PANEL ON PLANTS AND LIGHT

FRIDAY MORNING SESSION

December 16, 1955

The fourth session convened at 10:00 o'clock, President Fillmore presiding.

PRESIDENT FILLMORE: We are resuming the program of the Fifth Anniversary Meeting of the Plant Propagators Society with a presentation based primarily on scientific research It frequently happens in trying to set up a program of this kind that there is a considerable debate as to whom should be choosen to present a particular topic There may be several individuals of equal rank in the particular field under consideration. In such a case the Program Committee has a difficult job in making the choice. There is, however, one field of plant research in which there is no debate, in which there is one preeminent leader The preeminent leader in the field of light and plant growth is Dr. H. A. Borthwick of the United States Department of Agriculture at Beltsville, Maryland.

Dr. Borthwick will discuss light and plant propagation. I am now happy to present Dr. Borthwick.

Dr. Borthwick presented his paper entitled "Light and Some Plant Responses" (Applause)

LIGHT AND SOME PLANT RESPONSES

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We have long known that plants are influenced by light in many different ways. For example, the seasonal change in daily duration of light controls flowering of many species, some flowering only when days are short and others only when days are long. Daylength also determines the time of year at which many trees and shrubs cease expansion of new leaves and produce resting buds before the onset of winter. Light is required by some seeds for germination, but it prevents the germination of others It regulates elongation of stems of some plants and promotes coloration of the ripening fruits of others. It enters into the regulation of growth and development of plants in countless ways that are familiar to us and probably in many others that have not yet come to our attention.

In the last 4 or 5 years we have learned that a number of these seemingly unrelated responses of plants to light have some points in common. Several of them are, in fact, controlled by the same basic light reaction. This means that detailed studies of one response give us in-

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*Dr Borthwick's official title is Plant Physiologist, United States Department of Agriculture, Agricultural Research Service, Horticultural Crops Research Branch, Plant Industry Station, Beltsville, Maryland formation about the light reaction that is common to all. Thus a study of the light control of seed germination may give us information on how to manipulate light to promote or inhibit the growth of a tree or a shrub so that its wood will be in suitable condition for propagation at times of our choice.

The purpose of this discussion, therefore, is to describe several light responses of plants and to explain our present understanding of how light operates to produce them. The principles involved are basic not only to plant propagation but also to many other phases of plant culture.

The daylength responses of plants Let us first consider the effects of the daily duration of light on plant responses that are often attributed to temperature. The cessation of growth of various woody plants that occurs in late summer or early autumn results from the short days of that season, not from the low temperatures In fact, the stoppage of growth and the onset of bud formation frequently occur well in advance of the time when temperatures begin to fall. In addition to regulating growth of woody plants, daylength also controls other vegetative responses such as the formation of bulbs of onion, the runners of strawberry, the tubers of begonia, and the thickened roots of dahlia.

More widely known, however, are the regulatory effects of daylength on flowering. The flowering of chrysanthemum in autumn and that of poinsettia at Christmas are responses to the short fall and winter days. For that reason these plants and others of similar seasonal flowering habit were called short-day plants. Long-day plants, which flower best when the days are long and fail to flower when days are short, are also known. They include radish, spinach, beet, certain clovers and alfalfa and most of our cereals.

In addition to long and short-day plants, there are others that seem uninfluenced by daylength. Tomato is an example. Most of our commercial tomato varieties flower equally well on a wide range of daylengths, but flowering of certain types introduced from South America is somewhat dependent on this environmental factor. Another example is the Red Kidney bean, which initiates flower buds equally well under a wide range of daylengths. The subsequent maturation of flowers and production of pods by Red Kidney bean, however, are limited by daylength if the plants are grown within one range of temperature but not if they are grown within another Plants that do not usually exhibit a response to changes in daylength thus may do so under a certain combination of environmental conditions, and frequently they may have close relatives that are sensitive to daylength over a wide range of environmental conditions. Such observations suggest that the mechanism for daylength response may be rather universally present in all plants but that in some such as Red Kidney bean the mechanism, although present, does not function as a control on flowering except under certain conditions.

Discovery of daylength response. Our knowledge of the daylength response of plants began in 1920, when W. W. Garner and H. A. Allard, two plant scientists in the U.S. Department of Agriculture, reported their discovery of it They named the phenomenon "photoperiodism," a term coined to indicate the controlling action of daily duration of light or dark on flowering of some kinds of plants. In the 35 years since that time the photoperiodic response has been found to occur in a wide range of plants.

Application of controlled daylength to plant production. Artificial light, although very weak in comparison with sunlight, was found to substitute satisfactorily for it to extend the length of day and thus meet the photoperiodic requirements of plants. Plant breeders were quick to use this in a practical way to make plants of early and late varieties bloom simultaneously so that they could be hybridized. Breeders also induced plants to bloom out of season by appropriate use of light and thus hastened breeding projects through production of more than one generation a year.

Use of light on plants by commercial growers thus far has been largely confined to chrysanthemums Regardless of their natural time of bloom, flowers of many varieties of "mums" are now produced throughout the year in greenhouses by use of artificial light during the months when natural days are short and by shading to decrease the daylength when days are long. In the warmer southern parts of the country, where chrysanthemums can grow outside throughout the winter, artificial light is used over many areas of them during late fall and early winter to delay blooming until late winter and spring. As these practices become more widely known and understood they can no doubt be extended with similar success to a number of other crops grown outdoors in the south and can be used elsewhere to improve methods of production of greenhouse crops in addition to chrysanthemum.

It would seem that many phases of plant propagation and nursery practice might be benefited through the judicious use of light Maintenance of plants in condition for the production of cuttings by appropriate light treatments has already been mentioned. The rooting of cuttings of many plants is known to be favorably influenced by light, and the growth of seedlings and rooted cuttings of many woody plants can be continued for long periods or promptly brought to a halt at the will of the grower by his choice of light treatment Some examples include rooted cuttings of *Weigela* and seedlings of catalpa, American elm, some species of maple, certain pines and others. These various responses of woody plants to light need further research, but the possible practical application of facts already established needs the imaginative consideration of those who are actively engaged in the business

Night length, not daylength, the controlling condition Addition of light at the end of a naturally short day prevents the flowering of short-day plants and promotes flowering of long-day ones. This lengthens the day, but it simultaneously shortens the night; so one wonders whether these responses result from the longer days or the shorter nights. The term photoperiodism suggests that the duration of light may be the controlling factor, but this is incorrect. The daily duration of darkness is the condition that regulates flowering. Moreover, this darkness must be continuous to be effective. Twelve-hour dark periods, for example, may promote flowering of soybean plants very effectively, but if the dark period is interrupted near the middle with only a minute or two of light, thus dividing it into two 6-hour dark periods, flowering fails completely. Barley plants, on the other hand, are unable to flower when grown with 12-hour nights, but a brief interruption about the middle of the dark period causes them to flower normally. On long nights the short-day plant flowers and the long-day one fails to flower, but on long dark periods interrupted near the middle, the long-day one flowers and the short-day one fails to flower. A short-day plant thus is one that requires long dark periods for flowering and a long-day plant is one that requires short dark periods or continuous light.

Dark-period interruptions are also effective in maintaining woody plants in a continuing state of growth. Experiments of this type, although not numerous, have established the validity of the procedure. The minimum amount of light required as a dark-period interruption for controlling the growth of trees and shrubs that are known to be responsive to daylength has not been determined. For a few species, such as *Weigela,* catalpa, American elm and some maples, one or two hours was found effective, and it is probable that appreciably shorter periods may be sufficient. Much variability in minimal amounts of light required for control of flowering and certain other responses in different varieties of plants within a species has been found and is to be expected among related varieties within species of woody plants when these are adequately investigated.

Location of the flower-regulating reaction. The part of the plant that is active in regulating flowering is the leaf. Some plants such as soybean and cocklebur flower if a single leaf is subjected to dark periods of the proper duration even though all the other leaves receive dark periods of durations unfavorable to flowering. Soybean requires a succession of two or more long dark periods, but under ideal conditions a cocklebur will flower in response to a single long dark period. Flowers occur on parts of the plant situated some distance from the treated leaf, this would imply that some flower-inducing substance must be made in the soybean or cocklebur leaf during favorable dark periods and that this substance must move from the leaf to the growing points of the plant where it induces flowering. Such substances are thought to be special flower-forming hormones, have not been isolated and identified. Numerous attempts have been made to extract from a plant that is flowering materials that when applied to a non-flowering plant would cause it to flower. Such experiments have in general not succeeded, but the lack of success does not necessarily disprove the possible existence of such compounds in the plant.

Studies involving the grafting of leaves of the Agate soybean on plants of the Biloxi variety give further evidence of the importance of leaves in controlling flowering and show an important difference between early and late varieties of soybean. Both of these soybean varieties are of the short-day type, but the Biloxi variety requires very long dark periods for flowering, while the Agate variety is able to flower on considerably shorter ones. If a single leaf of agate is grafted to a Biloxi plant, the latter no longer requires such long dark periods for flower formation; its dark-period requirements then become the same as those of Agate. At least one cause of differences in earliness of varieties of soybean or varieties of other photoperiodically sensitive plants would thus seem to be differences in flowering-regulating reactions going on in their leaves during darkness. In Agate soybean, products of these reactions reach an effective level in a shorter period of darkness than in

Biloxi. This is one reason that Agate plants can be grown so much farther north, where dark periods during the growing season are too short for flowering of varieties such as Biloxi.

Kind and amount of light needed. The amount of light required to regulate flowering of many plants is very low. For barley, hemp, soybean, poinsettia and certain others, less than 50 foot-candle-minutes of light from an incadescent-filament lamp is sufficient. This can be given in various ways without greatly altering the result. One might use an intensity of 50 foot-candles for 1 minute or 1 foot-candle for 50 minutes with equal effectiveness. If dim light is used throughout the "dark period" the intensity required is about 0 03 foot-candle. Flowering of hemp and soybean occurs if the intensity drops below this value and fails if it exceeds it. Such intensity is roughly equivalent to the light from a 100-watt lamp at a distance of about 40 feet. Some plants, such as chrysanthemum and possibly beet, require somewhat more light than this. The reasons for the difference are not completely understood but are not thought to depend on any different basic principles. As mentioned earlier, comparable information for growth responses of woody plants is very scarce.

Knowledge of the relative effectiveness of different colors of light has given information of both theoretical and practical value about photoperiodism. We know, for example, that red light is the most effective to use in the middle of the dark period to prevent flowering of short-day plants. Similarly, it is the best to use in the middle of the night to promote flowering of long-day plants Blue light is also effective in both cases, but far less so than red. Green light, however, is only slightly effective in preventing flowering of short-day plants and in promoting flowering of long-day ones. Although the end results of a given light treatment are opposite in long and short-day plants, the similar relative effectiveness of the different colors of light in controlling flowering of the two kinds of plants strongly suggests that both kinds are controlled by the same basic photochemical reaction.

Relation of daylength and other light responses of plants. The light reaction causing the daylength response also controls various other responses of plants. Growth of bean leaves and stems, for example, is regulated by light and the relative effectiveness of the different colors follows the same pattern as in photoperiodism. If seedlings of these plants are grown in darkness, their stems become long and their leaves remain small. Very briefly daily periods of light of very low intensity cause their leaves to become appreciably larger and prevent their stems from becoming so long. Red light is more effective in causing these changes than any other kind just as it is in the daylength response.

Another response that is similarly dependent on red light is the germination of light-sensitive seeds such as those of some varieties of lettuce and tobacco. A single exposure of the seeds to a relatively small amount of light is sufficient to induce a high percentage germination. These responses of seeds and seedlings to light seem outwardly to have little in common with photoperiodism, but experimental evidence indicates that all are controlled by the same basic light reaction.

This finding in itself has been very useful because it enables one to study various aspects of this basic regulatory reaction of light in any one of these several phenomena. This has led to a discovery about photoperiodism that probably would not have been made by a direct study of that phenomenon. Investigation of the light reaction that controls seed germination showed that light near the limit of visibility at the red end of the spectrum, for convenience called the "far red," counteracts the action of red light Thus, moist lettuce seeds that are given red light for a few minutes will germinate when placed in the dark, but moist seeds given first red and then far red remain dormant. This reversing action of red and far red, moreover, can be repeated many times, the final germination response always being determined by the kind of light given last in a series of light alternations. As mentioned previously, the promotion of germination of seeds and the inhibition of flowering of short-day plants both require red light. Since far red reversed the action of red for seed germination, one naturally wondered whether it might not likewise reverse the action of red in controlling flowering of short-day plants. If it did, this would be powerful evidence confirming the belief that these two plant responses are controlled by the same light reactions. An experiment was made, therefore, to test for this far-red effect; and reversibility of the light reaction controlling flowering was discovered.

This means that one can destroy the flowering stimulus in a short-day plant by irradiating its leaves in the middle of the night with red light. He can then immediately regenerate the stimulus to flower by irradiating again with far red. These reversals can be made repeatedly just as they can with germination of seeds and as many as four complete reversals of control of flowering in cocklebur have been made successfully.

The same reversible reaction has also been found to control the growth habit of bean plants. One can transform bush beans into climbing ones by treatments with far-red light for as brief a period as 5 minutes once a day only two or three times during the seedling stage. The climbing response thereby induced in the plants can then be completely counteracted by giving them 2 minutes of red light after each treatment with far red Such reversals in bean can be repeated several times without appreciable decrease in responsiveness of the plants. The phenomenon occurs in many bush varieties and even in pole beans. In the latter the climbing habit is exhibited precociously if the young seedlings are appropriately treated with far red.

The same reversible reaction is also present in tomato fruits and is responsible for a difference in color between dark-ripened and light-ripened fruits of certain varieties. This color difference results from the presence of a yellow pigment in the outermost part of the skin of the light-ripened fruit and its complete absence in the skins of dark-ripened ones. If green tomatoes are given only a minute or two of weak red light each day and complete darkness all the rest of the time, the skins become as yellow as they would be if ripened in full sunshine. However, if the tomatoes are given some far-red light after each treatment with red, the action of the red is completely nullified and the skins remain as colorless as they would be if ripened in complete darkness. In tomato the reaction is also repeatedly reversible, thus showing this response to be under control of the same light reaction that regulates seed germination, photoperiodic response and growth of bean seedlings. Although flowering of tomato, as mentioned previously, is not controlled by daylength, the light mechanism for such control is thus shown to be present. This again suggests its rather universal occurrence in plants but again indicates that a plant does not always have to use this mechanism even though it is present.

Significance of photoreversible responses. The various ramifications of this discovery of photoreversibility in control of flowering and other light-regulated responses have not been fully explored, but the discovery opens up new avenues of experimental approach to the study of photoperiodism and control of flowering. Conversely, knowledge about the photoperiodic reaction is now brought to bear on the physiology of seed germination. Identity of the light reactions controlling the various phenomena mentioned strongly suggests the universal occurrence of this control mechanism in plants and reemphasizes the great importance of further basic study of its action.

Research of this nature is not directed primarily toward immediate practical application to specific plant production problems Instead, its purpose is a basic understanding of the biological principles involved. Almost invariably, however, research workers or others make practical use of the results. Knowledge of the great effectiveness of red light in controlling flowering thus underscores the importance of having a lamp that produces light rich in red. Such a lamp is the ordinary incandescent-filament bulb, inexpensive to buy but very effective in regulating flowering and other daylength responses of plants. Ordinary fluorescent lamps are relatively ineffective when used for this purpose on some kinds of plants. Knowledge of reversibility of seed germination by light raises questions about survival of weed seeds in soil and their subsequent germination. What part does light play in the eventual germination of these seeds? The success of pre-emergence herbicides in controlling weeds depends on various factors, one of which is avoidance of cultivation after application of the herbicide. If the surface soil is disturbed, new weed seedlings appear. Does this happen because light-requiring weed seeds brought to the surface by cultivation have their light requirement satisfied and are thus enabled to germinate? Choice of kind and amount of light and time of its application for best control of flowering and finding the principles involved in seed and other light-controlled dormancies are only a few of the problems that are finding solution or new experimental approaches through basic studies of the action of light in photoperiodism and related phenomena.

Although our knowledge of the action of light in regulation of growth and development of plants is still very far from complete, we can begin to recognize at least the outlines of a basic controlling reaction. That it is some kind of master reaction is shown by the diversity of responses that it controls and enough has been learned about the way it operates to serve as a guide to further experimentation The reaction is of widespread, perhaps universal, occurrence in plants including, of course, all those with which plant propagators are concerned. The possibilities for making use of this light-controlled regulatory mechanism are numerous and depend largely for their discovery and development on the ingenuity and imaginativeness of those immediately involved with the problems of the individual plants. These persons will find a sizeable backlog of unexploited scientific information already available. They must also remain constantly alert, however, to the outcome of current basic research any phase of which may yield results of special interest and importance to them.

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PRESIDENT FILLMORE. Dr. Borthwick, we are indebted to you for the excellent discussion which you have given us on the influences of light on plant growth. It has been very inspirational and I am certain that our group have a number of questions for you.

GERALD H. VERKADE (Verkade's Nursery, New London, Conn.): Is there also increased root growth resulting from the light treatments?

DR. BORTHWICK· We have not made careful measurements, so I cannot say.

CHARLES A. BURR (C. R. Burr & Co., Manchester, Conn.): Have you had any experience with light with respect to growth of rose bushes?

DR. BORTHWICK: I have not had experience with rose.

ALBERT LOWENFELS (White Plains, N.Y.): What is the effect of filtering out a certain amount of sunlight by protecting cuttings using mist, polyethylene covers, cheesecloth shade, etc.?

DR. BORTHWICK: You are cutting down the total intensity and you are not interfering with the of light coming through. The chances are that you still have enough light intensity to take care of the desired rooting response.

DR. L BAUMGARTNER (Baumlandia Hort. Res. Lab., Croton Falls, N.Y.): Is it necessary to have additional red light or is it sufficient to weed out the undesired portion of white light?

DR. BORTHWICK: The difficulty with trying to weed out the non-red light from an incandescent lamp or from sunlight is that it is hard to filter the far red from the red. It is better to select a source that has no far red in it and then to remove the red. To do that, one uses a fluorescent source, which has practically no far red in it, and then use a red filter.

DR. BAUMGARTNER: Is it necessary to supplement the red that normally comes from an incandescent light?

DR. BORTHWICK: Yes You understand that Mazda lamp has both far red and red light in it. They are working in opposition to each other and under some circumstances either one might get the upperhand. The red action so far surpasses the far red that Mazda light gives the red effect.

MARTIN VAN HOF (Rhode Island Nursery, Newport, R.I.): Does light play an important part in the germination of evergreen seeds?

DR. BORTHWICK: One of the men at the station has run germination tests on pine seeds. I do not know the species he used, but some were light sensitive. Knowing what we do about the germination of seeds of many kinds of plants, I think that light may be involved.

MR. VAN HOF: Would you advise us to apply light to yew seeds which take two years to germinate?

DR BORTHWICK: Let me say that there are many things which may keep a seed from germinating One might be a requirement for light, another a hard seed coat, a requirement for after-ripening, or incorrect temperature. I may have unduly emphasized the role that light plays in the germination of seed, but even with such things as yews, I would certainly try light.

HARVEY TEMPLETON (Phytotektor, Winchester, Tenn.): Is it true that chlorophyl is destroyed in light and regenerated in darkness?

DR. BORTHWICK: This is getting into a field I know relatively little about. I believe you are correct in assuming it is destroyed in light. It is not my understanding that it is formed in darkness however.

LESLIE HANCOCK (Woodland Nurseries, Cooksville, Ontario): Certain woody plants, which are brought inside in early spring for forcing, do not react to heat alone. Is that because they weren't receiving the right daylength?

DR. BORTHWICK: I haven't had experience with that. I do understand that plants which have not had an adequate amount of cold to release their growth capabilities can have it promoted by continuous light sometimes when long days will not suffice.

MR. HANCOCK: The practical question is this: We used to get woody plants in January and they would not break bud. Certain types responded to forcing but others did not. Do you think that increasing the length of day might help?

DR. BORTHWICK: I can't answer the question except to predict that it would have a good chance of working

DR WILLIAM E. SNYDER (Rutgers University, New Brunswick, N.J.): I would like to comment on this question. While at Cornell University, I worked on the effect of lenght of day on a number of woody ornamentals. It was found that if evergreens had received a cold treatment, they would respond to the length of day. For example, *Taxus* cuttings showed lateral bud growth thirty days after being placed under long-day conditions (16 hours of light daily), however, those maintained continuously under short-day conditions (8 hours of light daily) had not developed any new growth even after eight months.

FRANK TURNER (Springfield, Ohio): Can you give any estimate of the number of woody plants which will respond to this light treatment.

DR. BORTHWICK: Beyond what Dr. Nitsch discussed yesterday and what Dr. Snyder has just told you, I can state that about two-thirds of the native trees which we have tested at Beltsville were highly responsive to light treatments I have the feeling that a large number of plants will be found which are sensitive. I am also fully convinced that every plant has the mechanism in it, but whether or not this mechanism is used or not may be a different matter.

PRESIDENT FILLMORE: I am sorry that we will have to terminate the discussion of this topic. Dr. Borthwick, unfortunately, will have to leave us early this evening. Questions which you may have can be directed directly to him during the remainder of the day.

Again, I want to express our thanks to you, Dr. Borthwick, for being with us and discussing your interesting work on light.

The next discussion this morning will be concerned with the propagation of chrysanthemums by Mr. Vernon Gifford of Yoder Brothers, Barberton, Ohio.

Mr. Gifford is a graduate of Ohio State University. He was a student of Dr. Chadwick's while at Columbus Yoder Brothers is a major producer of rooted chrysanthemum cuttings. In fact their annual production of this crop alone is in the neighborhood of 75 million cuttings It would seem, then, that we have one of the best sources of information about rooting chrysanthemum cuttings.

Mr. Gifford presented his paper entitled "Propagation of Chrysanthemums by Cuttings." (Applause)

PROPAGATION OF CHRYSANTHEMUMS BY CUTTINGS

Vernon E. Gifford
Yoder Brothers
Barberton, Ohio

The new developments and progress made in flowering chrysanthemums in the past few years have also influenced the propagation of "mums"

It was not too many years ago that propagating mums was generally conceded to be a Spring and early Summer proposition. Plants to be used for stock were selected during the flowering season and held in a more or less dormant or inactive state during the winter. This was accomplished by replanting the selected stock in benches, flats or perhaps cold frames. Low temperatures and low moisture conditions were maintained for the winter period. Plants were held thusly until Spring when they were given conditions necessary for resuming their normal growth. This procedure is still followed in some greenhouses.

With the advent of year round flowering of mums which is becoming more and more a common practice, it was necessary that rooted cuttings be also made available any time of the year. The diligent work of several large concerns have made this possible so that now rooted chrysanthemum cuttings are available each week of the year

Propagation of mums by cuttings is by no means the only method of propagation. Seeds, grafting, and division are other methods of propagation. However, propagation by cuttings is probably the most important method. The following discussion will deal entirely on propagation by cuttings

In discussing propagation by cuttings a number of important aspects both physiological and environmental come to mind. Many of these