Dependence of photoperiodic response of growth cessation on the stage of development in *Picea abies* and *Betula pendula* seedlings

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Abstract

Dependence of photoperiodic response of growth cessation on the stage of development was examined in seedlings of Norway spruce (*Picea abies* (L.) Karst.) and silver birch (*Betula pendula* Roth) in greenhouses with 20 °C day and 10 °C night temperatures. Different combinations of photoperiod and stage of development were created by repeating sowing five times with 2 week intervals during the summer. During the experiment light conditions were natural but the daily temperature sum accumulation was regulated to be constant. Eight origins of spruce and seven origins of birch from different latitudes (60–67°N) in Finland were used. In the first growing season both Norway spruce and silver birch seedlings from the first sowings required a longer time for growth cessation than seedlings from the later sowings. However, because the seedlings from the first sowings ceased their growth on an earlier calendar date, the night length at the time of growth cessation was shorter for the seedlings from the first sowings. The results suggest that the variation in the timing of growth cessation of Norway spruce and silver birch seedlings during the first growing season was explained jointly by night length and stage of development. Seedlings from northern origins stopped their growth with shorter night length than those from southern origins. The effects of latitude and average temperature sum of the original growing site on the critical night length of growth cessation in the first growing season were stronger in Norway spruce than in silver birch. In the second growing season the sowing time did not affect the timing of the formation of the terminal buds, but slightly affected the timing of height growth cessation of Norway spruce and silver birch seedlings.

1. Introduction

The growth rhythm of woody plants in cool and temperate regions is controlled by both internal and environmental factors. Genotype is the internal factor that sets the limits, whereas environmental factors determine the actual growth rhythm. The major environmental factors affecting growth rhythm are photoperiod and temperature. In cool and temperate regions, woody ecotypes and species are adapted to the local seasonal photoperiod and temperature conditions (Sakai and Weiser, 1973).

According to prevailing theory critical night length causes growth cessation and acts as an environmental signal which ensures the beginning of the hardening processes already before the temperatures drop (e.g. Wareing, 1950a,b; Vaartaja, 1954, 1957, 1959; Dormling et al., 1968; Heide, 1974; Ekberg et al., 1979; Junttila and Kaurin, 1985). The critical night

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length shows clinal variation with latitude, i.e. the northern geographical origins react to shorter critical night lengths compared to the southern ones. Accordingly, tree species which have wide range form photoperiodic ecotypes. These ecotypes are adapted to the local combination of photoperiod and temperature. Vaartaja (1954, 1959) has demonstrated the presence of latitudinally and altitudinally oriented photoperiodic and temperature ecotypes in 31 species of forest trees.

Environmental factors such as temperature, water stress and mineral nutrition have a modifying influence on photoperiodic reactions affecting growth cessation (e.g. Heide, 1974). In addition, the timing of growth cessation has been explained with a joint effect of temperature sum accumulation and photoperiod (Koski and Selkäinaho, 1982; Koski, 1985; Koski and Sievänen, 1985; Paus et al., 1986; Partanen and Beuker, 1999). This kind of regulation system would provide more flexibility in the timing of growth cessation compared to a regulation based only on one factor. In particular, a response only to the night length signal would mean that the growth cessation would take place at a fixed calendar date from year to year. This is, however, contrary to experience.

Physiological processes of plants can be described quantitatively on the basis of the concepts of rate of biological maturation and physiological stage of development (Hari, 1968, 1972). It may be assumed that the stage of development of seedlings is determined by several environmental factors, such as night length, light intensity, temperature and nutrition. In the beginning of the growing season, the rate of development is regulated mostly by temperature, and accordingly the accumulated temperature sum estimates the stage of development at a certain moment. Later during the growing season, the role of photoperiod becomes more important (e.g. Fuchigami et al., 1982). Koski and Selkäinaho (1982) presented a simple experimental technique where different combinations of photoperiod and stage of development of the seedlings are created by repeating sowing in natural light conditions in two different temperature conditions where the daily temperature sum accumulations are kept approximately constant. By using this kind of experimental technique, the effects of night length and stage of seedling development on the timing of growth cessation can be tested.

The first aim of the present study was to examine the effect of night length and stage of development on the timing of height growth cessation in seedlings of Norway spruce (*Picea abies* (L.) Karst.) and silver birch (*Betula pendula* Roth) in the first growing season. Further, the effect of the sowing date on the timing of bud formation and height growth cessation during the second growing season were tested. The second aim of the study was to examine the genetic variation among origins in the environmental response of growth cessation in the first growing season.

2. Materials and methods

The experimental material was obtained from eight Norway spruce and seven silver birch origins. These origins were from regions with different light and temperature regimes in Finland (Table 1). The seedlings were raised and observed in greenhouses at the Punkaharju Research Station (61°48′N, 29°19′E) of the Finnish Forest Research Institute during 1997 and 1998 in natural light. The temperature in the greenhouses was kept at a constant 20 °C between 7 a.m. and 5 p.m. and at 10 °C between 7 p.m. and 5 a.m. During the intervening times the temperature was changed steadily at a rate of 5 °C per hour. From June until the end of August during warm and sunny periods with warm nights, however, the temperatures in the greenhouses were up to 7 °C higher, because no artificial cooling was available.

The seedlings were raised in plastic trays of 45 cells (190 cm^3) filled with commercial fertilized peat (Vapo peat for forest trees; N 9.7%, P 7.5%, K 14.4% and micronutrients) as described in Partanen and Beuker (1999). Sowing was repeated five times during 1997 (Table 2). The aim was to grow 20 seedlings per origin, 10 of which were chosen for the experiments. However, because of the low germination capacity of northern origins this was not always successful.

In October, 2 weeks before the seedlings were moved outside, the temperature in the greenhouse was lowered to a constant 5 °C in order to attain winter hardiness. The seedlings were removed from the greenhouse in 1997 on 30 October. All the Norway spruce seedlings and the shorter silver birch seedlings overwintered wholly under natural snow coverage,

Table 1

Geographical information and average annual temperature sums for the original growing sites of the origins of Norway spruce and silver birch used in the study

Origin	Latitude (°N)	Longitude (°E)	Altitude (m)	Temperature sum (>5 °C, dd)
Norway spruce				
Tammisaari	60°02′	23°03′	35	1334
Tuusula	60°21′	24°59′	60	1321
Punkaharju	61°34′	29°13′	105	1226
Vilppula	62°04′	24°29′	105	1172
Laihia	62°52′	22°02′	35	1144
Lieksa	63°04′	30°17′	170	1046
Pihtipudas	63°17′	25°27′	165	1050
Rovaniemi municipality	66°21′	26°41′	295	873
Silver birch				
Karjalohja	60°14′	23°43′	50	1322
Taipalsaari	61°16′	27°54′	80	1288
Joutsa	61°40′	26°15′	110	1220
Punkaharju	61°49′	29°18′	92	1235
Ruovesi	62°03′	24°15′	100	1179
Oravainen	63°17′	22°20′	10	1132
Rovaniemi municipality	66°52′	24°55′	140	836

whereas the longer silver birch seedlings were covered with snow only partially.

The effects of the first growing season on the growth cessation of the overwintered seedlings in the second growing season were studied by experiments under the same greenhouse conditions as in the first growing season. In 1998 the seedlings were transferred into the greenhouse on 18 May. After transfer the silver birch seedlings were transplanted into plastic pots of volume $450 \, cm^3$ containing fertilized peat (Vapo peat for forest trees; N 9.7%, P 7.5%, K 14.4% and micronutrients).

In the first and second growing seasons, the total height of 10 seedlings in each batch was measured and the timing of the development of the terminal bud was observed as described in Partanen and Beuker (1999). The temperature data was recorded hourly.

Table 2

Night lengths on the sowing dates

Sowing	Date	Night length (h)
1	29 May	5.08
2	12 June	4.28
3	26 June	4.18
4	10 July	4.82
5	24 July	5.88

Because the daily temperature conditions were kept approximately constant, the temperature sum accumulations (5 °C threshold) calculated from different sowing dates were almost linear. Accordingly, the temperature sum accumulation and the age of the seedlings were linearly confounded in this experiment. The night length for the date of growth cessation was given by the time interval between sunset and sunrise. In the calculations, the night length of Jyväskylä (62°13′N, 25°44′E) as determined by the University of Helsinki (Anon., 1996, 1997) was used.

For an individual seedling, growth cessation was defined as the instant at which 95% of the height growth had been achieved, and for individual origins and sowing dates as the average over the seedlings. The formation of the terminal buds was observed from individual seedlings. For individual origins and sowing dates it was defined as the average over the seedlings, i.e. as the time when 50% of the seedlings had set buds. The effect of the sowing date on (1) temperature sum and (2) night length required for the average terminal bud formation and height growth cessation over all origins was tested separately in both growing seasons using analysis of variance.

In the first growing season, for each individual origin and sowing date, the night length prevailing at the time of growth cessation was plotted against the

temperature sum accumulated until growth cessation. The lines that were fitted into these plotted observations, are called growth cessation lines. The relationship between accumulated temperature sum and night length at the time of growth cessation is symmetric and thus cannot be analysed in terms of dependent and independent variables. Therefore, the growth cessation lines were fitted using the maximum likelihood estimation presented by Lappi and Sievänen (1993). This was carried out separately for each of the eight Norway spruce and seven silver birch origins.

The genetic variation in the environmental response of growth cessation among origins was examined by comparing the properties of the fitted growth cessation lines of the different origins. The variation of the predicted night lengths between the different origins at fixed temperature sums and the variation in the slopes of the fitted growth cessation lines were analysed separately for Norway spruce and silver birch using linear regression analysis. The predictors in the regression analyses were latitude and average annual temperature sum of the original growing sites of the origins. The correlations between the latitude and average annual temperature sum of the original growing sites of the origins were also determined. For Norway spruce, the separate regression analyses were done at fixed temperature sums of 700, 800 and 900 dd, respectively. For silver birch, the analyses were done at fixed temperature sums of 900, 950 and 1000 dd, respectively. The fixed temperature sums were chosen to cover approximately the whole range of the growth cessation times for the experimental material.

3. Results

The length of the growing period of both Norway spruce and silver birch seedlings was dependent on the sowing time. Seedlings from the first sowings had a longer growing period (Tables 3 and 4), and thus also a greater temperature sum, at growth cessation than seedlings from the later sowings. However, because the seedlings from the first sowings stopped their growth on an earlier calendar date, the night length at the time of growth cessation was shorter for the seedlings from the first sowings than for those from the later sowings (Figs. 1 and 2). The average final height

Table 3
Average number of days from sowing to growth cessation and terminal bud formation of Norway spruce seedlings in the first growing season

Origin	Sowing				
	1	2	3	4	5
Days to growth cessation					
Tammisaari	86	75	66	53	41
Tuusula	81	79	64	51	38
Punkaharju	78	69	56	51	38
Vilppula	75	62	54	48	35
Laihia	71	63	55	47	34
Lieksa	69	59	54	46	33
Pihtipudas	73	64	60	45	35
Rovaniemi municipality	60	45	56	36	35
Days to bud formation					
Tammisaari	91	77	71	58	45
Tuusula	84	77	69	59	46
Punkaharju	82	72	55	57	45
Vilppula	79	63	55	53	40
Laihia	76	67	54	50	39
Lieksa	72	61	51	47	34
Pihtipudas	70	64	55	50	42
Rovaniemi municipality	59	55	43	39	36

of both Norway spruce and silver birch seedlings was also dependent on the sowing time decreasing from the first to the last sowing (Fig. 3). Before the height growth ceased, the seedlings from different sowing

Table 4
Average number of days from sowing to growth cessation and terminal bud formation of silver birch seedlings in the first growing season

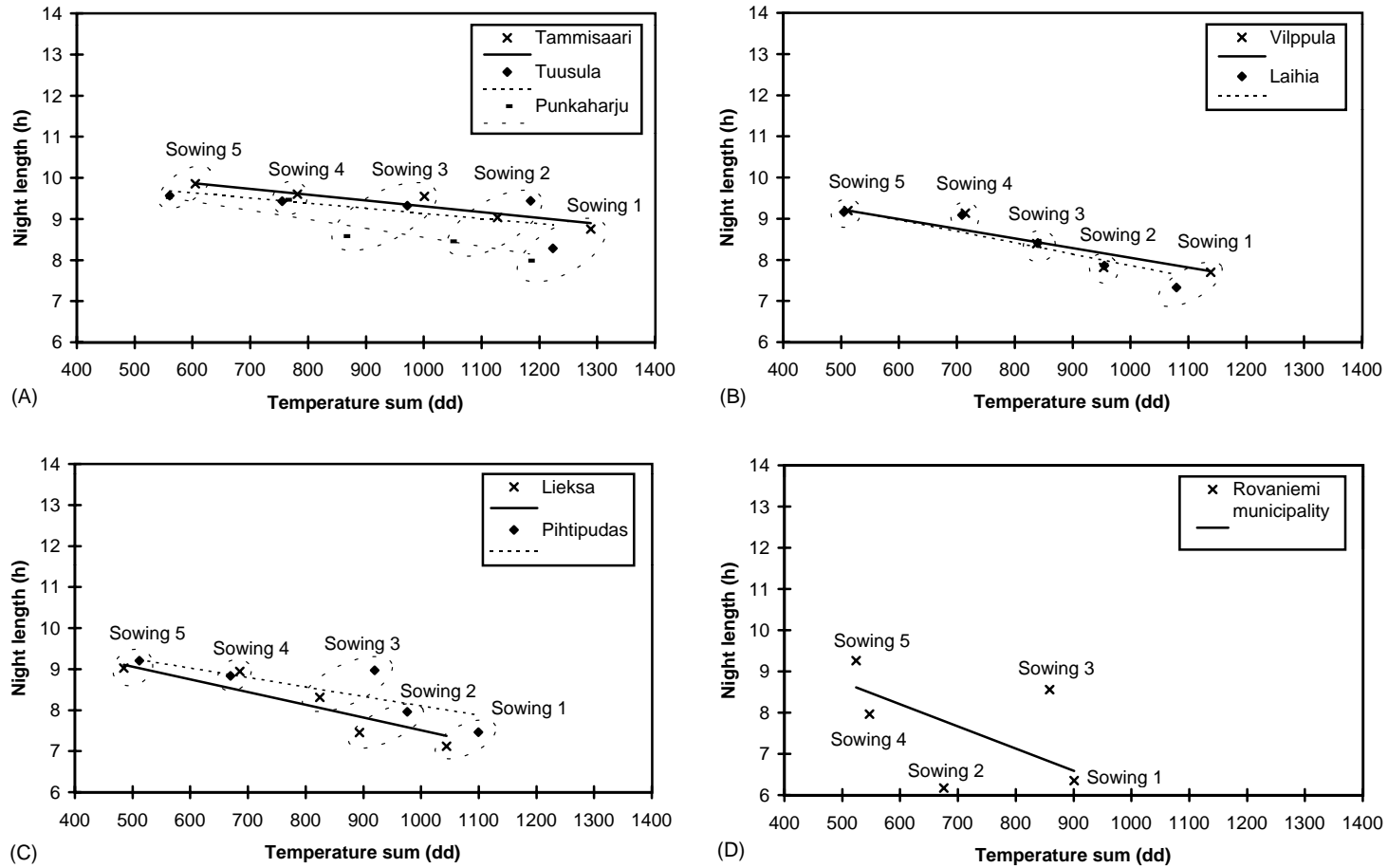| Origin	Sowing				
	1	2	3	4	5
Days to growth cessation					
Karjalohja	75	69	63	72	61
Taipalsaari	78	70	67	67	55
Joutsa	73	65	64	70	55
Punkaharju	76	68	60	67	58
Ruovesi	79	67	67	73	61
Oravainen	78	70	68	72	57
Rovaniemi municipality	67	65	59	61	47
Days to bud formation					
Karjalohja	84	79	64	74	64
Taipalsaari	81	73	62	68	77
Joutsa	79	72	63	71	64
Ruovesi	85	74	64	64	65
Punkaharju	83	71	60	82	73
Oravainen	78	71	62	71	73
Rovaniemi municipality	74	66	57	57	68

Fig. 1. Dependence of average timing of growth cessation on temperature sum and night length for different origins of Norway spruce seedlings in the first growing season.
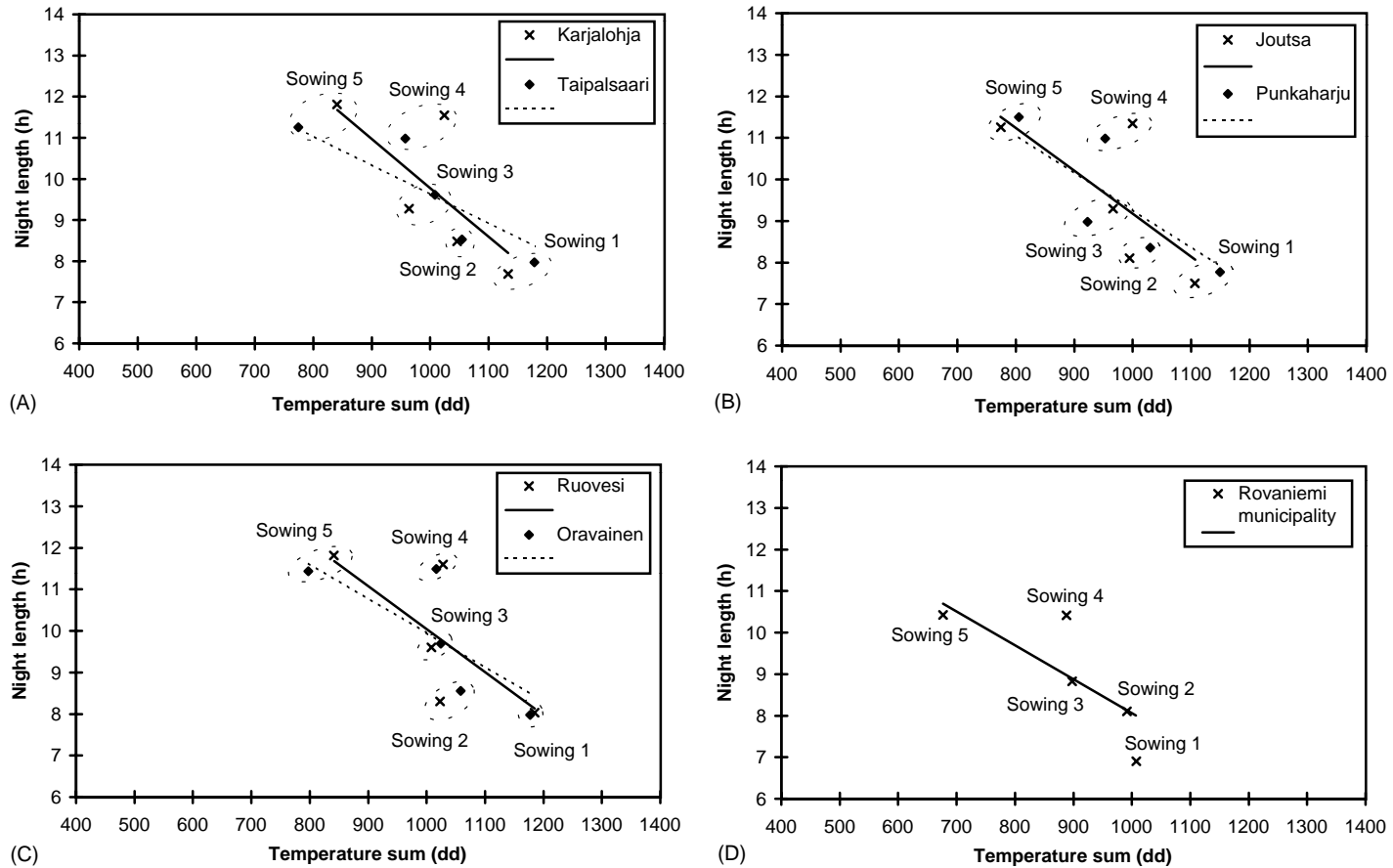
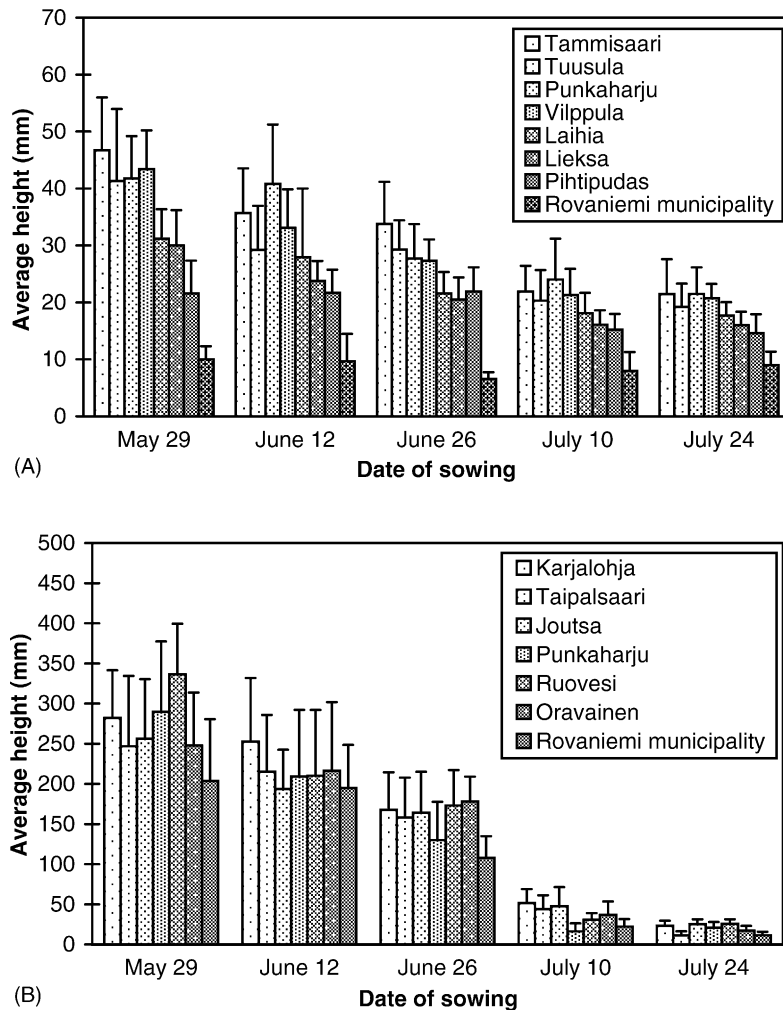Fig. 2. As Fig. 1, but for silver birch seedlings.

Fig. 3. Average final heights (±standard error) of the seedlings of Norway spruce (A) and silver birch (B) from different sowing dates and origins in the first growing season.

dates were at different developmental stages estimated with the temperature sum accumulation or, equivalently, with the age of the seedlings. Thus, the seedlings at earlier stages of development required a longer critical night length signal for height growth cessation.

There was latitudinal variation between southern and northern Norway spruce and silver birch origins both in the timing of height growth cessation and in the final height of the seedlings. Seedlings from northern origins generally stopped their growth earlier, i.e. with shorter critical night length than seedlings from southern origins (Tables 3 and 4). Correspondingly, the average final height of the seedlings from northern

origins was smaller than the average final height of the seedlings from southern origins (Fig. 3).

In the first growing season the growth of the Norway spruce seedlings from different origins ceased with a temperature sum accumulation between 480 and 1300 dd and night length between 6 and 10 h (Fig. 3). The growth of the silver birch seedlings, however, ceased with a temperature sum accumulation between 670 and 1200 dd and night length between 7 and 12 h (Fig. 4). Consequently, the fitted growth cessation lines for Norway spruce origins were more gently sloping than the corresponding lines for silver birch origins (Figs. 3 and 4). In other words, the change in stage of
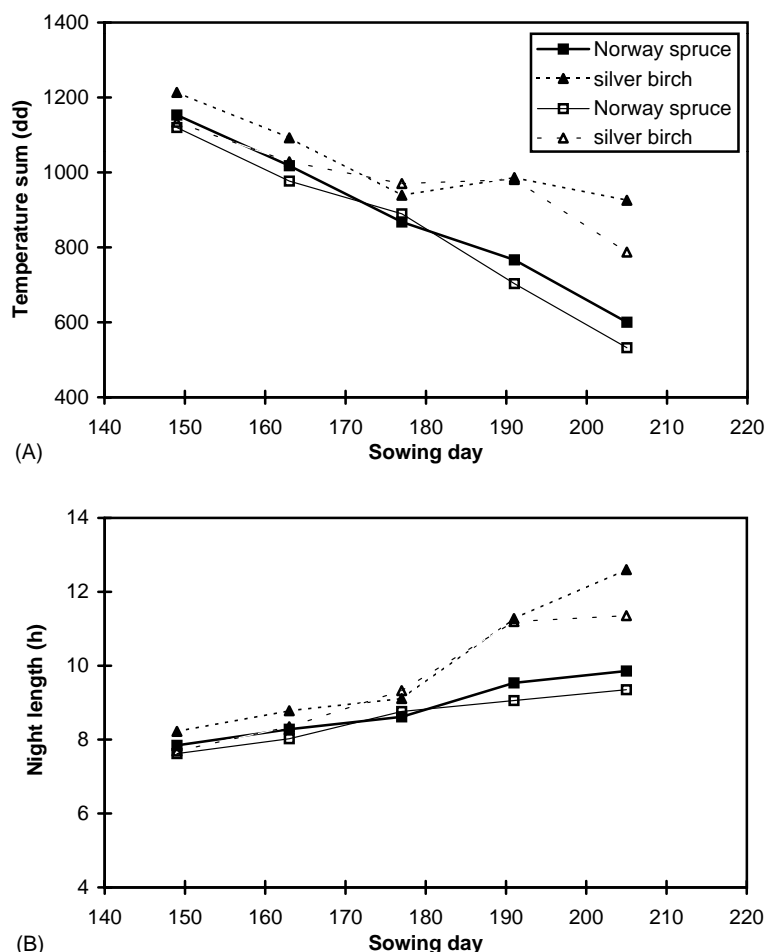
Fig. 4. Effect of sowing time (number of days from the beginning of the year) on temperature sum (A) and night length (B) required for average terminal bud formation (closed symbols) and height growth cessation (open symbols) of Norway spruce and silver birch seedlings in the first growing season. Pooled data over all origins.

development (estimated with temperature sum or, equivalently, with age of the seedlings) changed the critical night length of growth cessation more with silver birch than with Norway spruce.

For Norway spruce, latitude and average annual temperature sum of the original growing sites of the origins were strongly correlated ($r = -0.98$). Accordingly, either one of them alone can be used to predict the variation in the properties (= predicted night lengths at fixed temperature sums and the slopes) of the fitted growth cessation lines of origins. The linear regressions of the predicted night lengths of the fitted growth cessation lines at fixed temperature sums (700, 800 and 900 dd) using latitude or annual

temperature sum as predictor were all highly significant ($P < 0.001$) (Table 5). In all three cases, both predictors accounted for 93–96% of the variability. Accordingly, both latitude and average temperature sum of the original growing site of the origin had an effect on the critical night length of growth cessation of Norway spruce seedlings in experimental conditions. The seedlings from northern origins generally ceased their growth earlier (i.e. with shorter critical night length and with smaller temperature sum) than the seedlings from southern origins (Fig. 1). The slopes of the growth cessation lines were slightly more dependent on the latitude ($P < 0.001$) than on the corresponding annual temperature sum ($P = 0.001$).

Table 5
Linear regression analysis of the predicted night lengths at fixed temperature sums and the slopes of the fitted growth cessation lines of Norway spruce seedlings in the first growing season using latitude and average annual temperature sum of the original growing sites of the origins as predictors

Dependent	Predictor	P-value	R^2
Night length at 700 dd	Latitude	<0.001	0.95
Night length at 700 dd	Temperature sum	<0.001	0.93
Night length at 800 dd	Latitude	<0.001	0.95
Night length at 800 dd	Temperature sum	<0.001	0.93
Night length at 900 dd	Latitude	<0.001	0.96
Night length at 900 dd	Temperature sum	<0.001	0.93
Slope	Latitude	<0.001	0.92
Slope	Temperature sum	0.001	0.85

Table 6
Linear regression analysis of the predicted night lengths at fixed temperature sums and the slopes of the fitted growth cessation lines of silver birch seedlings in the first growing season using latitude and average annual temperature sum of the original growing sites of the origins as predictors

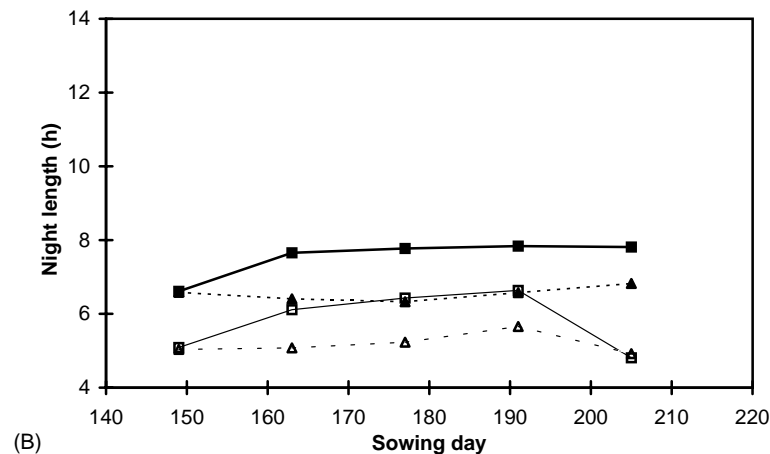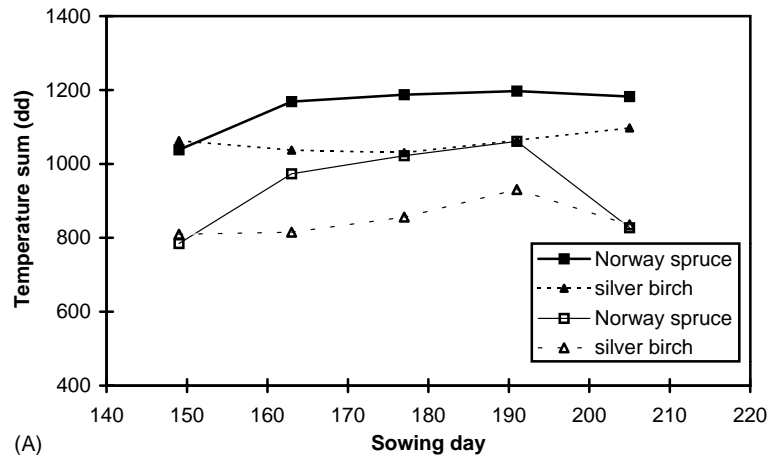| Dependent	Predictor	P-value	R^2
Night length at 900 dd	Latitude	0.035	0.62
Night length at 900 dd	Temperature sum	0.032	0.64
Night length at 950 dd	Latitude	0.041	0.60
Night length at 950 dd	Temperature sum	0.037	0.61
Night length at 1000 dd	Latitude	0.053	0.56
Night length at 1000 dd	Temperature sum	0.048	0.58
Slope	Latitude	0.287	0.22
Slope	Temperature sum	0.289	0.22

Fig. 5. As Fig. 4, but in the second growing season.

The latitude of the original growing sites of the origins accounted for 92% of the variability and the temperature sum for 85% of the variability (Table 5).

For silver birch, latitude and average annual temperature sum of the original growing sites of the origins were also strongly correlated ($r = -0.99$). The linear regressions of the predicted night lengths of the fitted growth cessation lines at fixed temperature sums (900, 950 and 1000 dd) using latitude or annual temperature sum as predictor were significant ($P \leq 0.05$) (Table 6). The dependence was, however, not so strong as in the case of Norway spruce. In all three cases, both predictors accounted for 56–64% of the variability. The difference in the timing of growth cessation between northern and southern origins was smaller in the case of silver birch than in the case of Norway spruce (Figs. 1 and 2). The slopes of the growth cessation lines, unlike in the case of Norway spruce, were not dependent on the latitude or annual temperature sum of the original growing sites of the origins ($P > 0.1$), which both accounted for only 22% of the variability (Table 6).

In the first growing season both the average formation of the terminal buds and the height growth cessation over all Norway spruce origins occurred with smaller temperature sum accumulation and shorter night length than the corresponding phenomena of the silver birch seedlings (Fig. 4). This difference was clearest in the fourth and the fifth sowings. In the second growing season, however, it was the silver birch seedlings that had the smaller temperature sum accumulation and shorter night length requirements (Fig. 5).

Both in Norway spruce and in silver birch in the first growing season, the differences of temperature sum and night length required for the formation of the terminal buds over all origins between different sowing dates were highly significant ($P < 0.001$) (Fig. 4). In the second growing season, however, these differences were not significant ($P > 0.1$) (Fig. 5). In other words, sowing time did not affect the timing of the terminal bud formation of either Norway spruce or silver birch seedlings in the second growing season. In both species in the first growing season, the differences of temperature sum and night length required for the height growth cessation between different sowing dates were highly significant ($P < 0.001$) (Fig. 4). In the second growing season, unlike in the case of

formation of the terminal buds, these differences were also slightly significant ($P < 0.05$) (Fig. 5).

4. Discussion

Sowing time had an effect on the timing of growth cessation of Norway spruce and silver birch seedlings in the first growing season. In first sowings, growing periods were longer and critical night lengths shorter than in later sowings. This is in accordance with earlier studies (Koski and Selkäinaho, 1982; Koski and Sievänen, 1985; Partanen and Beuker, 1999). In addition to the length of the growing periods, also the total height growth of the seedlings varied among sowing dates. Because the daily temperature sum accumulation in the experiment was kept constant, it is likely that the seedlings from different sowing dates were at different stages of development at given calendar dates (night lengths) before the height growth ceased. Accordingly, the results suggest that the variation in the timing of growth cessation in the first growing season was explained jointly by night length and stage of development of the seedlings, the latter estimated with the temperature sum accumulation or, equivalently, with the age of the seedlings.

Using constant 15 and 20 °C temperatures Koski and Selkäinaho (1982) detected that the growing periods of seedlings in the same sowings were longer in 15 °C than in 20 °C temperature conditions. A possible explanation for this is that the development of the seedlings was faster in 20 °C than in 15 °C temperature conditions. In earlier studies differences have also been found in the timing of growth cessation between experimental years (Koski and Selkäinaho, 1982; Partanen and Beuker, 1999). The existence of this year-to-year variation suggests that, in addition to photoperiod and temperature, other environmental factors like nutrition and light intensity have an additional effect on the timing of growth cessation.

In the present study both Norway spruce and silver birch origins displayed a latitudinal variation. Compared to southern origins, the growth cessation of the seedlings from northern origins generally occurred earlier. Correspondingly, the average final height of the seedlings from northern origins remained smaller. The presence of latitudinally oriented ecotypes has

been demonstrated in several tree species (Pauley and Perry, 1954; Vaartaja, 1951, 1954, 1959; Dormling et al., 1968; Håbjørg, 1972).

Short day treatment is commonly used in nurseries to stop the growth and to start the hardening of the seedlings. In this study the growth cessation lines were more gently sloping for Norway spruce origins than for silver birch origins. This sensitivity of Norway spruce to increasing night length during the first growing season has been detected earlier, e.g. by Vaartaja (1951), and makes it possible to stop the growth of Norway spruce seedlings by lengthening the night artificially (Rosvall-Åhnebrink, 1977, 1980, 1982, 1990; Dormling and Lundkvist, 1983).

The height growth of silver birch seedlings can be stopped by using short day treatment after the seedlings have reached a certain stage of development. An appropriate time to start short day treatment is when about two-thirds of the average annual temperature sum (threshold 5 °C) of the original growing site of the origin has been accumulated (Koski and Sievänen, 1985; Luoranen, 2000). Consequently, in central Finland the height growth of local silver birch can be stopped effectively with an 8 h short day treatment lasting for 2 to 3 weeks started at the earliest in July (Luoranen and Rikala, 1997; Luoranen, 2000). In the present study in the fourth and the fifth sowings, the height growth of silver birch seedlings occurred when the night length was already between 11 and 12 h. In these late sowings, the two-thirds of the average annual temperature sum (threshold 5 °C) of the original growing site of the origins had not been accumulated. Accordingly in late sowings, the night length over 11 h seemed to be the factor that forced the seedlings to cease their growth in spite of low temperature sum accumulation.

Unlike in the first growing season, the sowing date did not affect the timing of the formation of the terminal buds in the second growing season either in Norway spruce ($P > 0.1$) or in silver birch ($P > 0.1$) seedlings (Fig. 5). The sowing date, however, slightly affected the timing of height growth cessation in the second growing season both in Norway spruce ($P < 0.05$) and in silver birch ($P < 0.01$) seedlings. Koski and Sievänen (1985) did not find a correlation between the sowing date and the timing of growth cessation in the following growing season for Norway spruce and silver birch seedlings.

In conclusion, in the present study the growth of the seedlings from different sowing dates did not cease with the same critical night length, and the height of the seedlings also varied between sowing dates. The photoperiodic regulation of height growth cessation in the sowing year was dependent on the stage of seedling development estimated with the temperature sum accumulation or, equivalently, with the age of the seedlings. On the other hand, in similar photoperiodic conditions the height growth cessation was dependent on the latitude of the origin. Information about the effect of sowing time and the effect of photoperiodic conditions on the height growth and the growth cessation of the seedlings from different origins is needed when seedlings are produced in nurseries for forest cultivation.

Acknowledgements

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