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

III. Sequence of dormancy in trees growing in natural conditions

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It has been established by numerous investigators that the growth of shoots in the particular parts of the crown occurs at various rates, and buds are set on the shoot apexes not all at the same time (see review by Kozlowski 1964). This characteristic shoot growth in the crown is considered to be due to the activity of correlative growth inhibition factors mainly associated with the presence of leaves and of the growing parts of the crown (see reviews by Šternberg 1963, Champagnat 1965).

In natural conditions after the phase of correlated inhibition when the activity of the apical meristem enclosed in the bud is limited only by factors inherent in the plant but beyond the bud, in most trees there occurs a phase of rest, when only direct action on the bud may break its dormancy. The cause of rest lies in the bud itself (see reviews by Doorenbos 1953; Samish 1954; Romberger 1963; Vegis 1965).

Little is, however, known as yet if there exists any relation, and if so what relation, between correlated inhibition and the occurrence of rest in buds (Champagnat 1951, 1955, 1965; Libbert 1961a, b, 1964). This problem is the subject of the present study on *Populus* × *berolinensis*.

MATERIAL AND METHODS

The experiments were made in 1965 on 7-year-old *Populus* × *berolinensis* trees. They were 4.7 m high, breast-high diameter ca. 2.8 cm. The crown began at a height of 80 cm above the base of the trunk.

Bud opening was observed on the trees on April 25. The first to burst were those on the lower branches, and a few days later on the higher ones. After the period of spring growth, observations were started on bud setting on the tips of the lateral twigs which constituted a prolongation of the second-order axes (Fig. 1). On June 25 buds were already set in the lower part of the crown, on the average up to ca. 3.4 m of the tree height, i.e. to about 58 percent of the crown length. After one month, on July 22 it was found that the shoots grew only in the upper part of the crown, constituting 14 percent of its total length.

At the above mentioned dates, on the trunks of all the experimental trees the border was marked between the growing, and the dormant part of the crown. In the lower part of the crown ten shoots were chosen and marked, and so were five in the middle and five in the upper part. They were successively numbered 1—20 from below. On the shoots provided with labels the behaviour of the buds was followed

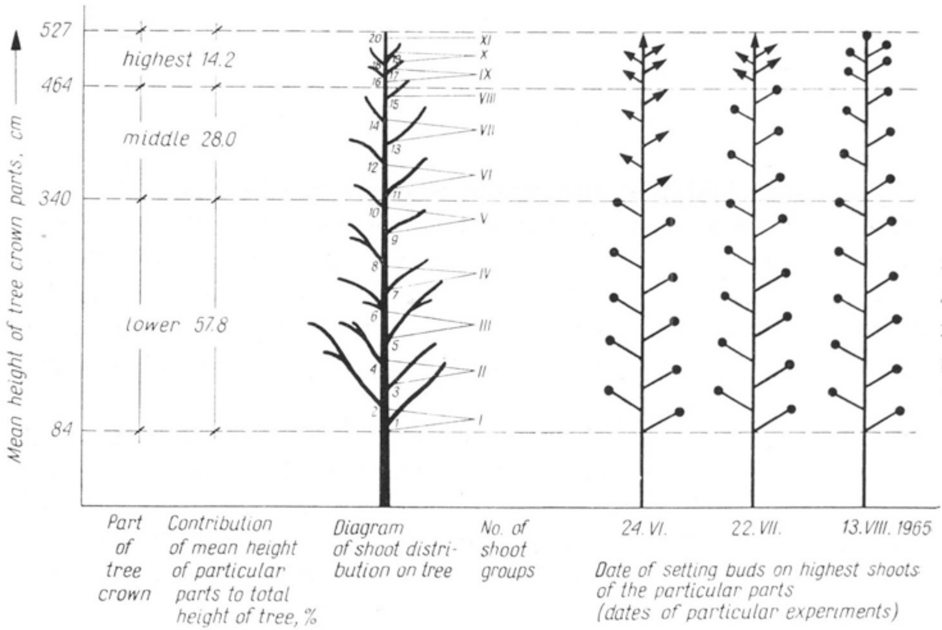

Fig. 1. Scheme of experiments

after the application of various experimental treatments. The observations involved both shoots on the trees and those detached and placed in beakers with water under glass bells with limited air access. The detached twigs (ca. 30—40 cm long) were placed in premises with natural daylight at a temperature favouring growth (mean 10-day air temperature 23—25°C).

Five trees were randomly assigned to each experimental treatment. In the elaboration of the results the shoots were assigned to the groups denoted by roman numerals (Fig. 1). The twigs of the lower crown tier were assigned successively by two to five groups (I—V), those of the middle and upper parts to six groups (VI—VIII and IX—XI). Since the number of twigs chosen for observation in the higher tiers was odd, each of the highest-situated groups (VIII and XI) consisted of one twig from each tree. Each result for a given group of shoots is, thus, a mean of the data for the buds on two successive twigs in five trees, with the exception of the highest groups of the middle and the upper tier.

The results of bud opening are presented in graphs with the use of the index of bud opening calculated by the formula (Witkowska-Żuk 1969)

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

where t — number of days required for opening of the terminal bud on each twig,
N — number of twigs in the experimental treatment.

The observations involved all kinds of buds on the twig, however, in view of the limited space, only the most interesting results obtained for the terminal buds of long shoots are presented.

RESULTS

Shoot length increment in various parts of the tree crown

In the autumn of 1965 the length increment for that year was measured on 20 shoots chosen in spring on five control trees not subjected to any experimental treatment (Table 1).

Table 1

Elongation growth of shoots on *Populus* × *berolinensis* trees in 1965 (mean from 5 control trees)

Part of crown	Group of shoots	Increment mm
Lower	I*	11
	II*	12
	III*	16
	IV*	45
	V*	79
Middle	VI*	193
	VII*	261
	VIII	298
Upper	IX*	371
	X*	494
	XI	600

* Mean from two successive shoots.

The lowest-situated shoots showed the smallest ca. 11 mm, and the apical shoots the largest (ca. 600 mm) length increments. Since the length of the growth period was known for the upper shoots in the particular parts of the crown, the average daily growth increment could be calculated. For the highest shoots of the lower part of the crown it was ca. 1.3, for those of the middle part ca. 3.3 and for the apical shoots ca. 5.4 mm.

Bud opening on shoots from various parts of the tree crown

a. Bud opening on shoots after removal of the growing part of the tree crown

In this experiment the behaviour of buds was observed on twigs of trees in which the growing part of the crown was cut off, and on twigs of trees on which from the remaining dormant part of the crown leaves were removed. At each successive date the same treatment as on the preceding dates was repeated (Fig. 1), thus:

on June 24 the observations involved two groups of trees:

1) with middle and upper part of crown removed, but with leaves left on the remaining part
2) with middle and upper par of crown removed, and the remaining part defoliated;

on July 22 — four groups of trees:

1) and 2) like on June 24 and
3) with upper part of crown removed, but with leaves left on the remaining part
4) with upper part of crown removed, and the remaining part defoliated;

on August 13 and September 12 six groups of trees:

1), 2), 3), and 4) like on July 22 and
5) trees with intact crown — foliated (controls)
6) ,, ,, ,, ,, — defoliated.

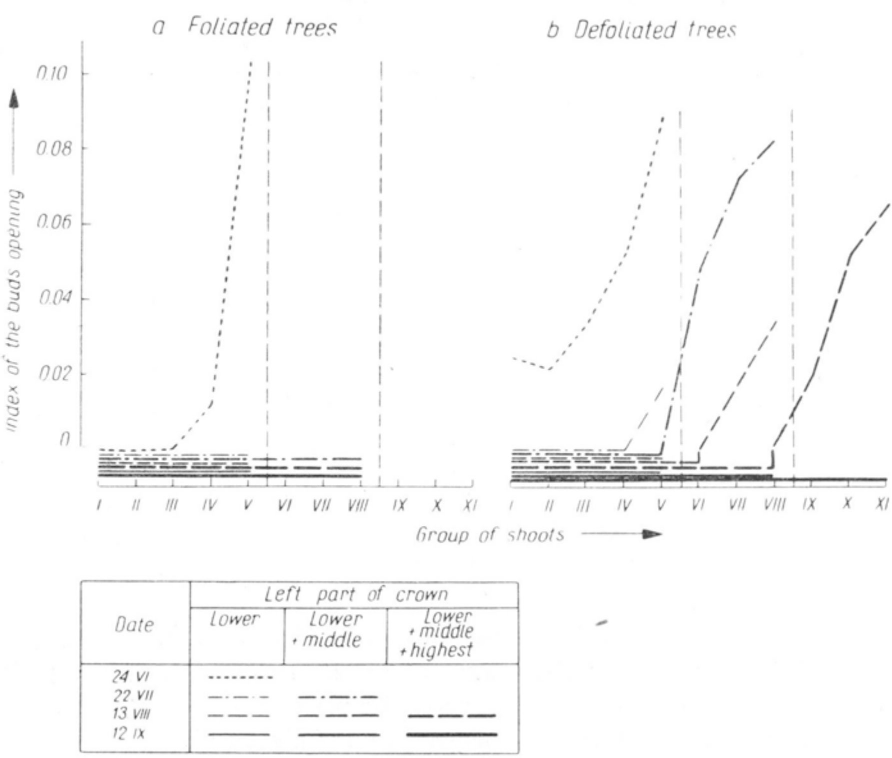

Fig. 2. Terminal buds opening on shoots of *Populus × berolinensis* trees on which particular crown parts were removed at four different dates in 1965

The results obtained in experiments with trees on which the particular parts of the crown were removed and the remaining part was not defoliated (Fig. 2a) indicate that only on June 24 opening of buds on the highest shoots of the lower part of the crown occurred. At all the remaining dates the buds did not open after removal of the growing tier.

Combination of removal of the growing part and defoliation of the lower part of the crown on which the shoots had already stopped growing resulted in an intensive opening of the terminal buds, though not on all the shoots (Fig. 2b). After the treatment of June 24, terminal buds opened on most shoots in the lower part of the crown. But when the same treatment was applied on July 22, only the buds on the highest shoots of the lower part of the crown burst. When at this date the growing part of the crown was removed, bud opening was observed only on the shoots of the middle part of the crown, on which buds had been set

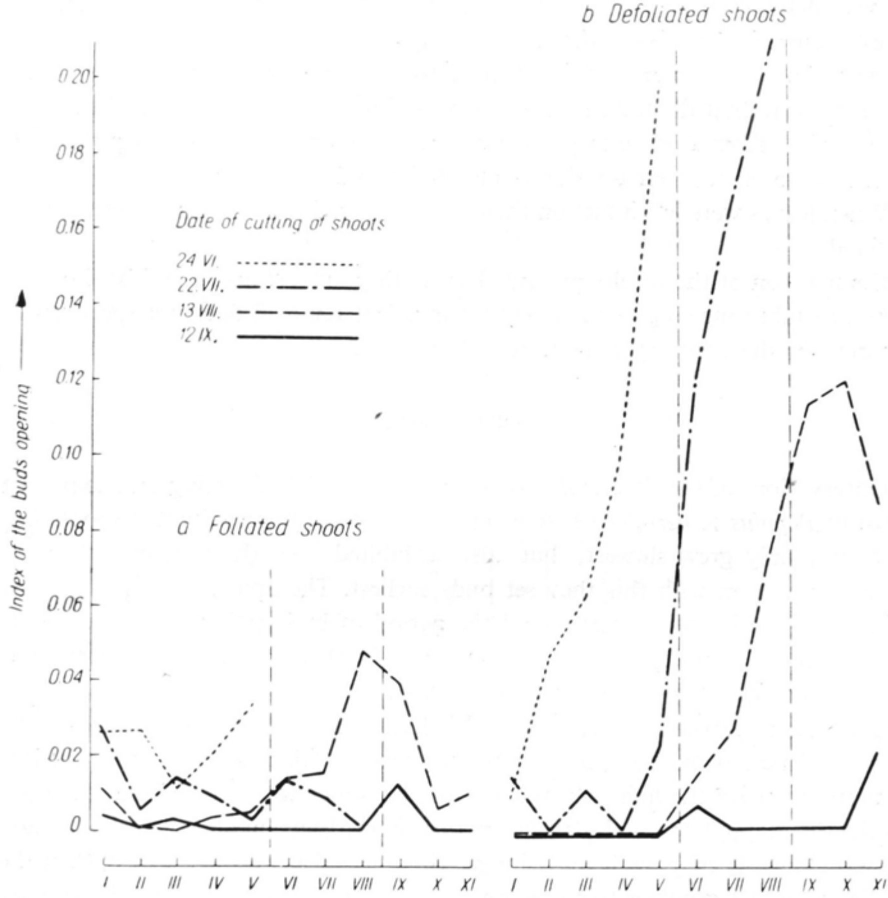

Fig. 3. Terminal buds opening on detached shoots of *Populus*×*berolinensis* cut off at four different dates in 1965

in the course of the previous month, whereas the buds in the lower part of the crown did not open. Similar results were obtained after the treatment of August 13, when, after defoliation of the whole crown, buds opened on the shoots of the upper tier, and after removal of the upper part of the crown they burst on several of the highest-situated shoots of the middle part of the crown. If only the lower part of the crown was left, no bud opening was observed on the shoots.

b. Bud opening on detached shoots from the particular parts of the tree crown

Twigs were used for the experiments detached from the particular parts of the tree crown after bud setting. On June 24 shoots were taken only from the lower part of the crown (nos 1—10), on July 22 from the lower and middle parts (nos 1—15), on August 13 and September 12 from the whole crown (nos 1—20). At each date the shoots were cut from different trees.

From each tree twice the number of the previously labeled shoots was detached. Very similar twin shoots were chosen in each pair. From each pair of twin shoots one was defoliated, and the foliated one was placed in water. Abscission of the leaves occurred after 6—15 days.

Opening of the terminal buds on the defoliated shoots is shown in Fig. 3 b. The results indicate that the higher the shoot was situated in the crown, and the shorter was the time from bud setting on it the more intensively its bud opened. Bud burst was observed even on shoots cut on September 12.

When leaves were left intact on these shoots (Fig. 3a), bud opening was generally inhibited.

Comparison of the results presented on both graphs (Figs 3a and b) shows that when a certain time elapses after bud setting, leaf removal does not speed up their opening, on the contrary it even retards it.

DISCUSSION

Observations of the date and succession of terminal bud setting on shoots in the crown of *Populus × berolinensis* trees indicate that the lowest-situated shoots in the crown not only grew slowest, but also exhibited the shortest growth period, and in connection with this they set buds earliest. The apical shoots grew fastest, their growth period was longest, and the period of bud setting latest. Relations of this type have been reported in a number of other species with a monopodial habitus (Wodzicki 1960; Kozlowski 1964).

The present experiments demonstrated that on defoliated shoots, both detached from trees and left on them, bud opening occurred with the same regularity; it was the more intensive the higher in the crown the shoot was situated and the shorter was the time lapse from bud setting on this shoot. Buds on detached shoots, however, were capable of growth for a longer time period from their setting than those on shoots of the growing trees. A similar relation was observed in the shoots of *Populus nigra* (Jost 1891). It is possible that detachment of the shoot from the parent plant was the cause which forced the shoot to start growth and regeneration of the whole organism (on the cut off shoots root formation was observed), although it cannot be ruled out that detachment of the shoot from the remaining part of the crown may have eliminated all inhibitory influences of the tree organism.

Fig. 4 presents schematically the occurrence of dormancy in the buds of *Populus* × *berolinensis* examined at four dates in 1965, according to the criterion by which the lack of opening of buds on detached defoliated shoots is considered as the beginning of rest (Jost 1891). These results seem to indicate a gradual sequence of rest in the buds of the particular crown parts. Chandler (1960) treats this process as an active translocation of rest from below towards the tree top.

Comparison of bud opening on shoots detached from trees and those remaining on them demonstrated that, in spite of the high ability of the buds for growth, their opening was inhibited by the leaves. It should be noted that the removal of the growing tier made bud opening possible on the highest shoots of the remaining part of the crown only on June 24. At other dates, if leaves were left intact on the remaining part of the crown, buds did not open. This might have been connected either with the diminished size of the actively growing part of the crown, or else with the increasing inhibitory influence of the leaves. The stronger influence of leaves than of the growing parts in inhibition of bud opening has been reported in other species (Smith 1944; Allary 1958; Cozens and Wilkinson 1966). Experiments in which various parts of the crown were removed at the same time and the remaining ones defoliated proved that when buds open on the upper shoots of the crown, those on the lower-lying shoots frequently do not burst, although they did begin to open when the part of the crown above them was removed. This

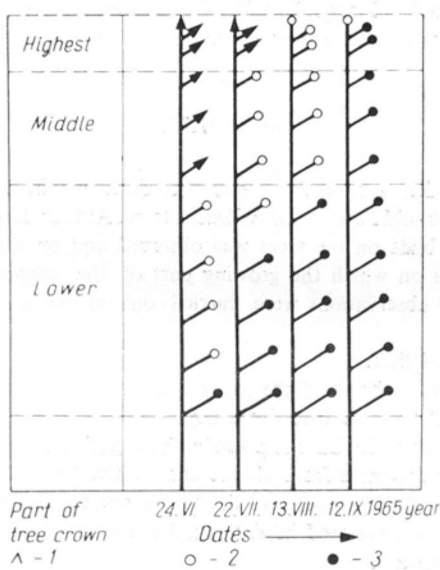

Fig. 4. Sequence of bud dormancy on shoots in various parts of the crown of *Populus* × *berolinensis* trees (schematically)

1 — growth of shoot, *2* — correlated inhibition *3* — rest would indicate an inhibitory influence exerted by the bursting buds of higher shoots on the buds of lower-lying shoots.

The results of observations on *Populus* × *berolinensis* allowed to determine the duration of correlated inhibition preceding rest for several shoots in the crown. For the highest ones in the lower part of the crown the period of growth was ca 90, correlated inhibition not less than 30 and not more than 50 days. For the highest shoots of the middle part of the crown growth lasted ca. 120, correlated inhibition not less than 22 and not more than 50 days. For the apical shoots of the trees the growth period was 140, and the correlated inhibition phase not less than 30 days, although it is not known when rest actually began, as further observations were not made. On account, however, of the low intensity of bud opening on the shoots detached on September 14 (thus 32 days after bud setting) it would seem that the buds were at this date in the preliminary phase of rest.

These results lead to the supposition that, independently of the length of the growth period, the rest of the buds on the above enumerated shoots was preceded by a period of correlated inhibition of a similar duration, probably not less than 30 and not more than 50 days. It is possible that in *Populus* × *berolinensis* the passing of buds to a state of rest is connected with long-lasting inhibition of growth of the apical meristem enclosed in the bud formed as the result of correlative inhibition. It also may be that correlated inhibition makes possible an accumulation of the inducing factor responsible for the entrance of the bud into a state of rest, and as suggested by numerous authors (Hemberg 1949; Wareing, Eagles and Robinson 1963; Libbert 1964), this factor may be of a hormonal character.

The authors are indebted to Docent T. J. Wodzicki for suggesting the scheme of experiments and to Professor J. Tomanek for making available to them the necessary facilities.

SUMMARY

Investigations were undertaken on the sequence of dormancy in the bud of shoots in various parts of the crown of 7-year -old *Populus*×*berolinensis* trees. At four dates in the course of the summer 1965 the setting of buds on the trees was observed and on shoots cut from the trees as well as on shoots in trees on which the growing part of the crown was removed, the bud opening was studied. The observations were carried out on two groups of plants: with leaves and defoliated.

The experiments proved that:

1) The buds on the lowest shoots of the tree crown are the earliest and those on the apical part of the crown the last to enter into dormancy.

2) The occurence of rest in the buds is preceded by a period of correlated inhibition, the duration of which is similar for buds from all the shoots investigated.

3) The growing parts of the crown and the leaves exert an inhibitory effect on the buds, causing probably a state of correlated inhibition; the inhibitory influence of leaves is stronger than that of the growth apexes.

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

III. Następowanie spoczynku w pączkach drzewa rosnącego w warunkach naturalnych

STRESZCZENIE

Przeprowadzono badania nad następowaniem spoczynku głębokiego w pączkach pędów w różnych częściach korony drzew topoli berlińskiej. Doświadczenia prowadzono na 7-letnich drzewkach rosnących na poletku doświadczalnym. Do celów eksperymentalnych wykorzystano fakt niejednakowego terminu zakładania pączków na pędach w różnych częściach korony drzewka. W czterech terminach lata 1965 roku obserwowano rozwój pączków na pędach ściętych z drzewek jak i na pędach drzewek, którym usuwano rosnącą część korony. Obserwacje objęły dwie serie roślin: ulistnione i defoliowane. Wyniki doświadczeń wykazały, że:

1) Pączki na najniższych pędach korony drzewa wchodzą w spoczynek głęboki najwcześniej, a na wierzchołkowych częściach korony najpóźniej.

2) Następowanie spoczynku głębokiego w pączkach jest poprzedzone przez spoczynek względny, którego długość jest podobna dla pączków na wszystkich badanych pędach.

3) Rosnące części korony i liście wywierają inhibitujący wpływ na pączki, prawdopodobnie powodując stan spoczynku względnego; hamujący wpływ liści jest silniejszy od wpływu rosnących wierzchołków.