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Photo- and thermoperiodic responses of different larch provenances (*Larix decidua* Mill.)

Foto- och termoperiodiska reaktioner hos olika lärkprovenienser (Larix decidua Mill.)

by

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ABSTRACT

The present investigation was undertaken in order to study the formation of the terminal buds, top shoot maturation, bud break and flushing as well as the amount of growth of the top shoot under different photo- and thermoperiodic conditions, in three larch provenances (*Larix decidua* Mill.). Two-year-old plants were tested under long- (LD = 16 h) and short-day (SD = 8 h) conditions and under various temperature combinations. The experiment went on for 59 weeks in a phytotron. The plants' growth activities were greatest under LD conditions. SD conditions were necessary for the plants to complete their vegetative growth. For bud formation and lignification of the leading shoot, relatively high temperatures were required under SD conditions. Under low temperatures, bud formation was incomplete and the leading shoot remained unlignified. The investigation showed that there is an interaction between photo- and thermo-period which determines the plants' vegetative cycle. In comparison with the climate of the place of origin of the larch, in northern Scandinavia the days are longer and the temperatures lower in the autumn. This is the reason why the introduced larch hardens poorly and too late, which in its turn makes it sensitive to early frosts.

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1. Introduction

Trees in autochthonous populations have their annual biological cycle adapted to the environment as a result of long-continued natural selection. In such populations only those individuals prosper, which are suited to the habitat. Consequently, the successful adaptation of an introduced species to a new habitat will depend upon its genetically controlled reactions to the new environment. The response of populations of different origin can be directly studied in provenance trials in the field or in laboratory experiments (e.g. in a phytotron). These two test methods are complementary. In many cases the observations made by the one method, must be checked with the other, before any correct and definite interpretation of the results can be given.

The present investigation* was undertaken in the phytotron at Stockholm in order to study the formation of the terminal buds, top shoot maturation, bud break and flushing as well as the amount of growth of the top shoot under different photo- and thermoperiodic conditions, in three larch provenances (*Larix decidua* Mill.).

The photoperiodism in different provenances of larch has been less investigated. Some of the photoperiodic studies carried out on various larch species are mentioned below.

Larix decidua: Wareing (1949); Zelawski (1954, 1956, 1957, 1960); Molski & Zelawski (1958); Leibundgut (1962); Kantor & Simancik (1966);
Larix sibirica: Bogdanov (1931); Moshkov (1932); Vaartaja (1954); Dafis (1962); Leibundgut (1962); Nagata (1966);
Larix dahurica: Bogdanov (1931);
Larix czekanowski: Bogdanov (1931);
Larix leptolepis: Downs (1962); Nagata (1966);
Larix laricina: Vaartaja (1957); Balatinecz & Farrar (1968);
Larix occidentalis: Downs (1962).

*) A preliminary mimeographed report of a part of this investigation (periods I—III) was distributed in 1967, entitled: Photo- and thermoperiodic responses of different larch provenances (*Larix decidua* Mill.).

2. Material and methods

The three autochthonous provenances of larch used in this experiment represent ecologically very different types. Blizyn is a hilly type from Poland, Ipoltica is a mountain larch from the Slovakian part of the Carpathians and Pragelato originates from the Western Alps in Italy. The distance between Blizyn and Pragelato is considerable; latitudinally they are six degrees apart, and vertically about 1600 m. Provenance Ipoltica is situated nearer Blizyn (Table 1).

The plants were grown in a nursery in Sundmo (lat. 63°30′ N, long. 16°41′ E, alt. 190 m). In autumn 1965 at the age of 2/0 years they were lifted after the vegetative growth had ceased, transported to Stockholm and stored in the open under snow. At the end of November they were individually planted in pots in a mixture of perlite, sand and gravel (1:1:2) and transferred to the phytotron of the Royal College of Forestry. From 29 November 1965 to 24 January 1966, the plants were kept in the phytotron under the following conditions (the term "Day" in the text denotes the light period and the term "Night" the dark period):

In the constant room of the phytotron:

16 days: Night 24 h, 5°C (for last 4 days weak artificial light).

Thereafter in the greenhouse of the phytotron:

7 days: Day 16 h, 15°C + Night: 8 h, 15°C.

33 days: Day 16 h, 20°C + Night: 8 h, 15°C.

At the end of these periods of adaptation (24 January 66) the buds on the plants had swollen so much, that it was possible to select individuals with good vigour (46 plants per provenance). The experiment was started on 24 January 1966 when the plants were transferred to the phytotron chambers. There were four series (A—D) for the photo- and thermoperiods and five periods for the time of treatment (I—V). The plan of the experiment is given in Plate I.

Table 1. Description of material.

Provenance No.	Locality	Latitude	Longitude	Altitude	Geog. region
707	Pragelato	44°57′	6°58′	1900 m	W. Alps
303	Ipoltica	49°00′	20°00′	800 m	Slovakia
102	Blizyn	50°50′	20°40′	330 m	Poland

Number of plants per provenance: In period I where the photo-termo conditions were the same in all the four series, 46 plants were tested. In period II: 9 plants/series; in period III: 7 plants/series; in period IV: 6 plants/series and in period V: 3+3 plants/series (see p. 18). The decreasing number of plants in later periods is due to the distribution of plants in four series and to the fact that some plants were used for various other studies (e.g. for wood anatomy).

Light: "Gro Lux" fluorescent tubes giving about 20,000 lux at the level of plants were used in the chambers.

Nutrition: From 20 December each plant was given modified Hoagland nutrient solution (cf. Went, 1957) twice a week.

Humidity: 75 per cent relative humidity of air.

The other conditions in the phytotron as also the working system are described by Gustafsson (1965) and von Wettstein (1967).

Measurements and observations: The height of plants was measured weekly. During the intensive growth period, it was not possible to determine the exact position of the growing point, because it was tightly covered by needles. The measurements were therefore made from the level of the pot rim to the needle-tips of the terminal shoot. This method of measurement gives constantly a slightly higher value (about 1 cm) than is really the case, but has the advantage that it is uniform, reproducible and does not damage the plants.

At each measurement the phenological stage of the plant was also noted. The different symbols used in this connection are explained in Plate II. At the end of the first and the second periods in each series one plant was taken for anatomical studies of wood development. The material was fixed in a mixture of glycerine and absolute ethyl alcohol (2:1), sectioned with a freezing microtome and stained in phloroglucine + 9 per cent HCl. The plants were photographed at different times, usually at the end of each period.

3. Results

The results are described separately for each period.

3.1. Period I (9 weeks, cf. Plate I)

LD-series A, B, C, D: Day: 16 h, 20°C+Night: 8 h, 15°C

During these two months the plants in all four series were kept under the same conditions as in the previous adaptation period (33 days).

This photoperiod of long day had a different effect on the rate of growth in each of the three provenances. In provenance Pragelato the individual plants reacted variably; 28 out of 46 formed terminal buds and ceased to grow completely or for a short time (Fig. 1). In provenances Ipoltica and Blizyn most of the plants grew continuously throughout this period.

The average increment in height calculated for all 46 plants in each provenance would not give a true picture because of the irregular rate of growth in some plants chiefly in provenance Pragelato. For this reason, the average values for the height increment of continuously growing plants (↑) only are given in Table 2. The results show that the greatest increment is in provenance Pragelato and that this value significantly differs from those of the other two provenances.

Table 2. Rate of growth and increase in height of plants during period I.

Provenance	n	Rate of growth[a]				Average height increment for ↑ plants, cm	Average weekly increment, cm
		↑	⫯	⫯×	⫯××		
Pragelato	46	18	19	8	1	33.6±1.158	3.7
Ipoltica	46	41	3	2	—	29.8±0.781	3.3
Blizyn	46	44	1	1	—	30.7±0.754	3.4

a For explanations of symbols, see Plate II.

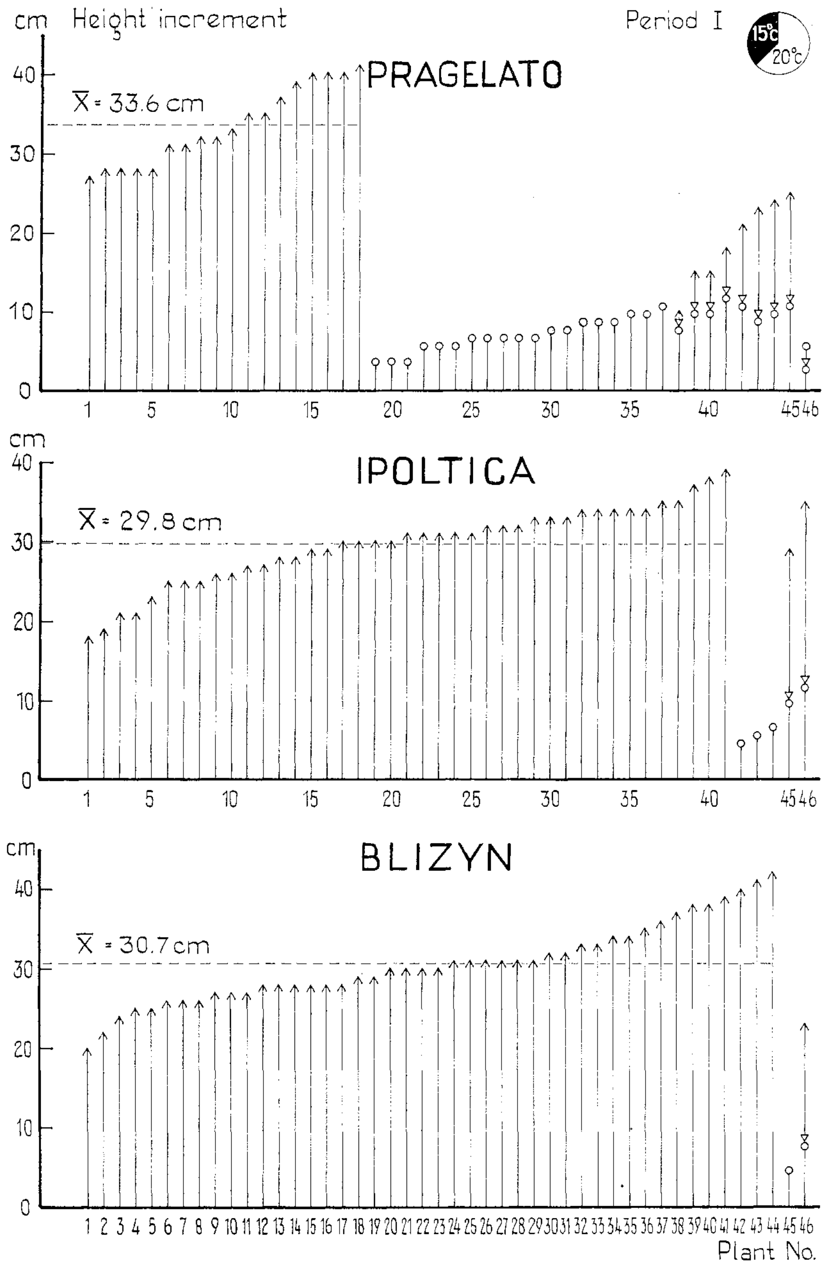


Fig. 1. Height increment during period I. For explanation of the symbols see Plate I and II.

3.2. Period II (13 weeks, cf. Plate I)

LD-Series A: Day: 16 h, 20°C + Night: 8 h, 15°C
» B: Day: 16 h, 20°C + Night: 8 h, 10°C
SD-Series C: Day: 8 h, 20°C + Night: 16 h, 15°C
» D: Day: 8 h, 20°C + Night: 16 h, 10°C

The plants tested in period II were distributed into four series (A—D) in each provenance: two in long day (A and B), and two in short day (C and D). As in long day (LD) so also in short day (SD), one series each (A and C respectively) had the same day and night temperatures as in period I. In the other two series (B and D respectively), the night temperature was lowered from 15°C to 10°C. Consequently, in series A of period II the same conditions as in period I were present. The number of individuals in each series in period II was reduced to 9 (cf. Fig. 2).

LD-series: Growth of the plants of provenance Pragelato was often interrupted by the sudden formation of a terminal bud. The average increment in height during period II in LD has been calculated only for plants having continuous growth (↑). Such individuals were available in sufficient number in

Table 3. Increase in height, rate of growth and degree of maturity of plants during period II (cf. Fig. 2). Number of plants in all series = 9.

		Average height increment in cm for ↑		Rate of growth[a]					Degree of maturity[b]				
Provenance	Ser.	Total	Per week	↑	↑○	↑↓	○|	○¦	1	2	3	4	5
Pragelato	A		—	2	—	3	—	4	9	—	—	—	—
	B		—	5	1	2	1	—	9	—	—	—	—
	C	—	—	—	—	—	3	6	—	—	2	3	4
	D	—	—	—	—	—	3	6	—	2	2	4	1
Ipoltica	A	39.6 ± 2.51	3.0	7	—	—	—	2	9	—	—	—	—
	B	41.8 ± 2.22	3.2	9	—	—	—	—	9	—	—	—	—
	C	—	—	—	—	—	—	9	—	3	4	—	2
	D	—	—	—	—	—	—	9	—	2	6	1	—
Blizyn	A	39.2 ± 2.56	3.0	9	—	—	—	—	9	—	—	—	—
	B	42.7 ± 2.45	3.3	9	—	—	—	—	9	—	—	—	—
	C	—	—	—	—	—	—	9	—	5	2	—	2
	D	—	—	—	—	—	—	9	—	5	3	1	—

a For explanation of symbols, see Plate II.
b Degree of maturity (increasing from 1 to 5):
1 = The whole plant is green.
2 = More than 50 % needles of the plant are green, the rest are yellow or have been shed.
3 = More than 50 % needles are yellow. The top portion of plant is always green.
4 = All needles are yellow and have partly been shed.
5 = More than 75 % of the needles have been shed.
2—5 = No growth activity.

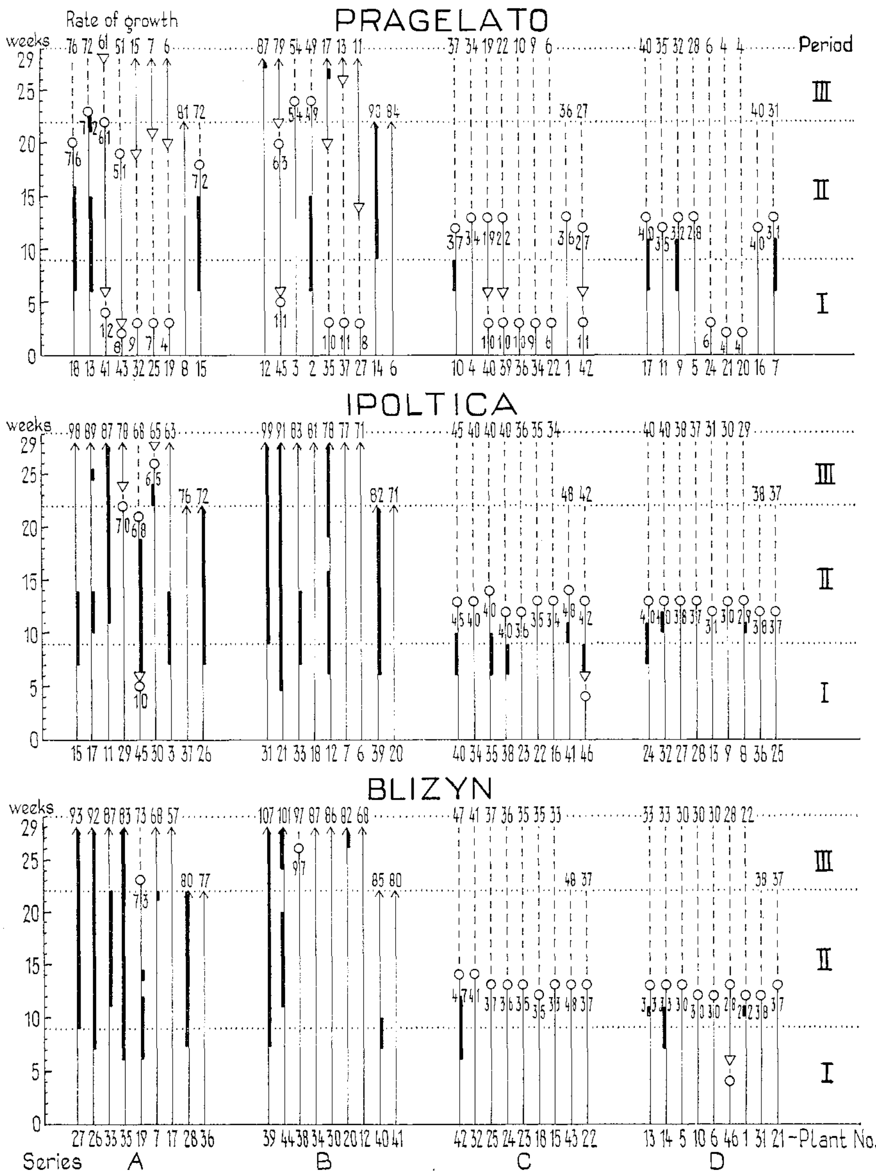


Fig. 2. Rate of growth during periods I, II and III. In each provenance 9 plants per series (A, B, C, D) were tested in the first two periods, and 7 plants in the third period. Each vertical line represents the growth history of a single plant. The plant numbers correspond with those in Fig. 1. The numbers beside the vertical line denote the height of plants in cm at the stage of growth marked by symbols just above them. The height increment during the three periods is represented by numbers at the top of vertical lines.

The reason why some plants do not show any height increment despite their growth activity as denoted in the figure, lies in the method of measurement. For instance, in plant 25 Pragelato, the terminal bud has sprouted, but the new needles are still shorter than the older ones, in relation to which the height increment was measured.

For explanation of the symbols see Plate II.

provenances Ipoltica and Blizyn. The increment in height for both provenances was nearly the same, but plants in series at lower temperature (B) showed greater increment than those at the higher temperature (A). However, the difference was not significant.

SD-series: Under SD, the plants in the three provenances stopped growing after 4 weeks, formed terminal buds, the needles turned yellow and fell (Table 3 and Fig. 4). The plants of provenance Pragelato reached the final degree of maturity earlier than those of provenances Ipoltica and Blizyn. The maturing of plants seems to have proceeded more slowly at lower temperatures (series D) than at higher ones.

3.3. Period III (7 weeks, cf. Plate I)

LD-Series A: Day: 16 h, 20°C + Night: 8 h, 15°C
» B: Day: 16 h, 15°C + Night: 8 h, 5°C
SD-Series C: Day: 8 h, 20°C + Night: 16 h, 15°C
» D: Day: 8 h, 15°C + Night: 16 h, 5°C

In period III series A and C were kept under the same conditions as in the previous period. The only change was in series B and D, where the day temperature was lowered from 20°C to 15°C, and the night temperature from 10°C to 5°C. The number of individuals in each series in period III was reduced to seven (Fig. 2).

Table 4. Increase in height, rate of growth and degree of maturity of plants during period III (cf. Fig. 2). Number of plants in all series = 7.

		Average height increment in cm for ↑		Rate of growth[a]				Degree of maturity[b]				
Provenance	Ser.	Total	Per week	↑	↕	⫯	⫯	1	2	3	4	5
Pragelato	A	—	—	3	1	2	1	7	—	—	—	—
	B	—	—	3 + 1[c]	1	—	2	7	—	—	—	—
	C	—	—	—	—	7	—	—	—	—	—	7
	D	—	—	—	—	7	—	—	—	—	—	7
Ipoltica	A	(15.8)	(2.6)	4	2	1	—	7	—	—	—	—
	B	12.1 ± 0.74	2.0	7	—	—	—	7	—	—	—	—
	C	—	—	—	—	7	—	—	2	3	—	2
	D	—	—	—	—	7	—	—	2	4	—	1
Blizyn	A	11.5 ± 2.07	1.9	6	—	—	1	7	—	—	—	—
	B	13.0 ± 1.63	2.2	6	—	—	1	7	—	—	—	—
	C	—	—	—	—	7	—	—	2	2	—	3
	D	—	—	—	—	7	—	—	3	3	—	1

a For explanations of symbols, see Plate II.
b Cf. Table 3.
c A lateral branch grew beyond the terminal shoot.

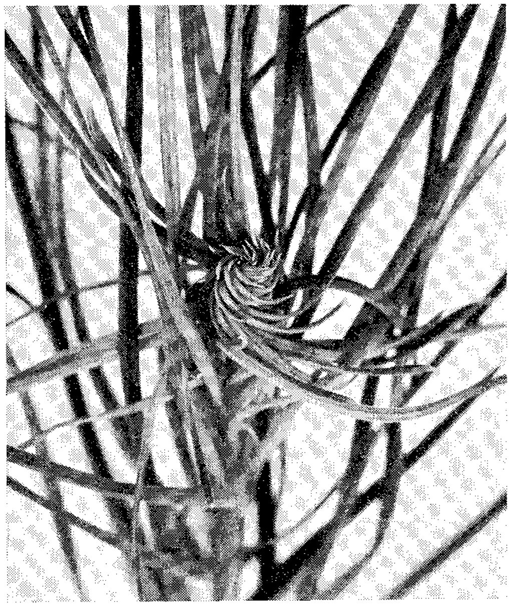


Fig. 3.
Spiral arrangement of needles formed during the intensive growth of terminal shoots. Left whorl. It is of interest to mention that the direction of whorling of the needles on a therminal shoot of a particular plant was always the same during the entire experiment.

LD-series: A similar rate of growth and degree of maturity as for period II were also observed in period III. However, there were slight differences. The weekly increase in growth in LD of period III was considerably lower than in period II (cf. Tables 3 and 4).

SD-series: In SD the clearest differences among the provenances were to be found in the degree of maturity. In provenance Pragelato at the end of period III, all plants had lost their needles (degree 5), but in provenances Ipoltica and Blizyn, many of them still possessed green needles (Fig. 4).

At the end of period III, the number of lateral shoots on that portion of the terminal shoot only, which grew during the periods I—III under LD conditions (in series A and B) was counted. Table 5 shows that the plants in provenances Ipoltica and Blizyn produce distinctly more lateral shoots than provenance Pragelato. This applies to both series. The values in series B for Pragelato and Blizyn are slightly higher than those in series A and significantly higher in provenance Ipoltica.

The anatomy of wood development was, in principle, the same for periods II and III. Only the results for period III are, therefore, summarised as follows:

a) Plants growing during the whole of the experiment in LD produced early wood only (Fig. 5, plant 102-27).

Table 5. Number of lateral shoots growing during periods I—III.

Provenance	Series A			Series B		
	No. of plants		Number of lateral shoots per plant	No. of plants		Number of lateral shoots per plant
	Total	With shoots		Total	With shoots	
Pragelato	7	2	0.3 ± 0.184	7	2	0.9 ± 0.705
Ipoltica	7	7	18.4 ± 4.603	7	6	31.1 ± 6.735
Blizyn	7	6	19.4 ± 3.754	7	7	20.1 ± 6.147

b) Plants which stopped growing in SD, formed a thin layer of more or less typical late wood (Fig. 5, plant 303-16). In Pragelato the late wood was less differentiated from early wood than in Ipoltica and Blizyn (Fig. 5, plant 707-40).

c) The interruption and renewal of growth in LD was not accompanied by changes in wood anatomy. The exception was plant 29 (Ipoltica) which formed a thin layer of cells with thickened walls on about one-quarter of the circumference of the stem. This may possibly be correlated with its interrupted growth in period III (Fig. 5, plant 303-29).

3.4. Period IV (18 weeks, cf. Plate I)

SD-Series A: Day: 8 h, 20°C + Night: 16 h, 15°C
» B: Day: 8 h, 15°C + Night: 16 h, 5°C
LD-Series C: Day: 16 h, 20°C + Night: 8 h, 15°C
» D: Day: 16 h, 15°C + Night: 8 h, 5°C

In this period, the LD from period III was changed to SD and *vice versa.* The temperature in all the series remained the same as before.

LD-series: The plants in series C and D which were kept under SD during periods II and III, were exposed to LD in period IV. Two weeks after this treatment, the buds began to develop leaves; the provenances Blizyn and Ipoltica more strongly than the provenance Pragelato. This was the case in both series C and D, but in series D, this process was faster and more uniform among the plants within a provenance than in series C. In Fig. 6 the development of each plant and provenance is shown schematically after six weeks' treatment in period IV.

After about ten to eleven weeks in this period the plants in all provenances began to put out new terminal shoots. Even plants in provenance Pragelato,

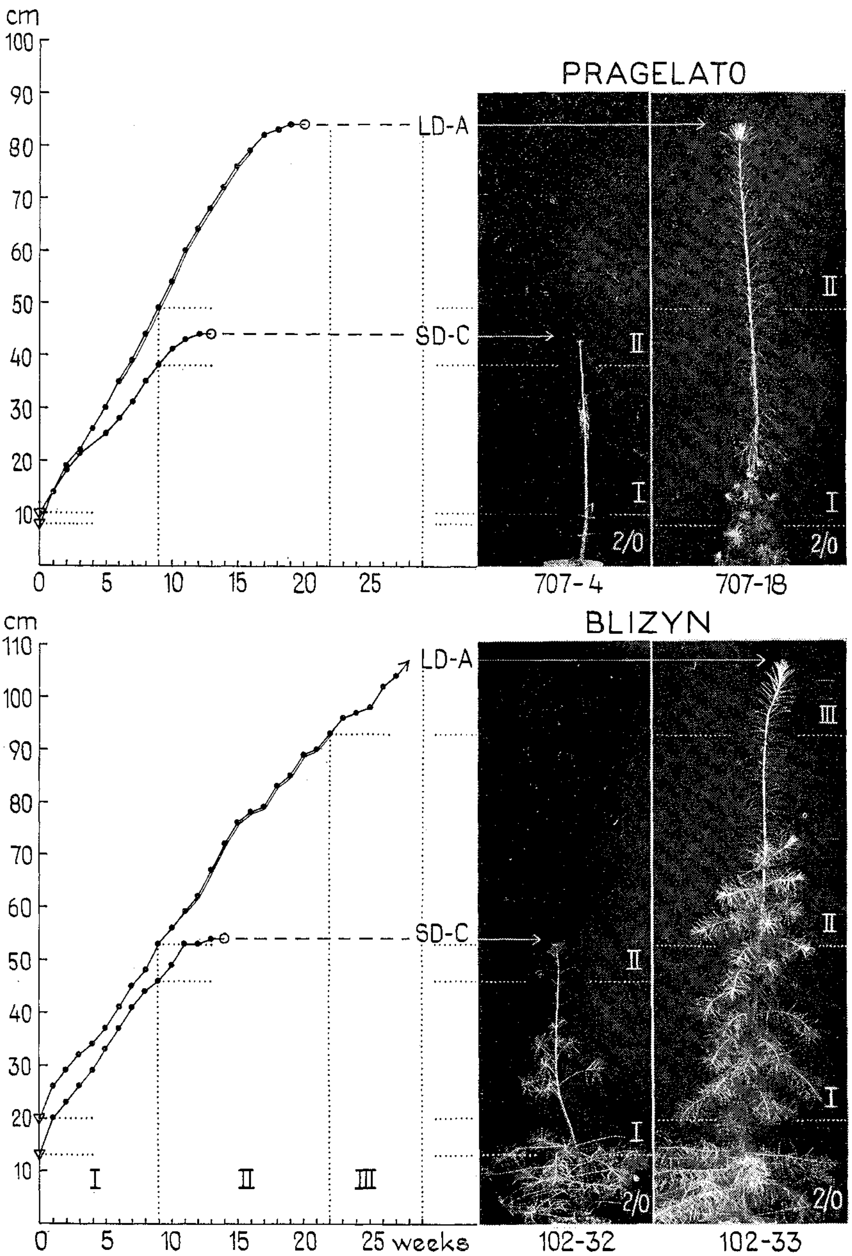


Fig. 4. Rate of plant growth during periods I—III in provenances Pragelato and Blizyn in LD and SD conditions (series A and C respectively). The double lines in the curves denote the time in which the whorls were observed on the top shoots. There are only dead needles hanging on the plant No. 707-04. The height of the 2/0 plants is also included in the total height of the plants.
For explanation of the symbols see Plate II.

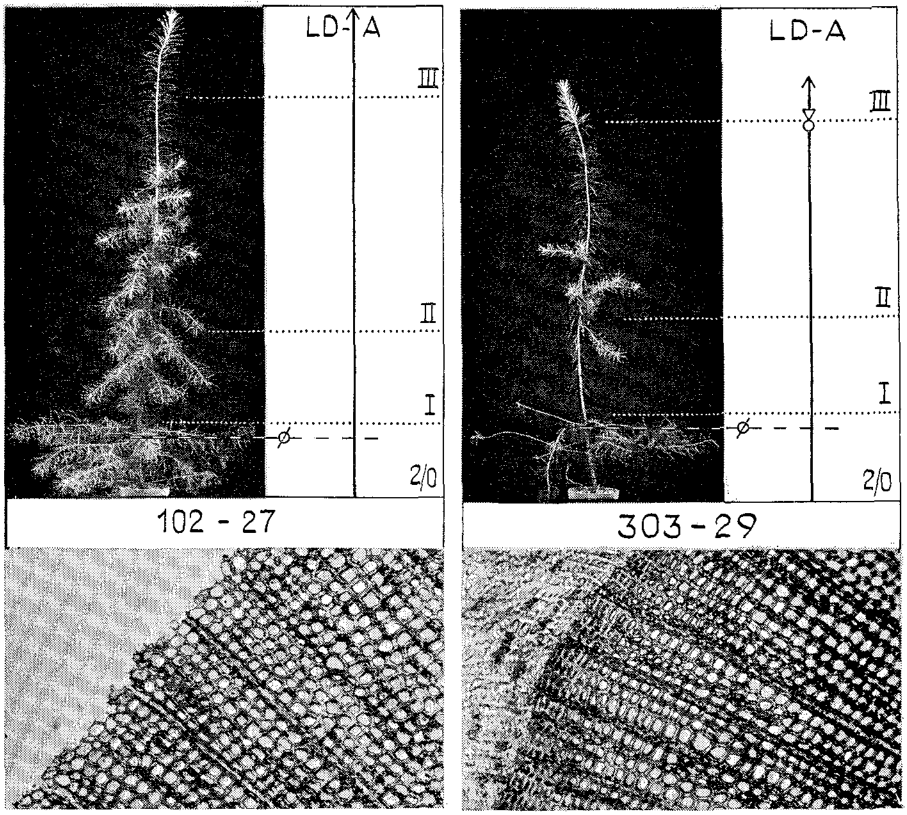


Fig. 5. Wood anatomy of plants growing under LD and SD conditions. Sections were cut 3 cm below the position in which the terminal bud was at the beginning of the experiment (Ø). The plant numbers correspond with those in Fig. 1 and 2.
LD-Blizyn-27: Only early wood was formed throughout the experiment.
LD-Ipoltica-29: 4—5 layers of late wood in the outermost xylem were formed in a fourth of the circumference of the stem.

which during period I (LD) had stopped growth activity and formed terminal buds (cf. plants No. 34, 36, 20, 21, 24 in Fig. 2) shot up. An exception was Pragelato plant No. 22, which had shown height growth only during the first four weeks in period I. Since this time, the terminal bud had been resting (cf. Fig. 2).

After 18 weeks' treatment in period IV, the plants of provenance Blizyn showed the highest and those of provenance Pragelato the lowest average height increment. This relationship is valid both for series C and D (Fig. 6). However, in series D, the increment was much lower than in series C. Increment per week was distinctly lower in period IV than in period I in all the provenances and in both of the series. However, different numbers of plants were compared in period I and IV.

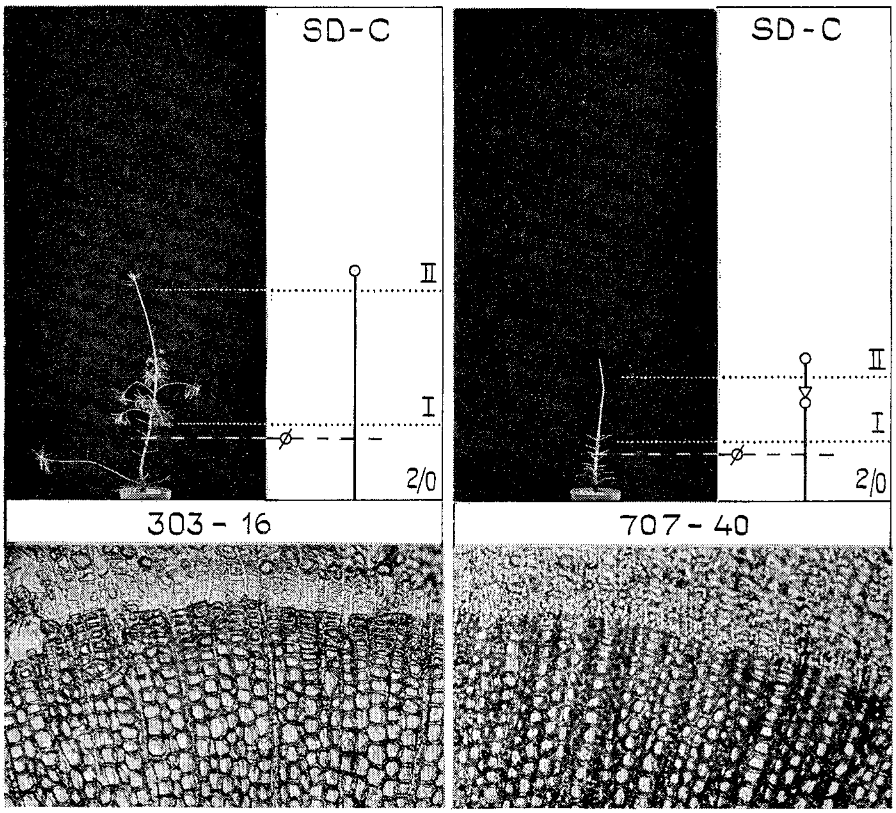
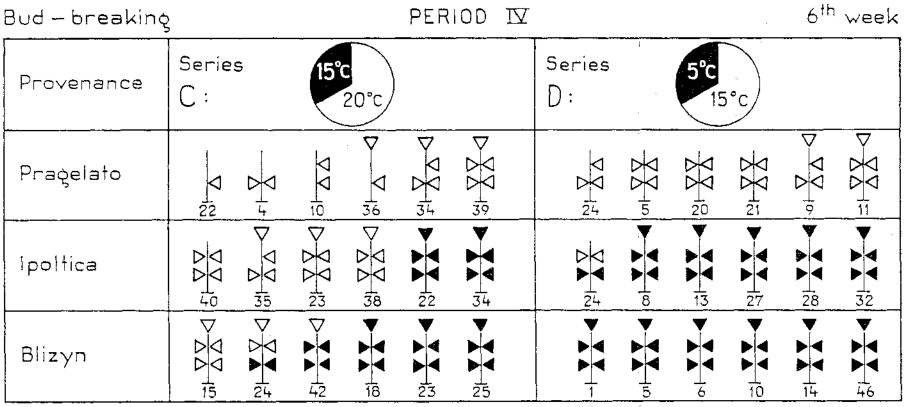


Fig. 5. (*Continued*).
SD-Ipoltica-16: 4—5 outermost layers of xylem were formed of late wood.
SD-Pragelato-40: The outermost layer in xylem had cells with narrower lumen but not thicker walls than those in the early wood.
For explanation of the symbols see Plate II.

SD-series: The maturing of the plants in series A and B under SD conditions was visible very soon. Four weeks after being transferred to period IV, the plants in all the provenances had more or less ceased vegetative growth. An evident cessation of growth activity was particularly observed in plants of series A, where all the plants began to form terminal buds, if they had not already done so in the earlier periods, as, for instance, Pragelato plants No. 13, 18, 43 (cf. Fig. 7 and 2).

After eight weeks in SD the maturation processes (yellowing and shedding of needles) had proceeded much further in plants of series A than in those of series B.

After fourteen weeks under SD conditions the plants of all the provenances in series A showed lignified top shoots and more or less well-differ-



Average height increment in cm for ↑ plants — 18th week

Provenance	Series C:	Series D:
Pragelato	18.2 ± 5.40	7.8 ± 2.10
Ipoltica	20.7 ± 2.92	15.1 ± 1.64
Blizyn	22.7 ± 2.54	17.7 ± 2.38

Fig. 6. The development of the plants after 6 and 18 weeks LD-treatment in period IV. For explanation of symbols see Plate II.

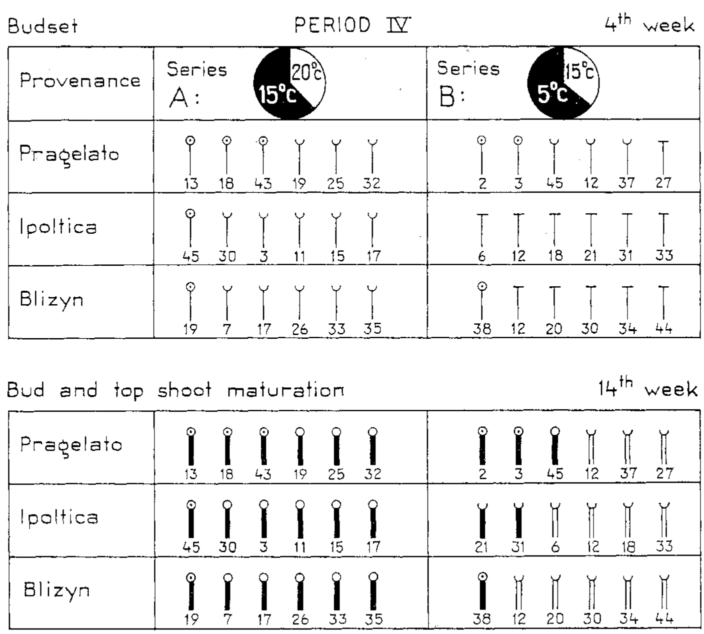


Fig. 7. The maturation of the plants after 4 and 14 weeks SD-treatment in period IV. For explanation of symbols see Plate II.

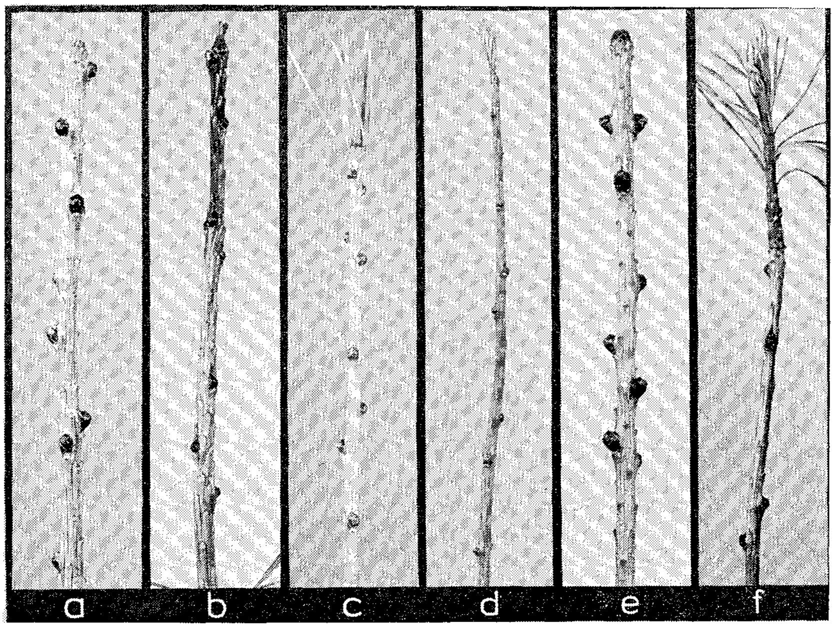


Fig. 8. The maturation of top shoot and bud formation at the end of period IV under SD conditions. a—c: Provenance Pragelato, a: at temperature of 20—15° C, bud initiation and formation already in period III, plant No. 43, b: at temperature of 15—5° C, plant No. 12, c—d: Provenance Ipoltica, c: at temperature 20—15° C, plant No. 15, and d: at temperature 15—5° C, plant No. 6. e—f: Provenance Blizyn, e: at temperature 20—15° C, plant No. 19, and f: at temperature 15—5° C, plant No. 20, bud initiation and formation already in period III. For corresponding plant numbers see Fig. 7.

entiated buds. As against this, at low temperature (series B) most of the plants still had immature top shoots and the terminal buds were poorly formed (Fig. 7 and 8).

On the whole, the maturation processes just described proceeded much faster at the higher temperatures (series A) than at the lower ones (series B). However, this may be due not only to the temperature differences in series IV, but also to those between series A and B in the previous periods.

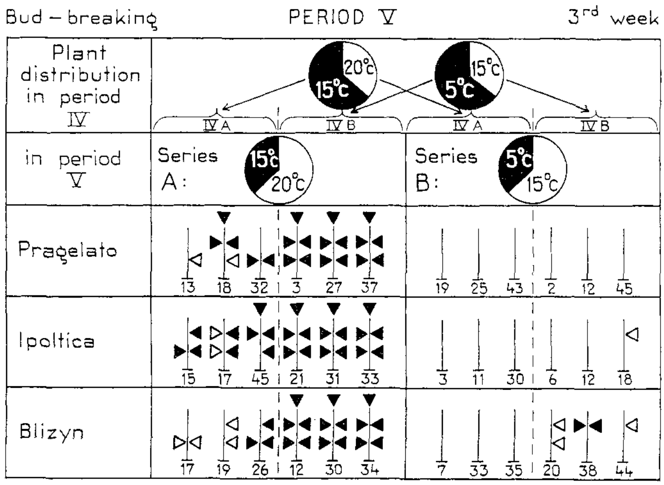


Fig. 9. The development of the plants after 3 weeks LD-treatment in period V. For each of the two series A and B in period V, plants from both temperature series A and B of period IV were selected. For explanation of the symbols see Plate II.

3.5. Period V (12 weeks, cf. Plate I)

LD-Series A: Day: 16 h, 20°C + Night: 8 h, 15°C (3 pl. from IV A + 3 pl. from IV B)

LD-Series B: Day: 16 h, 15°C + Night: 8 h, 5°C (3 pl. from IV A + 3 pl. from IV B)

SD-Series C: Day: 8 h, 20°C + Night: 16 h, 15°C (3 pl. from IV C + 3 pl. from IV D)

SD-Series D: Day: 8 h, 15°C + Night: 16 h, 5°C (3 pl. from IV C + 3 pl. from IV D)

In period V, the photoperiod which was LD in period IV was changed to SD and *vice versa*. Moreover, for each of the LD and SD series in period V plants from both temperature series of period IV were selected. With this arrangement it was possible to study the influence of different photothermic conditions in period IV on the growth activity in period V (cf. Fig. 9). Through this sampling the number of plants decreased to three per treatment, in consideration of the combined conditions between periods IV and V.

LD-series: Three weeks after the plants were transferred from SD (period IV) to LD, the buds began to open, but only in series (A) with high temperature. Moreover, the plants kept at a high temperature in the previous period (SD in IV A) formed needles more slowly than those kept at a low temperature previously (SD in IV B).

SD-series: After nine weeks in SD-series, the plants maintained at high temperature (SD in V C) were practically leafless, in contrast to those in series D (SD in V D), which still had most of their needles. No distinct influence of the different temperatures in the previous period IV was observable on the plants in period V.

It must be mentioned that in the last week of period IV, a technical accident occurred in series B. One night the temperature in the cold room (+5°C) for some unknown reason fell below zero and the top shoots of the plants were damaged by frost. The results in SD-series of period V should, therefore, be treated with reservation and will be excluded from the discussion.

4. Discussion

This investigation was carried out at the time when the phytotron at Stockholm first came into use and for technical reasons, the choice of plant number and the photo-thermal conditions was limited. Thus only photoperiods 16 hours as LD and 8 hours as SD were used. The latter lies below the critical short-day length for larch. Zelawski (1956, 1957, 1960), for instance, states that the vegetative buds in larch show the characteristic reactions for short day between 9 and 15 hours at an average temperature of 22°C. Also the combinations of temperatures were limited in the experiment. Moreover, the seasonal and the daily transfer of the plants between LD and SD as well as between different temperatures occurred abruptly, as against under natural conditions where the change takes place progressively. In spite of these methodical disadvantages the result of this investigation can serve as a good starting point for the further studies which should be carried out under controlled and more natural conditions. The results are given individually for each plant, as far as possible, because an average value per treatment often hides the very interesting behaviour of an individual. In order to present the growth history of each plant briefly it was necessary to introduce symbols, despite the fact that such forms of illustration may in some cases appear complicated. In the last weeks of the experiments, it would have been desirable to transplant the plants to larger pots, because the root system had become too large. But this was not done, in order to avoid checking of the plants.

The photoperiodic reactions of the three provenances investigated in this experiment are, in principle, the same; LD (16 hours) stimulates the growth activity, SD (8 hours) inhibits it. The length of LD photoperiod (here used) need not necessarily be the optimum for the growth of larch. So far as the increment in height in *Larix leptolepis* and *Larix occidentalis* is concerned it is known that they respond positively up to the maximum LD=24 hours (Downs, 1962). *Larix decidua* needs a long photoperiod even for the germination of seed. Kantor & Simancik (1966) have found that the optimum photoperiod for the best germination percentage for larch is 16 hours, whereas it is only about 8 hours for Norway spruce and Scots pine.

Moreover there are also differences in the photoperiodic responses among the three provenances. Whereas almost all plants in Ipoltica and Blizyn under LD grow continuously, the most individuals of Pragelato have an irregular growth, which often ceases. However, the plants of Pragelato provenance which grow continuously (↑ type in Fig. 1), show a greater increment in height than those of the other two. Nevertheless, the height increment in Pragelato provenance should be judged carefully, because through the elimination of about 50 per cent of plants with irregular growth from the calculation, a selection has been made which could favour only the best-growing individuals in this population. There were great differences amongst the individuals of provenance Pragelato concerning the rate of growth. It may be supposed that the light and temperature in this experiment probably lie at a threshold value, at which the photo- and thermoperiodic responses of this southernmost provenance alter. At the same time the genetically controlled individual variations are apparent. For instance, in Fig. 1 some plants of Pragelato in LD-series suddenly formed a terminal bud which sprouted after a very short rest, without going into deeper dormant condition (cf. Pragelato plant 45 in Fig. 1). Other individuals after forming a terminal bud remained in this condition for several weeks (cf. Pragelato, plants 25, 32, 37 in Fig. 2). In no case did the interruption of growth under LD conditions cause discoloration of the needles or their shedding. This and the fact that in most cases no false annual ring was formed in the wood in connection with the interruption of growth, indicates that it was not a question of true dormancy (cf. Vegis, 1963). Repeated bud-set, flushing, etc., as in Pragelato larch, were also observed by Dormling *et al.* (1968) in *Picea abies* of northern provenance, and by Downs (1962) in different tree species, when the plants had been kept under continuous long-day conditions. Individuals in a population which show such different photoperiodic reactions can have a practical use in tree breeding, in so far as these responses are genetically controlled, e.g. in the choice of suitable crossing partners, selection of individuals for artificially created populations, etc.

The non-formation of a false annual ring in the wood of larch with interrupted growth as also observed by Zelawski (1957), indicates that this is a case of "echte Johannestriebe" (according to Späth cit. in Burger, 1926). But in the case of plant 303-29 (Fig. 5), there is evidence that the size of xylem cells can also change due to interruption in growth (cf. Larson, 1962, in red pine). It would therefore be necessary to make detailed anatomical studies on a larger material with different types of plant concerning the growth rate, before the nature of the interrupted growth could be explained.

In connection with "Johannestriebe" (Lammas shoots) the formation of laterals which grow from the terminal shoot of the current year should be mentioned. Leibundgut & Kunz (1952), who call the lateral shoots "seitliche Johannestriebe" have found in experimental plots in Switzerland that these occur chiefly in provenances with large height increment, and in those which attain half of their height relatively late in the season. Consequently, the larches from lower altitudes which grow very intensively and stop growth relatively late in the season, distinguish themselves through the profuse formation of laterals from the shootless Alpine larches which stop growing early. These differences in habit of larches are known from different provenance plots and have also been observed in Sweden. The Alpine larch Pragelato did not form or formed very few lateral shoots, even under the extreme condition to which it was subjected in the phytotron. In spite of the fact that it was forced to grow continuously and intensively for a long time, lateral "Johannestriebe" were not formed (cf. Table 5). These results show that the formation of lateral shoots in larch is genetically strongly fixed in certain provenances and is less modified by photoperiodism, than is the case with other species (Bogdanov, 1931). The presence or absence of laterals in larches of unknown provenances can, therefore, be a good criterion for the identification of their origin (cf. Leibundgut & Kunz, 1952). The rate of growth has been followed weekly through the measurement of height increment. From the results it will be seen (Fig. 3 and 4), that the spiral arrangement of needles on the terminal shoot was mostly visible during the intensive growth of the terminal shoot. This character can, therefore, be valuable as a phenological criterion for the judgement of the growth activity in plants on experimental plots.

The plants in all three provenances when exposed to SD ceased growth after 3—4 weeks, a small terminal bud was initiated, the needles turned yellow and were later shed. Of the three provenances, Pragelato larch has reacted most intensively to SD conditions. In period III it had lost all its needles, whereas many of the plants of Ipoltica and Blizyn still possessed some of their green needles (cf. Table 4 and Fig. 4). This maturation process in SD seems to proceed faster in series III C at higher temperature, than in series III D at lower temperature. The initiation of bud formation on larch takes place sometime after its being subjected to SD conditions (cf. Molski & Zelawski, 1959) and the further maturation depends upon the temperature at this stage. Under SD: 20—15°C the buds became much enlarged by swelling and the top shoots were lignified very early (cf. IV A in Fig. 7 and 8). In contrast to this, the buds remained small and the shoots unlignified, when the temperature during bud maturation was as low as that in SD: 15—5°C (cf. IV B in Fig. 7 and 8). As a consequence of such poor bud formation, one would expect that flushing of the poorly developed buds would proceed slowly and the new shoot increment be delayed. However, this was not the case. These buds at SD: 15—5°C (series IV B) after exposure to LD: 20—15°C (series V A) conditions flushed more rapidly and the new top shoots were decidedly better than those for the plants originating from SD:20—15 °C with well-developed buds (series IV A in Fig. 7 and 9). The relatively low temperature SD: 15—5°C (in series IV B) is on the one hand responsible for bad bud formation, but on the other hand, this temperature is probably low enough to break the dormancy of the buds. According to Potapenko (cit. Vegis, 1961) the cold requirement of a bud can also be satisfied with a low night temperature (in this case at 5°C), instead of a continuously low temperature. As against this, the relatively high temperatures SD: 20—15°C in series IV A, which of course were suitable for the top shoot maturation (lignification) and bud formation, caused an effective bud dormancy. Consequently, after transfer of such plants to LD conditions in series V A, bud breaking was delayed and irregular (Fig. 9). Larch as well as other trees (e.g. Norway spruce: Dormling *et al.*, 1968), after bud maturation need a cold resting period in order to break dormancy, otherwise the flushing and growth of plants in LD conditions do not occur normally.

In this experiment, there were too few plants and combinations of treatment for it to be possible to investigate intensively the cold requirements of larch. However, the importance of the temperature for bud breaking and for the following plant growth could be partly studied from different times of treatment, photo- and thermoperiod combinations in Plate I and in the respective figures and tables. These show clearly that the time and intensity of the bud flushing etc. in a larch plant are controlled by rather complicated relationships between the time of treatment and the photo- and thermoperiodic conditions which begin to act in the very early stages of bud formation.

The transfer from LD to SD had also influenced the formation of late wood, which in SD-plants consisted of a few layers of cells with narrow lumen (Fig. 5, plant 303-16) or which was less differentiated from early wood (Fig. 5, plant 707-40). The association between late-wood formation and SD conditions in larch seedlings has been proved by Zelawski (1956), Molski & Zelawski (1958) and Wodzicki (1960, 1961). The impulses for the formation of early and late wood seem to originate from the terminal bud or from the apical meristem, which through the synthesis of growth promoters in LD (auxin, gibberellins) or inhibitors in SD influence the diameter of tracheids (cf. Larson, 1962; Wort, 1962 and the literature cited there; Dickerman, 1963). It has been proved experimentally, that also leaves and needles as assimilatory organs play an important role in the regulation of height and diameter increment of stem (cf. Moshkov, 1935; Wareing, 1949; Nitsch & Nitsch, 1959; Vegis, 1964 and the literature cited there; for larch cf. Chalupa, 1965). Moreover, there are also other factors which can influence the early or late wood formation, e.g. moisture in the soil (cf. Balatinecz & Farrar, 1967 and literature cited there).

In view of the reservation in the beginning of the Discussion about the material and the methods, it can be concluded that the bud initiation, formation, maturation, breaking-flushing and the amount of height increment of new top shoots in larch are processes which are highly regulated by photoperiodism and temperature. In all the processes during the vegetative cycle of larch discussed here, it was observed that the responses of the three provenances were very different. It may be concluded that these reactions can also be largely controlled by differences in the genetic constitution of the three provenances.

Practical applicability

The results of this laboratory experiment, together with those of field trials have some applications in practice. The autochthonous area of European larch lies between lat. 44° and 53° approx. (Ostenfeld & Syrach Larsen, 1930), in different isolated geografical regions. There are distinct racial differences between these regions.

The adaptation of tree provenances to various thermoclimates which exist at different altitudes of a certain geographical region can explain why populations growing in the same photoclimate but at different elevations form "races". The larch, which has a large vertical distribution in the Alps, is known to form different altitudinal types (Engler, 1905; v. Wettstein, 1946; Vincent, 1958). Wachter (1962) emphasized that for the formation of races in *Larix decidua*, the length of day and temperature of habitat are the deciding factors. Cieslar (1899) does not distinguish any altitudinal differences in Tirolian larch, but on the very same material Langlet (1938) pointed out their existence.

Through the introduction of this species to Scandinavia it is exposed to a longer photoperiod than is the case in its original habitat. Long days and relatively low temperatures in northern regions force larch to grow intensively up to late in the autumn, as has been proved experimentally on 55 provenances of *Larix decidua* in Remningstorp in Sweden (Exp. plot S:66 lat. 58° 28′ N, long. 13°33′ E, alt. 130 m). On the basis of direct measurements of height increment and the phenological observations during the year 1964, the termination of vegetative growth of larch in these plots occurred at the end of September. Before this time, there were several days and nights with temperatures below 0°C. Due to the relatively long photoperiod and low temperature at the end of the growth period, the lignification of the larch shoots was very incomplete (cf. Fig. 8 b, d and e), and consequently, these immature shoots were very easily damaged or killed by frost. The frost damage was found also in the cambium of the stem going deep down from the top of the plants, without any external symptoms. This cambial damage could have a negative influence on the height increment of plants in the following year (Simak, 1969).

Engler (1903), Burger (1926) and Leibundgut & Kunz (1952) give dates for the termination of vegetative growth of larch on experimental plots in Switzerland, which are a month or more earlier than those in Sweden (Remningstorp). Moreover, there are large differences among provenances as regards the cessation of growth. As against this, the termination of growth in all provenances in Remningstorp took place more or less simultaneously at the end of September in 1964. The different behaviour of larch in Switzerland and in Sweden can be attributed to its genetically controlled photo-thermoperiodical reactions to the different climatic conditions in the two countries.

The poor adaption of larch to northern photo- and thermoperiodic conditions may also be a reason for the frequently unsuccessful autumn planting of this species in Sweden. Larch plants lifted in the autumn from nursery beds are often incompletely hardened. In consequence, they are exposed to some degree of physiological shock, and on being planted in the autumn, they are readily frosted or killed.

The photoperiodic conditions are fixed for a particular habitat. Even if it is not possible to change them, one can while introducing larch, choose only such provenances which best fit the photoperiodic conditions existing there. The thermoclimate is more variable in a habitat and in this way the forester may be able to influence the results of plantations through the selection of suitable sites, e.g. planting under the canopy of trees, or on suitably exposed slopes. As is known, light and temperature act antagonistically during certain stages of annual growth; light promotes growth, whereas high temperature inhibits it through the formation of resting buds (Vegis, 1953). Consequently the higher the temperature of a habitat, the longer the photoperiod that can be allowed in order to bring about the formation of the buds and maturation of the shoots.

The photoperiodic reactions of tree species can be tested by different methods (Moshkov, 1935; Langlet, 1937, 1944; Schröck & Stern, 1952; v. Wettstein, 1954; Schmidt, 1957; Wiersma, 1958; Dafis, 1962; Leibundgut, 1962), which help the breeder in his selection work. The provenance trials give a suitable material for the vegetative reproduction of individuals which through their responses fit well with the required conditions; e.g. individuals with an early cessation of growth activity in autumn can be considered as less sensitive to early frost. In this way, it is possible for the breeder to create new populations in a much shorter time than nature would need through the process of natural selection.

Finally, in nurseries, etc., the effect of long day can be utilised for the production of plants of good quality in a short time through the prolongation of photoperiod by artificial light (Nagata, 1966). The same effect, but more economically, can also be attained by interrupting the "night" for a short time by artificial illumination (cf. Wareing, 1950, 1954; Giertych & Farrar, 1961). By contrast, through artificial shortening of photoperiod (shading), the maturation process in the plant can be hastened in order to avoid the risk of early frost damage. Such regulation of light and temperature conditions may be of current interest and can also easily be attained in practice, for instance, in plastic green houses.

5. Summary

Photo- and thermoperiodic responses of larch (*Larix decidua* Mill.) were studied in the Stockholm phytotron, using three provenances: Blizyn 330 m, Ipoltica 800 m and Pragelato 1900 m. Two photoperiods, long day (LD=16 hours) and short day (SD=8 hours) were used. Different combinations of thermoperiods were tested in the experiment. The plan of the photo- and thermoperiods tried is given in Plate I.

1. Under LD the growth activity was high. The cambium formed only early wood.
2. Under SD the growth in height stopped after 3-4 weeks, terminal buds were initiated, the needles turned yellow and were shed. The cambium produced only late wood, as long as the growth activity existed.
3. The formation of the terminal buds after their initiation in SD is dependent upon the temperature. At high temperature, the buds were large and swollen, at low, they were small and poorly developed.
4. The top shoots also required a high temperature for a good maturation (lignification) under SD conditions. At low temperature, the top shoots remained unlignified and therefore susceptible to frost damage.
5. The buds formed at high temperature were dormant. The dormancy could be broken only by a period of low temperature (cold requirement).
6. The time for bud breaking and flushing, as well as the amount of growth of top shoot, were dependent upon the photo- and thermoperiodic conditions during the entire course of bud formation, beginning from bud initiation.
7. There were considerable variations in the growth behaviour among the provenances. The plants of Pragelato grew irregularly in LD and often ceased their height increment for a short or long time, forming terminal buds. In provenances Ipoltica and Blizyn the rate of growth was constant and uninterrupted. The lateral shoots in these two provenances were numerous, but practically absent in Pragelato. Under SD conditions the plants of Pragelato matured earlier than those of the other two provenances. Also in bud breaking, flushing and in the amount of height increment of the top shoot, there were considerable differences between the Alpine provenances Pragelato and the other two provenances.

On the basis of these results in the phytotron and those of experimental trials in the field, some conclusions have been drawn regarding the introduction of larch to northern Europe.

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Plate I. Plan of the experiment.

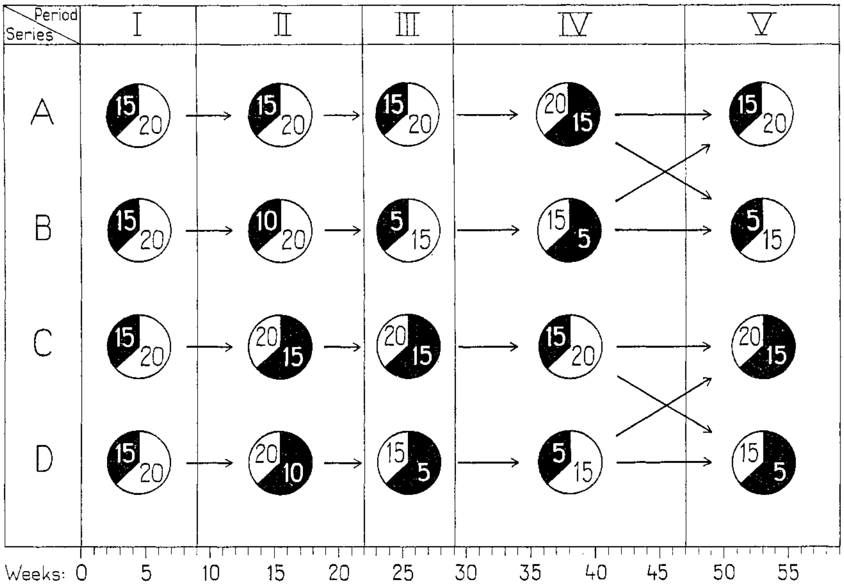


Plate I. The experiment was carried out for 59 weeks in five periods I—V and in four series A—D. The length of the photoperiod is given by a circle. The white sector in a circle denotes the day-length, the black one the night-length. Only two photoperiods were used: LD (16 hours) if the white sector in a circle is larger and SD (8 hours) if the white sector is smaller than the black sector. The corresponding temperatures in each sector are given in degrees Centigrade.

Plate II. Symbols used for the description of phenological stages of the plants.
(The symbols can be used in different combinations)

Top shoot

 Continuous growth of the top shoot.

 No growth activity during the time denoted by the dotted line.

 The thickened area on the right or left side of the vertical line denotes the time in which the right or left whorl respectively was observed for a particular plant.

 Growth of the top shoot stopped. No distinct initiation of a new terminal bud visible.

 Growth of the top shoot stopped. Initiation of a new terminal bud visible.

 Growth of the top shoot stopped. Terminal bud distinctly developed.

 Terminal bud had developed in one of the previous periods of the experiment.

 Breaking of the terminal bud (breaking = only the tip of green needles visible).

 Breaking and flushing (flushing = needles fully developed) of the terminal bud and growth in height of the new top shoot.

 Unlignified top shoot, with terminal bud not fully developed.

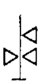
 Lignified top shoot with terminal bud distinctly developed.

Plant

 No bud on the plant breaking.

 Breaking of terminal bud and of less than 50 % of the buds in the lower half of the plant.

 Breaking of terminal bud and of more than 50 % of the buds in the upper half of the plant.

 No breaking of the terminal bud. Less than 50 % of the buds in the upper half and more than 50 % in the lower half of the plant are breaking.

 The black triangles denote quantitatively the same as the white ones, but the black ones represent fully developed needles.

Sammanfattning

Foto- och termoperiodiska reaktioner hos olika lärkprovenienser (*Larix decidua* Mill.)

I ett fytotronförsök undersöktes foto- och termoperiodiska reaktioner hos tre lärkprovenienser (*Larix decidua*: Blizyn 330 m, Ipoltica 800 m, Pragelato 1 900 m ö. h.). Tvååriga plantor odlades under lång dag (LD = 16 timmars ljus) och kort dag (SD = 8 timmars ljus) samt vid olika termoperioder. Försöksplanen är återgiven schematiskt i Plate I. Följande resultat har erhållits:

1. Plantorna visade en hög tillväxtaktivitet under LD, endast sommarved bildades i stammen.
2. Under SD avstannade tillväxtaktiviteten helt efter 3—4 veckor. Terminalknopp anlades, barren gulnade och föll av, höstved började bildas.
3. Knopputvecklingen under SD var beroende av temperaturen. Vid höga temperaturer blev knopparna stora och väl utvecklade, vid låga blev de svaga.
4. Terminalskotten krävde relativt hög temperatur under SD för att förvedas väl. Vid låg temperatur skedde ingen förvedning.
5. Knoppar som befinner sig i verklig vila kräver låg temperatur för att bryta detta tillstånd.
6. Knoppens anläggning och utveckling, knoppsprickningen samt tillväxten av toppskotten bestämdes av de foto- och termoperiodiska betingelser, som rådde innan och under dessa utvecklingsstadier.
7. De tre provenienserna odlade under likartade betingelser skilde sig från varandra i tillväxtaktivitet. Pragelato-proveniensen växte oregelbundet (under LD), höjdtillväxten avstannade ofta för kortare eller längre tid. Hos provenienserna Ipoltica och Blizyn var höjdtillväxten i LD konstant och oavbruten. Bildning av sidoskott på årets terminala skott förekom i stort antal hos de två sistnämnda provenienserna. Hos Pragelato bildades ej sådana skott. Under likartade SD-betingelser avmognade Pragelato snabbare än Ipoltica och Blizyn. Likaledes förekom tydliga skillnader i knopputvecklingen, höjdtillväxten m. m. mellan Pragelato å ena sidan och Ipoltica samt Blizyn å den andra.

Med ledning av resultat från denna fytotronundersökning samt från i Sverige anlagda fältförsök med olika lärkprovenienser kan dras vissa slutsatser beträffande lärkens introducering till nordligare breddgrader.