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

II. Role of leaves in the correlated inhibition phase

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It has been repeatedly observed that, after damage occurring to the leaves on a tree, buds start to grow in the same vegetation season in which they were formed (Goebel 1880; Späth 1912; Dostal 1926; Rose 1958). Bud opening, however may occur only in a certain period which differs for individual species (Perk 1960; Kulagin 1966). This period has been termed correlated inhibition of buds (Samish 1954), since its cause is inherent in the plant, but it lies beyond the bud.

It is known (Allary 1958) that, in dependence on the tree species, the axillary buds may be inhibited by incompletely developed or fully grown leaves or by a combination of both. The existence of an acropetal or basipetal shift (Champagnat 1951, 1955, 1965) of the inhibitory influence of leaves on the opening of axillary buds has been also demonstrated.

The present experiments on *Populus × berolinensis* were undertaken in order to elucidate further the influence of leaves on the buds in various stages of correlated inhibition.

MATERIAL AND METHOD

For the experiments twigs cut from about 15-year-old *Populus × berolinensis* trees were used. After terminal bud setting on the shoots, twigs which showed in the current year a length increment of about 30 cm were cut at successive dates from the trees. In view of their similar habitus and situation in the tree crown, it could be assumed that the buds on them formed at about the same time.

On the cut shoots leaves were removed in various ways, and placed under glass bells giving some air access from below. The end of the shoot was immersed in water. The premises were kept under natural daylight at a temperature favourable to growth (mean diurnal tempe-

perature 23—25° C). The bells were taken off every day to air the plants and remove the water vapour excess.

The observations on bud (terminal and axillary) opening were made every second day, and the dates of bud bursting on the particular shoots were recorded. The results are given only for terminal buds, since the axillary buds developed less intensively. For each treatment the following data are given: 1) the number of shoots on which buds opened and 2) the mean number of days required for bud opening. In the graphs an index of bud opening was introduced (Witkowska-Żuk 1969). The index was calculated from the formula:

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

where: t — number of days required for bud opening on each shoot,
 N — number of shoots in the experimental treatment

RESULTS

Experiments with leaves removal at various dates after cutting off of shoots from tree

On shoots cut at four different dates in the summer of 1965, leaves were removed according to the following schedule:

- 1) immediately after cutting off,
- 2) 2 days after cutting off,
- 3) 4 days after cutting off,
- 4) 6 days after cutting off,
- 5) leaves not removed.

It is seen from the data in table 1 that, both the number of shoots with buds opened and the time to their bursting varied in the particular treatments. Bud opening on the shoots cut in July occurred in all the treatments after a similar time of 4—8 days but the buds opened on the various number of shoots. In August it was observed that the later the leaves were removed the slower was bud opening. No differences were noted between the shoots of the treatment defoliated after six days and those with leaves intact. It was noted at the end of August that the buds on the shoots defoliated immediately after cutting and two days later opened distinctly quicker than on those of the remaining treatments, in which opening was the slower the later leaves were removed. The data also indicate that the earlier defoliation was performed after

Table 1

Opening of terminal buds on detached shoots of *Populus* × *berolinensis*, on which leaves were removed at various dates after collection (in each treatment 20 shoots)

Date of shoot collection		No. of experimental treatments									
		1		2		3		4		5	
Year	Month and day	Leaves were removed								Shoots with leaves not removed	
		immediately		after 2 days		after 4 days		after 6 days			
		Beginning of bud opening									
		no. of shoots	mean no. of days	no. of shoots	mean no. of days	no. of shoots	mean no. of days	no. of shoots	mean no. of days	no. of shoots	mean no. of days
1965	July 19	9	5	19	8	2	4	4	8	1	6
	Aug. 9	18	6	18	10	15	12	7	18	5	17
	Aug. 31	18	9	18	10	13	20	10	22	6	27
	Sept. 22	2	15	0	∞	0	∞	0	∞	0	∞

Table 2

Evaluation of the statistical significance of the difference in bud opening on shoots of *Populus* × *berolinensis* on which leaves were removed at various dates after collection. Chi-square test

Experi- mental treat- ments	5	4	3	2
1	+	+	+	—
2	+	+	+	
3	+	—		
4	—			

+ differences significant

— differences not significant

cutting off of the shoots the greater was the number of shoots with opened buds. The data statistically elaborated by the chi-square test (table 2) showed no significant differences in the number of shoots on which buds opened between the following treatment pairs:

- (a) defoliated immediately and after 2 days,
- (b) defoliated after 4 and 6 days,
- (c) defoliated after 6 days and with intact leaves.

Experiments with partly leaves removal on the shoot

Shoots were cut off at four dates in the summers of 1962 and 1965, and subjected to the following treatments:

- 1) all leaves removed on the whole shoot,
- 2) half of the leaves removed (alternately every second leaf on the whole length of the shoot)*
- 3) half of the leaves removed (all in the upper part of the shoot),
- 4) half of the leaves removed (all in the lower part of the shoot),
- 5) leaves not removed.

Table 3

Opening of terminal buds on detached shoots of *Populus x berolinensis*, on which various leaves were removed (in 1962 each treatment comprised 10 shoots, in 1965 — 20)

Date of shoot collection and defoliation		No. of experimental treatments									
		1		2		3		4		5	
		All leaves removed	Half of the leaves removed						Shoots with leaves not removed		
			every second leaf	in upper part of the shoot		in lower part of the shoot					
Year	Month and day	Beginning of bud opening									
		no. of shoots	mean no. of days	no. of shoots	mean no. of days	no. of shoots	mean no. of days	no. of shoots	mean no. of days	no. of shoots	mean no. of days
1962	June 20	10	6	—	—	7	5	0	∞	3	5 *
	July 10	10	6	—	—	10	6	4	7	1	6
	July 30	10	7	—	—	4	14	2	7	4	12
	Sept. 4	0	∞	—	—	0	∞	6	18	2	32
1965	July 19	9	5	10	5	19	4	3	7	1	6
	Aug. 9	18	6	8	14	13	13	11	10	5	17
	Aug. 31	18	9	15	22	13	19	5	21	6	27
	Sept. 22	2	14	2	28	2	18	5	18	0	∞

The data on bud opening on these shoots (Table 3) indicate that the buds on shoots cut at various dates and subjected to various treatments opened after different time periods and on a different number of shoots. The data of the shoot number with buds opened were elaborated statisti-

* treatment applied only in 1965

cally by the chi-square test (Table 4). It was found that in both the years of the experiments there were significant differences in the number of shoots with buds opened between the combinations with complete defoliation or with upper part of shoot defoliated, and those in which the leaves were not removed or left on the upper part of the shoot. Comparison of the results for shoots with foliation reduced by one half in various ways proved that, notwithstanding which leaves were removed, always a significantly more intensive bud opening was obtained than on the shoots with intact leaves.

Table 4

Evaluation of the statistical significance of differences in bud opening on shoots of *Populus × berolinensis*, on which various leaves were removed. Chi-square test

Year of experiments	Experimental treatments	5	4	3	2
1962	1	+	+	+	X
1965		+	+	—	—
1962	2	X	X	X	
1965		+	—	—	
1962	3	+	+		
1965		+	+		
1962	4	—			
1965		+			

+ differences significant

— differences not significant

DISCUSSION

The experiments were made on shoots cut off from the tree, thus isolated from its influence. Theoretically the opening of buds on such shoots is dependent solely on:

- (1) the potential growth ability of the buds,
- (2) the influence exerted on the buds by the leaves on these shoots.

It can be assumed that the potential ability of growth of the bud within a given period is represented by the bud burst on the shoots on

which leaves were removed immediately after cutting off. Thus the difference in bud opening on defoliated and foliated shoots shows the extent of the influence of the leaves present on the given shoot.

Fig. 1. Opening of terminal buds on detached shoots of *Populus × berolinensis*, on which leaves were removed at various time periods after cutting.

1 — immediately, 2 — after two days, 3 — after four days, 4 — after six days, 5 — leaves not removed

The results indicate (Fig. 1) that in the period from June to August the buds had a high growth ability, which they lost in September. In this period the leaves left on the shoots, although they fell off already after 7—10 days, exerted a strong inhibitory influence which made bud opening impossible.

Formation of the abscission layer and falling off of leaves on the branches of *Populus × berolinensis* was observed only when the shoots were placed under bells in conditions of high air humidity (80—100%). Otherwise the leaves dried up and remained on the branches which showed a high tendency to dying back. The abscission layer did not form if the base of the leaves was immersed in water. The same phenomenon has been observed in the lemon (Livingston 1950).

Although it has been repeatedly observed that in many tree species a long photoperiod delays the falling off of leaves (Walter 1931; Matzke 1936; Olmsted 1951; Nitsch 1962), the date of leaf shedding on the cut twigs of *Populus × berolinensis*, irrespective of the day-length applied, was similar (Witkowska-Żuk 1969).

It has been recently reported (Heinicke 1968) that on cut apple-tree branches covered with polyethylene bags, a strong increase of

the activity of peridermis or cambium cells occurs owing to the change in the atmosphere in the bags (reduced oxygen content and increased CO_2 and ethylene concentration), depending on the degree of their permeability. Similarly, in *Populus* $\times$ *berolinensis* shoots placed under bells, a strong activity of the cells forming callus on all the injured fragments (ends of cut leaf petioles, surface of shoot cutting etc.) was observed. This leads to the supposition that in the examined *Populus* $\times$ *berolinensis* branches, the increase in the activity of the cells of the abscission layer and the consequent leaf fall might have been caused by the change of the atmosphere under the bells. Since, however, in the experiments with *Populus* $\times$ *berolinensis* the shoots with leaves and those defoliated were placed always under the same bell, and the reaction of buds on the foliated and defoliated plants was different, it would seem that the atmospheric changes had no direct influence on the bud reaction, influencing only the falling off of leaves.

Fig. 2. Opening of terminal buds on detached shoots of *Populus* $\times$ *berolinensis*, on which various leaves were removed.

1 — all leaves on the whole shoot, 2 — half of the leaves (alternately every second leaf), 3 — half of the leaves (all in the upper part of the shoot), 4 — half of the leaves (all in the lower part of the shoot), 5 — leaves not removed

Notwithstanding whether leaf shedding was connected with a change in the water balance conditions in the cut shoots (Addicot, Lynch 1955), or whether it was associated with the composition of the atmosphere under the bells, the presence of leaves on the shoots had a decisive influence on the bud development ability as long as the leaves remained on the shoots. This is confirmed by the results of observation of shoots on which leaves were removed at various dates after cutting off (Fig. 1). The longer the leaves remained on the shoots the less intensive was bud opening on them. It would thus seem that the factor inhibiting bud opening is translocated from the leaves to the buds. That translocation occurs under the given conditions between the third and fifth day after cutting off of the shoot, whereas after about five days an abscission layer probably forms which makes contact between the leaf and the bud impossible.

Two years experiments on the influence of various kinds of leaves on the terminal bud in shoots partly defoliated demonstrated that in July an inhibitory influence is mainly exerted by young leaves in the upper half of the shoot, whereas already in August leaves of any kind left on the shoot cause a considerable inhibition of bud development. Also reduction of the number of leaves always accelerated bud burst (Fig. 2).

The results of experiments, in which the shoots lost their leaves even under conditions of high humidity, and did not nevertheless exhibit bud opening, do not seem to confirm the view that the inhibitory role of leaves is associated with their strong transpiration causing a deficient water supply to the buds (Perk 1960). The observed translocation of the inhibitory factor from the leaves to the bud, and the seasonal changes in the influence of leaves on bud opening in the period of correlated inhibition seem to suggest that the leaf—bud relation is of hormonal nature in agreement with the results of observations of other authors (Champagnat 1951, 1965; Allary 1958; Eagles and Wareing 1963; Kefeli 1965).

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SUMMARY

The experiments were made with *Populus × berolinensis* Dipp. trees, from which shoots were cut successively and subjected to defoliation. The following experiments were made: 1) the leaves were removed at various dates after collection of the shoot and 2) various leaves were removed from the shoot.

The observations of the opening of terminal buds of long shoots seem to suggest that in the correlated inhibition phase of the poplar buds (July—August), the agent inhibiting bud opening was translocated from the leaves to the buds. In

July mainly young leaves in the upper half of the shoot, exerted an inhibitory influence whereas in August all leaves exhibited this ability.

The results described seem to suggest that the leaf—bud relation is of hormonal nature.

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

III. Rola liści w okresie spoczynku względnego

Streszczenie

Celem pracy było określenie wpływu liści na pączki w okresie spoczynku względnego. Obiektem badań były drzewa topoli berlińskiej, z których w kolejnych terminach odcinano pędy i poddawano je różnego typu defoliacji. Obserwowano rozwój pączków wierzchołkowych długopędów.

Przeprowadzono doświadczenia, w których:

- 1) usuwano liście po różnym czasie od ścięcia pędu, w celu stwierdzenia, czy następuje przemieszczanie z liści do pączków czynnika hamującego rozwój i kiedy,
- 2) usuwano różne liście na pędzie w celu stwierdzenia, jaki jest wpływ liści na pączki w zależności od położenia liści na pędzie.

Uzyskane wyniki nasuwają przypuszczenie, że w okresie spoczynku względnego pączków topoli berlińskiej (lipiec—sierpień), między trzecim a piątym dniem po ścięciu pędów z drzewa, z liści do pączków przemieszczał się czynnik hamujący ich rozwijanie. W lipcu hamujący wpływ wywierały głównie liście młode, znajdujące się w górnej połowie pędu, natomiast w sierpniu wszystkie liście miały zdolność hamowania rozwoju pączków. Zawsze jednak redukcja ulistnienia przyspieszała rozwój pączków.

Powyższe wyniki są podstawą do przypuszczenia, że zaobserwowane zależności między liśćmi i rozwojem pączków na pędach mają charakter reakcji hormonalnych.