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

V. Relation between the growth apexes on neighbouring shoots

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Many authors have investigated the possibility of photoperiodic induction of growth apexes dormancy in some parts of woody plants. In the case when dormancy was induced on the apex of plants, the axillary buds or lateral shoots treated with long day grew continuously (Van der Veen and Meijer 1959; Wodzicki 1961; Wodzicki and Witkowska 1961). Nevertheless the observations of growth of two-branch plants (Kawase 1961; Nitsch and Nitsch 1959) may indicate that some growth-inhibitory effect was transported from the branches under short day conditions to those treated with long day.

On the other hand, the data concerning the breaking of bud dormancy proved, that sprouting of one or several buds on the shoot did not affect the development of the other buds on the same twigs (Coville 1920; Molisch 1930; Takahashi 1963). In this connection it was suggested, that dormancy is localized in the buds only (Denny and Stanton 1928). However a few authors obtained transfer of break of winter dormancy of buds (Krasnosselskaya and Richter 1942) as well as advance of the rest influence from basal parts of shoots to the apical meristems (Chandler 1960).

In order to elucidate whether a relation exists between the growth apexes on the neighbouring shoots of the woody plant, and how it is manifested, experiments with *Populus* × *berolinensis*, a species with known bud dormancy (Witkowska-Żuk 1969, 1970; Witkowska-Żuk and Kapuściński 1969) were made in the period of setting in and emergence from dormancy.

Experiment 1

The material, one-year-old plants of *Populus* × *berolinensis* were obtained from cuttings set in clay pots in greenhouse in February 1969 *). When the plants had reached a height about of 5 cm, they were cut so as to induce the growth of two equivalent twigs. The short-day treatment was started on May 26-th.

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*) In 1962 an experiment was performed with the plants of *Populus* × *berolinensis* growing in water culture. The results were similar to those obtained in 1969.

The plants were subjected to the following treatments:

1 — long day on both shoots (LD — LD)

2 — short day on both shoots (SD — SD)

3 — different photoperiodic conditions (long day or short day) on each shoot (LD — SD).

The plants were selected so as to have a similar height of all shoots at the end of the short-day period. The plants under 20-hrs day received beside normal day-light additional illumination of about 4500 lux from a system of high-pressure mercury vapour lamps (5—11 p.m. and 3—8 a.m.). Those under 10-hrs day were placed for the night in dark chambers in the same greenhouse. The pots with plants, in which only one shoot was treated with short-day conditions, were wrapped in black crepe paper so that only the shoot under long day emerged.

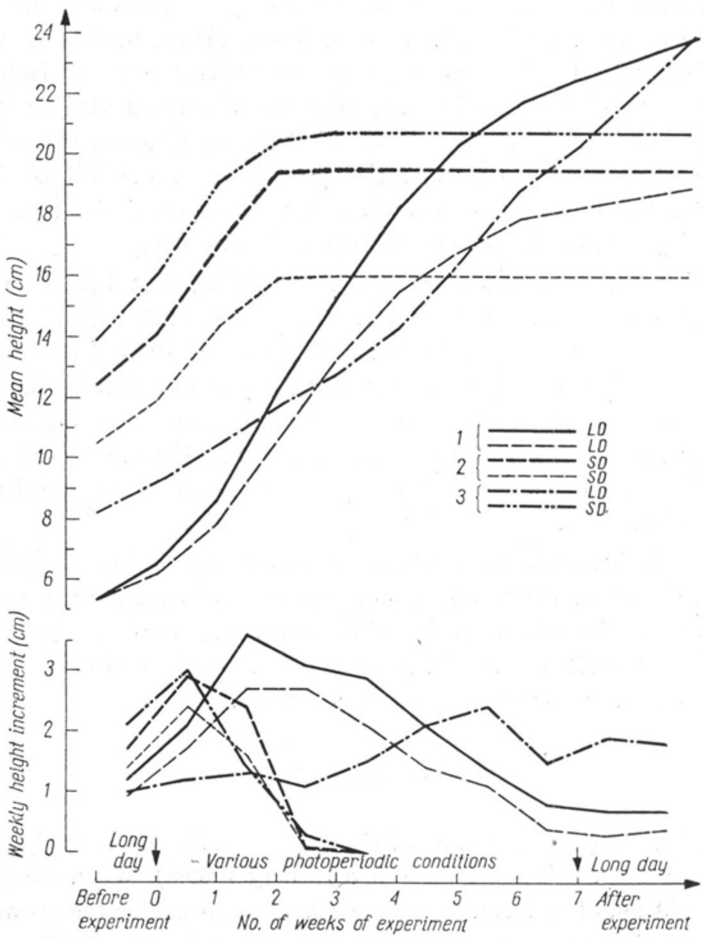

Fig. 1. Shoot growth of two-twig *Populus* × *berolinensis* plants in which shoots were kept under various photoperiodic conditions:

1 — long day on both shoots (means from 9 plants), *2* — short day on both shoots (means from 24 plants), *3* — different photoperiodic conditions on each shoot (means from 12 plants)

On the many experimental plants, in which the height of both shoots was different, the terminal bud was set on the lower shoot even under long day. These plants were excluded from the experiment and for final elaboration only those results were used, in which the shoots under long day showed continuous growth during a 7-week period of treatment. Taking into account the existant irregularity of growth of both shoots in one plant, the results were compared separately for the group of higher or lower shoots on the seedlings.

The observations comprised:

1) measurement of elongation growth at 7-day intervals
2) the date of terminal bud setting
3) the date of bud opening.

As seen from Fig. 1, the height of the shoots in the particular groups before the experiment was highly variable. In the treatment LD — LD the plants were smallest with minimal difference in the height of both shoots. In SD — SD treatment the plants were higher with a greater difference in shoot height. In LD — SD treatment the difference in shoot height was the greatest, but always the higher shoot was that treated with short day.

Table 1

Summed mean height (Σh) and weekly height increment (ΣΔh) of both shoots of plants in particular treatments (in cm)

No. of weeks of the experiment	Height (Σh) increment (ΣΔh)	Treatments: LD—LD long day on both shoots (means from 9 plants)	LD—SD different photoperiodic conditions on each shoot (means from 12 plants)	SD—SD short day on both shoots (means from 24 plants)
Before experiment	Σh	10.6±2.8 *)	22.1±4,5	22.9±3.8
	ΣΔh	2.1±0.6	3.1±0.8	3.1±0.5
0	Σh	12.7±2.9	25.2±4.8	26.0±4.1
	ΣΔh	3.8±1.0	4.2±0.8	5.3±0.6
5	Σh	37.1±4.1	37.1±4.9	—
	ΣΔh	2.5±1.2	2.4±0.6	
6	Σh	39.7±3.4	39.5±4.8	—
	ΣΔh	1.1±0.6	1.6±0.5	
7	Σh	40.8±5.1	41.0±4.9	—
	ΣΔh	1.0±0.5	1.9±0.7	
After experiment	Σh	41.8±4.7	42.9±5.2	—
	ΣΔh	1.1±0.6	1.8±0.7	

* error at $p = 0.95$.

The comparison of the weekly height increment before the experiment, when all plants were grown in LD conditions, showed that the longer was the plant shoot and higher the plant, the greater was their increment. The data combined in Table 1 confirm the existence of a dependence between the height increment and the length of the plant. After 2 weeks of SD-treatment the increment of growth decreased, irrespective whether the whole plant or one shoot of a plant was treated. After 3 weeks in all plants growth stopped and terminal buds set. The shoots which were in LD conditions grew continuously. In the LD — LD treatment the curves of height increment for both shoots were similar, however, the growth increment of the lower shoot was always less. The height increment of the LD shoot of the plants, in which the second shoot was SD treated, was at the beginning of the experiment much less than in LD—LD treatment. Nevertheless after 3 weeks of experiment the growth increment of shoots increased and after 4 weeks was equal with that of the LD — LD plants, and after 5 weeks it exceeded it a little.

When SD treatment was started, the height difference between both shoots of the plants of LD — SD treatment was 7 cm, and after 1 week of treatment it increased to about 9 cm. Nevertheless, the weekly height increment of the LD--treated shoots was not less than in the period, when both the shoots of the plant were in LD conditions, but the difference in their height at that time was less. When after 5 weeks of SD treatment the height and appearance of the plants in two treatments (LD — LD and LD — SD) was the same (Fig. 1, Table 1), the joint height increment of the plants was similar, irrespective if both shoots or one were growing. In the next weeks of experiment the height increment was larger in LD — SD treatment than LD — LD. In this connection it may be supposed that the original small height increment of the LD treated shoot in the LD — SD treatment was caused by a large difference in the height of both shoots on the plant at that time.

After 7 weeks of SD treatment all groups of plants were placed in long day conditions except the group from SD — SD treatment in which one shoot was LD treated and the other continued to be under SD.

No bud on the shoots of these plants began to grow in the following 70-day period. During this time the plants of the LD — LD treatment exhibited intermittent growth. The buds were set and then grew again. The behaviour of LD shoots of the plants of LD — SD treatment was similar. After this period one shoot of the plants previously treated with SD was placed in a warm water bath (30°C, 24 hrs). From among these 36 plants, only 5 opened buds (3 — from LD — SD and 2 — from SD — SD then one LD and one SD) and others were dormant.

Experiment 2

As plant material served 2—3-year-old twigs of *Populus × berolinensis* about 20—30 cm long, cut from trees growing in natural conditions. The detached twigs consisting in their upper part of a current year's long shoot (10—15 cm long) with a terminal bud on the apex, and a few axillary buds, and in their lower part, of one- or two-year-old short shoots (2—6 cm) each ending in a terminal bud. The twigs were treated with warm water bath and placed in beakers with water in laboratory conditions (air temperature suitable for growth, natural daylight).

Table 2

Bud opening on twigs of *Populus* × *berolinensis* treated with warm watern bath. Date of collection November 30, 1963. In each treatment 10 twigs. Data of bath-treated buds in bold type

Kind of warm water bath	Beginning of bud opening															
	on long shoots										on short shoots					
	terminal bud		first axillary bud under terminal bud		first axillary bud at base of long shoot		first of all the axillary buds with exception of buds under terminal bud and at the base of long shoot		more than 50% of all axillary buds		bud on short shoot near long shoot		first bud of any short shoot with exception of short shoot near long shoot		more than 50% of all short shoot buds	
	no. of twigs	mean no. of days	no. of twigs	mean no. of days	no. of twigs	mean no. of days	no. of twigs	mean no. of days	no. of twigs	mean no. of days	no. of twigs	mean no. of days	no. of twigs	mean no. of days	no. of twigs	mean no. of days
Whole twig immersed	**10**	**14**	**3**	**21**	**1**	**30**	**2**	**15**	**1**	**14**	**10**	**16**	**10**	**15**	**10**	**20**
Whole twigs treated except the surface of the shoot cutting	**10**	**15**	**1**	**37**	**3**	**22**	**6**	**25**	**3**	**25**	**6**	**17**	**10**	**18**	**7**	**20**
Only long shoot of twig treated	**10**	**15**	**1**	**42**	**4**	**26**	**9**	**21**	**3**	**27**	9	37	8	39	6	39
Only terminal bud of long shoot treated	**10**	**19**	9	39	2	43	9	40	6	41	9	41	10	39	9	42
Whole twig treated except terminal bud	10	31	**10**	**19**	**6**	**19**	**9**	**17**	**8**	**20**	**10**	**14**	**10**	**16**	**8**	**19**
Only lower part of twig (with short shoots) treated	10	39	3	41	3	40	4	40	2	42	**10**	**19**	**10**	**16**	**10**	**17**
Intact twigs (controls)	10	40	2	38	4	48	6	48	3	51	7	43	8	39	6	39

Table 3

Bud opening on detached twigs of *Populus* × *berolinensis* treated with warm water bath in 1961/62. In each treatment 10 twigs

Date of collection	Duration of bath, hrs	Treatments *)	Beginning of bud opening									
			terminal bud of long shoot		first of any axillary buds		more than 50% of all axillary buds		first of any short shoot buds		more than 50% of all short shoot buds	
			no. of twigs	mean no. of days	no. of twigs	mean no. of days	no. of twigs	mean no. of days	no. of twigs	mean no. of days	no. of twigs	mean no. of days
September, 29 1961	0	A	0	∞**)	0	∞	0	∞	0	∞	0	∞
	9	B	0	∞	0	∞	0	∞	0	∞	0	∞
		C	0	∞	0	∞	0	∞	2	37	0	∞
		D	1	15	0	∞	0	∞	7	16	2	21
	20	B	0	∞	0	∞	0	∞	0	∞	0	∞
		C	1	18	0	∞	0	∞	0	∞	0	∞
		D	10	12	5	14	4	14	9	13	9	14
October, 20 1961	0	A	0	∞	0	∞	0	∞	1	27	0	∞
	9	B	0	∞	0	∞	0	∞	0	∞	0	∞
		C	4	27	0	∞	0	∞	0	∞	0	∞
		D	1	13	4	15	0	∞	10	12	6	16
	20	B	2	18	0	∞	0	∞	0	∞	0	∞
		C	6	19	0	∞	0	∞	0	∞	0	∞
		D	10	14	5	20	2	29	8	14	7	19

November, 20, 1961	0	A	7	56	3	63	2	60	9	54	6	57
	9	B	8	29	0	∞	0	∞	3	47	0	∞
		C	10	17	0	∞	0	∞	0	∞	0	∞
		D	7	20	6	24	4	26	7	17	7	22
	20	B	9	24	0	∞	0	∞	5	47	3	47
		C	10	17	2	47	0	∞	3	47	2	47
		D	6	15	6	15	2	22	7	14	7	15
January 19, 1962	0	A	10	20	10	21	8	21	10	21	9	21
	9	B	10	14	6	23	5	21	10	21	8	24
		C	10	14	9	22	3	24	10	21	9	22
		D	10	14	5	23	4	19	10	12	9	12
	20	B	10	12	8	21	6	21	10	21	10	21
		C	10	11	8	30	5	28	10	21	7	21
		D	8	12	1	21	1	21	9	11	8	14
March 9, 1962	0	A	9	9	8	9	4	10	8	8	8	13
	9	B	10	9	9	11	9	14	10	10	9	12
		D	10	8	8	13	3	11	10	13	10	14
	20	B	10	8	9	14	8	12	9	8	8	12
		D	10	12	5	15	2	11	7	14	2	10

* A – intact twigs (control)
B – only the terminal bud of the long shoot treated
C – only the long shoot of the twig treated
D – whole twig treated

** no bud opened during 70 days after treatment.

The dates of opening of the buds were recorded at 2-day intervals.

a) Preliminary observations

The following questions were elucidated:

1) does the access of water to the vascular tissue across the surface of the shoot cutting induce bud opening?

2) is the velocity of bud opening dependent on the size of the twig part treated with water bath?

The twigs cut on November 30-th, 1963 were bathed (36—37°C, 9 hrs) in the following way:

1 — whole twigs,
2 — whole twigs except the surface of shoot cutting,
3 — only long shoot of twigs,
4 — only terminal bud of long shoot,
5 — whole twigs except the terminal bud,
6 — only lower part of twig (with short shoots).

The results of this experiment (Table 2) show that, since on the intact twigs the buds opened after 40 days, the water bath was used in the phase of emergence from rest. Only in two cases the opening of the buds on the twigs partly bathed differed from the development of buds on the intact twigs or those completely bathed, i.e.: 1) when only the terminal bud of the long shoot was bathed, its opening was less intensive as compared with those on the shoot bathed as a whole, 2) when the whole shoot with the exception of the terminal bud was bathed, the terminal bud opening was a little quicker than on the intact twigs.

b) Seasonal observations

In the autumn-winter season of the year 1961/62 observations were made of the reaction of buds of twigs partly treated with water bath.

The twigs were cut on successive dates and subjected to a warm water bath (34—35°C, 9 and 20 hrs). The water bath treatments were as follows:

1 — whole twigs,
2 — upper part of twigs (long shoot),
3 — only terminal bud.

The results of bud opening (Table 3) show, that in the period when buds on the control twigs did not open or opened very slow, the buds on the twigs bathed completely opened very quickly and numerously; when only one bud was treated — very slowly. On the detached twigs treated on successive dates, the terminal buds opening of long shoots was similar, independently of the size of the bathed part of the twig. Nevertheless in March bud opening on the twigs completely immersed decreased in comparison with bud opening on intact twigs. At all dates of the experiment the buds of short shoots on the part of twigs not subjected to bathing opened very similarly as on intact twigs.

DISCUSSION

The results of the experiment performed during the period of advance of photoperiodically induced dormancy of *Populus* × *berolinensis* showed, that the short-day treatment induced bud setting on one shoot of the two-twig plant, the other shoot of which grew continuously. Bud setting on these shoots occurred after a similar time period of SD treatment as on the shoots of plants exposed as a whole to SD. It has been shown previously, that dormancy may be induced on the terminal shoot apex, the growth of lateral shoots being continued in *Populus* (Van der Veen and Meijer 1959), *Larix polonica* (Wodzicki 1961) and *Picea abies* (Wodzicki and Witkowska 1961). In this case the dormancy induced on the shoot apex caused cessation of apical dominance. The relation between apical dominance, correlated inhibition and rest has been discussed repeatedly (Libbert 1961 a, b; Champagnat 1965). The previous data (Witkowska-Żuk and Kapuściński 1969) on the advance of rest in buds of *Populus* × *berolinensis* trees growing in natural conditions showed a dependence of bud setting from apical dominance and correlative inhibition. It was also concluded that the following advance of rest from the basal to the apical part of the tree, is dependent from the duration of the correlated inhibition phase.

In the present experiments plants weie used with two equivalent shoots or plants in which the growing shoot was smaller than the dormant one, in order to exclude the influence of apical dominance. It was found, that only in the initial period, when the LD-shoot was smaller than the SD-shoot, did the LD-treated shoots in plants each shoot of which was in different photoperiodic conditions exhibit a smaller increment than those on plants whole-treated with LD. When the difference of height between both shoots was smaller and the appearance of plants in both treatments was equal, the height increment of the LD-treated shoot in LD — SD treatments was the same as the sum of the height increment of both shoots in LD — LD treatment, and in the following period it was even larger.

In this connection we may suppose that the presence of a dormant shoot on the plant did not affect the growth of the neighbouring shoot. These observations on *Populus* × *berolinensis* did not confirm the results of the experiment with *Weigelia* (Nitsch and Nitsch 1959) and *Betula* (Kawase 1961).

The state of dormancy induced by SD was similar in the buds of plants whole-treated with SD and in those plants, in which the other shoot was LD treated. After 7 weeks of SD-treatment the buds were in the middle phase of rest, since long day or a warm water bath did not break the dormancy of buds in them (Witkowska-Żuk 1970).

The results of experiment on the breaking of bud dormancy at various times of the rest- and quiescence-phase performed on cut twigs of *Populus* × *berolinensis*, demonstrated a local influence of warm water bath and no sign of transmission of the promoting effect. These results are in accordance with reports of other authors, who localized the dormancy in the bud (Molisch 1909, 1930; Coville 1920; Denny and Stanton 1928; Takahashi 1963) and did not confirm the observations on *Populus suaveolens* and *Fraxinus* sp. (Krasnosselskaya and Richter 1942) which seemed to suggest the transport of break of winter dormancy along branches after a water bath.

In the experiment concerning the effect of a water bath on bud opening in *Populus × berolinensis*, the observations were ended after bud opening. The growth of shoots growing from these buds was not measured (because after sometime the cut twigs died in water culture). In view of this it is not known if the dormant part of the shoot induced an inhibitory effect on the shoots growing from these buds. In a few cases (September 29, November 20, 1961 and November 19, 1963), however, less intensive bud opening was observed, if only one bud was bathed, than when the whole shoot was treated. It is not excluded, that this effect was the result of imperfect technic of the water bath. Nevertheless there are reports, in which the weaker shoot developement was observed if the shoot was grown from a chilled bud on unchilled shoots. The explanation of this phenomenon was a lack of water supply and necessary nutrient substances by the unchilled, basal part of the shoot to the buds, which had emerged from the phase of rest (Nesterov 1956, 1960). Eventually this fact may be interpreted as an advancing inhibitory influence of rest through tissue between the buds (Chandler 1960).

In connection with the results of our experiments we can suppose, that as regards the process of advance and of emergence from rest of *Populus × berolinensis* there is a lack of relation between the particular shoot growth apexes.

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SUMMARY

The relations between growth apexes on neighbouring shoots of two-branched one-year-old *Populus × berolinensis* plants grown in greenhouse was investigated during advance of rest. The dormancy was induced photoperiodically. The experimental treatments were:

1 — long day on both shoots of the plant

2 — short day on both shoots of the plant

3 — different photoperiodic conditions (long or short day) on each shoot.

The relations between the particular buds on the cut twigs of *Populus × berolinensis* trees growing in natural conditions was investigated in the process of emergence from rest. Various parts of the detached twigs were treated with a warm water bath.

The results of the experiments seem to suggest a lack of relation between particular shoot growth apexes during advance of rest and emergence from it.

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

V. Związek między wierzchołkami wzrostu na sąsiednich pędach

Streszczenie

W okresie następowania spoczynku głębokiego pączków badano związek między wierzchołkami wzrostu sąsiednich pędów. W tym celu u hodowanych w szklarni dwu-pędowych sadzonek topoli berlińskiej indukowano spoczynek, stosując warunki krótkiego dnia. Rośliny poddawano następującym działaniom:

1 — warunki długiego dnia na obydwa pędy rośliny,
2 — warunki krótkiego dnia na obydwa pędy rośliny,
3 — każdy z pędów rośliny w różnych warunkach fotoperiodycznych (długiego lub krótkiego dnia).

Zależności w rozwoju pączków w czasie przerywania spoczynku badano używając odcięte gałązki topoli berlińskiej z drzew rosnących w warunkach naturalnych. W celu przerwania spoczynku pączków stosowano ciepłą kąpiel wodną na różne części gałązek. Po doświadczeniu wstępnym przeprowadzono doświadczenie sezonowe podczas fazy spoczynku głębokiego i narzuconego pączków.

Wyniki doświadczeń sugerowały brak związku między poszczególnymi wierzchołkami wzrostu podczas procesu następowania i przerywania spoczynku u topoli berlińskiej.