

ken zu können: Es war die Zeit, als die berühmt gewordenen Wiener Kaffeehäuser gegründet wurden.

Nach Erledigung dieser Präliminarien widmeten sich die WETTSTEINS den Wissenschaften, jetzt schon in mehreren Generationen. Auch übrigens in der jüngsten, 7 Enkelkinder warten bereits darauf. Und damit komme ich wieder auf eine Lesefrucht. „The sex factor in creativity“, überschrieb ALEX F. OSBORN ein Kapitel seines bekannten Buches „Applied Imagination“, das in der 21. Auflage erschien. Er ist der Schöpfer der „Creative Education Foundation“, deren Mitglied zu sein ich die Ehre habe. Seinem Buche konnte er ALBERT EINSTEINS Wort voranstellen: „Imagination is more important than knowledge“. Bekanntlich sind Frauen erfinderischer als Männer. Das kennt man. Aber es ist auch statistisch erwiesen. Die Johnson O'Connor Foundation fand durch Tests an 702 Frauen heraus, daß ihre creativen Fähigkeiten um 25% höher waren als bei Männern. Nun kann man sich vorstellen, was der Spruch bedeutet: „Tu felix Austria nube.“ (Bella gerant alliierte, heißt es weiter, nach dem Wiener Kongreß, wenn ich mich recht entsinne). Die WETTSTEINS, selbst creativ, heirateten in mehreren Genera-

tionen Frauen aus ebenfalls creativem Hause. Macht in der ersten Generation ein Plus von 25%, in der nächsten 125% plus 25%. Von 125%, versteht sich, also wieder eine Steigerung um 31% usw., um mathematisch präzise zu sein. Wolffangs Mutter stammt aus der Gelehrtenfamilie der KERNER VON MARILAUNS. Ein Sohn heiratete eine Tochter des schwedischen Genetikers GUSTAFSSON.

Kein Wunder, daß ich mir Wolffangs Schreibtisch nicht so leer vorstellen kann wie den Kaiser Franz Josephs. Der Fremdenführer im Schloß Schönbrunn bei Wien zeigt dessen Schreibtisch mit der Bemerkung, der Kaiser habe an ihm auch immer gefrühstückt. Er mußte also über Nacht bis zur Morgenfrühe von allen Aktenerinnerungen frei sein, der Schreibtisch. Aber das besorgen für einen Kaiser ja die Hofräte. Ich entsinne mich jedoch einer anderen großen Ähnlichkeit einiger Räume der Versuchsanstalt mit dem Schloß Schönbrunn. Man mußte Schloßpantoffeln über die Schuhe ziehen, um das wunderschöne Parkett zu schonen. Und das werden hoffentlich auch die Geburtstagsgratulanten tun.

The Experimental Control of the Life Cycle in *Picea abies* (L.) Karst.

I. Some basic experiments on the vegetative cycle

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Introduction

Since 2 to 3 decades are usually required in nature before a seedling of *Picea abies* comes to flowering, the most urgent problem to be solved in the genetics and breeding of *Picea abies* concerns the experimental reduction of the generation time. To produce inbred lines of *Picea abies* for heterosis breeding in a short time, on a reasonable large scale, and with the desired genotypes, one must be able to induce flowers on any seedling in the first or subsequent growth periods. In principle, several approaches to the solution of this problem are possible: (1) One can try to induce flowering by treating seedlings with growth retardants and hormones which promote flowering. (2) Artificial aging or shortening of the juvenile phase (16, 33) in a phytotron can be employed, whereby one tries to accumulate the 20 to 30 growth periods necessary for bringing the tree into the reproductive age in as short a time as possible. This can be achieved by alternating the optimal climate for growth with the optimal climate for the necessary periods of dormancy. (3) A combination of the two approaches, that is a certain amount of artificial aging followed by treatments with hormones inducing or promoting flowering, is most likely to succeed.

We have decided to study the problems of artificial aging in a central European provenance (Westerhof) and an arctic provenance (Laitamaa) of *Picea abies*. The optimal growth conditions for these two tree provenances at the seedling stage, at the age of 1 year, and at the age of 2 years have been determined earlier (9). This species of *Picea* grows optimally under long-day conditions at a temperature of 20° C. For the central European provenance a photoperiod of 16 hrs in a 24 hr day is sufficient, whereas the arctic provenance requires a photoperiod of 22 to 24 hrs for optimal continuous growth.

In this paper we present an analysis of the climatic control of budset, bud maturation, dormancy, and flushing.

Strict control of the vegetative cycle of *Picea abies* is accomplished by using a sequence of photoperiodic and thermoperiodic conditions. The amount of growth after flushing of the buds can be controlled with the day length and the temperature during bud maturation. With the central European provenance 4 weeks for bud maturation, 4 weeks for bud dormancy and 7 weeks for growth and budset, i.e. 15 weeks in total, are sufficient for a complete vegetative cycle. With the arctic provenance 4 weeks for bud maturation, 4 weeks for bud dormancy, and only 5 weeks for growth and budset, i.e. 13 weeks in total, are required. Under controlled climatic conditions at least 3 to 4 vegetative cycles per calendar year are feasible, which suggests that seedlings of *Picea abies* can be brought in 7 to 8 years perhaps even earlier into the reproductive phase by artificial aging.

Material and Methods

The experiments reported here have been carried out in the phytotron at Stockholm, described by (35). Temperature and day length conditions are given with the individual experiments. Sylvania Grolux (GL) lamps giving 2000 fc. at the level of the plants were used as light sources. A relative humidity of 70% was employed throughout the investigation. Seeds were sown in vermiculite and the seedlings transplanted after 2 (central European provenance) or 3 weeks (arctic provenance) into a mixture of gravel, sand, and perlite (2:1:1). Thereafter the plants received a modified Hoagland solution (34) twice a week. When a truck was transferred from long-day to short-day conditions, the plants received a 24 hr photoperiod followed by the first new dark period. Conversely when the plants were moved from short-day to long-day conditions the last light period was extended to 24 hrs and in the central European provenance this 24 hr light period was then followed by the first

new dark period. These transitions thus could involve considerable phase shifts in the circadian rhythms of the plants (cf. 2).

The "cold" treatments for removal of bud dormancy consisted of 4 weeks, the first 7 days at 10° C under an 8 hour photoperiod, the second at 5° C under an 8 hour photoperiod, the third at 0° C in darkness, and the fourth at 10° C under an 8 hour photoperiod.

The plants were measured and evaluated weekly. Height measurements were made from the level of the potrim to the needle tips of the apical and of the longest shoot.

As seed source for the arctic provenance we used a population of trees at Laitamaa in Northern Sweden (Latitude 66° 50', Longitude 23° 10', 200 m above sea level) and for the central European provenance trees at Westerhof in Lower Saxonia, Germany (Latitude 51° 47', Longitude 10° 09', 300 m above sea level).

Considerable variation in the growth rate of the individual seedlings from both provenances occurred. Up to five weeks the growth rate was very uniform, differences in seedling height being primarily due to differences in seed size. Thereafter differences in the growth rate of the individual genotypes became clearly expressed (cf. figure 2).

To demonstrate the variation between individual seedlings found in the experiments some details of the variability are given below for 2 growth curves of the Westerhof provenance depicted in figure 1 and for one growth curve of the arctic provenance in figure 4.

At the age of 17 weeks 22 Westerhof seedlings growing in long-day conditions varied in height between 118 and 235 mm, with a mean of 152.4 ± 6.3 (S.E.) mm. In spite of this large genotypic variation in the growth rate all seedlings responded to a short-day treatment during week 16 and 17 by cessation of growth and beginning of bud formation in week 17. This demonstrates a small or lack of genotypic variance in the response to this photoperiodic control of budset within the population (see curve labeled 20° 8 h in figure 1).

An additional 22 Westerhof seedlings growing in long-day conditions with a similar variation in growth rates were treated during weeks 16 and 17 with a decreased temperature of 10° C in continued long-day conditions (see curve labeled 10° 16 h in figure 1). This treatment also caused cessation of growth and budset but at very different times in the individual seedlings as is shown in table 1. Only after 33 weeks had all seedlings stopped their growth. Their height then varied from 143 to 357 mm with a mean of 242.3 ± 13.9 mm, i.e. a standard error more than twice that of the seedlings, in which budset was induced with short-days. No obvious correlation exists between the growth rate and the onset of bud formation in the low temperature treated seedlings. This behaviour indicates either a large genotypic variance in the response, which is independent of that of the growth rate or a general indeterminate response to such temperature conditions. In either case such treatments are useless for a strict control of this phase in the vegetative cycle. This situation is clearly expressed by the continuously decreasing slope of the average growth curve labeled 10° 16 h in figure 1.

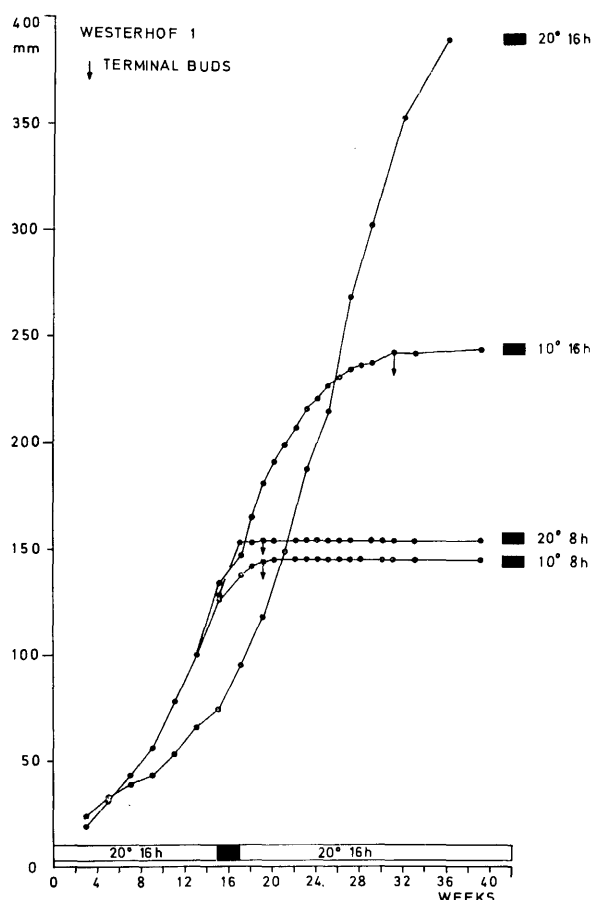


Fig. 1. — Growth curves of *Picea abies* seedlings provenance Westerhof subjected to different conditions during weeks 16 and 17. Continuous growth occurred under long-day conditions (photoperiod 16 hrs) at 20° C. A short-day treatment (photoperiod 8 hrs) at 20° C or 10° C induced budset. A low temperature treatment (10° C) under long-day conditions led to a delayed and variable cessation of growth and subsequent budset. (Each curve is mean of 22 seedlings.)

Seedlings of the arctic provenance Laitamaa grown in long-days ranged from 85 to 141 mm in height at the age of 18 weeks, which is at the end of a 2 week short-day treatment (figure 4 curve labeled 10° 16 h). The mean height of the 14 seedlings was 112.6 ± 4.5 mm. Cessation of growth had occurred in week 18 in all 14 seedlings. Only 5 of the 14 seedlings, however, remained dormant during the following 22 weeks in long-day conditions (table 2); the others were flushing after 6 to 14 weeks of dormancy in a highly variable fashion. As seen in table 2 the second growth period varied between 2 to 10 weeks and was followed by a new resting period. One seedling flushed a third time and went into a new resting period after 9 weeks of growth. Whereas the short-day treatment produced a uniform induction of the first resting period, thus revealing no genetic variance in this photoperiodic response of the seedlings, the further behaviour of the seedlings in long-day conditions reveals again either a high genetic variability or an indeterminate response to the unnatural conditions of long-days after budset. After 40 weeks the seedling height in this

Table 1. — Cessation of growth in 22 seedlings of the provenance Westerhof after a decreased temperature treatment (10° C) in long-day conditions during week 16 and 17 (cf. figure 1, 10° 16 h)

Weeks after end of temperature treatment	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Number of seedlings ending growth	1	3	2	3	2	1	2	1	1	—	2	—	3	—	1

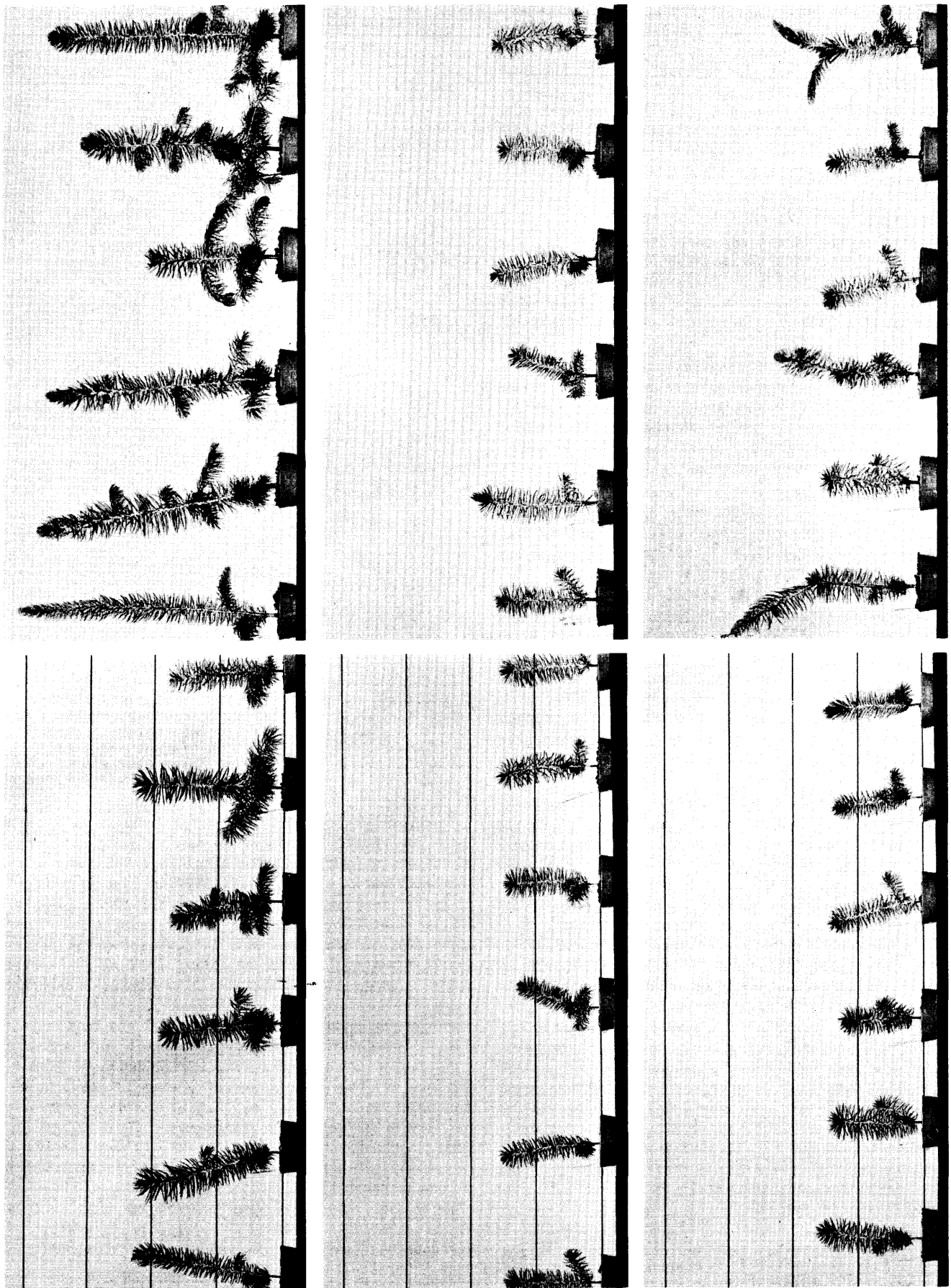


Fig. 2. — Examples of seedlings from the experiment in fig. 1. — Left: 20 week-old seedlings. Right: Same seedlings at 32 weeks. — Treatment during weeks 16 and 17. — Top: 10° C — 16 hrs photoperiod. Center: 20° C — 8 hrs photoperiod. — Bottom: 10° C — 8 hrs photoperiod; observe flushing of lateral buds with this treatment.

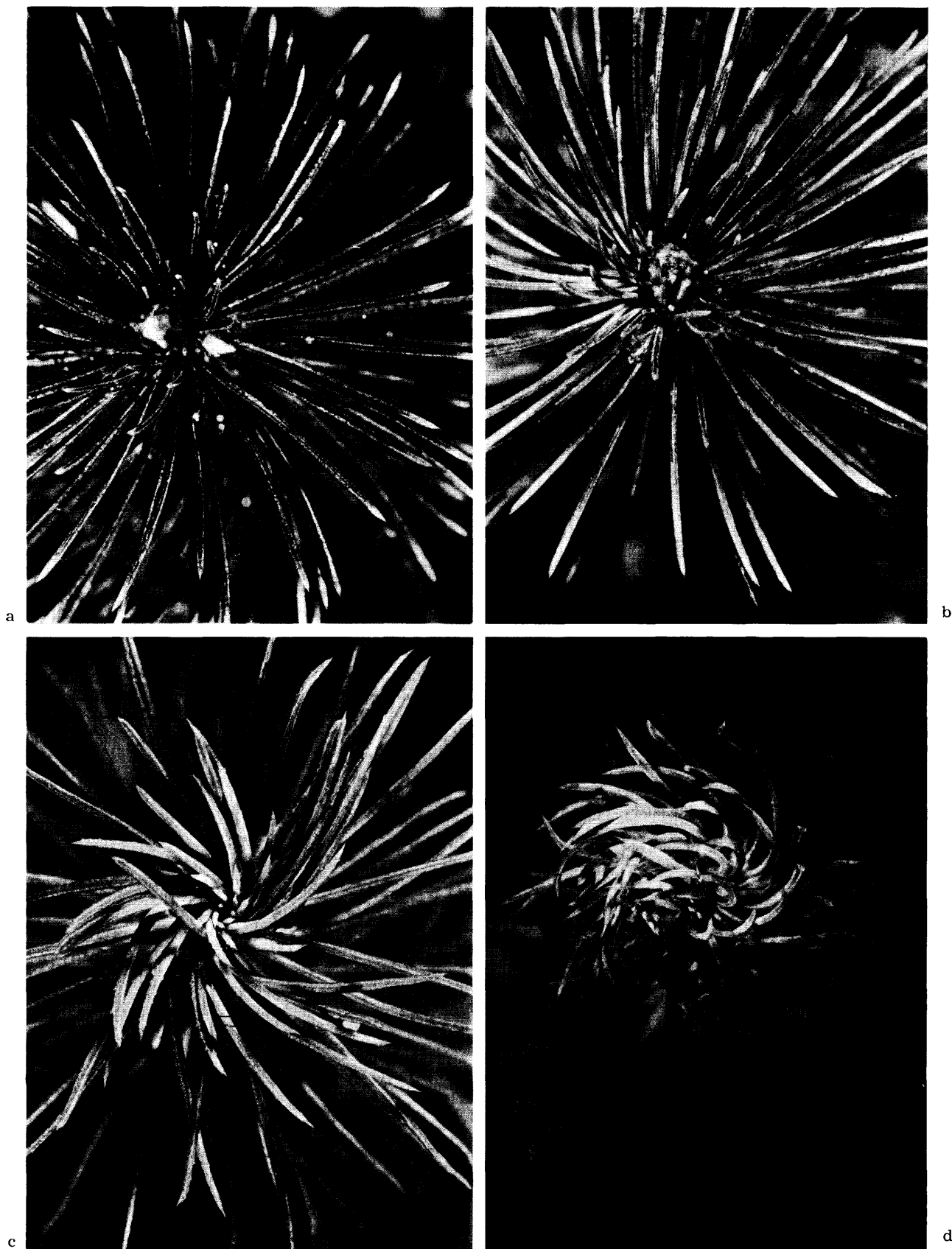


Fig. 3. — Examples of seedling shoot apices from the experiment in fig. 1. — (a) Terminal bud on 23 week-old seedling after short-day treatment (8 hrs photoperiod). — (b) Same seedling as in (a) at 33 weeks with huge swollen bud obtained by maturation in long-days (16 hrs photoperiod). — (c) Growing shoot apex on 23 week old seedling after low temperature treatment (10° C). — (d) Same seedling as in (c) at 33 weeks with newly formed terminal bud.

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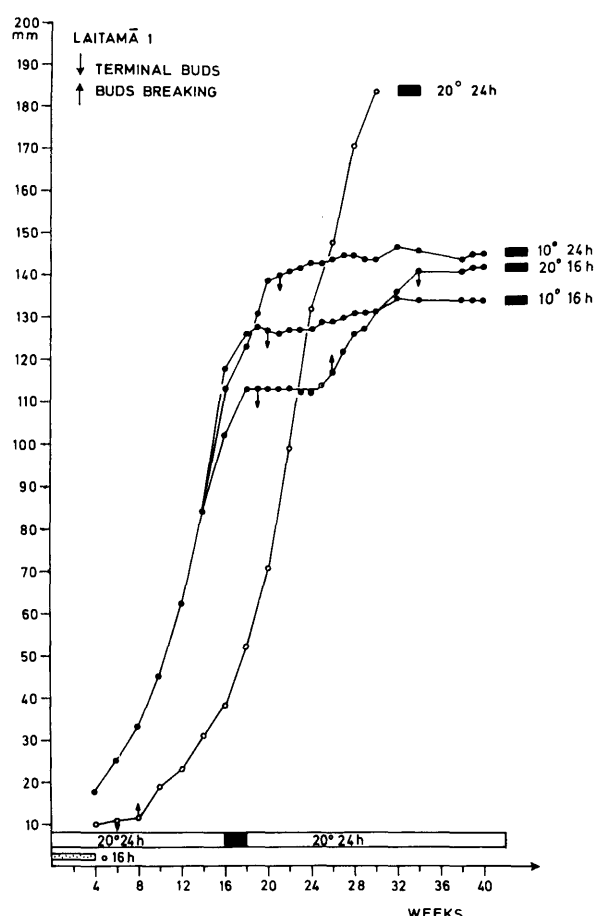


Fig. 4. — Growth curves of *Picea abies* seedlings provenance Laitamaa subjected to different conditions during weeks 17 and 18. Continuous growth occurred under long-day conditions (continuous light) at 20° C. A short-day treatment (photoperiod 16 hrs) at 20° C induced budset; after some weeks of dormancy the buds were flushing and limited growth occurred followed by a second budset. A low temperature treatment (10° C) under the long-day conditions led to a delayed and variable cessation of growth and subsequent budset. (Each curve is mean of 14 seedlings.)

material of the arctic provenance ranged from 91 to 196 mm with a mean of 142.6 ± 9.5 mm.

The large variance in the growth rates of individual seedlings leads to differences in the mean height of the seedling groups within a provenance which are to be compared for the effect of various photoperiodic and thermoperiodic treatments. To eliminate the growth rate differences from the curves presented in figures 7, 8, 9, 11, 12, 14, 17 and 19, the mean growth curves of the groups of seedlings have been normalized by proportional adjustment to a height of 50, 75 or 100 mm at the time of the first induction of budset.

The height value chosen for normalization of each seedling group was the closest to its mean.

The black, broken, and stippled bars at the bottom of the diagrams mark the time for specific treatments. The nature of the treatments during this time is indicated on each individual growth curve.

Results

1. The photoperiodic control of budset

Seedlings of the central European provenance Westerhof kept at a constant temperature of 20° C and a day length of 16 hours will grow continuously for at least 36 weeks as shown in figure 1. This growth curve is taken from one of the earliest experiments in the phytotron and the seedlings had a slower average growth rate than was achieved in the later experiments recorded in figure 1. A short-day treatment with an 8 hr photoperiod during weeks 16 and 17 resulted in cessation of growth in week 17. After an additional two weeks apical buds were visible on most of the seedlings. As long as they were kept in long-day conditions the buds grew bigger and matured but did not break. A decrease in temperature from 20° to 10° C during week 16 and 17 under continued long days did not lead to an immediate and uniform budset (figure 1). The growth rate was slower during the 2 weeks but resumed its original value when the seedlings were returned to the higher temperature. As shown in table 1 and discussed on p. 45, cessation of growth and bud formation occurred little by little over a period of 16 weeks after the end of the temperature treatment. In a third group of seedlings the short day treatment was combined with a decrease in the temperature from 20° C to a constant 10° C (figure 1; 10° 8 h). This treatment resulted first in a retardation of growth and then in its cessation over a 2 week period. The low temperature delayed the transformation of the growing shoot apex into the bud forming one, revealing the temperature sensitivity of this process (see also figure 12). The terminal buds formed did not break as long as they were kept in long-day conditions at 20° C. On about 50% of the seedlings, however, lateral buds were flushing 4–6 weeks after the end of the low temperature treatment, which was sufficient to break the dormancy of these buds (figure 2, lower right).

In figure 2 examples of the seedlings from the experiments just discussed at the age of week 20 (left) and week 32 (right) are given. The effect of the short-day treatment (center) as compared to reduced temperature treatment (top) is striking. In figure 3a the terminal bud of a seedling six weeks after the end of the short-day treatment is shown. Ten weeks later (figure 3b) the bud has developed to a huge swollen organ as a consequence of its continued stay under long-day conditions. For comparison a growing shoot

Table 2. — The growth history of 14 seedlings of the provenance Laitamaa in long-day conditions after cessation of growth with short-day treatment up to 40 weeks (cf. figure 4, 20° 16 h).

Number of seedlings	3	2	1	1	1	1	5
Weeks of bud maturation and dormancy after cessation of growth at week 18	6	7	8	11	12	14	22
Second growth period in weeks	4, 6, 10	4, 7	6	9	4	2	—
Second dormancy period in weeks	12, 10, 6	1, 8	8	2	6	6	—
Third growth period in weeks	—, —, —	9, —	—	—	—	—	—
Third dormancy period in weeks	—, —, —	1, —	—	—	—	—	—

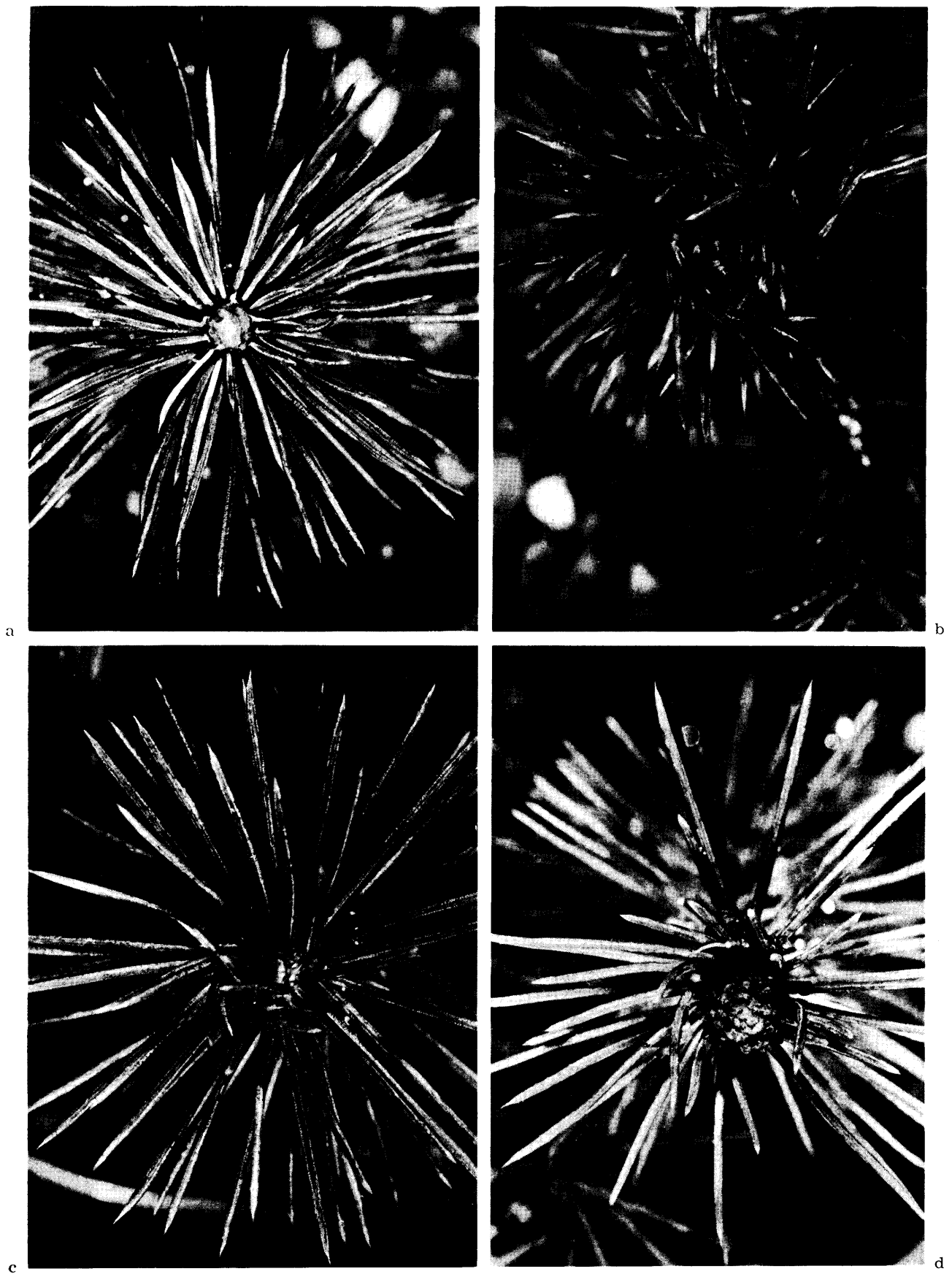


Fig. 5. — Examples of seedling shoot apices from the experiment in fig. 4. — (a) Terminal bud on 24 week-old seedling after short-day treatment (16 hrs photoperiod). — (b) Same seedling as in (a) at 34 weeks with newly formed terminal bud after second growth period. — (c) Terminal bud on 24 week-old seedling after low temperature treatment (10° C) under long-day conditions (continuous light). — (d) Same seedling as in (c) at 34 weeks with huge swollen bud obtained by maturation in long-days.

apex of a seedling six weeks after a reduced temperature treatment is reproduced in *figure 3 c* and the same shoot ten weeks later after cessation of growth in *figure 3 d*.

A similar set of experiments has been performed with the arctic provenance Laitamaa (*figure 4*). Constant temperature and continuous light resulted in vigorous and uninterrupted growth over 30 weeks (curve labeled 20° 24 h). The seedlings received, as indicated, a 16 hour day during the first 4 weeks of their life, which resulted in prompt formation of terminal buds two weeks later in spite of transfer to long-day conditions. The buds flushed, however, in the following week, whereafter continuous growth ensued. The seedlings of this provenance responded uniformly and even faster than the Westerhof provenance with cessation of growth and budset upon a 2 week short-day treatment with a photoperiod of 16 hrs or 8 hrs (not shown). A reduced constant temperature treatment (10° C) instead of the short-day treatment produced the same effect as in the Westerhof provenance — a variable cessation of growth and budset spread over a long period of time. A reduced temperature during the short-day treatment uniformly retarded in this provenance also the processes leading to cessation of growth and terminal budset, whether they were induced with a 16 or 8 hr photoperiod.

As already described on p. 45 and in *table 2* many of the buds matured in long-day conditions on the arctic provenance seedlings were flushing after 6 or more weeks. To a certain extent, this was also the case, when a short-day treatment was given with a decreased temperature or when

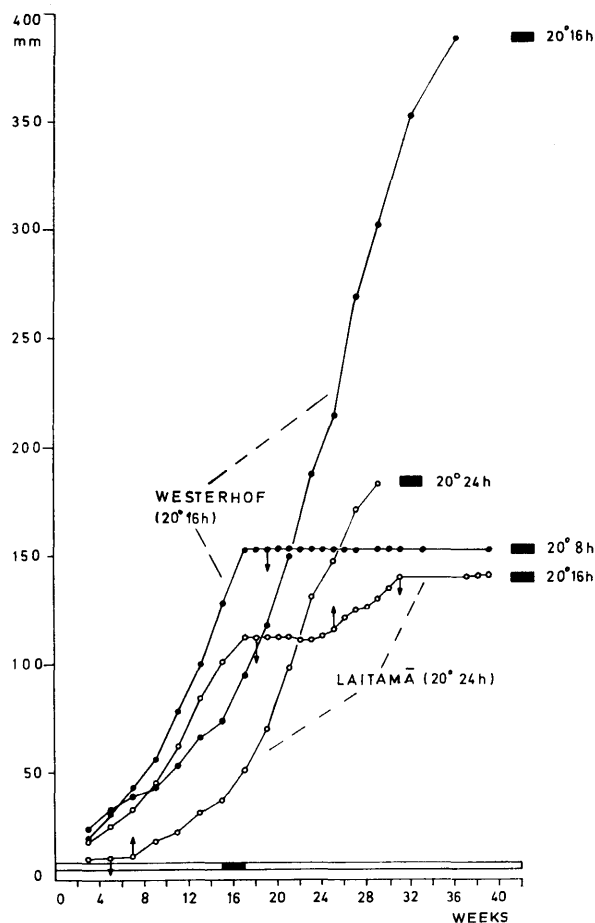


Fig. 6. — Comparison of growth curves for seedlings from the provenances Westerhof and Laitamaa. Long-day resulted in continuous growth in both provenances. Short-day conditions for 2 weeks resulted in growth cessation and budset.

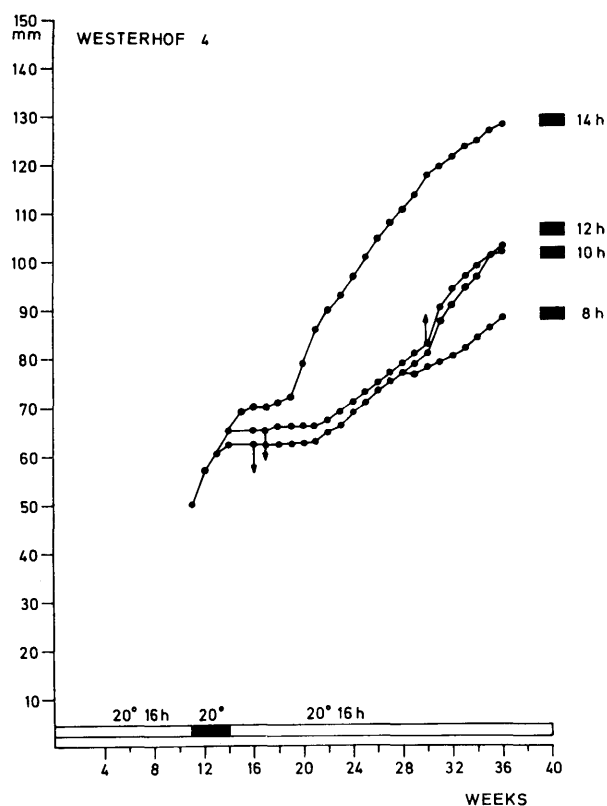


Fig. 7. — Growth curves for *Picea abies* seedlings of Westerhof provenance which were treated with reduced photoperiods of 8, 10, 12, or 14 hrs during 3 weeks. (Each curve is mean of 20 seedlings.)

the budset was caused only by low temperature treatment. The second growth period, where it occurred, was of variable length but resulted eventually in new apical bud formation without a second short-day treatment. The first short-day treatment appears to have induced in some seedlings an "annual periodicity" of growth and resting phases. These phases, however, vary highly in length and duration from individual to individual.

An example of a bud formed on a seedling of the arctic provenance 6 weeks after the end of the short-day treatment is given in *figure 5 a*. Ten weeks later (*figure 5 b*) the seedling has completed a second growth period. The apical shoot in *figure 5 c* from a seedling subjected to the reduced temperature treatment has ended its growth and after an additional 10 weeks in long days formed the huge swollen bud reproduced in *figure 5 d*.

The continuous growth curves and the budset in response to a 2 week short-day treatment of the arctic and central European provenances are compared in *figure 6*. The slower growth of the arctic provenance than the central European population as well as the genotypic adaptation of these two provenances to very different photoperiodic conditions is clearly illustrated. The critical night length for continuous growth versus budset lies between 8 and 16 hrs for the central European provenance and between 0 and 8 hrs for the arctic provenance.

To determine the critical day length or better the critical night length for budset in the two provenances the experiments presented in *figures 7 and 9* have been performed. For Westerhof the critical night length lies between 10 and 12 hrs, if a 3 week treatment is used (*figure 7*). A night length of 12 hrs led to cessation of growth in all 20 seedlings after 3 weeks, whereas a night of 10 hours produced

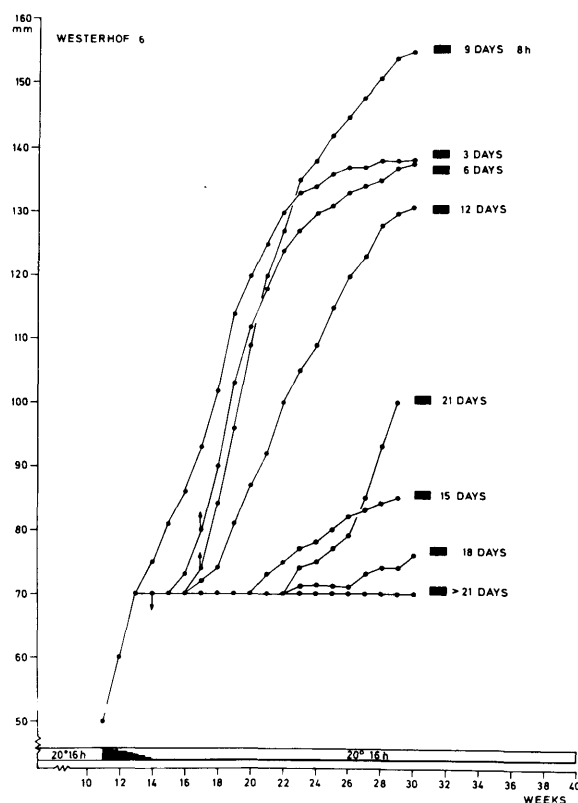


Fig. 8. — Growth curves for *Picea abies* seedlings of Westerhof provenance which were transferred into short-day conditions (photoperiod 8 hrs) for 3, 6, 9, 12, 15, 18, 21, or > 21 days. A short-day treatment of 6 days is sufficient to induce cessation of growth and bud formation. Prolonged dormancy require short-day conditions over a longer period. (Each curve is mean of 10 seedlings.)

this result only after 5 weeks. For Laitamaa the critical night length lies between 4 and 6 hrs (figure 9). A night of 2 hrs for 3 weeks hardly retarded the growth of the seedlings (figure 10 a). With a 4 hr night cessation of growth had occurred in all seedlings after 5 weeks, whereas a night length of 6 or 8 hrs achieved this in 1 week (figure 10 b).

We have further studied the minimum number of short-day cycles necessary to induce budset. For the provenance Westerhof 3 short-day cycles with a photoperiod of 8 hrs are not sufficient to induce budset, but 6 cycles are clearly enough for this purpose (figure 8). Similarly, between 3 and 6 short-days with a photoperiod of 16 or 18 hrs were required to produce budset in the arctic provenance. With a photoperiod of 20 hrs 6 to 9 cycles are necessary for cessation of growth in this provenance after 3 to 5 weeks.

Finally it should be mentioned that exposure to low light intensity for 1 hr in the middle of a 16 hr dark period prevented budset in seedlings of the central European provenance growing under short-day conditions. The same treatment could not prevent budset of the arctic provenance, probably because this light break did not split the night into periods shorter than the critical length of 4 hrs.

In conclusion, the induction of budset in *Picea abies* — as previously shown for this species (10), and many other woody plants (25, 27, 29, 33) — is a photoperiodic response, which follows the regularities established for other photoperiodic phenomena (19, 22, 26). Although increasing night length leads to budset, the critical length is very different for the two populations; for the arctic provenance about 4 hrs and for the central European provenance about 10 hrs. The day length response is considered quantitative

rather than qualitative, as long as indefinite continuous growth of *Picea abies* has not been proven to occur.

II. The photo- and thermoperiodic control of bud maturation, dormancy and flushing

The day length and temperature during maturation of the terminal bud determines the amount of dormancy obtained, the time of bud breaking, and the amount of growth obtained in the next flush. These responses will therefore be treated together. Extended dormancy of the resting apical bud can be induced by a 2 or 3 week treatment with short-days in both provenances (figures 1 and 4). After transfer of the seedlings into long-days at a temperature of 20° C, the buds of some seedlings, especially of the arctic provenance, will eventually break. According to figures 7 and 9 the length of dormancy of the terminal bud in long-days is evidently a function of day length during cessation of apical growth and the formation of the apical bud.

The critical day length during a 3 week treatment for the induction of a dormancy exceeding 1 week is 12 hrs for the Westerhof provenance and 18 hrs for the arctic provenance, which are the same times required for instantaneous cessation of growth. With decreasing day length the dormancy period seems to increase. That the length of the dormancy period is a result of the intensity as well as duration of the short-day treatment is also borne out by the experiment in which seedlings from the Westerhof provenance were transferred for various length of time into 8 hr short-day conditions (figure 8). Only after 15 or more days of short-day treatment was a prolonged dormancy period of at least 7 weeks obtained.

If bud maturation is carried out under short-day conditions, the buds remain small and are often difficult to recognize macroscopically (cf. figure 13 d). These buds matured at 20° C can be uniformly flushed by transferring the seedlings into long-days as shown for the Westerhof provenance in figure 11 (20° 8 h). When the maturation is carried out in short days at a higher temperature, e.g. 25° C, the buds cannot be flushed uniformly just by a transfer into long-days; only some of the seedlings flush and the amount

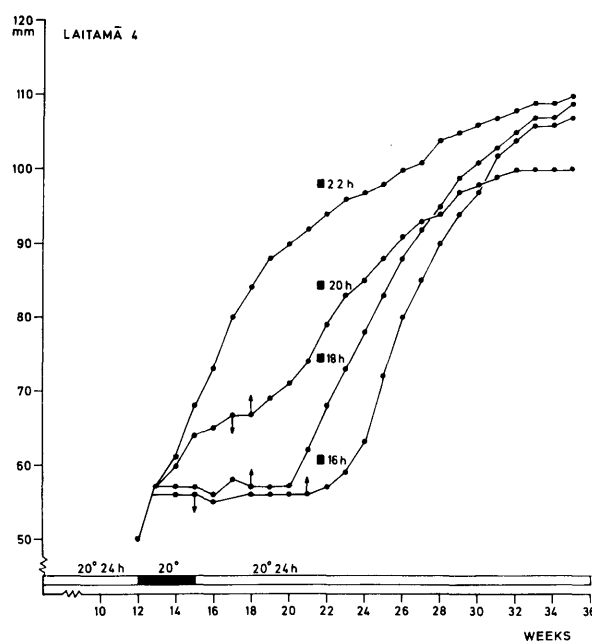


Fig. 9. — Growth curves for *Picea abies* seedlings of Laitamaa provenance which were treated with reduced photoperiods of 16, 18, 20, or 22 hrs during 3 weeks. (Each curve is mean of 20 seedlings.)



Fig. 10. — (a) Growing shoot apex on 18 week-old seedling after treatment with a 22 hr photoperiod (cf. fig. 9). — (b) Terminal bud on 18 week-old seedling after treatment with a 16 hr photoperiod (cf. fig. 9). — (c) and (d) The effect of a cold treatment on bud flushing in 31 week-old seedlings provenance Westerhof (cf. fig. 11). The growing shoot apex in (c) is from a bud that has been induced and matured under short-day conditions (photoperiod 8 hrs) and transferred to long-day conditions (photoperiod 16 hrs) for bud breaking. The growing shoot apex with long slender needles in (d) has received a cold treatment.

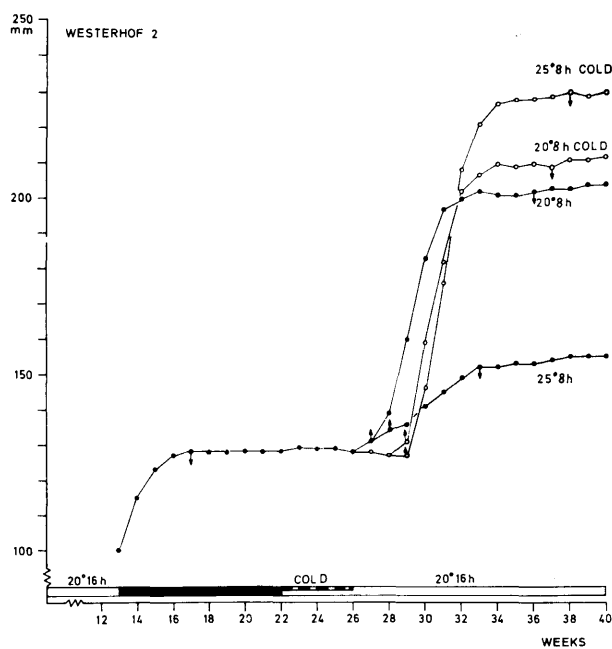


Fig. 11. — Growth curves of *Picea abies* seedlings provenance Westerhof. Budset was induced with an 8 hr photoperiod and the bud matured under these short-day conditions at a temperature of 20° C or 25° C. One half of the seedlings with dormant buds at each temperature received a cold treatment for 4 weeks the others did not. For bud breaking the seedlings were transferred into long-day conditions (photoperiod 16 hrs). More vigorous growth is observed with the cold treatment at both bud maturing temperatures. At 25° C a cold treatment is required for a normal growth period. (Each curve is mean of 9 seedlings.)

of growth obtained is very limited and irregular (cf. figure 11, 25° 8 h). This defect caused by bud maturation at high temperature can be overcome if a cold treatment reaching 0° C is given prior to the transfer into long-days (figure 11, 25° 8 h COLD). Not only do the seedlings flush in a synchronized fashion but they also grow as tall or taller in the second growth period as those matured at 20° C. A high temperature during bud maturation thus causes a dormancy which requires a cold treatment for breakage.

A cold treatment of the buds matured in short-days at 20° C resulted in a very uniform flushing and vigorous growth (figure 11, 20° 8 h COLD), although the total length of the seedlings was not significantly greater than that of those flushed in long-days without a preceding cold treatment. In both cases the growth period of 4 to 5 weeks was followed by a cessation of apical growth and then a new budset in long-day conditions. The cold treatment produced a drastically different habitus of the plants even if the seedling height was not affected (e.g. 20° 8 h photoperiod, figures 13 a and b). The shoots emerging from the flushing apical and lateral buds developed much longer and more slender needles, when the buds had received a cold treatment then without such a treatment. A comparison of figure 10 d with c and of figure 13 b with a demonstrates this difference in the shoot habitus as seen during and at the end of the growth period.

Lower temperatures of 15° C and 10° C during the induction and maturation of the terminal buds in short-days have also been tested (figure 12). As described earlier (p. 48) this treatment delays bud formation and maturation. No dormancy requiring a cold treatment for bud breakage, however, is caused by low temperature as was the case with the high temperature. The amount of growth achieved after

flushing was comparable to that found after bud maturation in short-days at 20° C.

In certain respects the arctic provenance responds more strongly to temperature treatments during bud maturation and to a cold treatment of the resting bud, than the central European provenance. The very different growth rates caused by these treatments after flushing can be evaluated from figure 17. Bud maturation in short-days (16 or 8 hrs photoperiod) at 10° C gives under all circumstances a smaller amount of height growth than if the buds are matured at 20° C. Without cold treatment bud maturation at the shorter day length of 8 hrs produces superior growth at both temperatures than at the 16 hr short-day. After bud maturation with the latter photoperiod at 10° C neither uniform flushing nor growth is obtained. The cold treatment can overcome this difficulty but cannot restore the growth normally obtained with a maturation temperature of 20° C. The cold treatment increased the growth of the seedlings kept at 20° C for bud maturation with both photoperiods but was most effective with the longer short-days of 16 hrs.

Typical examples of the seedlings in these experiments from the provenance Laitamaa are presented in figure 18. The terminal shoot of the seedling in a) has a bud which was matured in short-days at 20° C. After transfer to long-days (24 hrs) the bud is flushing as shown in b), and after a period of growth the shoot is ending its second growth period as shown in c). The shoot in d), which had received a cold treatment prior to its transfer into long-day conditions for flushing, is of similar age than that in c) and in the middle of its growth period. As in the central European provenance the cold treatment induces a vigorous growth of the newly developed needles into a long and slender form.

Summarizing the experiences with the two provenances, a cold treatment does not appear necessary to break the resting buds in *Picea abies*, if they have been matured long enough in short-day conditions with an optimal temperature. A transfer to long-days alone suffices. Suboptimal temperature conditions — too high or too low —, ineffective short-day conditions, or long-day conditions lead to dor-

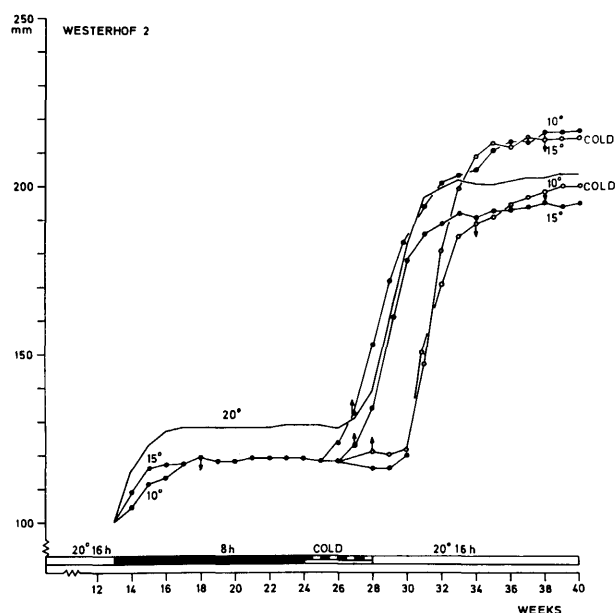


Fig. 12. — Same as fig. 11, but buds induced and matured at 15° C or 10° C. — No significant differences in the amount of growth after flushing are found with these treatments. (Each curve is mean of 9 seedlings.)

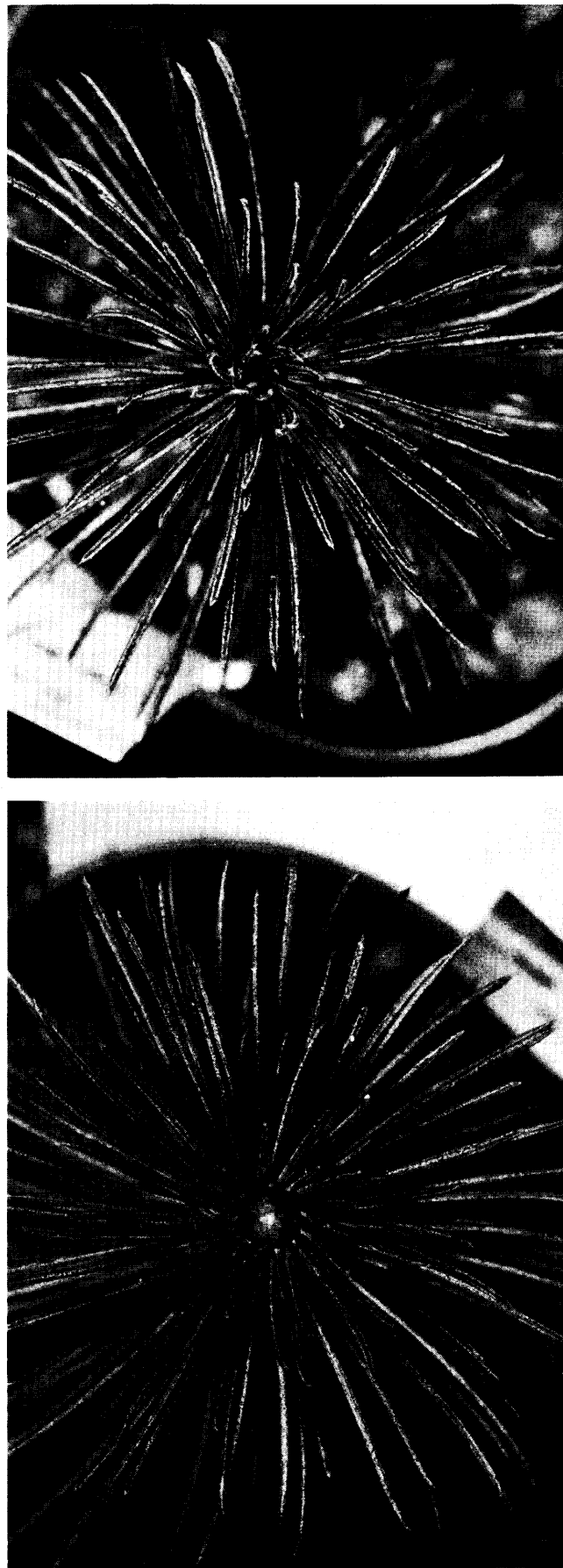


Fig. 13 — (a) and (b) Examples of seedlings from the experiment in fig. 11 at week 34. The buds were matured at 20° C in short-day conditions (photoperiod 8 hrs) and then transferred to long-day conditions (photoperiod 16 hrs). Only the seedlings in (b) received a cold treatment. Observe the long and slender needles on the latter. — (c) and (d) Terminal buds on seedlings of the experiment presented in fig. 14 at week 21. (c) Huge bud induced by short-day treatment (photoperiod 8 hrs) and matured in long-day conditions at 20° C (photoperiod 16 hrs). (d) Small bud induced and matured in the short-day conditions.

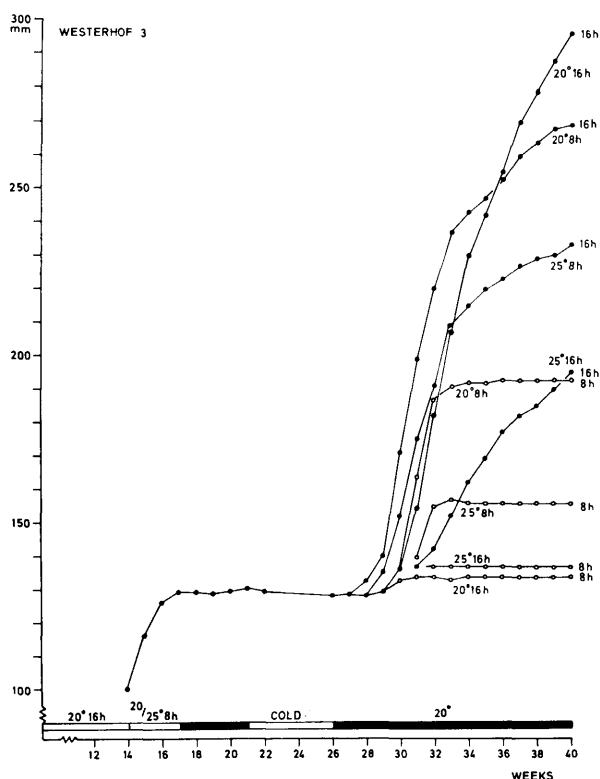


Fig. 14. — Growth curves of *Picea abies* seedlings provenance Westerhof showing the effect of temperature and photoperiod during bud maturation on their growth after bud breaking in long-days (photoperiod 16 hrs) or short-days (photoperiod 8 hrs). All seedlings received a cold treatment. Buds matured under long-day conditions at both temperatures cannot flush in short-day conditions. Limited growth is obtained in short-day conditions from buds matured under short-days. Long-days can induce breaking of buds which have been matured under short- or long-day conditions. A high temperature and long-days during bud maturation increase dormancy. High temperature reduces amount of growth obtained. (Each curve is mean of 10 seedlings.)

mant buds which require a cold treatment for uniform flushing and normal growth. The experiments done so far cannot answer the question, whether the low temperature *per se* or the extreme short-day conditions during the metabolic inactivity around 0° C remove the dormancy of the buds. A cold treatment, however, gives optimal synchronization of flushing and maximal needle growth, and we have therefore included a cold treatment in the following experiments and in the routine procedure for artificial aging. Figures 14, 15 and 16 contain the results of investigations on the effect of temperature and photoperiod during bud maturation on the subsequent growth of provenance Westerhof seedlings in long-days and short-days at 20° C. All growth curves are labeled at their right hand end with the photoperiod under which the seedlings were placed for flushing at the end of week 26, i.e., the end of the cold treatment (16 h = long-day; 8 h = short-day). To the left of this identification each curve is labeled with the temperature and photoperiod during bud maturation from week 18 to 21. Cessation of growth and induction of budset was achieved by short-days at 20° C or 25° C.

Buds matured at either temperature in long-days cannot flush in short-days, despite the cold treatment. They require long-days for breaking. Buds matured in short-days will flush in short-days but height growth is limited and a new terminal bud is rapidly formed. If temperatures are suboptimal during bud maturation, such as 25° C the amount

of growth in comparison with that obtained at the optimal temperature is reduced.

The amount of growth obtained in short-day conditions is, as far as can be judged from figure 14, dependent on the time of bud breaking. The buds matured at 20° C with an 8 hr photoperiod break first under short-day conditions and, therefore, reach the largest height before cessation of apical growth is accomplished by this very treatment. The buds matured at 25° C in short-days require a longer time to break their deeper dormancy and, therefore, are much shorter when apical growth is checked by the short-day conditions. The buds matured in long-days never enter flushing before the short-day conditions have induced the processes which lead to growth cessation.

Long-days remove the dormancy of all buds matured under the various conditions employed in the experiment of figure 14. Again, the time until bud breaking varies but in all cases the seedlings flush earlier than in short-day conditions. Upon transfer to long-days the dormancy of the buds matured in short-days (8 hr photoperiod) at 20° C ends before that of those matured in short days at 25° C. Buds matured in long-days at 20° C and 25° C flush last.

The major period of apical growth lasts 5 to 7 weeks in all groups of seedlings, whereafter the plants reduce their growth and finally cease growing one by one even under long-day conditions. The amount of growth obtained is partly a function of the time of bud break — the earlier flushing plant groups grow faster and higher — and partly a function of the conditions during bud maturation. High maturation temperature reduces the height. Long-day maturation at optimal temperature can produce as good or slightly better total growth in spite of late flushing, than short-day maturation.

Photographs of the seedlings from the experiment in figure 14 are given in figures 13 c, d, 15 and 16. Figure 13 c shows the huge bud obtained after long-day maturation at week 21 just prior to the onset of the cold treatment and figure 13 d a bud matured in short-days. In figure 15 the effect of photoperiod and temperature during bud maturation on flushing in long- or short-days is visible. The early flushing and vigorous growth of the plants in figure 15 b right is caused by bud maturation in short-days at 20° C, followed by transfer into long-day conditions after the cold treatment. On the other hand the plants in figure 15 c or d left did not flush because their buds were matured in long-days and then transferred to short-days. The plants reproduced in figure 15 b and d, which comprise the 20° C bud maturation series are shown at the end of the growth period in figure 16. The plants flushed in long-days (bottom) are superior to those flushed in short-days (top), while bud maturation in short-days (right) is superior to that in long-days (left). Under short-days no flushing occurred in plants, whose buds were matured under long-days.

Analogous experiments with the arctic provenance yielded the same results (figures 19 and 20). In contrast to the experiment with the central European provenance, all seedling groups were treated for 3 weeks with long-days to end the dormancy and obtain uniform breaking of the buds (figure 19). This procedure was successful with buds matured in short-days (16 hrs photoperiod), but only a few buds broke after long-day maturation. After the 3 weeks half of the seedlings in each group were transferred to short-days. Maximal height growth of the plants was obtained after short-day bud maturation regardless whether the plants were growing in long- or short-days after the bud

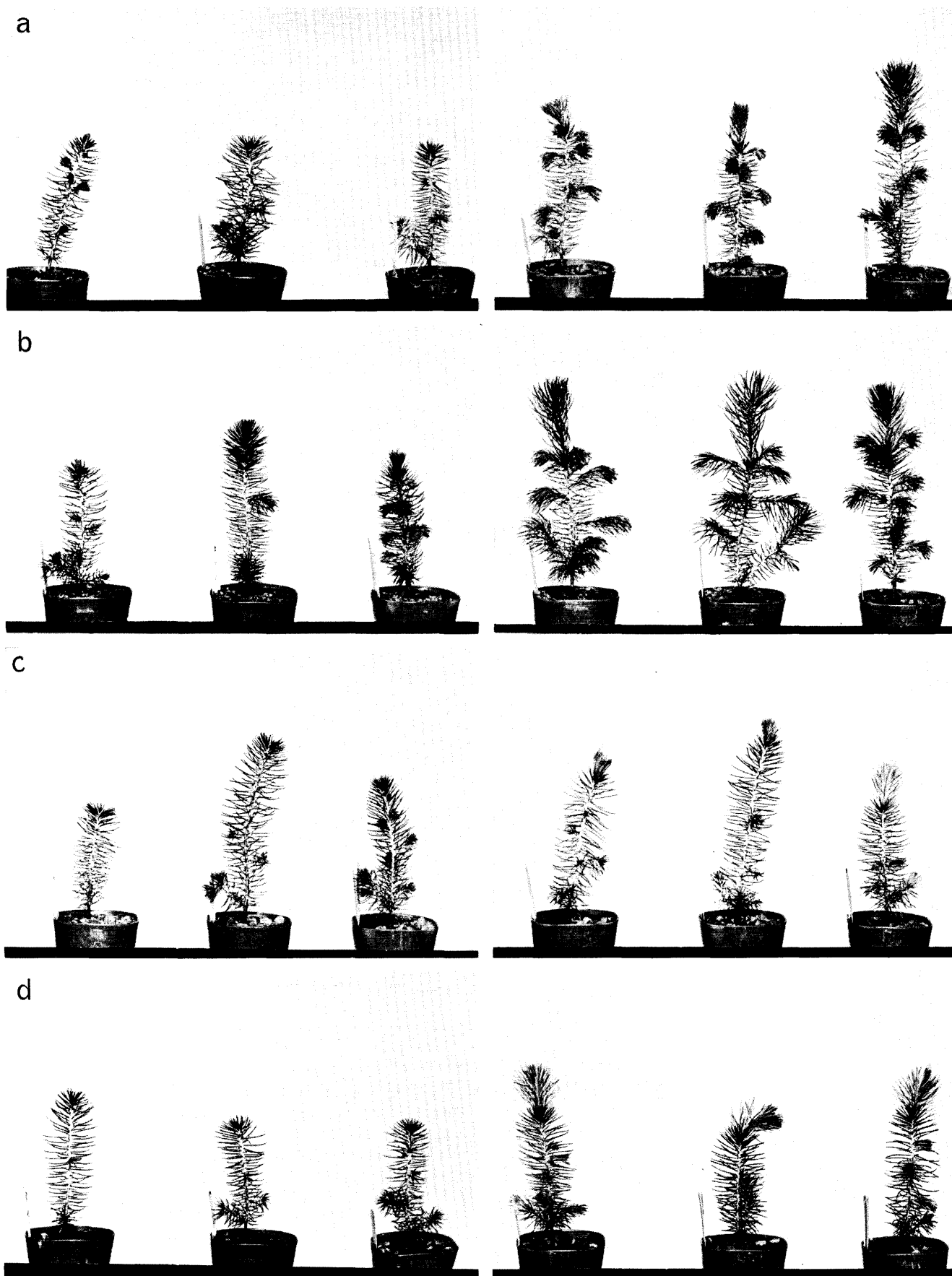


Fig. 15. — Examples of 31 week-old seedlings, i. e. during flushing from the experiment in fig. 14. *Left:* Buds matured in long-day conditions (photoperiod 16 hrs). *Right:* Buds matured in short-day conditions (photoperiod 8 hrs). — (a) Buds matured at 25° C, flushing in long-day conditions. (b) Buds matured at 20° C, flushing in long-day conditions. (c) Buds matured at 25° C, flushing in short-day conditions. (d) Buds matured at 20° C, flushing in short-day conditions.

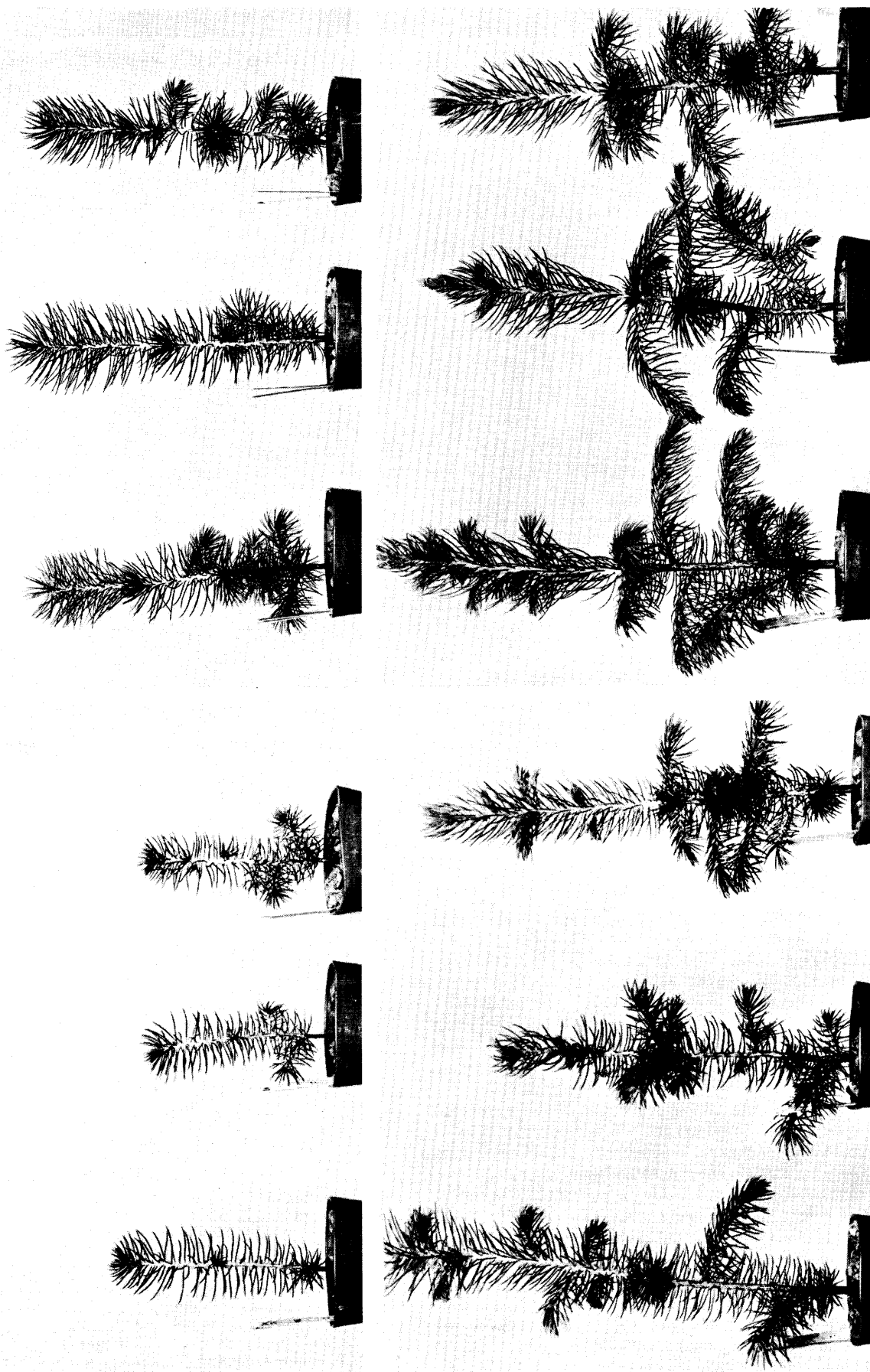


Fig. 16. — Same seedlings as in fig. 15 (b) and (d) at week 36, i. e. at the end of the growth period. (Only 20° C series is represented). — Left: Buds matured under long-day conditions. — Right: Buds matured under short-day conditions. — Bottom: Flushed in long-day conditions. Vigorous growth is obtained if buds are matured in short-days and flushed in long-days.

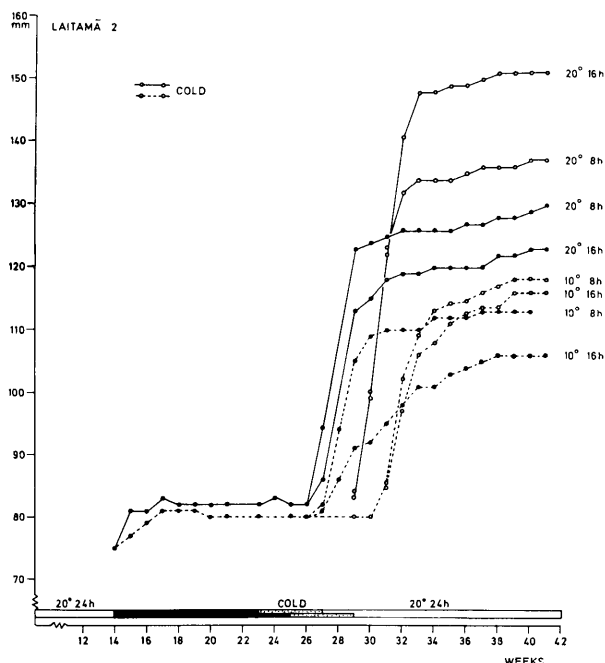


Fig. 17. — Growth curves of *Picea abies* seedlings provenance Laitamaa showing the effects of temperature (10°C or 20°C) and day length (photoperiod 16 and 8 hrs) during bud maturation on the subsequent growth of the seedlings in long-day conditions (photoperiod 24 hrs). The effect of a cold treatment after bud maturation is also studied. A temperature of 10°C during bud maturation gives less growth under all conditions than a temperature of 20°C does. A cold treatment increases the amount of growth obtained. (Each curve is mean of 9 seedlings.)

breaking had occurred (figure 20 right). Again buds matured in long-days could only be broken after a long time in long-day conditions and then they grew unevenly (figure 19, 20 lower left). In short-day conditions no growth is obtained from these buds in spite of the 3 weeks long-day treatment (figure 19, 20 upper left). Figure 19 also shows that a low (10°C) or high (25°C) night temperature during bud maturation in short-days decreases the growth of the plants by roughly 50%.

The major growth period of the Westerhof provenance was ended in long-day conditions by uniform cessation of growth and budset in the experiments on the effect of cold treatments (figure 11). Such uniform budset was not obtained in long-day conditions in the experiment described by figure 14. This difference could have been caused by the longer bud maturation period employed in the former experiment (9 weeks) than in the latter (7 weeks). Cessation of growth and budset in long-days is actually not expected from the results of the experiments with seedlings in their first growth period. It could well be that the first induction of a budset and resting period induces or synchronizes the "annual" periodicity, to which the plants thereafter tend to adhere. In some cases several growth and resting cycles may be necessary to establish the periodicity more firmly.

The major results of this study are summarized in figure 21. In d) terminal buds are shown which have been induced by short-days in the arctic provenance Laitamaa. The left-hand large bud was matured in long-days and the right-hand small one in short-days. In b and c the response to day length during bud maturation at 20°C on the subsequent growth in long- (left) or short-days (right) is recognizable. Parallel responses are obtained in the central European (b) and arctic provenance (c). With short-days during bud induction, short-days during bud maturation

followed by a cold treatment, and long-days during flushing as well as the major growth period, the vegetative cycle of *Picea abies* is optimally controlled. Reduction in growth results from suboptimal temperature (25°) during bud maturation as in figure 21 a.

The amount of growth is easily regulated in 4 different ways:

- 1) High or low night temperature during bud maturation can be used to decrease the amount of growth in the subsequent flush.
- 2) Long-days during bud maturation can be used to delay bud breaking in long-days, whereafter an early return to short-days during flushing can reduce the amount of growth.
- 3) Flushing in short-days can be used to reduce the amount of growth.
- 4) Transfer to short-days during flushing can be used to reduce the amount of growth.

A vegetative cycle with optimal growth will comprise maximally 4 weeks of bud maturation (short-days), 4 weeks of bud dormancy during cold treatment, 4 weeks of flushing and growth (long-days) and 3 weeks of budset (short-days). In the arctic provenance the flushing period will take only 3 weeks and the budset period 2 weeks. By regulating the amount of growth with the above parameters, we can age the plants artificially by cycles with either large growth steps or small growth steps. Various alternations of cycles with large and small growth steps can now also be tried for shortening the juvenile phase in *Picea abies*.

Discussion

Many of the individual responses to day length and temperature occurring in the various phases of the vegetative cycle in *Picea abies* are similar to those established for conifers and other woody plants. Perhaps the most

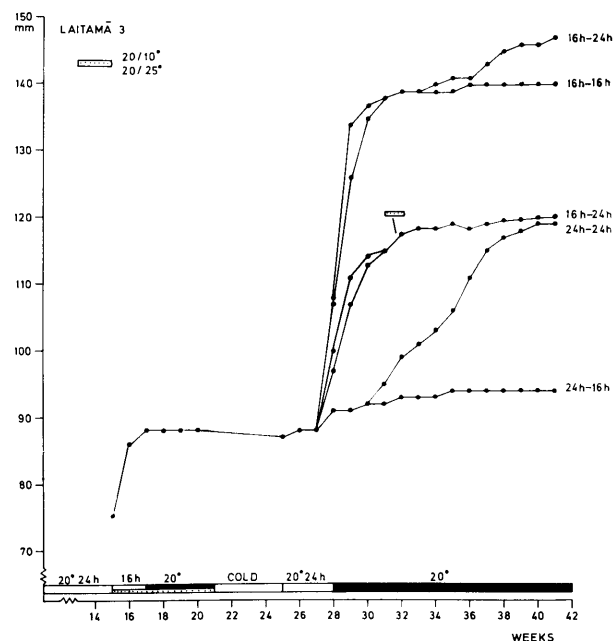


Fig. 19. — Growth curves of *Picea abies* seedlings provenance Laitamaa showing the effect of day length and night temperatures during bud maturation on the subsequent growth of the seedlings in long-day (photoperiod 24 hrs) and short-day conditions (photoperiod 16 hrs). Buds matured under long-day conditions require long-days for flushing. Bud maturation in long-days or at sub-optimal night temperatures reduces the amount of growth obtained. (Each curve is mean of 10 seedlings.)

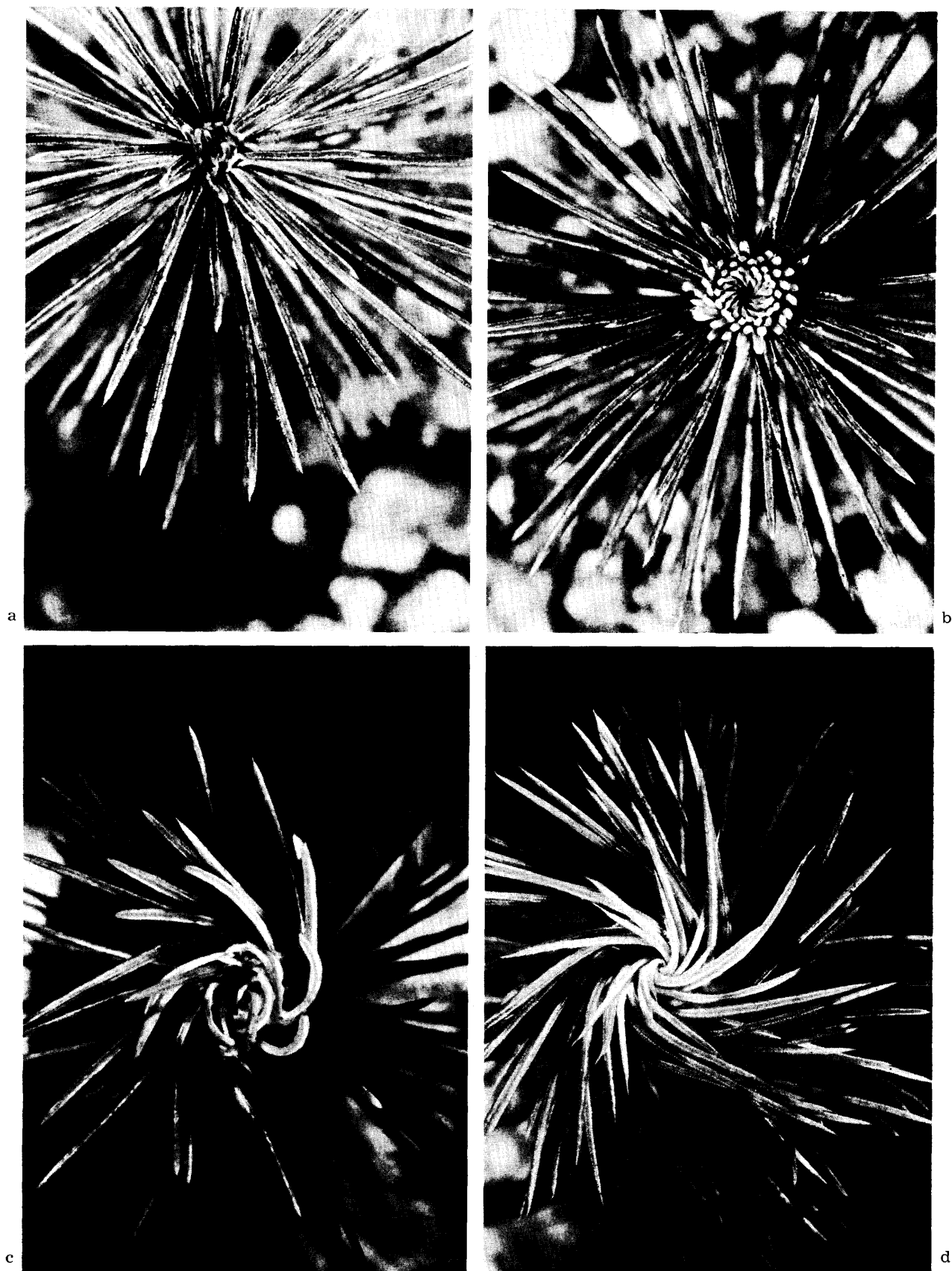


Fig. 18. — Examples of terminal shoots from seedlings in the experiment of fig. 17 at 20° C. (a), (b), (c) Same seedling at 23, 26, and 32 weeks respectively after planting. (a) Bud induced and matured in short-days (photoperiod 16 hrs). (b) Bud breaking in long-days (photoperiod 24 hrs). (c) Terminal shoot at the end of growth period. (d) Terminal shoot of 30 week-old seedling but with a cold treatment of the bud. Observe the long slender needles.

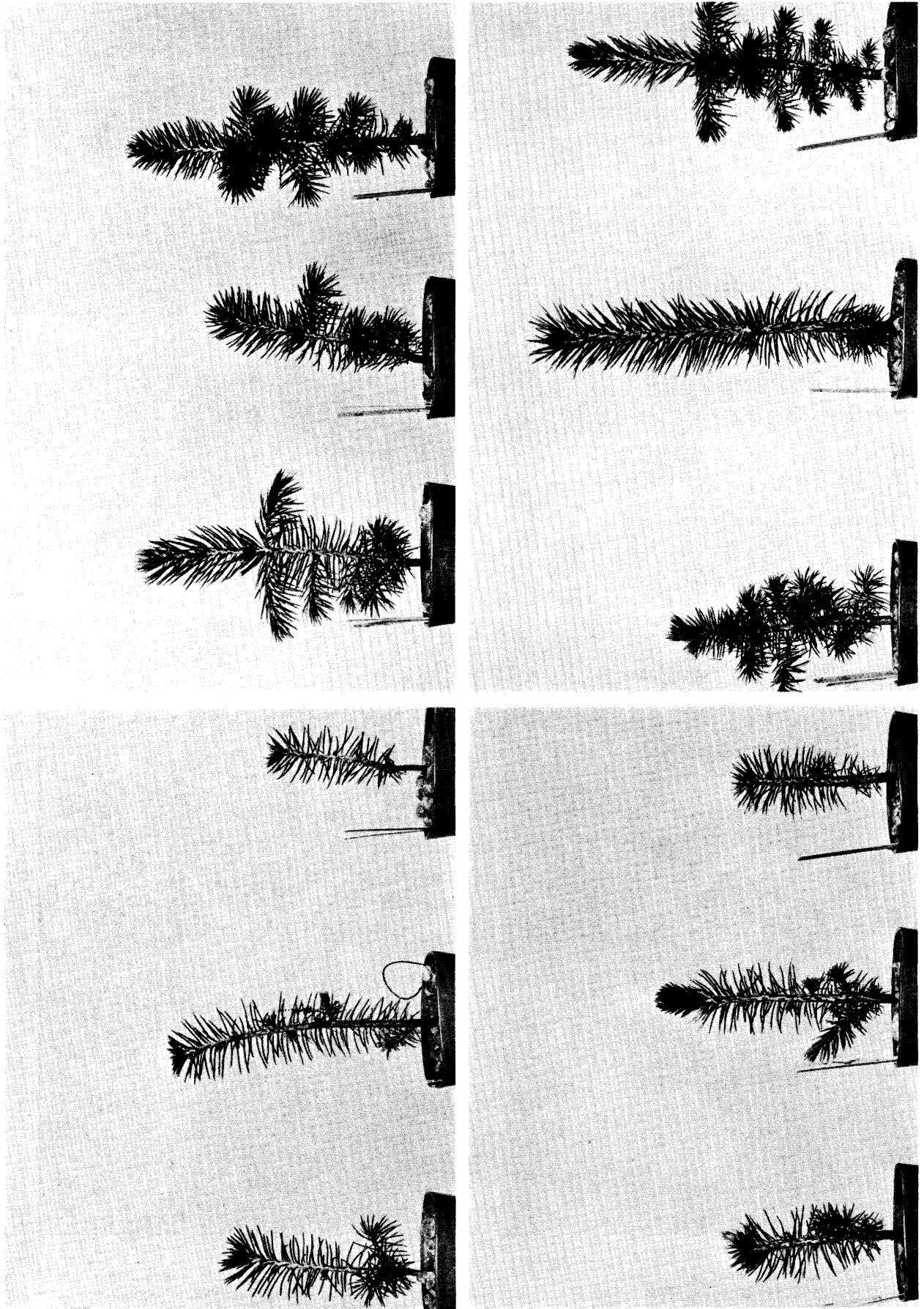


Fig. 20. — Examples of 37 week-old seedlings from the experiment in fig. 19. — *Left*: Buds matured in long-day conditions (photoperiod 24 hrs) at 20° C. — *Right*: Buds matured in short-day conditions (photoperiod 16 hrs) at 20° C. — *Top*: Flushing in short-days (16 hrs). — *Bottom*: Flushing in long-days (24 hrs).

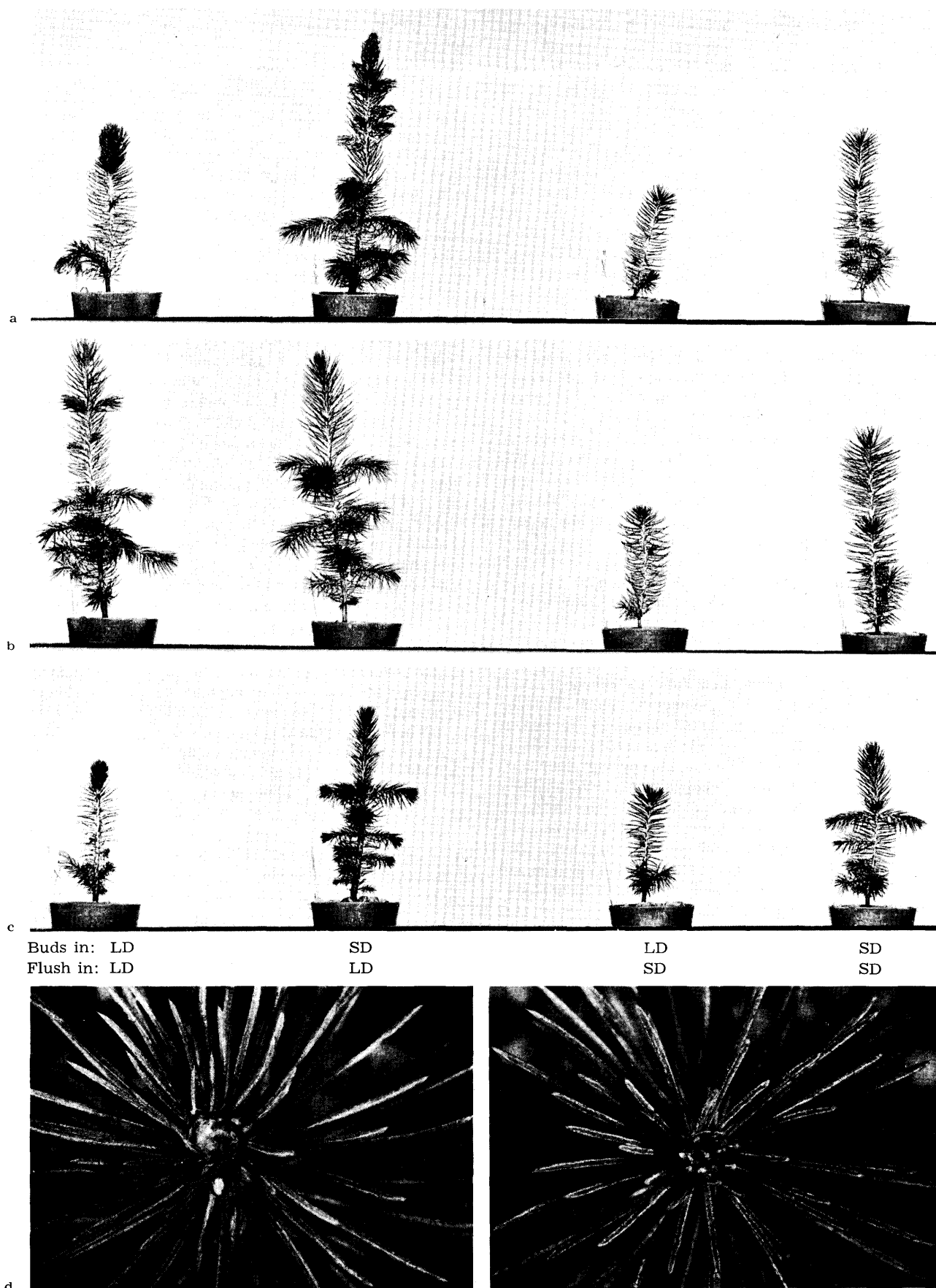


Fig. 21. — Summary of results (LD = long-day; SD = short-day). — (a) Effect of day length during bud maturation at 25° C on subsequent growth in long- or short-days visible on 36 week-old seedlings of Westerhof provenance. (b) Same as (a) but maturation of buds at 20° C. (c) Effect of day length during bud maturation at 20° C on subsequent growth in long- or short-days visible on 38 week-old seedlings of Laitamaa provenance. (d) Terminal buds induced by short-day treatment and matured in long-days (left) or short-days (right) on 21 week-old seedlings from the provenance Laitamaa.

ubiquitous of the phenomena, which have been extensively reviewed by VEGIS (28, 29) is the cessation of growth and induction of budset by short-day treatments, for example in *Pinus*, *Picea*, *Larix* and other conifers (1, 30, 31, 32, 27, 10, 25). The hastening of dormancy by short-days is also well known for woody plants (29). That high temperatures during bud maturation increase dormancy has been shown by VEGIS (29) for *Stratiotes* and is found in fruit trees. Our results give a clear example how temperature and photoperiodic conditions during bud maturation determine whether breaking of bud dormancy requires a cold treatment, a long-day treatment or both. The diversity in such requirements reported for various woody species (33, 36) probably reflects differences in the experimental conditions rather than species specificities. In *Pinus sylvestris*, *Picea abies* and many deciduous trees, the climatic conditions during bud induction and maturation largely determine the amount of height but not diameter growth in the following season (15, 6, 18). The experiments reported in this paper demonstrate this in *Picea abies*. Since the amount of height growth in *Picea* is so easily regulated by the temperature conditions during bud maturation, plants of this species represent a very suitable material to analyze the theory that the quantity of carbohydrates stored during bud initiation and maturation is a limiting factor in the height growth produced in the following flush.

Since the vegetative cycle of *Picea abies* can be experimentally controlled, the question can be asked whether the flower inducible, i. e. adult, stage is attained with a certain minimum number of growth cycles or with a certain minimum amount of juvenile growth. Continuous growth under long-days overcame or reduced the juvenile stage in *Betula verrucosa* (23), *Pinus taeda* (14), and *Rhododendron* (8). Although seedlings, 1 and 2 year-old plants of *Picea abies* have been kept as long as 36 weeks in continuous growth under long-days, they all eventually ceased to grow and formed terminal buds, e. g., after they had been transplanted to larger pots. Repeated budset and flushing has been observed under these conditions in the northern provenance. The diverse responses — continuous growth, repeated flushing, or eventual setting of dormant buds after repeated flushing — have been noted earlier by DOWNS (10) for different tree species when kept under continuous long-days. Very likely ecotypes of the same species may also respond differently to continuous long-day conditions. The juvenile phase of the *Picea* provenances studied here probably cannot be overcome by a procedure with uninterrupted growth under long-days.

To find out if total size in *Picea abies* is the factor determining the end of the juvenile phase two approaches can be used: a) Short-day treatments for 6 days give cessation of growth and flushing of the bud after return to long-days in 2 to 3 weeks (figure 8). If such a treatment is repeated every 10 weeks, longer periods of dormancy may be avoided and large size achieved fast. b) The alternative is to employ the vegetative cycle giving maximal height growth (p. 58), i. e., bud maturation in short-days, cold treatment, flushing in long-days, and budset in short-days after growth has occurred.

If the number of growth cycles is the significant factor, cycles of the shortest duration (p. 58) will be most advantageous.

For budset in the central European provenance the critical day length is 14 hrs. A day length longer than 14 hrs exists at Westerhof between April 18 and August 24. Similarly, a day length longer than the critical length of 20 hrs for

the arctic provenance is found at Laitamaa between May 24 and July 19.

The climatic varieties (ecotypes) discovered by CIESLAR (3, 4, 5, 7) and ENGLER (11, 12, 13) in *Picea abies* emerge as populations which are adapted to latitude and elevation by means of a genetically fixed critical day length response of budset or continuous growth. By his investigations of *Picea* provenances LANGLET (20, 21) has elucidated the importance of a timely budset and plant maturation for resistance against autumn and winter frosts. VAARTAJA (27) has recognized photoperiodic ecotypes in several species of *Picea* and many other trees. He considers the genetic adaptation to photoperiods as a means by which trees adapt indirectly to the seasonally changing climatic factors at different latitudes and altitudes. Since plants have evolved pigment systems and mechanisms to measure day length precisely, it is not surprising that adaptation to day length is often used instead of direct adaptation to the more inconsistent temperature periodicities. Specific photoperiodic adaptations are also encountered among the arctic and alpine ecotypes of other plants, e. g. *Oxyria digyna* (24). In an elegant analysis HOLZER (17) has proved that the critical day length for terminal bud formation is the most reliable criterion for identification of altitude ecotypes of *Picea abies*. Low altitude ecotypes have a shorter critical day length for uninterrupted growth than high elevation ecotypes, which may require more than 16 hrs light. This behaviour is expected for an indirect adaptation by day length to a short growing and plant maturing season at high altitudes.

In our study we find that the optimal growth and bud maturing temperature is the same (20° C) for both the central European and the arctic provenance. Under 20° C during growth and bud maturation the northern provenance, however, grows less in height than the central European one and concentrates its growth to a shorter period. In agreement with the previous findings by ENGLER and LANGLET, the arctic provenance starts to flush earlier after the end of the cold treatment than the central European provenance. More important for the provenance problem is the finding that the day length and temperature during bud maturation can have a decisive influence on the time of the initiation of flushing. The very accurate adaptation of various provenances to day length will allow clarification on the conditions for frost resistance at various stages of the vegetative cycle in phytotron experiments.

The clear cut photoperiodic adaptations of the *Picea* ecotypes make them a favourable material for the analysis of the genetic basis of the mechanism by which plants measure day length. Determination of the critical day lengths for budset in a complete series of latitudinal or altitudinal populations should reveal, if the critical day length can be genetically fixed at any given day length or if only a certain number of discrete day lengths differing, for instance, by 30 or 60 min. are possible. Determination of the critical day lengths for F₁ seedlings from crosses between distinct photoperiodic ecotypes may give a hint as to whether the product of one or many genes determines what a plant considers critical day length. Particularly interesting in this respect would be crosses between northern and alpine ecotypes which respond to the same critical day length.

Acknowledgements

We would like to dedicate this paper to Professor Dr. WOLFGANG VON WETTSTEIN at the occasion of his 70th birthday.

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Summary

The vegetative cycle of *Picea abies* can be controlled by a sequence of photoperiodic and thermoperiodic conditions. These have been defined for a central European and an arctic provenance.

- 1) Optimal growth occurs in both provenances at 20° C in long-days.
- 2) Induction of terminal budset is a short-day response. The critical day length for the central European provenance lies around 14 hrs, for the arctic one around 20 hrs.
- 3) Photoperiod and temperature during bud maturation have a decisive influence on the time of the initiation of flushing as well as the amount of growth during the flush.
- 4) An optimal vegetative cycle for the central European provenance is obtained in 15 weeks and comprises 4 weeks of bud maturation in short-days, 4 weeks of bud dormancy with a cold treatment, 4 weeks of flushing and growth in long-days, and 3 weeks of budset in short-days.
- 5) An optimal vegetative cycle for the arctic provenance is obtained in 13 weeks as only 3 weeks are required for the flushing period and 2 weeks for budset.
- 6) The amount of height growth during the flush can be regulated in 4 different ways:
 - a) High or low night temperatures during bud maturation reduce the amount of growth in the subsequent flush.
 - b) Long-days during bud maturation delay bud breaking in long-days; whereafter an early return to short-days during flushing reduces the amount of growth.
 - c) Flushing in short-days reduces the amount of growth.
 - d) Transfer to short-days during flushing reduces the amount of growth.

Zusammenfassung

Der Wechsel von Wachstum und Ruhe in der vegetativen Phase von *Picea abies* kann durch eine Folge photo- und thermoperiodischer Bedingungen gesteuert werden. Diese Bedingungen wurden für eine mitteleuropäische und eine arktische Provenienz bestimmt.

- 1) In beiden Provenienzen erfolgt optimales Wachstum bei 20° C im Langtag.
- 2) Die Induktion der Terminalknospenbildung erfolgt durch Kurztag. Die kritische Tageslänge für diese Reaktion liegt für die mitteleuropäische Provenienz bei 14 Stunden und für die arktische bei 20 Stunden.
- 3) Tageslänge und Temperatur während der Knospenreife haben einen entscheidenden Einfluß auf den Zeitpunkt des Treibens der Knospen sowie auf das Höhenwachstum des neuen Triebes.
- 4) Ein optimaler vegetativer Wachstumszyklus von 15 Wochen umfaßt für die mitteleuropäische Provenienz 4 Wochen Knospenreife im Kurztag, 4 Wochen Knospenruhe mit einer Kältebehandlung, 4 Wochen Knospentrieb und Wachstum im Langtag, sowie 3 Wochen Terminalknospenbildung im Kurztag.
- 5) Für die arktische Provenienz kann der Wachstumszyklus auf 13 Wochen verkürzt werden, da nur 3 Wochen zum Trieb und 2 Wochen zur Terminalknospenbildung benötigt werden.
- 6) Der Höhenzuwachs kann durch 4 verschiedene Behandlungen reguliert werden:
 - a) Hohe oder tiefe Nachttemperaturen während der Knospenreife vermindern den Zuwachs des neuen Triebes.
 - b) Langtag während der Knospenreife verzögert den Knospentrieb im Langtag. Eine darauffolgende frühe Rückführung der wachsenden Triebe in den Kurztag begrenzt den Höhenzuwachs.
 - c) Knospentrieb im Kurztag begrenzt den Höhenzuwachs.
 - d) Überführung in den Kurztag während des Austreibens begrenzt den Höhenzuwachs.

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Vererbungsverhältnisse in einer Halbgeschwisterfamilie von *Picea abies* (L.) Karst f. *virgata* (Jacques) Rehd.

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Im Herbst 1958 wurden im Botanischen Garten in Maria-brunn zwei frei abgeblühte Zapfen einer Schlangenfichte (*Picea abies* [L.] KARST. f. *virgata* [JACQUES] REHD.) geerntet; von deren Samen gelangten 36 Sämlinge zur Aufzucht. Diese wurden 1961 verschult und 1964 nochmals im Weitverband (1 × 1 m) ausgepflanzt. Da im Laufe der Jahre fünf Pflanzen eingegangen sind, mußte die Auswertung der Ergebnisse auf insgesamt 31 Halbgeschwister beschränkt werden.

Im Laufe der Beobachtungsjahre 1962 bis 1967 wurden einige Merkmale, wie Austrieb, Höhenwachstum und dergleichen, wiederholt aufgenommen; andere Merkmale, wie Knospenöffnung und Gallausbefall wurden nur in den letzten Aufnahmejahren registriert. Insgesamt wurden dabei 20 Merkmale aufgenommen, wodurch infolge einiger Wiederholungen zusammen 48 Einzelaufnahmen zu den Vergleichen herangezogen werden konnten. Eine Übersicht über sämtliche Aufnahmedaten ist in *Tabelle 3* dargestellt.

Als besonders augenscheinliches Merkmal wurde der Grad der Schlangenform (S) im Jahre 1963 und erneut 1966 aufgenommen, wobei vor allem bei den Zwischenformen geringfügige Verschiebungen in der Beurteilung festzustellen waren. Als stärkste Änderung tritt hier eine Pflanze auf, bei der auf Grund ihres langsamen Wachstums im Jahre 1963 die Zugehörigkeit zu dieser Familie sehr zweifelhaft erschien; diese Pflanze war im Alter von fünf Jahren 14 cm hoch gegenüber einer Höhe von 25–76 cm bei den übrigen Pflanzen; bis zum Jahre 1966 entwickelte sich diese Pflanze jedoch zu einer eindeutigen Schlangenfichte mit langsamem Wuchs (jährlich etwa 2–10 cm Zuwachs) (*Abb. 2 c*). Wie die erste Aufnahme des Grades der Schlangenform (1963) ergab, entfielen auf die 5 ausgeschiedenen Klassen (keine : schwache : mittlere : starke : sehr starke Schlangenform) 22 : 3 : 4 : 5 : 2 (zusammen 36) Pflanzen. Dieses Verhältnis hat sich nach den letzten Aufnahmen (insgesamt 6 Klassen) folgendermaßen verschoben 15 : 6 : 3 : 1 : 5 : 1 (zusammen 31 Pflanzen infolge von Ausfällen), wobei vor allem die vorerst nicht genau bestimmbaren Zwischenformen eine Verschiebung erfuhren.

Aus diesen Aufspaltungszahlen müßte man folgendes

schließen: Die aus 2 Zapfen stammenden Nachkommen dieser Schlangenfichte als Mutter müßten zum Teil durch Pollen der im Arboretum benachbart stehenden Rückkreuzungsform einer Schlangenfichte mit einer normalen Form und zum Teil durch normalen Fichtenpollen bestäubt worden sein, um das aufgetretene Aufspaltungs-verhältnis erklären zu können. Bei der Annahme von zwei nicht gekoppelten Genen *a* und *b* für die Ausbildung einer Schlangenfichte müßte das Gen *a* stärker wirksam sein als das Gen *b*; die Mutter dieser Halbgeschwisterfamilie hätte die Kombination *aaBb*, d. h., das homozygote Merkmal *aa* wirkt stark auf die Ausbildung der Schlangenform und wird durch das heterozygote *Bb* nur wenig gestört. Der Pollenspender hingegen, in Arboretum bezeichnet mit „*virgata* × Normalform“, der erst im Alter die Einkreuzung einer Schlangenfichte erkennen läßt, hät-

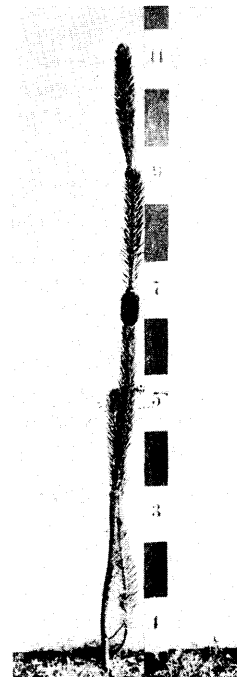


Abbildung 1. — „Astlose“ Fichte (Maßstabteilung in 5 cm).

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Tabelle 1

					Klasse	Anzahl	Ausbildungsform
aB	AB	Ab	aB	ab	1	1	AaBB = Normalform
					2	2	AaBb = in früher Jugend ± Normalform
					3	1	Aabb = ± Kreuzungsform
	AaBB	AaBb	aaBB	aaBb	4	1	aaBB = ± Kreuzungsform
					5	2	aaBb = Schlangenfichte
	ab	AaBb	Aabb	aaBb	6	1	aabb = astlose Fichte