DORMANCY IN BETULA AS A QUANTITATIVE STATE 1, 2
MAKOTO KAWASE 3
DEPARTMENT OF FLORICULTURE & ORNAMENTAL HORTICULTURE, CORNELL UNIVERSITY, ITHACA, NEW YORK

Klebs (12) reported in 1914 that the growth of beach, oak, ash, and hornbeam could be maintained even in winter if they were placed under continuous electric light. Since Klebs' report on the effect of day length on the growth of woody plants, there have been many studies pertaining to photoperiodism and dormancy in woody plants. They were amply reviewed by Samish (21), Wareing (24, 26), and Nitsch (16). In general, a short photoperiod induces a reduction in growth of woody plants through a shortening of internodes and a decrease in the number of new nodes formed. These same plants would grow continuously under long photoperiods. The breaking of dormancy induced by either artificial or natural short photoperiods has been accomplished by three different treatments: A: long photoperiods (7, 10, 18, 19, 22, 23, 25, 27); B: chilling (2, 5, 7, 9, 19), and C: application of gibberellic acid (1, 3, 4, 6, 13, 14, 15). Previous workers such as Van der Veen (23) and Downs and Borthwick (7) have suggested that, when leaves remain on the plant and are subjected to short days after visible growth has ceased, dormancy becomes increasingly more difficult to break. This project was undertaken to study the effect of photoperiods on dormancy with special consideration on the degree of dormancy.

MATERIALS & METHODS

Seedlings of Betula pubescens Ehrh. 4 and Betula lutea Michx. 4 = B. alleghaniensis Britton were used.

In all experiments the seedlings were grown under 18-hour photoperiods (abbreviated as LD) in the greenhouse for approximately six months until the start of the treatments. The seedlings ranged from 1 to 2 feet in height at the beginning of an experiment, and were selected for uniformity of size. The temperature of the greenhouse was controlled at 21 C minimum during day and 15.5 C minimum at night.

Because of the lack of a cooling system, maximum temperature could not be controlled. All plants received 9 hours of natural light from 8:00 AM to 5:00 PM. From 5:00 PM to 8:00 AM darkness was produced by means of thick, black sateen cloth to eliminate all natural light. Under the black cloth, 60 w incandescent lamps were lighted from 5:00 PM to 2:00 AM for the LD treatment and from 5:00 PM to 6:00 PM for the 10-hour photoperiod treatment (abbreviated as SD). The bulbs were hung 2 to 3 feet above the top of the plants, and gave an approximate light intensity of 15 to 30 ft-c as measured with Weston illumination meter, model 603, at the tips of the plants.

During the experiments, stem elongation and the numbers of new, macroscopically visible nodes were measured once a week. To eliminate any secondary effect from branching, all auxiliary buds were cut off as soon as they started to swell. Thus, the growth studies concerned main stems only.

RESULTS

I. GROWTH OF BETULA PUBESCENS SEEDLINGS UNDER DIFFERENT NUMBERS OF 10-HOUR PHOTOPERIODS. Five groups of 15 seedlings each were treated with SD for the last 0, 1, 2, 3, or 4 weeks of their experimental periods in such a manner that all treatments terminated on March 19, 1958. As shown in figure 1, growth of the seedlings was retarded by 1 week of SD and stopped completely after 2 weeks of the treatment. Thus, seedlings kept under SD for more than 2 weeks appeared to be in a dormant condition without any measurable growth. A similarity in growth curves of stem elongation and of the numbers of newly developed nodes was seen not only in this phase of the study but also in all others. Therefore, only one measure of shoot growth, namely the elongation of the stem will be discussed for the remainder of the studies. The actual growth curves of the numbers of newly developed nodes are presented in (11).

II. RESUMPTION OF GROWTH OF DORMANT BETULA PUBESCENS SEEDLINGS UNDER DIFFERENT DURATIONS OF 18-HOUR PHOTOPERIODS. Plants were subjected to SD for 4 weeks continuously and then given LD for the last 0, 2, 3, 4, 5, or 6 weeks of their experimental periods in such a manner that all treatments terminated on July 23, 1958. After 4 weeks of SD treatment, plants became completely dormant. At the end of the experiment, resumption of growth

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3 Present address: Department of Horticulture, Purdue University, Lafayette, Ind.
4 The seeds of Betula pubescens and Betula lutea were obtained from the Herbst Brothers Seedsmen, Inc., 678 Broadway, New York 12, N. Y. and Mr. F. W. Schumacher, Sandwich, Mass., respectively.
was noted in 9 plants (60\%) out of 15 which received 6 weeks of LD, in 5 plants (33\%) of those treated with 5 weeks of LD and in one plant (7\%) of those treated with 4 weeks of LD. No plants resumed growth in the treatments of 2 weeks or 3 weeks of LD. If the average growth resumption of 15 plants including both dormant and non-dormant plants is calculated at the end of the experiment, the following is noted.

<table>
<thead>
<tr>
<th>Photoperiods</th>
<th>6 weeks</th>
<th>5 weeks</th>
<th>4 weeks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avg. growth in cm</td>
<td>12.0</td>
<td>3.0</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Those that had received 4 consecutive weeks of SD apparently needed at least 4 weeks of the LD treatments to resume growth. Once dormancy was completely broken, the plants started to grow vigorously. The individual growth curves are presented in (11).

### III. Quantitative Character of Dormancy Induced by 10-Hour Photoperiods

From the previous results one can conclude that a minimum of 4 weeks of 18-hour photoperiods is required to break the dormancy induced by 4 weeks of 10-hour photoperiods in *Betula pubescens*. The following experiments were conducted to determine the quantitative character of the degree of dormancy in two species of birch: *Betula lutea* and *Betula pubescens*.

A. *Betula lutea*. Thirty six seedlings were divided into four treatments of nine plants each. These four treatments were 0, 3, 4, and 5 weeks of SD. The SD treatments were started and spaced so as to have them terminated on Aug. 22, 1958, at which time all 36 plants were brought back under LD to study the resumption of growth (fig 2).

*Betula lutea* seedlings needed 4 weeks of SD to completely stop their growth, although 3 weeks of SD treatments were sufficient to retard growth. Plants in all treatments resumed their growth within the experimental periods but the rate of recovery varied. Plants treated with 3, 4, and 5 weeks of SD needed LD treatments of approximately 2, 3, and 4 weeks, respectively, to resume their growth. The fact that there was a correlation between the number of LD required for the resumption of growth and the increase in the number of SD of the prior treatment, indicates that for *Betula lutea* there is a quantitative relationship between the degree of SD induced dormancy and the duration of the SD treatment.

B. *Betula pubescens*. Four plots of 15 plants each were treated as follows: A: 9 weeks of LD. B: 2 weeks of LD + 2 weeks of SD + 5 weeks of LD. C: 4 weeks of SD + 5 weeks of LD. D: 9 weeks of SD. All treatments terminated May 22, 1959. The results are presented graphically in figure 3. Resumption of growth required 2 weeks of LD if the plants had been previously treated with SD for 2 weeks; 5 weeks of LD were necessary when the plants had been treated with 4 weeks of SD. Both SD treatments induced dormancy, but the number of LD

![Graphs of growth of Betula seedlings](image-url)
cycles required for growth resumption was quite different. This indicates that the growth-inhibitory stimulus accumulated in the plants beyond a minimum level which is sufficient to stop growth. In other words, growth-promoting and growth-inhibiting effects due to LD and SD are quantitative. More long days are required for the resumption of growth when the number of short day cycles is increased.

IV. Growth of Betula pubescens Under Different Combinations of Photoperiods. In order to compare different photoperiods in respect to the promotion of plant growth, the following experiments were conducted.

Fifty Betula pubescens seedlings were divided into three lots. One lot of 20 was treated with 14-hour photoperiods, a second lot of 10 received 16-hour photoperiods, and a third lot of 20 received 18-hour photoperiods for 9 weeks starting March 9, 1959. On May 11, half the plants which had been treated with 14-hour or 18-hour photoperiods were transferred to 16-hour photoperiods. Growth measurements were recorded weekly starting 3 weeks before May 11 and continuing for 3 weeks after May 11 (fig 4).

Plants subjected to the 14-hour photoperiods showed very little growth. However, the growth of plants in the 16-hour or 18-hour photoperiods was very pronounced, with the plants subjected to the 18-hour photoperiods showing the greatest growth rate. A modification of growth was obtained when photoperiods were altered May 11. Transferring plants from the 18-hour to the 16-hour photoperiods caused a little retardation of growth, while transferring the plants from the 14-hour to the 16-hour photoperiods speeded up the growth rate.

The quantitative character of photoperiodic treatments, which was indicated by the results in previous sections, can be extended further within the range of 10-hour to 18-hour photoperiods in Betula pubescens. It is evident that the photoperiodic effect in the direction of either promotion or retardation is due not only to the number of photoperiodic cycles given but also to the length of the photoperiod. There may be a critical day length, which when exceeded, results in growth; conversely when the day length is less than the critical, growth does not occur or growth is greatly retarded. The critical day length in the present case may be somewhat shorter than 14 hours.

V. Effect of Alternating Short Day & Long Day Treatments on Growth of Betula pubescens. It was clear from the foregoing experiment that the modification of growth follows if plants are transferred from one to another photoperiod. It would be interesting to know how plants behave in respect to their growth if one treats plants repeatedly with two kinds of photoperiods one after another. Betula pubescens seedlings were used in the following experiments. Four groups of 15 plants each were grown under 10-hour, 14-hour, 16-hour, or 18-hour photoperiods for 10 weeks, starting June 2, 1959. Another three groups of 15 plants each were treated with 14-hour, 16-hour, or 18-hour photoperiods, respectively, during the odd-numbered weeks while during the even-numbered weeks all 45 plants were treated with 10-hour photoperiods throughout the period from June 2 to Aug. 10, 1959 (table I).

In this experiment, continuous 14-hour, 16-hour, and 18-hour photoperiods induced vigorous growth and even the 10-hour photoperiod under which Betula pubescens stopped growth within 2 weeks in previous cases, showed some growth. This point will be further explored in the final discussion of all the experiments. It is quite an interesting point that plants showed a rather constant growth even under photoperiods which were changed weekly. It may mean that under the extended treatment, a combination of long and short photoperiods produced an intermediate effect. The 10-hour photoperiod which was given

| Table I |
|-----------------|-----------------|-----------------|-----------------|
| **Week** | **18 hr** | **18-10 hr** | **16 hr** | **Treatments** | **16-10 hr** | **14 hr** | **14-10 hr** | **10 hr** |
| 1 | 5.7 | 6.0 | 6.7 | 6.8 | 5.0 | 6.0 | 4.9 |
| 2 | 13.1 | 12.5 | 15.4 | 12.1 | 12.1 | 10.9 | 9.4 |
| 3 | 20.4 | 17.8 | 23.0 | 16.6 | 17.6 | 15.1 | 11.6 |
| 4 | 29.3 | 22.9 | 32.6 | 21.1 | 23.5 | 16.7 | 12.9 |
| 5 | 41.4 | 35.1 | 45.0 | 30.1 | 36.2 | 22.7 | 15.3 |
| 6 | 51.9 | 46.3 | 56.1 | 40.0 | 47.2 | 31.8 | 17.8 |
| 7 | 67.2 | 61.8 | 71.2 | 54.0 | 63.4 | 46.0 | 21.8 |
| 8 | 78.8 | 73.3 | 83.6 | 64.8 | 73.7 | 56.4 | 24.4 |
| 9 | 89.7 | 82.0 | 93.7 | 74.3 | 84.2 | 64.1 | 26.4 |
| 10 | 104.7 | 95.7 | 108.9 | 83.9 | 98.9 | 73.7 | 28.1 |

Unit : cm

10 hour, 14 hour, 16 hour, or 18 hour: 10-, 14-, 16-, or 18-hour days, respectively; 14-10 hour, 16-10 hour, or 18-10 hour: 14 hour, 16 hour, or 18 hour during the odd-numbered weeks, however, all three groups of plants under 10 hour during the even-numbered weeks.

**Fig. 4.** Combination of different photoperiods. 14 hour, 16 hour, or 18 hour: under 14-hour, 16-hour, or 18-hour days, respectively; 14-16 hour: 14-hour for the first 3 weeks, thereafter under 16 hour; 18-16 hour: 18 hour for the first 3 weeks, thereafter under 16 hour; the arrow shows the time at which photoperiods were changed.

**Fig. 5.** Inactivation of short-day effect by night interruption or by gibberellic acid. LD or SD: 18-hour or 10-hour days, respectively; GA: SD with a 50 ppm solution of gibberellic acid every 2 weeks; NI: SD with dark period interrupted with pink fluorescent lamp.

**Fig. 6.** Two-branch plants. LD or SD plants: both branches kept under single treatment, 18-hour or 10-hour days, respectively; LD and SD branches: one branch subjected to LD, the other to SD.

**Fig. 7.** Effect of cold pretreatment and long photoperiods on breaking dormancy. C 10, C 15, or C 18: cold pretreatments followed by 10-hour, 15-hour, or 18-hour days, respectively; W 18: non-cold pretreatment followed by 18-hour days; numbers in brackets: percentages of plants which resumed growth by those dates.
during odd-numbered weeks did, however, cause different growth retardations, depending on the length of photoperiods with which the 10-hour photoperiod was combined. If one considers the last 3 weeks when all curves became linear and calculates the growth rates, the following is noted.

Photoperiods

<table>
<thead>
<tr>
<th>10 hr</th>
<th>14-10 hr</th>
<th>16-10 hr</th>
<th>18-10 hr</th>
<th>14 hr</th>
<th>16 hr</th>
<th>18 hr</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>9.2</td>
<td>10.0</td>
<td>11.3</td>
<td>11.8</td>
<td>12.6</td>
<td>12.5</td>
</tr>
</tbody>
</table>

Growth rate (cm/week)

These data show that one can not calculate mathematically the growth rate for 14-10 hour, 16-10 hour and 18-10 hour as an average of the two photoperiods. The average would be 7.0, 7.4, and 7.3 cm per week for 14-10 hour, 16-10 hour, and 18-10 hour, respectively, and these numbers are lower than the observed values. Thus, one must multiply some factors by the growth rates of 14-hour, 16-hour, or 18-hour photoperiods before adding to the 2.1 cm per week of 10-hour photoperiod. These factors are calculated as 1.38, 1.42, and 1.64 for 14-hour, 16-hour, and 18-hour photoperiods, respectively. Thus, in the case of the 18-hour photoperiod, one can calculate 11.3 cm per week for 18-10 hour photoperiod as follows.

\[
\frac{12.5 \text{ cm/week} \times 1.64 + 2.1 \text{ cm/week}}{2} = 11.3 \text{ cm/week}
\]

If one is allowed to use these ratios as comparable numbers between different photoperiods, one can say that 14-hour, 16-hour, and 18-hour photoperiods promoted growth of *Betula pumescens* seedlings with a ratio of 1.38 : 1.42 : 1.64.

VI. Inactivation of Short Day Effect with Interruption of Night & Application of Gibberellic Acid. Forty *Betula pumescens* seedlings were divided into two groups so that ten plants would have continuous LD and 30 plants would have SD. The latter group was subdivided into three subgroups of ten plants each. The first subgroup was treated with SD throughout the experimental period. In the second subgroup, a dark period of 14 hours was interrupted at its mid-point (1:00 AM to 1:30 AM) throughout the experimental period with 30 minutes of light from a 15-w pink fluorescent lamp 2 feet above the plants. The lamp had an intensity of 10 to 15 ft-c as measured with a Weston illumination meter, model 603, at the tips of plants. In the third subgroup, the growing points were treated with one drop of an aqueous solution (50 ppm) of gibberellic acid at intervals of 2 weeks beginning Nov. 1, 1958, when all the treatments were started. One drop of the above mentioned solution contains approximately 2 gammas of gibberellic acid.

The results presented in figure 5 show that plants grew vigorously under LD, and SD induced dormancy after 2 weeks. The interruption of the dark period and the gibberellic acid treatments, however, reduced the growth-inhibitory effect due to SD. Growth of the gibberellic acid treated plants was somewhat greater than plants with interrupted night. Development of new nodes was associated with the growth curves except in the case of the gibberellic acid treatment, where the number of nodes increased remarkably. Finally, there was no difference in the number of new nodes formed between the SD and gibberellic acid treatments, in spite of their difference in height at the conclusion of the experiment.

VII. Two-Branch Test. Thirty *Betula pumescens* seedlings were grown under LD so as to have two equal sized branches originating from adjacent basal buds. One group of seven plants was shifted to LD and a second group of seven plants to SD. A third group of 16 plants was treated so as to have one branch subjected to LD and the other to SD (both are abbreviated as “LD branch” and “SD branch” in the following discussion). To restrict the photoperiod treatment to one branch, a thick, black sateen curtain was drawn between the two branches from 5:00 PM to 8:00 AM. A photoperiod of 18 hours was given to one branch and 10-hour photoperiod to the other. Before beginning the study on Jan. 10, 1959, as well as throughout the experimental period, the leaves near the base of the plants were removed to facilitate the movement of the curtain (fig 6). The plants which received SD or LD on both branches reacted similarly to those mentioned in previous experiments, namely a cessation of growth after 2 weeks of SD and continuous growth under LD. On the other hand, plants which received SD on one branch and LD on the other showed the following results: the SD branches stopped growing just as did the SD plants, while the LD branches grew, but far less than the LD plant. These facts may indicate that some growth-inhibitory effect was transported from the SD branches to the LD branches.

VIII. Effect of Cold Temperature & Long Photoperiods on Breaking Dormancy. In the greenhouse 120 *Betula pumescens* seedlings were subjected to SD for 4 weeks starting Jan. 19, 1960. Thereafter, seedlings which had been in dormant condition were divided into two groups of 60 plants each. In the first group, plants were kept in a cold frame which was located outside of the greenhouse and controlled so as to maintain the inside temperature of 4.5°C minimum, while plants in the second group were kept continuously in the greenhouse. The photoperiod was not controlled at all so that both groups were exposed to a natural day length with either cold or warm temperature for the period of 4 weeks. At the end of treatment, plants in the cold frame showed different degrees of cold injury with brown leaves and leaf abscission. Some plants completely lost their leaves. On March 16, plants were shifted from the cold frame to the greenhouse and these plants as well as the plants continuously kept in the greenhouse were each subdivided into three
groups and subjected to the following three photoperiods: 10-hour, 15-hour, or 18-hour. Thereafter, resumption of growth in the six subgroups was observed for 12 weeks. Dormancy was broken by either cold treatment or longer photoperiods (fig 7). In cold-treated plants, the longer photoperiods induced quicker resumption of growth and the subsequent growth was more rapid. The plants kept continuously in the greenhouse resumed their growth only when they were kept under 18-hour photoperiods. Conclusively it can be said that the dormancy of terminal buds can be broken most effectively when plants are subjected first to cold and then to longer photoperiodic treatments.

**Discussion**

The quantitative character of dormancy was clearly demonstrated in this study. Once plants cease their growth under SD, subsequent SD treatment apparently does not further modify growth. The degree of dormancy, however, depends on the number of photoperiods which are shorter than a critical threshold. The number of long days necessary for the resumption of growth in plants which had become dormant under the influence of short days increased as the duration of short day treatment was increased. This effect occurred in both *Betula lutea* and *Betula pubescens* (figs 2, 3) and is in agreement with the findings of Van der Veen (23) and Downs and Borthwick (7). Thus, in some way, the growth-retarding effect caused by a given number of short days must accumulate in the plant itself. Therefore, dormancy is not typical of the all-or-nothing characteristic which was first discussed by Borthwick in 1871 (8) with respect to muscle contraction. The dormancy is, however, capable of full gradation in depth.

The length of a daily photoperiod has, on the other hand, an important quantitative implication on the photoperiodic control of growth in *Betula*. It is demonstrated in figure 4 that 14-hour, 16-hour, and 18-hour photoperiods promote growth of *Betula pubescens* seedlings; the longer photoperiods causing more growth. As calculated from the data in table I, 14-hour, 16-hour, and 18-hour photoperiods promoted growth of *Betula pubescens* seedlings with a ratio of 1.38:1.42:1.64. The growth of seedlings of *Betula pubescens* under the 10-hour photoperiod (in table I), however, can be questioned. Seedlings of *Betula pubescens* ceased their visible stem elongation under this photoperiod within 2 weeks (figs 1, 3, 5, & 6). This contradiction could be explained by the possibility that high summer temperatures in 1959 might have somewhat lengthened the critical day length of this species. The temperature in the greenhouse where this experiment was carried on was not recorded but the weather report from Caldwell Field Station of Cornell University (this station is located approximately 1.5 miles NE of the greenhouse) stated that the mean temperature was 1.3 C higher in August of that year than the 20-year average for this month. This explanation is probably not in variance with the results of Downs and Borthwick (7). They said that the induction of dormancy in trees took a greater number of short days under high temperature than under lower temperature and also that trees ceased growth under relatively longer photoperiod when plants were grown at temperatures below 21.1 C. The strong modifying influence of temperature on photoperiodic growth control was discussed by Nitsch (16). He said that photoperiodism seems to be operative inside a given temperature range; the whole mechanism is ineffective at temperatures below or above certain limits.

The length of a daily photoperiod also has an important quantitative bearing on the photoperiodically induced dormancy. Figure 7 shows that 10-hour, 15-hour, and 18-hour photoperiods induce resumption of growth in dormant *Betula pubescens* seedlings when photoperiodic treatments are followed after cold treatment, the longer photoperiod resulting in higher percentages of resumption.

It is clear, therefore, that a photoperiod regulates the degree of dormancy by means of its attributes. At least two of these are important as far as the present results are concerned, A: length or kind of photoperiod, B: duration or cycle of photoperiod.

It is difficult to know what is the intermediate mechanism between photoperiod and growth. Figures 2 and 3 imply that the change in state of dormancy is quite gradual in the direction of either induction of initial dormancy under SD or breaking of dormancy under LD. This type of close relationship between photoperiod and dormancy may lead one to believe that a substance exists between the photoperiodic stimulation and growth reaction, the level of which is controlled by the photoperiod, which in turn controls the growth. This kind of speculation is not in disagreement with the results presented in figure 6. In a two-branch plant (see fig 6) there must be some inhibitory effect moving from the SD branch to the LD branch. Although the inhibitory stimulus coming from the SD branch did not stop the growth of LD branch, it greatly reduced it.

Downs and Borthwick (7) said that dormant *Betula manchurica* apparently needs a cold treatment in order to break the dormancy of the terminal buds. However, *Betula pubescens* and *Betula lutea* used here, showed the resumption of growth without cold treatment if the day length was long enough (figs 2, 3, 7). Gibberellic acid application (3, 4, 13, 14, 15, 17) and dark period interruption (20, 27, 28) have been reported by many workers to nullify the short day effects. The present results shown in figure 5 are in agreement with those reported results.

**Summary**

The growth of leafy seedlings of *Betula pubescens* and *Betula lutea* was studied under different photoperiods.

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*Plant Physiology*
In both species:

I. To induce dormancy 2 to 4 weeks of 10-hour photoperiods were required.

II. Short day induced dormancy was broken by long photoperiods.

III. The degree of the short day induced dormancy depends on the number of short days given. The greater the number of consecutive, short days, the longer it took to break dormancy with long days.

In Betula pubescens:

IV. Breaking of dormancy was induced by cold treatment but this effect was more pronounced when longer photoperiods followed after cold treatments.

V. The rate of growth was markedly varied by the length of a daily photoperiod, being greater under the longer photoperiod with the photoperiod range between 10-hour and 18-hour.

VI. An interruption of the long night at mid point or the application of gibberellic acid nullified the effect of short days when the short days were given.

VII. When one branch of the two-branch plant was kept under short days growth retardation was noted on another branch kept under long days.

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LITERATURE CITED


