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Aim and Scope Silva Fennica publishes original research articles, critical review articles, research notes reporting preliminary or tentative results, and discussion papers. The journal covers all aspects of forest research, both basic and applied subjects. The scope includes forest environment and silviculture, physiology, ecology, soil science, entomology, pathology, and genetics related to forests, forest operations and techniques, inventory, growth, yield, quantitative and management sciences, forest products, as well as forestry-related social, economic, information and policy sciences.

SILVA FENNICA

a quarterly journal of forest science

Special Issue on

Adaptation of Tree Breeding to Changing Circumstances and Demands

Vol. 28(4), 1994

The Finnish Society of Forest Science

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Foreword

This issue is composed of papers presented at the scientific meeting of the Nordic Group of Forest Genetics and Tree Breeding held in Finland August 30–September 2, 1994. The Nordic Group of Forest Genetics and Tree Breeding is one of the permanent working bodies of the Board of Cooperation in the Nordic Forest Research, SNS (Samarbetsnämnd för Nordisk Skogsforskning). The Nordic Group of Forest Genetics and Tree Breeding has arranged annual meetings in each country in turn. The meeting and the subsequent excursion were organized by the team: Mr. Matti Haapanen, Mr. Martti Lepistö, Ms. Seija Nurminiemi, and Dr. Pirkko Velling, conducted by Prof. Veikko Koski.

Seventeen papers covering a wide variety of topics under the theme were presented in three sessions: Response to Declining Demand for Genetically Improved Reforestation Material, Wood Quality Rehabilitated, and Biodiversity and Environmental Change. The papers published in this special issue were not selected to cover a particular session nor to represent the wide range of subjects under the theme of the meeting. Each speaker had the opportunity to submit a manuscript expanding the presentation in the meeting. The manuscripts that survived the peer review process are published in this issue. The topics extend over the adaptation mechanisms of trees in boreal forests, the genetic diversity of natural and planted forests, the seed production of micropropagated trees and, the interaction of genotype and silvicultural practices to timber quality.

If this issue reflects any significant trends in the research of tree breeding, they could be outlined as developments of incorporating genetic, silvicultural and economic aspects in wood production, and the demand of integrated knowledge on adaptation mechanisms of trees to the environment and responses of trees to environmental changes. Dialogue is encouraged between tree breeders, ecologists and economists.

Eeva Korpilahti *Veikko Koski*

Second and Third Growth Period Responses of *Picea abies* Families to First Growth Period Photoperiodic, Light Intensity and Temperature Treatments

Hyun Kang, Inger Ekberg, Gösta Eriksson and Johan Ununger

Kang, H., Ekberg I., Eriksson, G. & Ununger, J. 1994. Second and third growth period responses of *Picea abies* families to first growth period photoperiodic, light intensity and temperature treatments. Silva Fennica 28(4): 215–232.

Seedlings of *Picea abies* (L.) Karst. full-sib families of contrasting origin were cultivated in a phytotron under different photoperiodic, light-intensity and temperature treatments during their first growth period. The effects of the treatments on juvenile growth traits – whether enhanced or delayed maturation was induced – were observed during the two subsequent growth periods. The following hypotheses were tested: (A) Enhanced maturation can be induced after treatments in the first growth period from sowing with (i) a long period of continuous light during active growth (24 weeks vs. 8 weeks); (ii) a shorter night during bud maturation (12 h vs. 16 h); a high temperature (25 °C vs. 20 °C) during (iii) active growth, growth cessation and bud maturation; and during (iv) the latter part of growth cessation and bud maturation only. (B) Delayed maturation can be induced after (i) a low light intensity during growth cessation and bud maturation (114 µmol m^{-2} s^{-1} vs. 340 µmol m^{-2} s^{-1}); a low temperature (15 °C vs. 20 °C) during (ii) active growth, growth cessation and bud maturation; and during (iii) the latter part of growth cessation and bud maturation only.

The most dramatic treatment effect was 24 weeks of continuous light during active growth. All traits showed a significantly more mature performance in the second growth period compared with the control. The effect for all but one trait was carried over to the third growth period. This is in accordance with the hypothesis that the activity of the apical shoot meristems controls the maturation process. For the other treatments there was only weak or no support for the hypothesis of inducing enhanced or delayed maturation. Strong family effects were observed for all traits. Differential responses of the various latitudinal families were observed, suggesting that family effects must be considered to predict and interpret correctly how plants will respond to environmental effects.

Keywords environmental effects, genetic effects, maturation, juvenility, growth, seedlings, *Picea abies*.

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1 Introduction

Growth rhythm is crucial for plant survival and future growth of *Picea abies* (Langlet 1960, Dietrichson 1971, Krutzsch 1975). Too early bud flushing and too late inwintering may both be detrimental for successful reforestation. There is a dramatic change in the point of time for these two traits with age (Ununger et al. 1988) such that bud flushing occurs later with increasing age of the plant simultaneously with an earlier inwintering. This means that the probability for frost exposure of *Picea abies* seedlings is considerably reduced with time. Together with date of bud flushing and inwintering, free growth is another juvenile trait which disappears with time. Ekberg et al. (1991) showed that it declined from 65 % to 8 % over growth periods 3 to 8 in southern families. The southern entries kept the juvenile growth performance longer than the northern. In spite of a shorter growth period at later ages the leader length increases, which means that the growth rate during the period of active growth is higher at later ages.

Since plants can respond to different cultivation conditions by altering growth in ways (cf. Schmid 1992) that may carry over to subsequent years, it is of practical interest to try to induce a non-juvenile growth pattern in young seedlings. Such effects carried over to subsequent growth periods were referred to as preconditioning by Rowe (1964). Preconditioning effects may gradually disappear with time, or could permanently change the ontogeny of the tree.

Some variations in light and temperature appear to have only short-term impacts on subsequent seedling growth and development, but the continuous light applied to *Picea pungens* seedlings by Young and Hanover (1976) produced a lasting effect. Preconditioning effects induced during embryo development – i.e. environmental conditioning during this ontogenetic stage – or perhaps earlier, can influence juvenile plant phenology in subsequent years (Bjørnstad 1981, Dormling and Johnsen 1992). Furthermore, treatments during the first growth period might influence ontogenetic development, implying that an accelerated or delayed maturation was caused by enhanced or retarded growth, respectively (e.g. Hackett 1985, Longman 1987, Poethig 1990). This effect on the ontogeny of a plant is primarily manifested during the juvenile stage. Whether this effect also influences the growth capacity or phenology of the adult tree is not known.

Previous studies have shown that seedlings of *Picea* species grown under long periods of continuous light during the first year pass the juvenile stage rapidly and mature sooner than those grown under normal light conditions (Young and Hanover 1976, Bongarten and Hanover 1985). In addition, studies of other species have shown that extended photoperiod combined with favourable temperature, water, and nutrient conditions can reduce the juvenile phase (Rudolph 1966, Robinson and Wareing 1969, Zimmerman 1972, Cecich 1981, Hackett 1985). Low light intensity, on the contrary, applied in the first growing season of *Pseudotsuga menziesii* seedlings resulted in earlier bud break and a higher frequency of a second flush in the next year (Drew and Ferrell 1977) indicating that the juvenile phase can be prolonged. High autumn temperatures caused delayed bud break in *Picea* the following spring (Heide 1974, Malcolm and Pymar 1975), and various temperature regimes during the first growth period from sowing have been shown to influence shoot length in the second growth period in *Picea abies* (Dormling et al. 1968, Heide

1974) and *Pinus sylvestris* (Junttila 1986). Temperature effects during the latter part of summer are considered to be critical because this is the period when needle and reproductive primordia are formed (Lanner 1976, Pollard and Logan 1977, 1979, Cannell 1978, Ununger et al. 1988, Kremer and Larson 1983, Deal et al. 1990). The physiological, biochemical and molecular processes behind the enhanced or delayed maturation caused by accelerated or retarded growth is unknown, but as stated by Greenwood and Hutchinson (1993) "continuing cell division of an apical meristem may be the actual mechanism that drives the maturation process". The importance of passing through "a certain number of cell divisions" for inducing phase change from juvenile to mature (flowering) condition was discussed by Robinson and Wareing as early as in 1969.

There is a clear need to improve our knowledge of the pattern of growth, seedling adaptation to new environments, and seedling maturation by obtaining a better understanding of how plants respond to different environmental conditions. This knowledge can be used in nurseries to apply cultivation regimes that would change the growth rhythm to produce more frost tolerant plants when outplanted on frost-prone sites. A reduction of the length of the juvenile phase could also be favourable for early tests in plant breeding and for induction of early flowering. The opposite treatment – to keep the plants longer in the juvenile phase or even rejuvenate them – could be of value for cutting production in clonal forestry if the motherplants could be kept a longer time in the juvenile phase without any reduction of the rooting ability of the scions or changes in the growth habit of the cuttings. In addition, Hänninen (1990) pointed out that besides a better understanding of seedling responses to different environmental conditions, knowledge of the seedling maturation during the juvenile phase should also be considered when developing mathematical models for bud-dormancy release in conifers.

The main objective of this study was to estimate the magnitude and duration of impact of different photoperiodic, light-intensity and temperature treatments on seven juvenile traits in *Picea abies* families of widely different origin. We intended to test the following hypotheses. (A) Enhanced maturation can be induced after treatments in the first growth period from sowing with (i) a long period of continuous light during active growth (24 weeks vs. 8 weeks); (ii) a shorter night during bud maturation (12 h vs. 16 h); a high temperature (25 °C vs. 20 °C) during (iii) active growth, growth cessation and bud maturation; and during (iv) the latter part of growth cessation and bud maturation only. (B) Delayed maturation can be induced after (i) a low light intensity during growth cessation and bud maturation (114 µmol m^{-2} s^{-1} vs. 340 µmol m^{-2} s^{-1}); a low temperature (15 °C vs. 20 °C) during (ii) active growth, growth cessation and bud maturation; and during (iii) the latter part of growth cessation and bud maturation only. The hypotheses are summerized in Table 3.

2 Material and Methods

We selected for this study six full-sib families of *Picea abies* with contrasting origin to ensure a large variation in phenology and growth traits (Table 1).

The seedlings were cultivated from sowing for three consecutive growth periods – GP1, GP2 and GP3, respectively – in the Phytotron at the Swedish University of Agricultural Sciences, Stockholm, Sweden. One growth period corresponds to one growing season (one year's growth) in the nursery. Following seed germination, the

Table 1. Origin and classification of full-sib families of *Picea abies* used in this study.

Family number	Crossing	Designation
1	Belgium × Germany	S × S
2	France × France	S × S
3	central Sweden × central Sweden	C × C
4	northern Sweden × Belgium	N × S
5	northern Sweden × northern Sweden[1)]	N × N
6	northern Sweden × northern Sweden[2)]	N × N

[1)] Included in the photoperiod and light intensity treatments only.
[2)] Included in the temperature treatments only.

Table 2. Cultivation conditions during phase I–III of the first growth period for the photoperiodic and light-intensity treatments and for the control. Photoperiods and temperature for the control during phase I–III are specified in Fig. 1. The temperature was 20 °C during phase I–III for all treatments and the control. Comparisons with the control are indicated in bold type.

Cultivation conditions	Growth-period phase I	II	III	Treatment type
Weeks	8	12	8	Control
Night length (h)	0	1→12	16	
Light intensity (µmol m^{-2} s^{-1})	340	340	340	
Weeks	8	12	8	ph12LI
Night length (h)	0	1→12	**12**	
Light intensity (µmol m^{-2} s^{-1})	340	340	340	
Weeks	8	12	8	ph16li
Night length (h)	0	1→12	16	
Light intensity (µmol m^{-2} s^{-1})	340	**114**	**114**	
Weeks	**24**	12	8	PH16LI
Night length (h)	0	1→12	16	
Light intensity (µmol m^{-2} s^{-1})	340	340	340	
Weeks	**24**	12	8	PH12LI
Night length (h)	0	1→12	**12**	
Light intensity (µmol m^{-2} s^{-1})	340	340	340	
Weeks	**24**	12	8	PH16li
Night length (h)	0	1→12	16	
Light intensity (µmol m^{-2} s^{-1})	340	**114**	**114**	

Table 3. Cultivation conditions during phase I–III of the first growth period for thhe temperature treatments and for the control. Photoperiods and temperature for the control during phase I–III are specified in Fig. 1. The light intensity was 340 µmol m^{-2} s^{-1} during phase I–III for all treatments and the control. Comparisons with the control are indicated in bold type.

Cultivation conditions	Growth-period phase I	II	III	Treatment type
Weeks	8	12	8	Control
Temperature (°C)	20	20	20	
Night length (h)	0	1→12	16	
Weeks	8	5 7	8	TEMP20–25
Temperature (°C)	20	20 **25**	**25**	
Night length (h)	0	1→12	16	
Weeks	8	5 7	8	temp20–15
Temperature (°C)	20	20 **15**	**15**	
Night length (h)	0	1→12	16	
Weeks	8	12	8	TEMP25
Temperature (°C)	**25**	**25**	**25**	
Night length (h)	0	1→12	16	
Weeks	8	12	8	temp15
Temperature (°C)	**15**	**15**	**15**	
Night length (h)	0	1→12	16	

seedlings were transplanted to pots with mineral wool. A complete nutrient solution (Ingestad 1979) of low concentration (100 mg N l–1) was provided at most twice a day or every second day dependent on the developmental stage of the plants. The proportions of N:P:K were 100:65:13. Relative air humidity was maintained at 75 %. The light intensities were supplied by Osram HQIR 250W, NDL lamps (providing 340 µmol m^{-2} s^{-1} or 114 µmol m^{-2} s^{-1} at 400–700 nm). The plants were continuously lowered on the growth trucks to ensure as constant a light intensity as possible at the top of the canopies. Between the growth periods the seedlings were transplanted into larger pots. To provide space for the larger pots the number of plants studied was randomly reduced with each growth period. The number of plants per family per treatment during each growth period was: 20 in GP1, 16 in GP2, and 12 in GP3. A randomized complete block design was used with one quarter of the plants per block.

Two main types of treatment – photoperiodic, light-intensity treatments and temperature treatments – were applied to the seedlings during GP1, and the effects of the treatments were analyzed during the following two growth periods except for two treatments (ph12LI and PH12LI, for explanation of the treatment symbols see Table 2) which were not continued to GP3. The two types of treatment could not be carried out simultaneously but consecutively owing to the space limitations in the phytotron. Each treatment type had therefore its own control, but the environmental conditions were set to be equal for both controls. The control conditions were defined based on information accumulated in over 25 years of studies of *Picea abies* in the Stockholm phytotron (e.g. Dormling et al. 1968, Dormling 1982, Ununger et al. 1988).

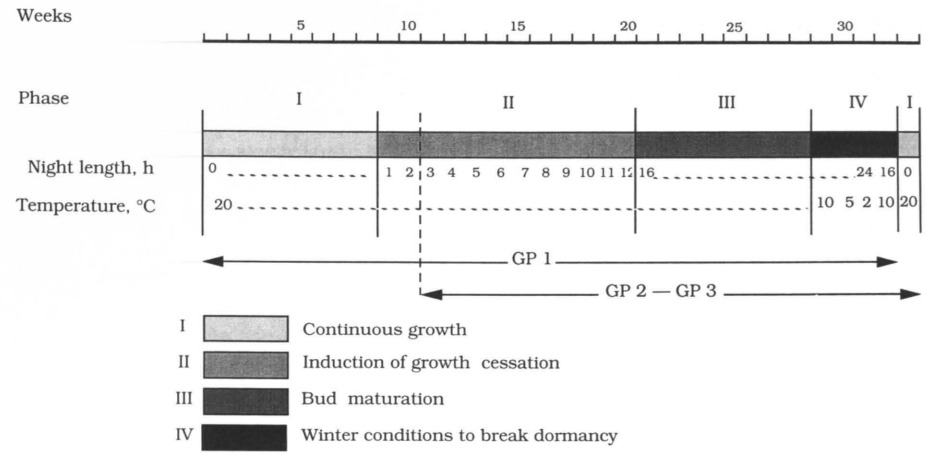


Fig. 1. The night lengths and the temperatures in the phytotron during all growth periods for the control plants are given. From phase IV (week 29) in the first (GP1) growth period and during the second (GP2) and third (GP3) growth period, the cultivation conditions were identical for the control and all the treatments. The light intensity was 340 µmol m^{-2} s^{-1}. The cultivation conditions during phase I–III in GP1 for the photoperiodic and light-intensity treatments and the temperature treatments are given in Tables 2 and 3, respectively.

The photoperiodic and temperature regimes and their duration for the controls during GP1 and for all seedlings during dormancy break and in GP2 and GP3 are outlined in Fig. 1. The light intensity was 340 µmol m^{-2} s^{-1} for the controls in GP1 and for all seedlings during dormancy break and in GP2 and GP3. The temperatures were the same during day and night. After germination, the control seedlings were grown in continuous light for 8 weeks (phase I), a photoperiod that keeps *Picea abies* seedlings in continuous growth. After that the night length was prolonged by 1 hour per week until 12 h was reached (phase II). This increase in night length induced growth cessation, budset and the initiation of needle primordia in the buds. The seedlings were then given 16 h nights for 8 weeks (phase III) for bud maturation. During phase I–III the temperature was 20 °C for the controls. Chilling treatments with 4 weeks of temperatures between +2 °C and +10 °C and long nights were applied to ensure a rapid and regular budburst. In GP2 and GP3, after one week in continuous light, all seedlings were given the same thermo- and photoperiods as for the controls in GP1 but starting with 3 hours per night.

To facilitate the understanding of the experimental design and the results of the treatment, we have compiled the treatment conditions for the control and photoperiodic and light-intensity treatments in Table 2 and Fig. 7, and for the control and temperature treatments in Table 3 and Fig. 11. Note that the numbering of the weeks is not the same in Fig. 1 and Fig. 7. The latter figure also includes the 24-week treatments that had to start 16 weeks earlier in order to reach the night prolongation at the same time as the 8-week treatments.

In the photoperiodic and light-intensity treat-

ments the control was compared with three categories of light treatments (Table 2, Fig. 1): (i) 8 weeks (control) vs. 24 weeks (PH16LI) of continuous light during active growth (phase I); (ii) 340 µmol m^{-2} s^{-1} light intensity (control) vs. 114 µmol m^{-2} s^{-1} light intensity (ph16li, PH16li) during the induction of growth cessation and budset (phase II) and during bud maturation (phase III), and (iii) 16 h nights (control) vs. 12 h nights (ph12LI, PH12LI) during bud maturation (phase III). The two last treatments (ph12LI, PH12LI) were not continued to GP3. The temperature was 20 °C (day/night).

In the temperature treatments the control was compared with 4 temperature regimes (Table 3, Fig. 1): 20 °C (control) vs. (i) 25 °C (TEMP20–25) or vs. (ii) 15 °C (temp20–15) during the last 7 weeks of bud formation (phase II) and during bud maturation (phase III), and 20° (control) vs. (iii) 25 °C (TEMP25) or vs. (iv) 15 °C (temp15) throughout phase I–III. There were no temperature shifts between day and night. The photoperiods applied are shown in Table 3.

2.1 Assessments

During the second and third growth period, leader growth was measured and the occurrence of lateral shoot elongation was assessed twice per week during rapid growth. The variables generated from the recordings were:

D10: number of days between day 0 and when the leader reached 10 % of final length,
D90: number of days to reach 90 % of final leader length,
DUR: duration of 80 % of the shoot-elongation period (D90-D10)
FGP: period (days) of lateral shoot elongation (free growth) on the leader.
LEN: final leader length (cm),
GRT: growth rate (mm/day) during the shoot-elongation period (D90-D10).

The percentage change of the duration of the shoot-elongation period (DUR) and of the free-growth period (FGP) in relation to the control in the second and third growth periods have been calculated. Percent plants showing free growth was also recorded.

The technique used for calculating the number of days for reaching a specific developmental stage is found in Eriksson et al. (1978).

In a preliminary study, it was found that the length of lateral shoots on the leader was correlated with the amount of free growth ($R^2 = 0.89$, Ununger et al. 1981). The lateral shoot-elongation period also coincided with the free-growth period. Therefore, the lateral shoot-elongation period was taken as a measure of the free-growth period.

A more mature performance compared with the control implies that
- D10 and GRT increased
- D90, DUR, LEN, and FGP decreased (Ununger et al. 1988).

2.2 Statistical Methods

For all traits except free-growth period, SAS Procedure GLM was used in analyses of variance with the model:

$$y_{ijk} = \mu + f_i + t_j + (fxt)_{ij} + e_{ijk},$$

where

y_{ijk} represents a trait in the k^{th} plant of the i^{th} family and j^{th} treatment
μ represents population mean
f_i represents i^{th} family effect, i = 1,...,5
t_j represents j^{th} treatment effect, for photoperiodic and light-intensity treatments j = 1,...,6 in GP2 and j = 1,...,4 in GP3, for temperature treatments j = 1,...,5 in GP2-3
$(fxt)_{ij}$ represents the interaction effect, and
e_{ijk} represents ijk^{th} error, k = 1,...,16 for GP2, k = 1,...,12 for GP3.

As the families and the treatments were considered as fixed, the error mean square was used in the F-tests.

The block effects were excluded from the analyses of variance as they were never significant.

T-tests and Tukey's Studentized range tests were used to compare different treatment means and family means. T-test uses the comparison-wide error rate to control the type I error, and Tukey's test uses the experimentwide error for the same purpose. Tukey's test is considered more conservative than the t-test in that a significant difference between two means under a t-test can be nonsignificant under Tukey's test.

As the trait free-growth period (FGP) frequently attained the value 0, the treatment effects were compared by applying homogeneity tests using SAS procedure FREQ. The frequency classes were defined as 0, (0,10], (10,20], (20,30], etc. In some cases, the right-most classes were pooled in order to fulfil the requirement of an expected frequency of at least 5 in every class. Separate homogeneity tests were carried out in which each treatment was compared with its control treatment. In order to control the experiment-wise error as for the t-test and Tukey's test above, a method based on Bonferroni's inequality was used (Miller 1966). The inequality implies that if a comparison within a group of c comparisons shall be considered as significant, the significance level in the separate comparisons must be at least c times smaller.

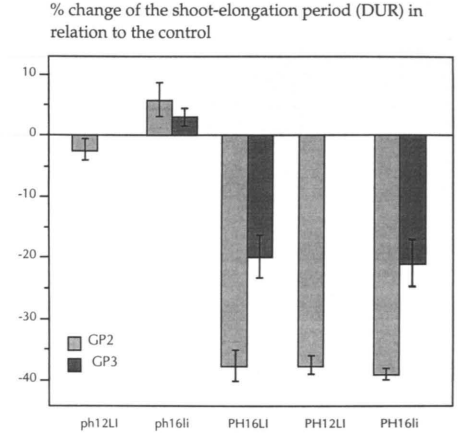


Fig. 2. Percentage change of the duration of 80 % of the shoot-elongation period (DUR) in relation to the control (mean ± SE) in the second (GP2) and the third (GP3) growth period as a result of the photoperiodic and light-intensity treatments in the first growth period (pooled data). Note that treatments ph12LI and PH12LI were not continued to GP3. Treatment symbols are given in Table 2.

3 Results

3.1 Photoperiodic and Light-Intensity Treatments

Since the families included in this investigation strongly vary in their natural phenology, the percentage change of the duration of the shoot-elongation period in relation to the control for the individual treatments in GP2 and GP3 is given in Fig. 2. The most conspicuous change was the large reduction of the shoot-elongation period following treatment with 24 weeks in continuous light during active growth before the onset of the growth-cessation treatment (PH16LI, PH12LI, PH16li) as compared to the control that was grown in 8 weeks. Moreover, the small standard errors during GP2 for these treatments indicate a fairly similar response of the individual families when expressed as percentage change. The data of Fig. 3 illustrate that the reduction of the shoot-elongation period was caused by both a later bud flushing and an earlier budset in all types of families included in this investigation. These treatments thus led to a more mature phenological behaviour of the seedlings during GP2. This was also the case for GP3 (Fig. 2).

The percentage reduction in plants with free growth in GP2 was most pronounced in families 3 (C × C) and 5 (N × N), the two families of northern origin (Fig. 4). A significant reduction of free-growth period in GP2 was observed for all 24-weeks treatment in continuous light during active growth (Fig. 5, pooled data, and Fig. 7). Thus, the more mature plant characteristic of a low amount of free growth was observed already in GP2. The data in Fig. 6 illustrate the spontaneous maturation for the reduction of percentage plants with free growth and the reduction of free-growth period from GP2 to GP3 for the control and the PH16LI treatment. Spontaneous maturation for treatments was calculated by subtracting the effect in GP3 from the effect in GP2 divided by the effect in GP2 and expressed in percentages. The two families – Nos. 1 and 2 – with a high capacity for free growth (Fig. 4),

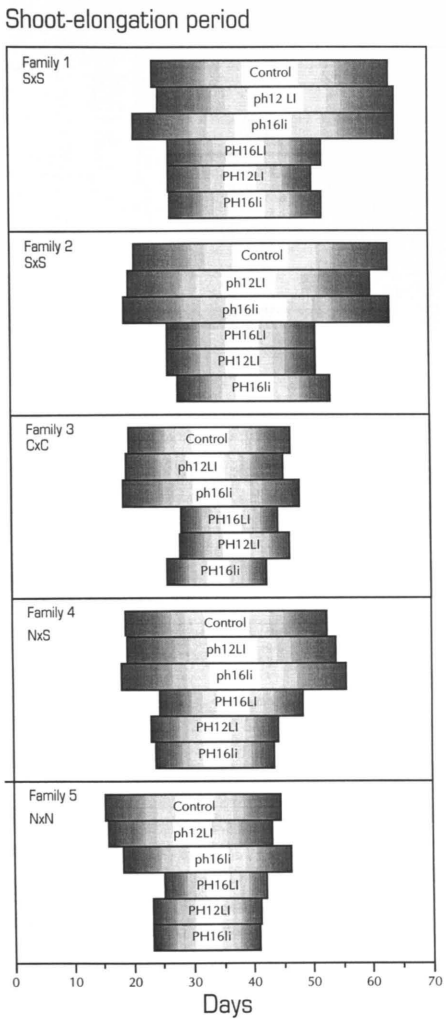


Fig. 3. Duration and timing of 80 % of the shoot-elongation period (DUR) in the second growth period for the five full-sib families as a result of the photoperiodic and light-intensity treatments in the first growth period. Origins of the families are given in Table 1 and treatment symbols in Table 2.

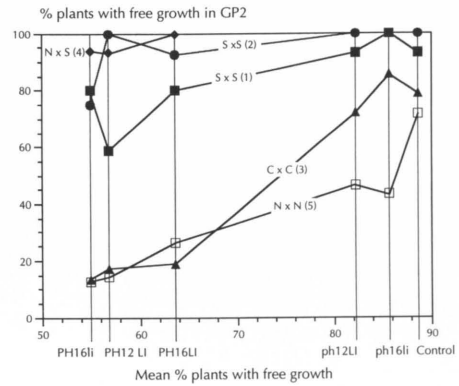


Fig. 4. Percentage plants with free growth in the second growth period (GP2) for the five full-sib families as a result of the photoperiodic and light-intensity treatments in the first growth period. The mean for each treatment and the control are given on the x-axis. Origins of the families are shown in Table 1 and treatment symbols in Table 2.

showed the largest reduction of percentage plants with free growth between GP2 and GP3 after PH16LI treatment compared with the other families. Also in the control, these two families showed a much less reduction of percentage plants with free growth. Thus, for families with a high capacity for free growth, the reduction of plants with free growth appeared later compared with the other families, but earlier compared with the control.

The data of Table 4 reveal that only the growth rate in treatment PH16LI deviated significantly from the growth rates of the other treatments including the control. Thus, only this trait showed a significant difference among the three 24-week treatments. The growth rate was significantly higher after longer nights during bud maturation (PH16LI) as compared to shorter nights during bud maturation (PH12LI) or low light intensity during night prolongation and bud maturation (PH16li).

The compilation of the results from the statistical analysis of the effects (Fig. 7) confirms the data presented in the graphs; all the 24-week treatments with continuous light caused a more

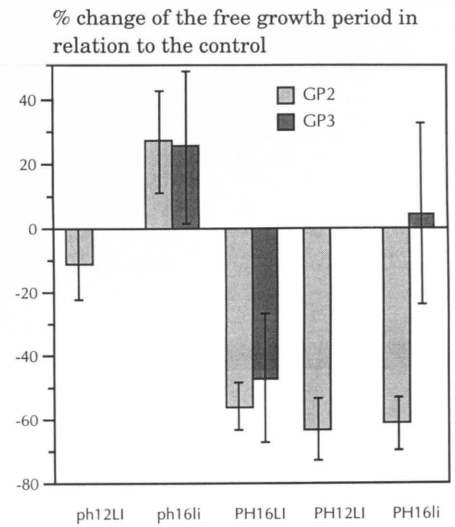


Fig. 5. Percentage change of the free-growth period in relation to the control (mean ± SE) in the second (GP2) and third (GP3) growth period as a result of the photoperiodic and light-intensity treatments in the first growth period (pooled data). Note that treatments ph12LI and PH12LI were not continued to the third growth period. Treatment symbols are given in Table 2.

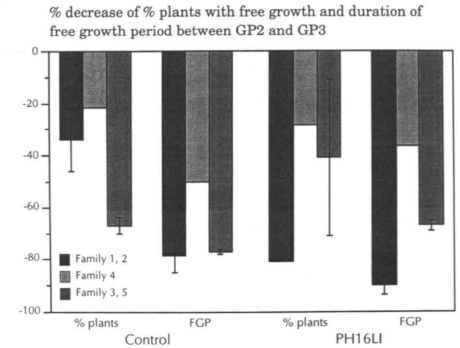


Fig. 6. Percentage decrease of % plants with free growth and the percentage decrease of the duration of the free-growth period (FGP) between the second (GP2) and the third (GP3) growth period (spontaneous maturation) for the control and the treatment with 24 weeks in continuous light during active growth (PH16LI) in the first growth period. Mean ± SE for family 1+2, and family 3+5 and mean for family 4 are shown. Origins of the families are given in Table 1 and treatment symbols in Table 2.

mature growth pattern during GP2. Moreover the effect lasted in most cases to GP3.

3.2 Temperature Treatments

On an average, the percentage change of the duration of the shoot-elongation period tended to be towards a more juvenile performance (Fig. 8). In contrast to the photoperiodic treatments the standard errors were large. Thus, there was no consistency among the families in how they responded to the same temperature treatment. Both families with a mature and a juvenile performance were recorded.

The percentage change of the duration of the free-growth period was more consistent among families in GP2 (Fig. 9). Including both GP2 and GP3, the two treatments with high temperature

Table 4. Mean values for growth rate (mm/day) in the second growth period (see Table 2 for explanation of the treatment symbols).

Control	ph12LI	ph16li	PH16LI	PH12LI	PH16li
5.93[a]	5.56[a]	5.58[a]	7.03[b]	6.15[a]	6.15[a]

Figures with the same letters do not differ significantly at $p < 0.05$.

(TEMP20–25 and TEMP25) caused a reduction of the free-growth period in all but one case, indicating a more mature performance, whereas the low temperature treatments (temp20–15 and temp15) caused an increase suggesting a more juvenile performance.

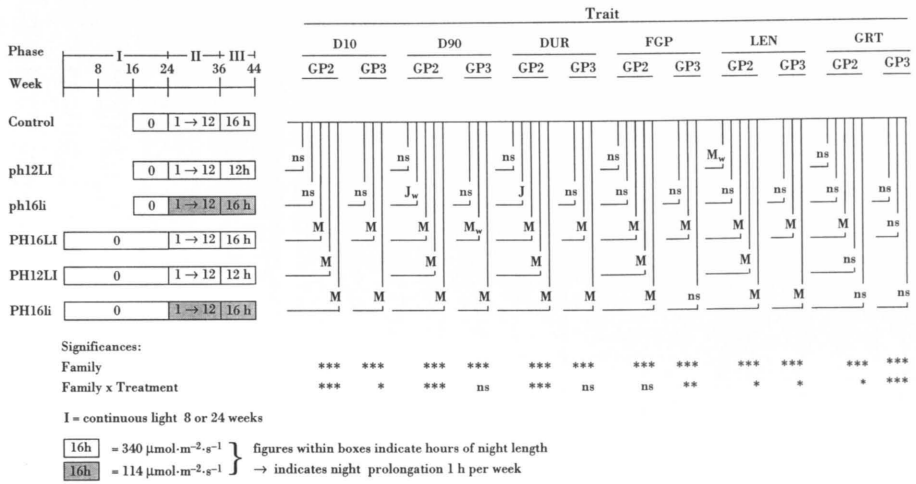


Fig. 7. Pairwise comparisons between different treatment means and the control with respect to the traits observed in the second (GP2) and third (GP3) growth period. Explanations of the trait symbols are given in Material and Methods. The photoperiodic and light-intensity treatments used in the first growth period are shown to the left. Treatment symbols are given in Table 2. Note that the control, ph12LI and ph16li treatments with 8 weeks in continuous light from sowing comprised 28 weeks and started 16 weeks later than the treatments with 24 weeks of continuous light from sowing. Note also that treatments ph12LI and PH12LI were not continued to GP3. M or J indicate that the treatment mean is significantly ($\alpha = 0.05$) greater or smaller than the corresponding control mean in showing a more mature performance or a more juvenile performance; M_w or J_w indicate that the treatment mean is significantly ($\alpha = 0.05$) greater or smaller than the corresponding control mean according to t-test, but not according to Tukey's test (similarly, the Bonferroni method was used for the duration of the free-growth period, FGP); ns indicates that the treatment mean is not significantly different from the corresponding control mean. Significances for the family effects and family x treatment effects are also given (*** = $p < 0.001$; * = $p < 0.05$; ns = non-significant).

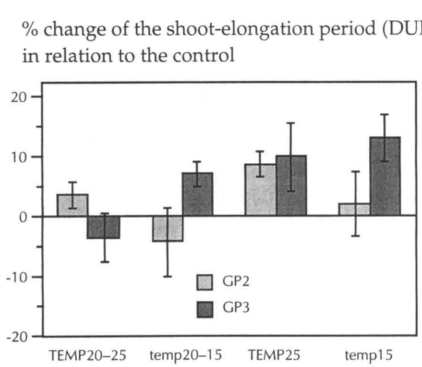


Fig. 8. Percentage change of the duration of 80 % of the shoot-elongation period (DUR) in relation to the control (mean ± SE) in the second (GP2) and the third (GP3) growth period as a result of the temperature treatments in the first growth period. Treatment symbols are given in Table 3.

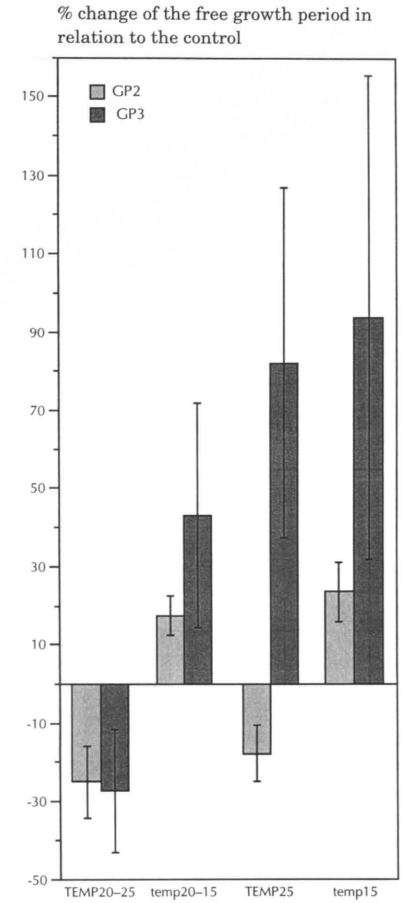


Fig. 9. Percentage change of the free-growth period in relation to the control (mean ± SE) in the second (GP2) and third (GP3) growth period as a result of the temperature treatments in the first growth period (pooled data). Treatment symbols are given in Table 3.

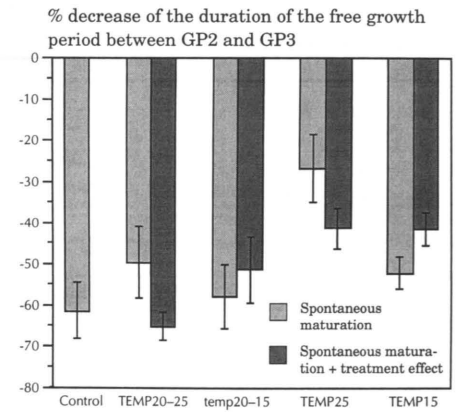


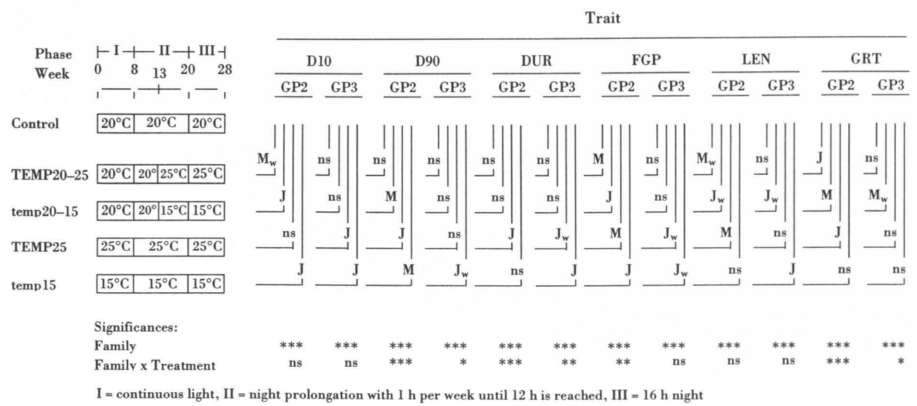
Fig. 10. Percentage decrease of the duration of the free-growth period (FGP) between the second (GP2) and the third (GP3) growth period for the control and the temperature treatments (pooled data). Spontaneous maturation and spontaneous maturation+treatment effects are shown separately. Treatment symbols are given in Table 3.

There was a dramatic percentage decrease, >60 %, in free growth from GP2 to GP3 in the control plants (spontaneous maturation), always larger than the spontaneous maturation in the four treatments (Fig. 10).

The data from the statistical analysis compiled in Fig. 11 reveal that the temperature treatments gave a more erratic pattern than the photoperiodic and light-intensity treatments.

3.3 Family Differences

The strong significances of the family effects both in the photoperiodic and light-intensity treatments (Fig. 7) and temperature treatments (Fig. 11) were expected considering the wide origin of the families with associated variation in phenology traits and in free growth. The family × treatment effects were significant for most traits (Figs. 7 and 11). Families of southern origin exceeded those of northern origin for duration of the shoot-elongation period (DUR, Fig. 3), % plants with free growth (Fig. 4), leader length (LEN) and growth rate (GRT) in GP2 for the photoperiodic and light-intensity treatments. Thus, most of the family pairs with non-significant mean differences came from the same origin. Growth rate during GP3 deviated from this general pattern with both highest and lowest values in families of southern origin.



I = continuous light, II = night prolongation with 1 h per week until 12 h is reached, III = 16 h night

Fig. 11. Pairwise comparisons between different treatment means and the control with respect to the traits observed in the second (GP2) and third (GP3) growth period. The temperature treatments used in the first growth period are shown to the left. Explanations of the trait symbols are given in Material and Methods. Treatment symbols are given in Table 3. For further explanations see legend of Fig. 7.

To get a better understanding of the plant growth pattern we estimated the growth rates between D10–D25, D25–D50, D50–D75, D75–D90. For the photoperiodic and light-intensity treatments there was a tendency for families 3–5 (northern origin and hybrid) to have their peak growth rates at D50–D75 in contrast to the two other families with their peaks at D25–D50. The two temperature treatments with 25 °C resulted mostly in the lowest growth rates during the entire growth period without any clear family differences.

4 Discussion

4.1 Outline of the Main Results

A summary of the results presented in Figs. 7 and 11 is given in Table 5. It should be remembered that some of the traits listed in Table 5 are not independent. Among the 5 treatments expected to cause a more mature performance only 2 behaved according to the hypothesis, i.e. the treatments with 24 weeks in continuous light with 16 h or 12 h nights in phase III, respectively, (PH16LI, PH12LI). The high temperature treatments (TEMP20–25, TEMP25) showed a more mature performance in a few cases only.

Among the 4 treatments expected to cause a more juvenile performance 2 cases out of 4 gave a weak support to the hypothesis (temp20–15 and temp15). The strong effect of the 24 weeks in continuous light masked a potential effect of low light intensity applied during the subsequent night prolongation and 16 h nights (PH16li).

High temperature during phase I–III (TEMP25) tended to cause a more juvenile behaviour. The same type of treatments with low temperatures indicated a more juvenile performance for the treatment with low temperature during phases I–III (temp15).

4.2 Effects Caused by the Transition from GP2 to GP3

Ununger et al. (1988) showed that families of *Picea abies* had a continuous reduction in the shoot-elongation period during the first four to five growth periods owing to a later budburst and an earlier budset. The capacity for free growth also decreased and thus contributed to the earlier

Table 5. Significances for more mature or juvenile performance for 6 traits compared with their respective controls. (See Tables 2 and 3 for treatment symbols.)

	Mature	Non-significant	Juvenile
Treatments hypothesized to cause a more mature performance			
ph12LI	1	5	0
PH16LI	11	1	0
PH12LI	5	1	0
TEMP20–25	3	8	1
TEMP25	2	4	6
Treatments hypothesized to cause a more juvenile performance			
ph16li	0	10	2
PH16li	9	3	0
temp20–15	3	5	4
temp15	1	4	7

budset. This may be an essential feature of early seedling development and perhaps an important adaptation mechanism. However, this means that any effect of treatments in this investigation is confounded with a spontaneous maturation effect. With increasing age as well as with strong maturation effects on traits during GP2 it becomes harder to trace any significant treatment effects during GP3. Ultimately there will be no free growth left even in the control. In spite of this, half of the significant treatment effects observed in GP2, were carried over to GP3 when including both photoperiodic, light-intensity and temperature treatments. The absence of any significant reduction of free growth in treatments PH16li in GP3 (Fig. 7) compared with the control may be attributed to a confounding with spontaneous maturation. The data for temperature treatments in Fig. 10 illustrate that the total effect of treatment and spontaneous maturation for some treatments turned out to be lower than the spontaneous effect alone (temp20–15 and temp15). This must be attributed to a more juvenile performance caused by these treatments.

4.3 Impacts on Phenology

The strong effect of the 24 weeks of continuous light during phase I of GP1 in causing a more mature performance in GP2 and GP3 is consistent with the findings of Young and Hanover (1976) for *Picea pungens*. They observed that seedlings of *Picea pungens* subjected to a long period of continuous light during the first year seemed to pass the juvenile stage more rapidly than those given a short period of continuous light.

As regards the impact of low light intensity, Drew and Ferrell (1977) reported that a low light intensity in autumn caused seedlings of *Pseudotsuga menziesii* to flush earlier the next spring, resulting in a high frequency of frost injury. Rostad (1988) interpreted a later budburst in *Picea abies* as caused by a low light intensity during bud maturation in climate chambers. According to our findings following low light intensity after 8 weeks in continuous light (ph16li), family Nos. 1–4 showed a tendency to earlier budburst (more juvenile) but the most northern family No. 5 had a later budburst than its control (Fig. 3). This resulted in non-significant difference compared with the control (Fig. 7). A significant juvenile performance (Fig. 7) was noted for growth cessation (D90) and for duration of the shoot-elongation period (DUR). As remarked above, the impact of low light intensity could not be studied in the corresponding 24-week treatment (PH16li) owing to the strong maturation effect of this treatment.

A night length of 12 h during bud maturation was expected to allow the apical meristems to be active longer than with 16 h nights, resulting in a more mature behaviour, provided that this meristem activity is photoperiodically controlled. This expectation was only fulfilled for leader length (LEN) in GP2. Again the impact could only be studied for the 8-week treatment.

Temperature conditions during bud formation and bud maturation are known to influence phenology during the next growth period. If the temperature conditions have been above average, a deeper bud dormancy can be reached and the possibility to build up sufficient frost hardiness increases. In the next spring, this results in an early budburst, provided that proper chilling

requirements are met and that temperatures needed to initiate budburst are reached. This has repeatedly been observed in *Picea abies* (e.g. Dormling 1982). Temperatures below average during autumn, on the contrary, can cause an incomplete bud maturation and inwintering leading to a late budburst in the spring. Our results seem to be inconsistent with these findings but more consistent with the observations by Heide (1974) who showed that high autumn temperature caused a late budburst in *Picea abies*, and by Malcolm and Pymar (1975) who showed that a low autumn temperature induced an early budburst in *Picea sitchensis*. As regards our findings that 15 °C from sowing induced an earlier budburst (earlier initiation of shoot elongation, decreased D10) than the control can be interpreted as mainly an effect of a slowing down of the apical-meristem activity leading to a more juvenile behaviour, e.g. earlier budburst. This interpretation is based on the assumption that almost the same degree of bud dormancy and frost tolerance was reached at 15 °C as at 20 °C, i.e. this temperature difference did not influence the time of budburst to such an extent that the potential juvenation effect was eliminated. The inconsistency shown for the 25 °C treatments can be due to the two counteracting forces: a high meristem activity expecting to lead to a more mature performance – late budburst – and the build-up of a high degree of bud dormancy and frost tolerance resulting in an early budburst.

4.4 Impacts on Free Growth Capacity

As the capacity of free growth disappears with age in *Picea abies* (e.g. von Wuelisch and Muhs 1986, 1991, Ununger et al. 1988, Ekberg et al.1991), it is an excellent trait for estimating whether a treatment has accelerated or delayed maturation. As remarked earlier, in our preliminary experiment we found that the length of lateral shoots on the leader was correlated with the amount of free growth in *Picea abies*. Therefore, we studied lateral shoots instead of the apical shoots since there is no sharp transition zone between predetermined and free growth on the apical shoot in young plants of *Picea abies* (also observed by von Wuelisch and Muhs 1986). The behaviour of lateral shoots was strongly influenced by the photoperiodic and light-intensity treatments (Figs. 4, 5, 6, 7). All 24-week treatments affected the free-growth period in a more mature direction whereas the low light intensity after 8-weeks in continuous light tended to cause a more juvenile performance (Fig. 5), however non-significant (Fig. 7). Drew and Ferrell (1977) noted not only an earlier budburst the next spring but also more lammas growth next summer after treatment of *Pseudotsuga menziesii* seedlings with low light intensity. Similar observations were made by Aldén (1971) in seedlings of *Pinus sylvestris* when given poor growth conditions (low levels of CO_2, water and nutrient content) during the first growing season: an early budset was followed by increased frequency of lammas and proleptic shoots in the next summer. Nutrients applied at different times during GP5 of *Picea abies* plants either increased or decreased the the free growth capacity in GP6 (von Wuelisch and Muhs 1991). These results can be a parallel to our findings that the duration of the free-growth period tended to increase in GP2 when low light intensity (or poor growth conditions) was applied in GP1 thus indicating a more juvenile behaviour. This is in accordance with the hypothesis that the number of cell divisions can be one important mechanism determining the maturation stage of the meristems (Greenwood and Hutchinson 1993). A reduction of needle primordia initiation, and thus cell divisions, by more than 40 % was reported for *Picea glauca* at low light intensity (Pollard and Logan 1979).

Furthermore, families behaved differently depending upon origin. For families of southern or hybrid origin with the largest capacity for free growth the treatments mainly affected the *period* of free growth and there were only a few plants that completely lost free growth in GP2, i.e. the percentage of plants with free growth was much less affected (Fig. 4). For families with a high capacity for free growth, the reduction of plants with free growth did not occur until GP3 (Fig. 6). The two families of Central and North Swedish origin with a moderate free growth capacity lost free growth to a great extent already in GP2. The same tendency was observed for the control when passing from GP2 to GP3: the percentage reduction of plants with free growth for the northern families was about double that for the two southern families (Fig. 6). This indicates that the treatments with 24 weeks in continuous light during active growth did not change the pattern of free growth reduction.

Also the temperature treatments significantly influenced the free-growth period but not so dramatically as did the 24-week treatments with continuous light. In accordance with the hypothesis, the two 25 °C treatments caused a more mature performance in GP2 and the two 15 °C treatments induced a more juvenile performance.

4.5 Impacts on Leader Length and Growth Rate

Environmental conditions during the bud maturation period in late summer are known to have a significant impact on the number of needle primordia formed in the buds, a critical determinant for shoot growth in the following growth period (Cannell 1978, Kremer and Larson 1983). In a previous section, we suggested that different photoperiodic and light-intensity treatments applied during the bud maturation did not influence the duration of the shoot-elongation (DUR) in the following growth period except for a significant increase after the low light-intensity treatment in plants grown in continuous light for 8 weeks (ph16li). Therefore, we are interested in knowing if these treatments during the bud maturation period influenced the growth rate. Fig. 7 shows that growth rate (GRT) in GP2 of 24-weeks plants with 16 h nights during bud initiation and maturation (PH16LI) is significantly higher than the control, indicating that a long period of continuous light from sowing influenced the growth rate in GP2. This influence was not carried over to GP3. The statistical significance was largely contributed by family 4, the hybrid between northern Sweden and Belgium origins. When this family was removed from the analysis, the statistical significance disappeared.

Even though the statistical evidence is weak, there exists a consistent pattern indicating that also photoperiodic and light-intensity treatments during the bud maturation period influenced growth rate in the subsequent growth period (Table 4). Treatments with 12 h nights or with a lower light intensity seemed to decrease growth rate for 8-weeks plants (ph12LI and ph16li: 6 % non-significant decrease) and for 24-weeks plants (PH12LI and PH16li: 12 % significant decrease compared to the 24-week treatment with 16 h nights) in the following growth period. A possible interpretation is that seedlings under 24-weeks treatments had lost a larger amount of their capacity for free growth reflected by a significantly shorter period of lateral shoot-elongation period as compared to the control. The growth rate is expected to be lower during free growth compared with predetermined growth because free growth implies both formation and elongation of new needle primordia whereas during predetermined growth only elongation of preformed (last year's) needle primordia occurs. In *Picea abies* plants exhibiting both predetermined and free growth, von Wuelisch and Muhs (1986) observed that the growth rate of the predetermined growth was larger than that of the free growth. The difference increased with age.

Temperature treatments appeared to have more consistent impacts on growth rate (GRT, Fig. 11) than the photoperiodic and light-intensity treatments. The two high temperature treatments with 25 °C (TEMP20–25, TEMP25), reduced growth rate significantly. However, the reduction in growth rate due to high temperature applied from sowing (TEMP 25) was about double that of high temperature treatment starting during the latter part of bud initiation and continuing during bud maturation (TEMP20–25). On the other hand, a low temperature, 15 °C, during the same period (temp20–15) increased growth rate, whereas 15 °C from sowing did not affect the growth rate significantly. These results were not in accordance with our hypothesis that high temperatures would cause a more mature behaviour – high growth rates – compared to the control owing to more active apical meristems. Accordingly, low growth rates were expected for the low temperature treatments. As discussed above, there are counteracting physiological processes that mask for example the potential maturation effects. One such process can be differences in build-up and release of bud dormancy. The high temperature treatments can have built-up a high degree of bud dormancy that was not completely broken before the start of GP2 (cf.

Dormling et al. 1968). A possible consequence can be a slow-down of the growth rate. A late budbreak observed for the high temperature treatment during bud maturation and part of the bud initiation can indicate incompletely broken bud dormancy. For the low temperature treatments the opposite reasoning can be applied: complete release from bud dormancy resulting in a high growth rate. In *Pinus sylvestris*, Dormling (1989) observed that budburst rate was higher after 8 weeks with dormancy-breaking treatment than after 4 weeks at temperatures between +2 °C and +5 °C. This was most apparent after the treatment that induced the deepest bud dormancy, i.e. 25/15 °C compared to 25°/5 °C day/night temperature during night prolongation in the preceding growth period. As regards the length of the chilling treatment applied in this study (4 weeks in +2C° to +5 °C), we can add that 8 weeks in 16 h nights preceding chilling also act as dormancy-releasing treatment (Dormling 1993, Qamaruddin et al. 1993).

4.6 Family Variation

Differential responses of the various latitudinal families makes it clear that one must consider family effects to correctly interpret how plants will respond to environmental effects. Furthermore, the range of variation among families is greater than that of responses to the varying environments. Therefore, proper interpretation of physiological processes depends on understanding their genetic basis as well.

4.7 Practical Implications

Some fast-growing *Picea abies* seedlings have a growth rhythm that makes them susceptible to early autumn frost injuries because of late growth cessation and bud formation. This study indicates that these genetically nonhardy seedlings can be modified by treatments applied in GP1 so that they become more frost-hardy in subsequent growth periods. Furthermore, our technique for producing plants with a more mature performance can be applied in early tests and in early flowering-induction treatments for which the reduction of the juvenile phase is desirable. For cutting production in clonal forestry, on the other hand, it is desirable to be able to keep the ortets in a juvenile stage for a longer time than is possible today. Our results indicate that it can be possible to produce plants with delayed maturation but the results were not so clear-cut as for enhanced maturation. However, it is necessary to observe the changes beyond 3 years of age before a concrete recommendation can be made.

Seedling phenology can also be used to better understand long-term dynamics of populations. To better explain causes of change in ecosystems and help predict their dynamics, it is necessary to translate physiological processes, in terms of fitness of individuals and populations, into ecosystem processes. Estimating genetic variation and phenotypic plasticity of fitness characters will allow ecosystem researchers and modellers to assign the likelihood of survival for a species in an ecosystem (Stern 1964, Kang 1993). Physiological and genetic information about the adaptation and reaction norms of young seedlings, in terms of changes in phenology, to new environments can be extremely valuable in this regard.

By studying early growth of Norway spruce seedlings, we can obtain insights into three interrelated aspects of plant growth and development: (1) pattern of growth; (2) seedling adaptation to (new) growing environments; and (3) maturation. This study generated new information about the above three criteria. Although not in complete factorial form, the two sets of experiments in this study helped to improve our understanding of the relative impacts of various environmental treatments on different growth characters during ontogeny.

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