EFFECT OF VARIATION IN LENGTH OF DAY ON GROWTH AND DORMANCY OF TREES

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(WITH FOUR FIGURES)

Introduction

One of the outstanding characteristics of the woody plants that are native to the temperate zone is the periodicity of their growth. This periodicity has commonly been assumed to depend largely if not entirely on the periodicity of temperatures favorable to growth. There are reasons, however, for doubting that temperature is the only important factor affecting the length of the growing season. Even in the tropics where the temperature is always high enough to permit growth, many species show a definite periodicity. In the temperate zone the growing season of most species is relatively short, growth ceasing and in some cases leaf abscission beginning long before the occurrence of frosts. Even evergreen species have a limited growing season which usually ends before the advent of temperatures low enough to check growth appreciably. Furthermore, many species of trees brought into the greenhouse in the summer and kept there during the autumn and winter cease stem elongation and the production of new leaves as soon as trees of the same species that are left out-of-doors.

Dormancy in such cases is evidently not the result of decreasing temperature, but is caused by some other factor which operates inside as well as outside the greenhouse. The only such factor which varies with the season is length of day. In the latitude of Durham, North Carolina, where these observations were made, there is a difference of about five hours between the longest and the shortest days of the year and this difference becomes progressively greater with increasing distance from the equator.

As a result of the work of GARNER and ALLARD (**6, 7**) and others, it is well known that the length of day or photoperiod is an important factor in determining the time of flowering and amount and nature of vegetative growth of many species of herbaceous plants. References to the extensive literature on this subject are given in the papers of GARNER and ALLARD (**6, 7**), KELLERMAN (**11**), LAURIE and POESCH (**16**), and RAMALEY (**21**), so no review of the work on herbaceous plants will be made here.

KLEBS (**13**) was one of the first to investigate the effects of length of day on woody species. He reported that beech, oak, ash, and hornbeam grew all winter when placed under continuous electric light. GARNER and ALLARD (**7**) also experimented with several species of woody plants, including apple, yellow poplar, box elder, winged sumac, and smooth sumac. They found that yellow poplar, given daylight supplemented by electric light

until midnight, grew all winter, while smooth sumac treated in the same manner retained its leaves during the winter but made no growth. Leaf fall was retarded only a few weeks by this treatment in the case of winged sumac. Apple made more growth with a 10-hour day than with the normal long days of midsummer, but box elder grew better with the long summer days. GARNER and ALLARD concluded that the length of day might be an important factor in determining the time both of beginning and of ending the dormant period. ADAMS (**1**) reported that sugar maple given electric light at night produced leaves no sooner in the spring than trees receiving only daylight. MOSHKOV (**17, 18, 19**) reported that certain southern tree species, such as *Robinia pseudoacacia* and *Salix babylonica,* when grown at Leningrad where the maximum length of day is 20 hours, continued to grow until killed by frost instead of becoming dormant at the end of the summer. If the photoperiod was artificially shortened such species ceased growth earlier in the season and were not injured by cold. He also found that the morphology of certain species was altered. *Robinia,* for instance, with short days branched less than with normal day, formed scales instead of thorns, and produced fewer pairs of leaflets. BOGDANOV (**3**) also found that the length of growing season and resistance to cold of a number of species of trees were affected by the photoperiod with which the plants were grown. Further details of the Russian work may be found in a recent paper by GEVORKIANTZ and ROE (**9**). DARROW and WALDO (**4**) found reason to believe that the rest period in the strawberry may be a result of nutritional conditions caused by short days and low temperatures. They believed that this might also be true of the rest period of other plants, including woody ones.

Since so few species had been investigated, it seemed worth while to investigate the behavior of other species under various lengths of day. The species studied were: white ash (*Fraxinus americana* L.), green ash (*F. pennsylvanica* var. *lanceolata* Sarg.), beech (*Fagus grandifolia* Ehrb.), black locust (*Robinia pseudoacacia* L.), yellow poplar (*Liriodendron tulipifera* L.), red or sweet gum (*Liquidambar styraciflua* L.), post oak (*Quercus stellata* Wang.), northern red oak (*Q. borealis maxima* Ashe), white oak (*Q. alba* L.), and loblolly pine (*Pinus taeda* L.).

The experiments with these species extended over three growing seasons, although not all of the species were studied through all three seasons. The following report is a brief summary of the important results obtained during the three seasons.

Methods and results

Most of the plants used in these experiments were one or two years old, but a few of the oaks and red gums were grown from seed. All the plants

were grown in ordinary garden soil in 6- and 8-inch clay pots, one plant being grown in each pot.

The most extensive series of experiments was conducted in the following manner. During the early part of the summer, groups of 10 to 15 trees of each species to be studied were placed under various lengths of day. One series received the normal length of day, which varies from 14½ hours in June to 9½ hours in December. Another series received full daylight supplemented by electric light. The electric light was controlled by an automatic time switch and as the days changed in length the lights were turned on for a longer or shorter period of time, so that the plants continued to receive approximately 14½ hours of light or a photoperiod equal to the longest summer days. The light was supplied by ordinary 200-watt mazda lamps. The light intensity at the surface of the soil varied from 100 to 200 foot-candles. A third series was given an 8½-hour day by covering the trees from 4:45 P. M. to 8:15 A. M. with black cloth shades suspended over a framework about 6 feet above the plants. All the plants were subjected to the daily and seasonal variations in temperature which usually occur in a greenhouse. The differences in temperature between the groups under different lengths of day did not exceed two or three degrees. Appreciable variations in temperature are undesirable, for BERKELEY (**2**), GILBERT (**10**), and others have shown that differences in temperature may exert a marked effect on photoperiodic reaction.

All of the species just listed were grown under normal length of day. Stem elongation and the production of new leaves ceased in the autumn as soon in those trees growing in a warm greenhouse as in trees of the same species left out-of-doors. The leaves of beech and yellow poplar abscissed as soon indoors as outside, but the two species of ash, yellow locust, red oak and post oak retained their leaves in a living condition somewhat longer indoors than outside. Most of the leaves of the red gum and white oak remained green until early spring when new leaves began to appear.

White ash, yellow poplar, red gum, post oak, white oak, and loblolly pine were grown under short day conditions. All of these species except white oak made less growth and became dormant sooner than the trees exposed to normal length of day. There was no appreciable difference between the normal and short day white oak.

All of the species received long day treatment and all of those so treated except white and green ash and red oak grew later in the autumn and made greater shoot growth than trees exposed to the normal photoperiod. Loblolly pine grew all winter with the 14½-hour day (figs. 1, 2). Yellow locust and yellow poplar continued to grow until late December when an outbreak of mealy bugs and red spiders killed most of the leaves. Other experiments indicate that with a 16-hour day these species will grow all winter.

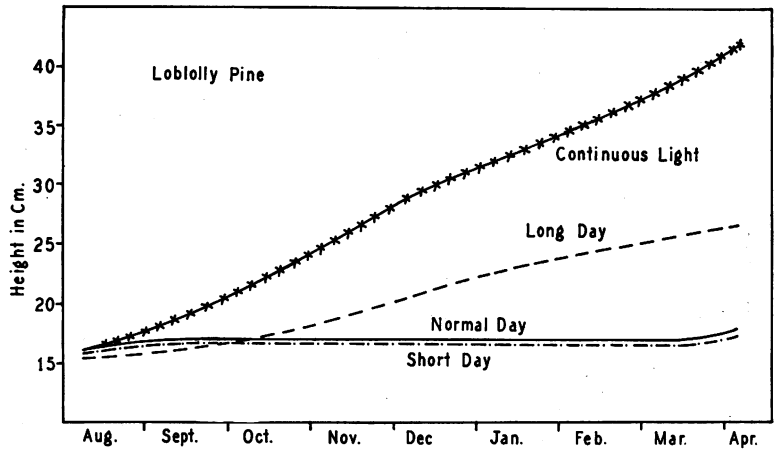

FIG. 1. Shoot growth of loblolly pine with photoperiods of various lengths.

In another series of experiments red gum, yellow poplar, and post oak were exposed to electric light until midnight. The yellow poplar continued stem elongation and the production of new leaves during the entire winter and the red gum and post oak continued to grow much later in the autumn than the trees receiving the normal length of day. Yellow poplar, loblolly pine, and red gum given electric light all night made even more growth than those receiving long day (figs. 1–3). The long day post oak did slightly better than those receiving continuous light, but this experiment must be repeated to determine whether or not this is the characteristic reaction. The growing season of green ash was not lengthened by continuous light. There was a tendency for some of the red gum plants to cease growth toward spring and become dormant for a time. This might possibly have resulted from a deficiency of minerals, but further investigation of this is necessary.

Two series containing yellow poplar, red gum, red oak, and white ash were placed outside the greenhouse. One series received the normal length of day, while the other series received a 14½-hour day. The red gum and yellow poplar grew about two weeks later in the autumn with extra light, but the growing season of the red oak and white ash was not extended. In the spring there was no difference between the time at which dormancy was broken in the normal and in the long day series. Apparently the days had already lengthened sufficiently no longer to constitute a limiting factor, and all of the trees were in a condition to resume growth as soon as the temperature was favorable.

Dormant seedlings of beech, yellow poplar, red gum, and red oak were brought indoors early in January and subjected to long and short days. In all instances the trees receiving additional light resumed growth sooner

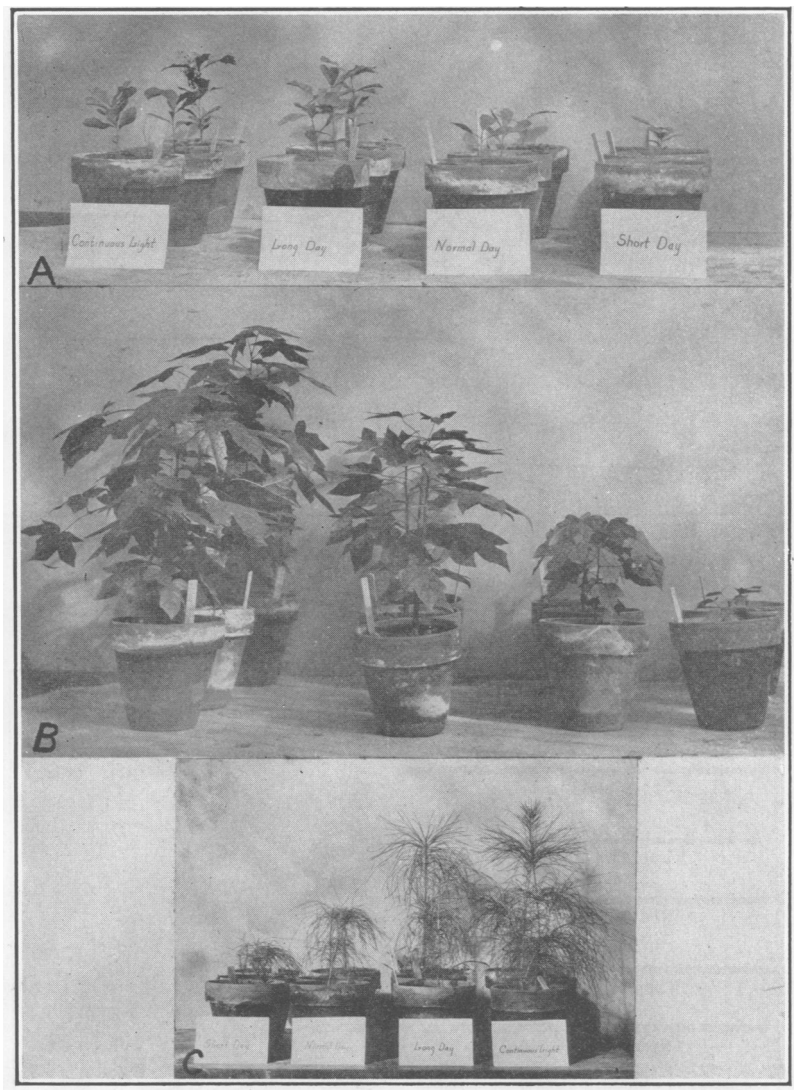

FIG. 2. *A*, post oak; *B*, red gum. In *A* and *B* the photoperiods are, from left to right: continuous light, long day, normal day, short day. *C*, loblolly pine. From left to right the photoperiods are: short day, normal day, long day, continuous light.

than those with a short day. Some of the results of this experiment are shown in figure 4. Certain short day red gum trees kept in the greenhouse all winter resumed growth as soon as normal day trees, but only the lateral buds opened, growth was very slow, and the leaves were small in size

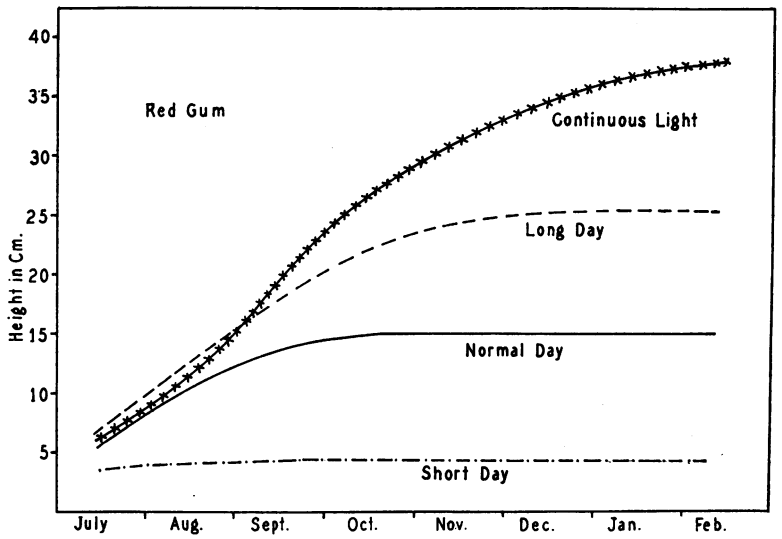

FIG. 3. Shoot growth of red gum with photoperiods of various lengths.

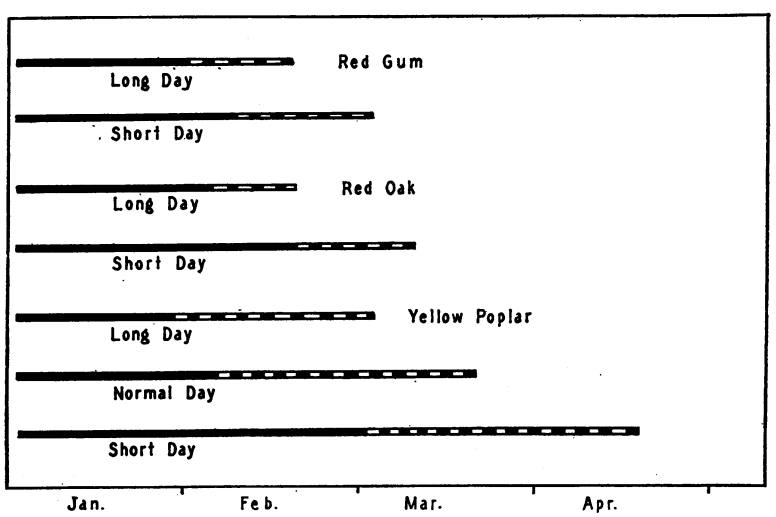

FIG. 4. Length of time required to break dormancy in trees brought into the greenhouse and subjected to various photoperiods. Solid line represents completely dormant condition; barred line, interval from opening of first buds until all buds were open.

and pale in color. These trees never caught up with the trees receiving normal or long photoperiods.

Discussion

The results of these experiments indicate that with certain species the time at which dormancy begins and ends is closely related to the length of day. Certain other species such as white and green ash do not seem to be affected by variations in length of photoperiod. It is possible either that these species are not sensitive to length of day or that the proper combination of photoperiod and temperature has not been tried. A classification of the species studied into long and short day types is not possible at present. Thus far the reaction to an increased photoperiod has been much more marked than has the reaction to a shortened photoperiod. GARNER and ALLARD (**7**), however, found that a certain variety of apple made more growth with a 10-hour day than with a 14- or 15-hour day, and other cases of this type will doubtless be found. As pointed out by GARNER (**5**), the original classification of GARNER and ALLARD is based on the effect of length of day in initiating or suppressing sexual reproduction. The studies on trees have thus far been concerned solely with length of growing season and amount of vegetative growth, and it may be questioned whether or not they should be classified as long or short day types on this basis. Since we are chiefly interested in their vegetative growth, however, and since there are obvious difficulties which will probably prevent any very extensive investigation of the response of flowering and fruiting to length of day, it may be justifiable to classify them as long, short, or insensitive types on the basis of vegetative growth.

It is probable that in nature the beginning of dormancy is more dependent on length of day than is the ending of dormancy. The shortening days of late summer may bring about the cessation of growth in some of the more sensitive species considerably before it would be stopped by decreasing temperature alone. On the other hand, in many instances it is probably the occurrence of temperatures high enough for growth rather than the length of day which determines the time of resumption of growth in the spring. It is likely that in some regions the days have lengthened sufficiently no longer to constitute a limiting factor before the temperature is high enough to permit the full resumption of growth.

It seems possible that differences in the length of the growing season of various species in the same locality may result from differences in their reaction to seasonal variations in photoperiod. KIENHOLZ (**12**), working at Keene, New Hampshire, found that *Pinus resinosa* began growth in late April and ceased growth about the middle of August, with a total growing season of 105 days; while *Abies balsamea* began growth late in May and ceased growth late in July, with a growing season of 65 days. These differences could scarcely have resulted from differences in temperature, moisture, or

the supply of minerals, but may have been caused by differences in tolerance to length of day.

Although length of day seems definitely to control the length of growing season of some tree species, it should be regarded as an *indirect* rather than as a *direct* causal agency in initiating or breaking dormancy. Changes in dormancy, flowering and fruiting, root-shoot ratios, and other growth phenomena are the direct result of changes in the internal physico-chemical processes and conditions of the protoplasm. Within the limits of the hereditary potentialities of any particular species or individual, such changes in internal processes and conditions may be brought about by one or several environmental factors acting singly or in combination. This viewpoint was set forth by KLEBS (**14**) many years ago. It is supported by the work of ROBERTS (**22**), who found that no separate environment had a consistently unique effect upon the internal composition or behavior of apple trees, but that similar changes in composition and behavior might result from different treatments. Thus short day trees not supplied with nitrogen behaved much like long day trees with nitrogen.

It may be that a state of equilibrium exists in respect to the complex of internal physiological processes, and by shifting this equilibrium in one direction dormancy results while a shift in the other direction results in the resumption of growth. Several different environmental factors acting separately or in combination may produce a sufficient shift in this equilibrium to result in cessation or resumption of growth. The most important factors are probably the supply of water and minerals (especially nitrogen), the temperature, and the photoperiod.

As yet the manner in which variation in length of day produces such marked reactions in plant behavior has not been satisfactorily explained. Experiments on herbaceous plants have shown that there are changes in hydrogen-ion concentration and hydration of tissues (**8**), carbohydrate-nitrogen relations (**20, 24**), root-shoot ratios (**25**), and catalase activity (**15**), and similar changes doubtless occur in woody plants. The rate and amount of photosynthesis is doubtless affected and it has been shown that in some plants the utilization of nitrates is also affected (**20**). ROBERTS and KRAUS (**23**) have suggested that photoperiodic responses are caused by changes in type of daily respiratory rhythms. These changes in rate of respiration are probably not the cause but the result of more fundamental changes resulting from photoperiodic activity. It is probable, however, that all these phenomena are correlations or indirect causes and that the real cause lies in changes in cell metabolism. Much more work on the fundamental physiological processes governing growth will be necessary before this problem can be explained.

It seems that information concerning the photoperiodic reactions of

various tree species would be of use in several ways. It may explain differences in length of growing season of various species growing in the same region. It may also explain why some species do not thrive when moved to a different latitude even though climatic conditions seem favorable. Knowledge of the optimum photoperiod should aid in predicting whether or not a given species is suitable for growth at any given latitude. In connection with research in forestry, horticulture, and pathology, it is frequently desirable to control the growing season so that growing material is available whenever needed. This can be done with some species by exposing them to the proper photoperiod. Seedlings of some species will also make much more rapid growth if given additional light and thus are ready for use sooner than if grown with normal length of day.

Summary

1. The behavior of potted seedlings of white and green ash, beech, yellow locust, yellow poplar, red gum, post oak, northern red oak, white oak, and loblolly pine was observed under various lengths of day. With normal length of day all of these species ceased growth as early in the autumn in a warm greenhouse as out-of-doors, although most species did not lose their leaves as soon indoors. All of the species except white and green ash and red oak made more growth and grew later in the autumn when daylight was supplemented by electric light to give a total photoperiod of 14½ hours. Several of the species were grown with an 8½-hour day and most of these made less growth and became dormant sooner than with normal day.

2. With a 16-hour day, red gum grew nearly all winter and yellow poplar grew all winter; both species grew all winter with continuous light. Loblolly pine grew all winter with a 14½-hour day, but made better growth with continuous light.

3. Dormant trees of beech, yellow poplar, red gum, and red oak were placed under various lengths of day in midwinter. In all species resumption of growth was hastened by additional light and retarded by shortening the photoperiod below the normal length of day.

4. The results of these experiments indicate that variations in length of day may, to a considerable extent, control the duration of the growing season of certain tree species. These results also strongly support the view that dormancy is not caused by any inherent rhythm in plants, but is produced by the action of various environmental factors on the complex of internal physico-chemical phenomena controlling growth.

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