 18
Shrubs, 320
Silage, 29, 297
Slit panel technique, 154
Smuts, resistance to, 193
Soil moisture, 44
South Australia, habitat, 100
Sowing: technique, 11; time, date, 63, 67, 227, 266
Spacing, of plants, 227
Spectrograph, 135
Spike, development, 57, 97
Spikelet formation, 59
Spring: habit, 35, 54, 55, 64, 68, 232; habit, defined, 265
Staining, in diagnosis, 76
Stalks, 37
Starvation, technique, 75
Stem(s): plasm, 34; length, 113
Stomata, 85
Strains, from different latitudes, 216
Subtropics, 113, 211
Sugar content, 27, 85, 107, 179, 195, 200
Succulence, of leaves, 136
Suction force, 85
Sunlight, effect of, 44
Sweden, environment, 127
Synapsis, 47
Syngamy, 47

Tashkent, environment, 239
Taxonomy, 54; and photoperiodism, 126
Technique: adjusting air flow, 125; photoperiodic studies, 250; studying light perception, 154; vernalization, 248, 249
Temperature: accessory factor, 123; and photoperiodism, 76, 108, 116, 117, 130, 310; decisive factor, 12, 26, 41, 43, 61, 65, 107, 149, 220, 246, 274; effect on transmission of response, 175; following photophase, 146; high, 70, 72
Thermo-phase, 22, 37, 41, 61, 65, 67, 68, 123, 140, 190, 200, 201, 220, 239
Thermoperiodism, 61, 79, 81, 82, 84, 86, 87, 88, 310
Tillering, 37, 158, 164, 257
Training, Lysenko method, 264
Translocation, 85; hormones, 168, 174
Transmission, of flowering response, 154
Transplant experiments, 54, 89
Trees, 255; forest, 323; fruit, 320
Tropical plants, 29
Tropics, 113, 211, 244
Tuber: formation, 28, 126, 282

U.S.S.R., area sown with vernalized grain, 249

Varieties, composition, 99
Vegetables, 251, 298
Venation, leaf, 88
Vernalin, 16, 171
Vernalization, 12, 13, 15, 18, 31, 33, 34, 42, 56, 57, 62, 66, 140, 180, 240, 246, 247, 257, 269; and biochemistry, 179; and disease, 193; and enzymes, 179; by short day, 18, 67, 68, 124; diagnosis, 76; hormonal interpretation, 159, 161, 163; location of response, 150; natural, 90, 199, 221; origin of term, 64
Victoria, Australia, environment, 228
Vitamin B, 172
Vitamin content, 224

Wageningen, Laboratory for Plant Physiological Research, 222
Wales, oats, 100
Washington, D.C., environment, 211, 214
Washington (State), environment, 212, 225
Water relations, 12, 61, 108, 113, 123, 188, 207
Weed control, 175, 176
Winter: habit, 35, 54, 55, 62, 64, 68, 232; habit, defined, 261, 265; hardiness, 16, 27, 55, 192, 194, 196, 202, 203, 221

Xanthophyll, 177