

Investigations on the bud dormancy of *Populus* × *berolinensis* Dipp.

IV. Sequence of dormancy in plants under controlled photoperiodic conditions

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It is well known that the growth of trees can be controlled by photoperiodic conditions (Garner and Allard 1923). On the shoots of most woody plants of the moderate zone buds are set under short-day conditions, this giving rise to a period of dormancy (Wareing 1949, 1956; Downs and Borthwick 1956a, Nitsch 1957a, b, 1962).

It has been observed that, in dependence on the tree species, the photoperiodically induced dormancy of the buds may be broken if: 1) foliated plants are exposed to long day (Wareing 1954; Downs and Borthwick 1956b; Kawase 1961); 2) the plants are defoliated (Downs and Borthwick 1956a, b; Nitsch and Nitsch 1959), 3) the plants are chilled (Van der Veen 1951).

The present paper describes investigations on the course of bud dormancy taking into account its state in *Populus* × *berolinensis* growing under controlled photoperiodic conditions.

MATERIAL AND METHODS

The experiments were made with 1- or 2-year-old *Populus* × *berolinensis* plants grown from cuttings set in clay pots, in the greenhouse. In the night they were exposed to the light of mercury 400 W lamps so as to obtain a 20- or 24-hr period of light. The mean 24-hr maximal and minimal temperature was 25.5° and 12.5°C, respectively, maximal and minimal relative air humidity was 97.5 and 64.5 percent.

When the plants had reached a height of 20–30 cm, a part was subjected to 12-hr day, by placing them for the night in dark chambers in the same greenhouse.

In 1968 the culture of the experimental plants from the cuttings was started in the second half of February under a 24-hr photoperiod. Short day was applied to the first group of plants from May 13.

In 1967 the outset material consisted of 1-year-old, 10-cm high plants which after hibernation in natural conditions were brought to the greenhouse on March 30 and kept under 20-hr day till May 2 when they were transferred to short day.

The cuttings in 1965 were set on January 29 under 20-hr day conditions and transferred to short day on April 15.

The observations comprised: 1) measurement of elongation growth at 7-day intervals, 2) the date of terminal bud setting and of their opening on plants subjected to various treatments, noted at 2-day intervals. Bud opening was expressed by an index taking into account both the number of plants on which buds opened and the number of days necessary for their development (Witkowska-Żuk 1969),

$$W = \frac{\frac{1}{t_1} + \dots + \frac{1}{t_n}}{N}$$

where t — time required for terminal bud opening on each plant

N — number of plants in given treatment.

RESULTS

Growth of plants under different numbers of 12-hr photoperiods

Six groups including six plants each were exposed to short day during the last 0, 1, 2, 3, 4 and 6 weeks of the experiment so as to end all the treatments up to June 24, 1968. The material was selected so as to have plants of similar mean height in each group at the moment when induction with short day was started (Table 1).

Table 1

Mean height (cm) of *Populus × berolinensis* plants under different numbers of 12-hr photoperiods and then transferred to 24-hr light

Symbol of treatment	At beginning of experiment	At beginning of short-day treatment	At end of short-day treatment and beginning of long-day	At end of experiment
6WSD	33.0	33.0	42.0	58.8
4WSD	27.4	32.1	39.0	50.3
3WSD	23.2	32.9	37.9	47.6
2WSD	22.9	37.7	43.4	58.4
1WSD	20.0	34.9	37.2	50.2
LD	19.9	—	38.9	53.2

As shown in Figs 1 and 2, the growth of the plants was retarded after one week of short-day treatment and ceased completely after three weeks, most of the plants having set terminal buds.

Growth of plants under 24-hr light after exposure for a different number of 12-hr photoperiods

The same plants which had previously been kept under short day for 0, 1, 2, 3, 4 and 6 weeks were subjected from June 24, 1968 to long day.

As seen from Figs 1 and 3, the plants which had been growing under short day

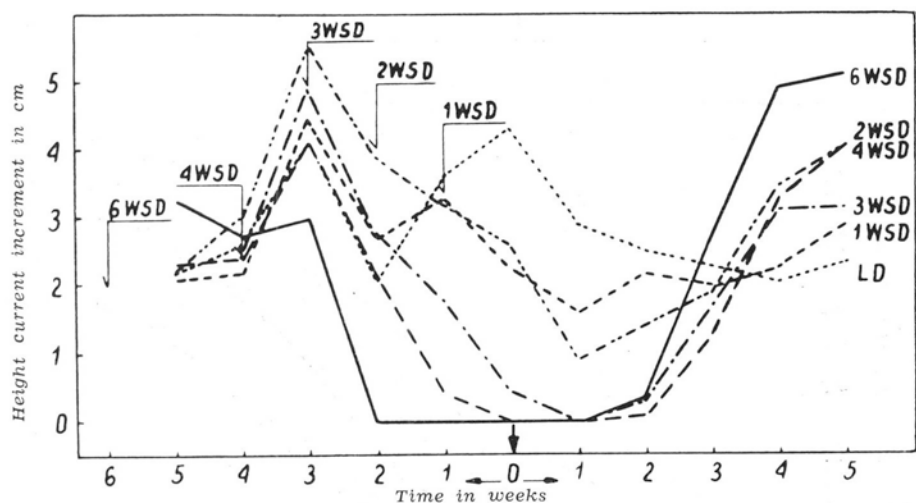


Fig. 1

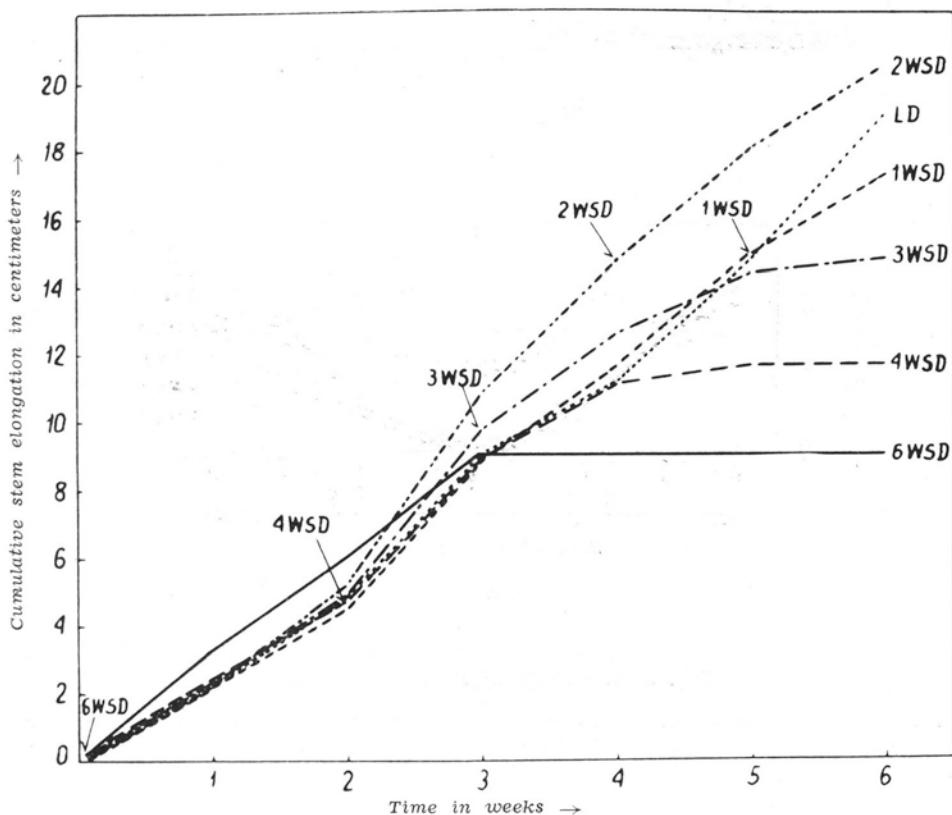


Fig. 2

Figs. 1, 2. Growth of *Populus × berolinensis*

Fig. 1. Height current increment of plants after various numbers of 12-hour photoperiods and after transfer to long day conditions. LD — under continuous light; 1WSD, 2WSD, 3WSD, 4WSD or 6WSD: under 12-hour day for 1, 2, 3, 4 and 6 weeks, respectively. The light and heavy arrows show the dates at which the 12-hour day treatments were started and terminated, respectively. Fig. 2. Growth retardation due to 12-hour day treatment. The arrow shows the dates at which the treatment was started.

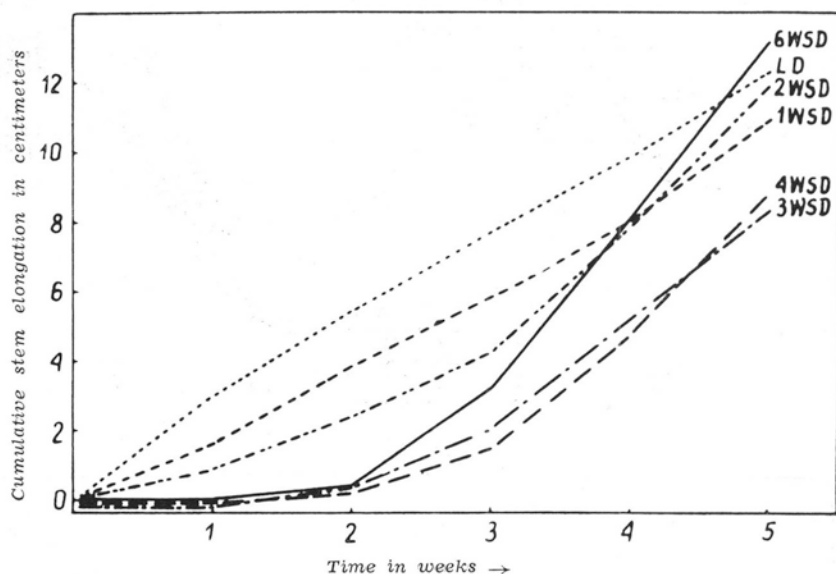


Fig. 3

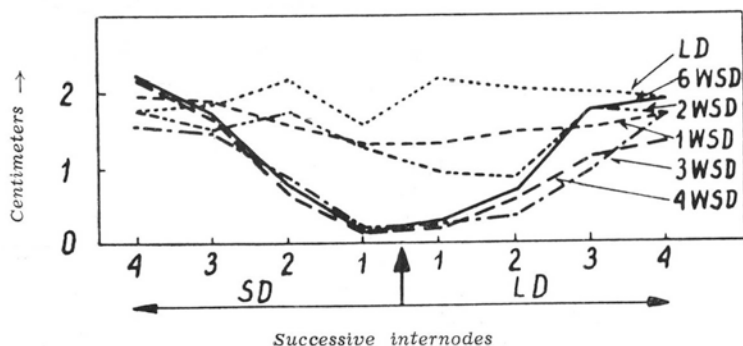


Fig. 4

Figs. 3, 4. Growth of *Populus × berolinensis*

Fig. 3. Resumption of growth under continuous light (LD) after 12-hour day (SD) treatment. Fig. 4. Length of successive internodes on *Populus × berolinensis* plants subjected for various time periods to 12-hr photoperiod, and then placed under continuous illumination

for less than 3 weeks continued to grow, although their growth increment was smaller than in the control plants treated the whole time with long day. Only after, a period of 2 weeks under long day did the growth increment begin to increase and after 3 weeks it attained the same level as in the control plants or even slightly exceeded it.

The plants growing for three and more weeks under short day had set buds at the moment when they were transferred to long day conditions. Resumption of growth and elongation were noted only as late as the second week after the change of light conditions. Later growth of these plants was rapid and after 4 weeks their growth increments were larger than in the controls.

The length of the successive internodes formed by the plants under short, and after transfer to long day, as measured in the end phase of the experiment, showed that even one week under short day reduces the length of the internodes as compared with the corresponding ones in plants under long day (Fig. 4).

State of photoperiodically induced bud dormancy

The data from the experiments in 1968, shown in Fig. 5 expressed as the index of bud opening, indicate that bud opening on foliated plants previously treated for 3, 4 and 6 weeks with short day, occurs with varying intensity after transfer of the plants to long-day conditions. The buds on plants subjected for 3 weeks to short day opened most rapidly, on the average after 5 days, whereas those on plants kept 4 and 6 weeks under short day opened later, on the average 10 and 12 days, respectively.

In 1967 for determining the kind of bud dormancy plants exposed to 12-hr daylight for 4, 6, 8 and 10 weeks were subjected to the following experimental treatments:

1. foliated plants were transferred to long day,
2. defoliated plants were transferred to long day,
3. defoliated plants were left under short day.

After 10 weeks of exposure to short day a single additional treatment was applied consisting in bathing the defoliated plants kept under short day (water temperature 30°C, duration of bath 24 hr.) Each treatment comprised 4 plants which were under observation for the following 4 weeks.

The results shown in Fig. 5 as the bud opening index prove that on the foliated plants kept under short day for 4—6—8 weeks buds opened at similar times, on the average after 20, 17 and 16 days. A distinctly lower index than for these plants was noted for plants under short day for 10 weeks — the buds opened only on one half of the experimental plants on the average after 22 days. On the plants defoliated after 4 weeks of exposure to short day, buds burst sooner than on the foliated ones, after 11—10 days, both under long and short day. The plants defoliated after 6 weeks of short-day treatment exhibited bud opening only on the specimens transferred to long day conditions after 17 days on the average. After treatment with 8 and 10 weeks of short day no bud burst was observed on the defoliated plants. The bath applied after 10 weeks of short day caused a rapid opening of the buds (after ca. 8 days).

In 1965 an additional experiment was performed in which, after 4 and 10 weeks of exposure to a 12-hr photoperiod the plants were subjected to the same treatments

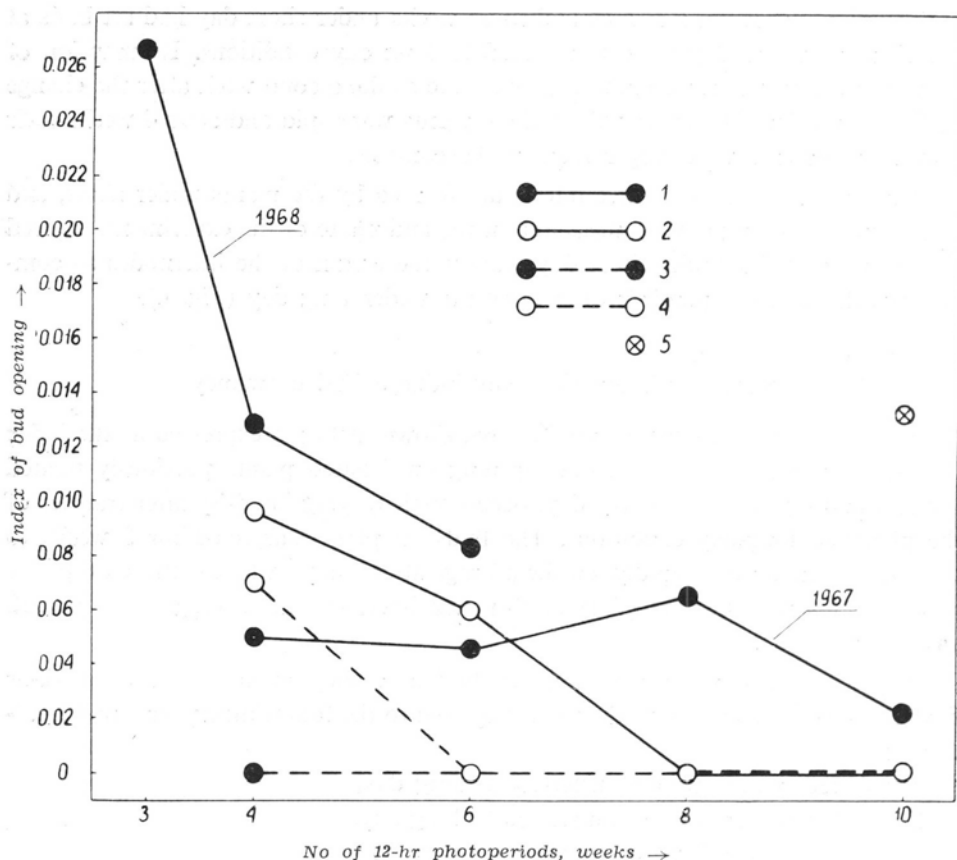


Fig. 5. Terminal bud opening on *Populus × berolinensis* plants subjected for various numbers of 12-hr photoperiods, and then subjected to various treatments.

1 — foliated plants transferred to long-day conditions, 2 — defoliated plants transferred to long-day conditions, 3 — foliated plants kept further under short-day, 4 — defoliated plants kept further under short day, 5 — defoliated plants subjected to warm water bath and further kept under short day

as described in the experiments of 1967. Each combination comprised 5 plants. After the treatment which followed 4 weeks of growth under short day, terminal bud opening was observed on all the plants after an average of 7 days (6–9). The plants kept 10 weeks under short day and subjected to a water bath (temperature 35°C, duration 9 hrs) exhibited bud burst after an average of 3 days (2–6). On the remaining plants no buds opened over a period of 10 weeks after the treatment, therefore on September 2 they were immersed again in a bath under the same conditions. Since no bud burst was observed after this treatment, the plants were placed on November 8 on an experimental plot and subjected to natural chilling until March 12. When brought into a warm greenhouse they developed buds after 3 days.

DISCUSSION

The results of experiments seem to indicate a certain succession in the influence of short day on *Populus x berolinensis* — beginning with reduction of elongation growth, thus shortening of internodes already after one week of short day, up to a fully formed bud with stipules transformed to scales, after 3 weeks. This occurred contrary to Nitsch's (1962) supposition based on the observation of *Populus canadensis* that the influence of transfer of the plants from long to short day is in the first place manifested by the transformation of leaf primordia to scales; he therefore supposed that elongation of the particular internodes may continue.

Plants previously treated for 1 or 2 weeks with short day required respectively 2 and 3 weeks of long day to attain a growth increment equal to that of control plants under long day. The plants which under short day conditions set buds, exhibited after two weeks of exposure to long day a slight growth increment which after 3—4 weeks of long day became equal to that in control plants and then exceeded it, irrespective of the time for which the plants had been kept previously under short day. Although, in view of the small number of plants in the particular combinations, the conclusions are very restricted, it seems, however, that the plants inhibited in growth for a longer period (6 weeks under short day) showed a higher growth increment. In those growing the whole time of the experiment under long day, or only one week under short day, the increments in the end period were the lowest, this indicating a certain decrease of their growth potential.

Distinct differences in starting growth by plants exposed to a different number of short-day photoperiods could be detected when the process of growth initiation was expressed in the number of days after which opening of buds was observed. It would thus seem, that the elongation growth of the plants does not fully reflect the development possibilities of the buds, and bud burst seems to be the most characteristic.

The experiments performed in 1968 demonstrated that, the longer the period of exposure of the plants to short day the more delayed was bud opening, after transfer to long day conditions, this seemingly indicating a gradual deepening of dormancy.

The experiments of 1967 demonstrated that after 4 weeks of exposure to short day, it was sufficient to remove the leaves in order to induce bud burst. If the plants were not defoliated and subjected to long day, the buds opened after a longer time lapse. Probably the leaves which in many species are the receptors of the photoperiodic stimulus (Moškov 1935; Wareing 1954; Downs and Borthwick 1956b; Nitsch and Nitsch 1959), were under short-day conditions the inhibitory organ, and after transfer of the plant to long day conditions they still inhibited bud opening for a certain time until a change occurred in their function in growth processes. Observation of plants after 6 weeks of short day treatment demonstrated that for bud development on defoliated plants, the long-day stimulus is necessary. This leads to the supposition that, for a certain time after bud setting, the apical meristem in *Populus x berolinensis* is sensitive to the length of the photoperiod

as has been observed in other species (Bulgakova 1937; Gustafson 1938; Wareing 1953, 1954).

The above described behaviour of buds on the plants during a further 3-week period of exposure to short day, after previous bud setting in the same conditions allows to designate this phase of bud dormancy as correlated inhibition.

After 8 weeks of treatment with short day, only those plants showed bud opening, in which leaves received the light stimulus. As shown by the experiments of 1967 and 1965, after 10 weeks of exposure to short day, dormancy had to be broken by an external factor such as a bath or chilling. Without these treatments buds opened only exceptionally.

It would seem, therefore that in plants which have set buds and are still kept under short day, rest occurs 5—7 weeks after bud setting.

The results obtained in the particular years, differ numerically. This was probably connected with the differences in plant material as regards growth, and the nonuniform conditions in the greenhouse in the particular experiments. Additional observations indicated that smaller plants required more short days for setting buds, therefore also the course of dormancy may have had a different rhythm in them. Temperature could also have exerted a modifying influence on the reaction of plants to short day, as described in numerous reports (Downs and Borthwick 1956a; Kramer 1957; Kawase 1961; Nitsch 1962).

Kawase (1961) observed that *Betula pubescens* seedlings, after exposure to short day for 4 weeks, require the same number of long days for resumption of growth. He concluded therefrom that the photoperiodically induced dormancy is of quantitative character. Downs and Borthwick (1956b), on the other hand, established that *Weigelia florida*, even after exposure for a period as long as 3 months to short day, opened buds when exposed for 1 week to long day, thus almost as soon as immediately after their setting. The results obtained with *Populus × berolinensis* confirmed the observations of Van der Veen (1951) that by means of exposure to short day rest may be induced.

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SUMMARY

The sequence of bud dormancy and its state in *Populus x berolinensis* were investigated under controlled photoperiodic conditions. The experiments were made with 1- or 2-year-old plants reared in a greenhouse.

It was found that the plants under 12-hr daylight set buds within three weeks, that is entered into dormancy. For the next three weeks, under short day, the buds were in a state of correlated inhibition, since removal of the leaves was sufficient to stimulate their growth. Further 2- to 4-week exposure of the plants to short day caused a gradual transition of the bud dormancy from correlated inhibition to rest, which could only be interrupted by an external factor (warm water bath or chilling).

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Badania nad spoczynkiem pączków topoli berlińskiej
(*Populus × berolinensis* Dipp.)

IV. Następowanie spoczynku w pączkach roślin rosnących w warunkach kontrolowanej długości dnia

Streszczenie

Przeprowadzono badania nad następowaniem spoczynku z uwzględnieniem jego głębokości u topoli berlińskiej rosnącej w kontrolowanych warunkach fotoperiodycznych. Doświadczenia prowadzono na 1- lub 2-letnich sadzonkach hodowanych w szklarni.

Wyniki doświadczeń wykazały, że sadzonki wymagały 3 tygodni 12-godzinnych dni do założenia pączków, a więc do wejścia w stan spoczynku. Przez następne 3 tygodnie przebywania w warunkach krótkiego dnia pączki ich znajdowały się w spoczynku względnym, ponieważ już samo usunięcie liści pobudzało je do wzrostu. Dalsze 2- do 4-tygodniowe działanie krótkich dni na rośliny powodowało stopniowe przejście pączków ze spoczynku względnego w spoczynek głęboki, który mógł być przerywany tylko działaniem czynnika zewnętrznego na pączki (kąpielą wodną lub przechłodzeniem).