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Day Length and Crop Yields

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In the present emergency and the years ahead, American farmers will be called upon to produce many crops that are new to them. New crops inevitably bring new problems of production. Much waste of effort and invested capital may often be prevented by knowing the areas to which these new crops are adapted.

There are three important environmental factors affecting the adaptability of plants to a given area—soil, climate, and length of day. In agricultural research and in farm practice much attention has been given to the soil and climatic requirements of plants, but less attention has been paid to the day-length requirements. Nevertheless, existing knowledge in this field is now being used in crop production and breeding and results of research have helped to eliminate crop failures and have guided farm practices throughout the world.

This publication¹ summarizes many of the agricultural applications that have resulted from studies of the influence of day length on plant development and calls attention to the effect of day length on such strategic crops as soybeans, sugar beets, and hemp.

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Day Length and Crop Yields

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The successful production of crop plants is dependent upon many factors, such as relative fertility of the soil, rainfall, soil moisture, temperatures prevailing at different times of the year, and light conditions. It is seldom that all these factors are present in any given locality in such combination that it is not possible for man to modify them to the extent that more abundant crop yields of better quality are secured. Indeed, such modification of the environment in which plants grow and the selection of plants adapted to specific environments constitute a large part of agricultural practice. It is the special duty of the experimentalist to find ways and means of accomplishing these desired results in the most direct and economical manner possible. The search for and the substitution of more effective practices for those which are less efficient are the marks of progress of an ever-changing agriculture.

It has long been known that light conditions affect plants in a variety of ways. Many studies have shown, for example, that the intensity of light is an important factor in determining the character and rate

Timothy, a hay crop, heads during the long days of early summer.

Strawberries produce abundant fruit when the day length is 14 or 15 hours, but they usually do not flower when the day length is only 10 or 11 hours.

of plant growth. The shading of certain crops, such as tobacco and coffee, has become an established field practice, whereas the elimination of shade through removal of trees or other obstructions has been found advantageous for various other crops. Despite these general observations, certain details of plant behavior remained unexplained on the basis of variations in light intensity only. Among these was the fact that in nature many plants bloomed only at definite seasons of the year. Some plants, such as poinsettia, could be propagated by means of cuttings made at various times of the year, but all the new plants, large and small, generally bloomed at approximately the same time. Various economic plants when grown in the North bloomed and set seed but did not do so in the South. Similarly, many kinds grown from seeds were leafy and grew luxuriantly when sown at certain seasons of the year but remained small and went to seed quickly at other seasons. From time to time many explanations for these various behaviors were advanced, but none adequately accounted for them.

Some soybean varieties do not produce seed when the photoperiods are long; the same varieties on shorter photoperiods produce abundant seed.

It was while working with Maryland Mammoth tobacco prior to 1920 that W. W. Garner and H. A. Allard, two scientists of the United States Bureau of Plant Industry, discovered that the plants came into flower only when the period of illumination each day was relatively short. When the light periods were long the plants remained vegetative. Subsequent experiments on many kinds of plants showed clearly that they differ greatly in their growth and flowering responses with respect to the relative lengths of the periods of illumination and darkness to which they are exposed. This discovery represented a distinct departure from the then-prevalent idea that intensity of illumination was the principal factor concerned in the determination of the characteristic growth, flowering, and fruiting of plants. This newer concept placed emphasis principally on the influence of successive, rhythmic occurrence of light and dark periods and the relative lengths of such periods rather than on light intensity only.

On the basis of these experiments Garner and Allard further determined that for many plants there is a certain critical length of the light period at which they flower. If this light period is lengthened some kinds will bloom more quickly and perhaps even more profusely. Such varieties are called long-day plants. On the contrary, certain others will not bloom if the light period is lengthened but will do so provided it is made shorter than the critical. Such plants are classified as short-day plants. There is a third, day-neutral group, so called because they flower whether the day length is relatively long or short.

In addition to these effects of day length upon the production of flowers and fruits, Garner and Allard also reported in their early work that other characteristics of plant development were influenced by this factor. They found that formation of bulbs, tubers, and thickened roots, the production of pigments, and the initiation of dormancy were in a large measure controlled by the daily duration of light.

Photoperiod

Scientists studying the influence of the relative length of light and dark periods upon plant growth have performed many experiments in which the length of the combined dark and light periods has been more or less than a 24-hour day. For convenience in discussing such experiments, as well as those based on a natural 24-hour day, any single combination of light and dark periods of whatever length has come to be designated as a "cycle," and the light portion of such a cycle has been designated as the "photoperiod" rather than the day length. For brevity and ready reference the behavior of plants in relation to the relative lengths of alternating periods of light and darkness is now called photoperiodism.

More recently the relation of other factors to the photoperiod

When planted in the spring sugar beets grow and accumulate sugar during the summer, but generally do not produce seeds. When sugar-beet seeds are sown in the autumn, however, and the plants are properly overwintered in the field, they produce seed the following summer.

has been critically investigated. It has been learned that many kinds of plants are much more sensitive to photoperiodic conditions when grown at certain temperatures than at others. Some varieties become more sensitive after they have been subjected to certain temperatures for various periods of time. Such exposure is often referred to as preconditioning. This relation to temperature is of great economic importance, as shown by peach and apricot trees, which leaf out very slowly in the spring or shed their flower buds prematurely unless they have experienced a certain number of hours or days of relatively low temperature during the winter or early spring. Many bulbous plants, some grains, and various other crops grow more

vigorously after they have been subjected for a time to low temperatures. Plants may be preconditioned during the seed stage, during periods of relative dormancy, or while they are in active growth. Preconditioning may occur naturally in northern latitudes at certain times of the year, or it may be provided readily wherever facilities for cold storage are available.

The photoperiodic conditions of a region are the most nearly constant recurrent environmental factors to which plants are subjected. The photoperiod and the temperature which pre-

Some onion varieties when grown where the photoperiod is long produce and mature bulbs, but they fail to form bulbs when grown where the photoperiod is short.

Pyrethrum produces flowers, which are the source of insect powder, only when grown in localities where the photoperiods are long. Under short photoperiods the plants remain as rosettes.

vail in any given region are as important as moisture and soil fertility in determining the specific behavior and economic value of varieties which it may be desired to grow. Although the length of photoperiod in any particular locality changes from day to day throughout the season, the photoperiods of corresponding days in successive years are always of the same length. Therefore, the seasonal variations in this environmental factor can be predicted far more accurately than the variations in temperature, moisture, or soil fertility.

It is not a difficult task to determine under controlled experimental conditions many of the special photoperiodic and temperature requirements of individual varieties. By making such determinations one can readily tell in advance whether certain varieties of soybeans, peas, onions, barley, and many other plants are adapted to the photoperiodic conditions known to prevail in a given locality. Such detailed experiments can be substituted, at least in part, for the far more costly necessity of growing or attempting to grow crops in any given locality to obtain the same information. If a variety were found by experiment to be unadapted, it would not be grown in the field. Either an existent variety that was adapted to the locality would be chosen, or if none was known, one or more which would be suitable could be bred.

This is no visionary ideal. These principles have already been brought to bear in improving agricultural practices. By proper selection of adapted varieties, choice of proper planting dates, and the use of storage for treating planting stocks over proper periods at correct temperatures, it has been possible to place certain farm practices on a more profitable basis. Special strains of crops such as wheat, soybeans, and sugar beets have been developed for planting in specific regions. The use of cold storage for holding planting stocks of potatoes, onions and other bulbs, and seeds to improve the rate at which the subsequent crop grows is standard practice. Now that the effects of photoperiod are coming to be more clearly understood, there is a sharper realization of the very marked effects which a difference of a few hours or even minutes in the length of the period of illumination each day may have upon the character and rate of growth, blooming, and fruit and seed production. This means a more intelligent selection and use of varieties which are photoperiodically adapted and the abandonment of attempts to grow those which are not suitable.

Controlling Length of Photoperiod

In the cases of several crops grown especially for their flowers, either in greenhouses or under field conditions, it is possible to shorten or to supplement the hours of natural daylight by shading or artificial illumination. Thus, in the case of chrysanthemums and some other flowers, it is commercially feasible to use existent varieties and to manipulate the light conditions under which they are grown so as to obtain certain desired results.

Timothy, grown in many sections of the northeastern United States as a hay and pasture crop, is a long-day plant. During the shorter days of the year it forms leafy rosettes, but after the cold temperatures of winter and during the increasingly longer days of spring and early summer the stems elongate, and the plants head out and become tall and stemmy. Most commercial stocks consist of a mixture of types which vary in the degree of their response to photoperiodic conditions. Such a mixture produces fair yields throughout regions having a wide range of prevailing photoperiods, because it is made up of seeds some of which will develop into plants whose requirements would be similar to the conditions prevailing in the specific locality where they are sown. But for any given locality greater yields would be obtained if a more uniform stock containing a higher percentage of specially adapted seed were used. Various native species of grasses likewise consist of mixtures of types which vary greatly in their response to both photoperiod and temperature. Thus, certain species which have extensive ranges north and south show a different proportion of these types when the seeds are obtained from the southern

Light for an hour in the middle of the dark period delays the blooming of chrysanthemums.

Hemp, used for cordage and sometimes for linen, grows rapidly and finally flowers on relatively long photoperiods.

limits of their ranges as contrasted with seeds from the northern limits.

Most varieties of strawberries grown in the Northern States form their flower buds during short days, but they flower and fruit during the long days of early summer. If attempts are made to grow most of these northern varieties in the South, where daylight periods are shorter, they form weak rosettes but bloom very sparsely or not at all. They produce little or no fruit. This is true despite the fact that temperature and other environmental conditions are favorable. Varieties adapted to the shorter day lengths occurring during the winter months in Florida and other Southern States can be bred and selected. The probability of their proving successful from the standpoint of photoperiodic adjustment can be readily determined by first growing them in a greenhouse where a photoperiod approximating that prevailing in the South is created either by shading during daylight hours of summer or by using supplementary artificial illumination in winter. If they do not flower and fruit under such experimental conditions, they are not likely to prove successful out of doors under the field conditions which the experimental conditions approximate.

Selection of Varieties for Specific Photoperiods

Soybeans are now widely grown in both the Northern and Southern States, with two principal objectives in view. One of these is the production of seeds used in the making of oil, plastics, and several food products. The other is the use of the whole plant for forage or for turning back into the soil in order to improve its texture and fertility. Many varieties are grown. Each has some particular quality of special value. Some, especially the variety Biloxi, do not bloom unless the light period to which they are exposed each day is less than 15 hours. In the North, Biloxi has little value as a crop and does not bloom sufficiently early to mature seeds before frost. In the Southern States, however, there is a sufficiently long interval after the periods of daily illumination become short enough for flowering to permit the seeds to mature. Other varieties develop flowers during the long days of northern summers and mature abundant crops of seed before killing frosts. The variety Agate will develop flowers under continuous illumination, although it flowers more abundantly if the light periods are shorter and it is exposed to a dark period each day.

The soybean well illustrates a crop of which there are many well-recognized varieties that show a wide range of photoperiodic adaptation. Whatever other desirable qualities a variety may have, if it is to be grown for seed production it is necessary that it be adapted to the photoperiodic conditions which prevail in the locality where it is to be grown. Failure to recognize this fact is one of the factors which limit

Leaf fall of the tuliptree and many others may be delayed when the photoperiod is long.

profitable production. New and more specifically adapted varieties of soybeans are constantly being selected, so increasing acreages of this very important crop are being grown more economically throughout wider and wider areas.

Recent experiments to develop sugar-beet seed furnish one of the most striking examples of the possibilities of securing newer and better varieties of a crop that is very sensitive in its responses to photoperiod and temperature. Only a few years ago the United States imported from Europe nearly all the sugar-beet seed needed. While developing strains of sugar beets resistant to curly top it became necessary to multiply as rapidly as possible the stocks of seed within the United States.

Previous experience in the southwestern United States indicated that field plantings made in late summer or early fall would successfully overwinter and produce seed. This method of production depends in part upon exposure of the plants during winter months to moderately low temperatures. This exposure does not injure the plants, but it preconditions them so that they will develop seed the following summer. Such a procedure eliminates many labor-consuming operations characteristic of the European method and results in the efficient production of profitable yields of seed.

On the basis of the knowledge that the production of sugar-beet seed is favored by long photoperiods, especially at certain temperatures or after a rather short exposure to relatively low temperatures, it has been possible to select localities that are much better suited to

its production. For example, very excellent yields of sugar-beet seed are now being produced in certain areas of the Pacific Northwest where the temperatures are sufficiently mild to permit overwintering and the longer summer photoperiods are especially favorable. As a result of these recent developments the United States now produces enough sugar-beet seed for its own use.

Onions also show a range in sensitivity and adjustment to photoperiod, not only in flowering but particularly in bulb production. Failure of certain varieties to produce marketable bulbs in one locality and their successful production in another often result from their relative degrees of adjustment to the photoperiods prevailing in such localities while growth and bulbing should be taking place. Because of this fact attention must be given to the determination and selection of localities where the largest crops can be most economically and successfully produced. As in the case of other types of plants, testing the varieties under experimental conditions will give exact information on their probable success or failure with respect to the

Many varieties of potato generally fail to mature the berrylike seed balls but do so when the photoperiod is sufficiently long.

Varieties of sugarcane may require different photoperiods for blooming. Simultaneous flowering of some of them could be induced by subjecting them to the proper photoperiods.

photoperiodic conditions in any area. If no such photoperiodically adapted varieties are available, they may be developed.

Experiments of the United States Bureau of Plant Industry are now in progress toward the development of new strains of onions resistant to diseases and insects and adapted to the photoperiodic conditions in various sections of the United States. By making the desired crosses and then growing the seedlings under experimental conditions in which the temperature and photoperiod are carefully controlled, those which are unfit are being eliminated. Only those that are most likely to succeed under the specific natural conditions prevailing in those sections where it is desirable to produce them are retained. After selection these plants serve as parents for further crosses that provide the seeds for use in the test plots to be grown in the different chosen regions. In simplest terms, what this procedure provides is a more ready means of selection and increase of new photoperiodically adapted varieties which may combine the desirable qualities of varieties now grown.

More than half the time required to establish the foundations of new strains of onions may be saved by planting the seed under controlled environment as soon as it matures in the summer instead of waiting until the following year to plant it in the field. Also, such seed stocks are of known higher quality and greater uniformity than if there has been only general selection under field conditions.

This same general procedure may be applied to testing and improving many vegetables, especially those classed as biennials. By combining these methods with those followed in the efficient production of sugar-beet seed, the problem of growing large crops of good seed in much less time may be more readily solved.

Many plants grown principally for their flowers are similar in photoperiodic behavior to food and forage crops. In many instances seasons of bloom are directly related to the seasonal temperatures and particularly to the length of the periods of daylight prevailing at different seasons. This is especially noticeable in northern latitudes. In many plants photoperiodic adaptation is a definitely fixed character, and their period of blooming is regulated by it. But as flowers are generally cultivated on a less extensive scale than are most food crops, it is commercially feasible to give them much more detailed attention. In greenhouses and to some extent out of doors, artificial regulation of the temperature and photoperiodic conditions may be done with profit. Any prevailing natural or seasonal photoperiod can be shortened by completely darkening the plants each day with black cloth or by placing them in dark chambers. It may be lengthened by the use of electric light. Both practices are now widely used by florists to hasten or to delay the blooming of chrysanthemums and some other crops and thus to gain advantage of market demands.

Prolonged artificial lengthening of the light period could prove relatively expensive if electric current costs were high. Recently, however, it has been shown that it is not necessary to supply illumination for the full length of time which would be required to provide the equivalent of a long photoperiod. The photoperiodic effect of interrupting the dark period for a few minutes to an hour near its middle is similar to the effect produced when light is used continuously to extend the natural photoperiod. Not only does this result in reduction of the cost for light, but often the plants and flowers produced are commercially superior to those grown with extended periods of artificial illumination. The length of the interruption and the time of its application should be determined experimentally.

Selection of Localities with Suitable Photoperiods

Pyrethrum, a relative of the chrysanthemum, is used for the manufacture of an insect powder. Large quantities are needed annually. Since the insecticidal constituent occurs in the flowers, it is desirable that plants produce a large number of flowers. It is possible to grow this crop commercially in the United States, but to do so care must be taken to select the proper localities. Pyrethrum is a plant of the long-day type, and its period of blooming is also dependent upon the prevalent temperature conditions. Selection of suitable sites should take into consideration both the temperature and light conditions occurring throughout the year.

Hemp, too, is photoperiodically sensitive and, although this fact is seldom realized or given the attention it deserves, the selection of the locality in which to grow hemp should be a matter of definite concern because of the influence exerted on both the amount and quality of the fiber obtained. Hemp plants are of two sexes. The males, which produce pollen, are generally somewhat smaller and more slender than the females, which bear the seeds. Under conditions of short photoperiod there is a tendency for relatively more male plants to develop than under long photoperiods. Such an increase in numbers might well result in a change in the quality and quantity of fiber produced in various regions, depending on the prevailing photoperiod of any region or on the season of the year when the plants are grown.

Seasonal leaf fall of many native trees and shrubs is as much a response to the prevailing seasonal day length as to other environmental factors. When attempts are made to cultivate such photoperiodically limited species in other parts of the world, failure is as often due to their lack of adjustment to light conditions as to other environmental factors. In cities, leaves on branches of street trees illuminated by electric lights often remain green much longer than those not so exposed.

Some of the earlier equipment employed by Garner and Allard, who used many kinds of wild and cultivated plants.

Photoperiod an Aid in Plant Breeding

The photoperiodic behavior of many varieties of plants is of great economic significance in the development of new varieties. In many localities the common potato as grown in the field frequently produces large numbers of flowers but few seeds. In the commercial production of potatoes this is no detriment because they are grown by planting whole tubers or pieces of them. But if a new variety of potato is desired, it is most quickly obtained by growing the seeds and selecting the type desired from among the seedlings. Seeds are now readily obtained by growing potato plants in greenhouses, where the photoperiod can be lengthened to suit their requirements for seed development. When this is done and after pollination has been effected, a number of varieties which usually do not set seed well do so very readily.

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.

A greenhouse equipped for present-day photoperiod studies on economic plants at the Bureau of Plant Industry Station, Beltsville, Md. The results of many studies here and elsewhere have helped to eliminate crop failure and have modified agricultural practices throughout the world.

Recently crosses were made between a wild species of sugarcane (*Saccharum spontaneum*) from Turkistan, which blooms in July, with cultivated sugarcane (*S. officinale*), which blooms in November or December. By appropriate manipulations of photoperiod for each plant the times of flowering were synchronized so that crosses could be made between them. The blooming period of the hybrids was found to be intermediate between those of the parents. The illustration on the cover page shows a progeny from such a cross. The purpose of these hybridizations was to combine those factors that contributed cold hardiness to the wild species with the factors for yield and quality present in the cultivated sugarcane.

A list of plants which are photoperiodically sensitive would include most of those of economic importance grown in the United States.

The crops which have been mentioned illustrate clearly some of the various responses which different plants may show. Suggestions for practical application have grown out of past experiments, and others will follow from other experiments still in progress.

The equipment with which Garner and Allard first worked was relatively simple. Similar apparatus is still extremely useful in photoperiodic studies, but it has been essential to supplement it for closer observation and more detailed experimentation. Their plants were grown in pots. Some of them were placed on trucks which could be conveniently moved into dark houses nearby so that the plants could be exposed to any determined photoperiod.

Garner and Allard also used a small chamber. This was so arranged that boxes containing living plants could be fitted into the side of it, and the whole was left open or darkened at will. The illustration on page 18 shows clearly how a single plant may exhibit two responses to photoperiod at the same time. The shorter, more bushy plant is a species of *Sedum*, or liveforever, and the other is a species of *Rudbeckia*. The half of each plant outside the box has been exposed each day to the natural period of illumination prevailing during the summer in Washington, which reaches a maximum of approximately 15 hours. As a result of exposure to this relatively long photoperiod the stem has elongated and the plant has come into flower. The other half of each plant, inside the box, has been exposed to photoperiods of but 10 hours each day. Although there has been some growth, the rosette stage still persists and there are no evidences of flower buds or flowers. This is a particularly striking demonstration of how the effects of photoperiod may at times be very precisely localized.

Such localization of photoperiodic response does not always occur, for in many instances such responses may be shown by portions of the plant at some distance from the part directly exposed to light. Such an instance is especially well illustrated by the Jerusalem-artichoke, which produces tubers in darkness below ground when the leaves are subjected to conditions of short photoperiod. If the leaves are exposed to long photoperiod, no tubers are formed. The response to photoperiod is indicated mainly by the extent of tuber formation rather than by any readily observable effects on the leaves.

The necessity for closer observation and more detailed experimentation has increased as understanding of the problem has progressed, and its greater complexity has become more clearly recognized. This is particularly true in attempts to study and evaluate the relative effects of photoperiod and temperature and their possible interrelationship. As a result, it is necessary to devise ways and means by which most environmental conditions, especially temperature and light, can be much more precisely controlled. A greenhouse well equipped for making such studies on photoperiodism is illustrated.

After the grafting of a leaf of Agate soybean onto a Biloxi plant the latter was induced to flower.

Plants are grown on benches and on trucks, which may be readily placed in dark houses whenever essential. Ample provision is made for artificial illumination by means of electric lamps. Beneath the glass jars plants may be grown with different amounts of moisture or any desired combination of gases in the atmosphere. All these factors influence photoperiodic sensitivity, and it is important that they be studied critically because they represent natural conditions prevailing in some sections of the United States or in other agricultural countries.

Painstaking detail in experimentation constantly increases understanding. One of the most significant findings of detailed experimentation is the fact that in general the leaves of a plant are the organs through which photoperiodic conditions primarily influence it. It is not necessary, for example, to expose an entire Biloxi soybean to short photoperiods to induce it to bloom; it will bloom promptly if only a few of the leaves are subjected to a short photoperiod, even though all the rest of the above-ground parts receive long photoperiods. Moreover, if a single leaf of a variety such as Agate soybean, which blooms readily even when photoperiods are long, is grafted to Biloxi, which normally requires short photoperiods for blooming, the Biloxi plant is thereby enabled to bloom on long photoperiods also. This, together with much other evidence based on critical experiments, indicates that under certain conditions the plant forms some substance which may be transported to other parts of a plant or to another plant where the production of flowers occurs. A similar situation, resulting in tuber formation underground, occurs in the Jerusalem-artichoke.

It is not too much to hope that eventually substances which when applied may aid in the control of growth and flowering may be either obtained directly from plants or manufactured artificially. Two substances, ethylene and acetylene, have already been shown to hasten flowering when properly applied to pineapple plants. They have already been used for this purpose under field conditions. Undoubtedly others will be discovered and put to use.

From the instances just cited, it is clear that at present means are available and practices have been established whereby it is possible, commercially, to take advantage of the part which photoperiod plays in the way plants develop or to offset such disadvantages as it may impose. Once the facts and details are established it is not difficult to work out ways and means of turning knowledge of them to immediate use.