

Critical night length for bud set and its variation in two photoperiodic ecotypes of *Betula pendula*

ANNELI VIHÄRÄ-AARNIO,^{1,4} RISTO HÄKKINEN² and OLAVI JUNTILA³

¹ Finnish Forest Research Institute, Vantaa Research Unit, P.O. Box 18, FIN-01301 Vantaa, Finland

² Finnish Forest Research Institute, Unioninkatu 40 A, FIN-00170 Helsinki, Finland

³ Department of Biology, University of Tromsø, N-9037 Tromsø, Norway

⁴ Corresponding author (anneli.vihera-aarnio@metla.fi)

Received August 2, 2005; accepted November 20, 2005; published online May 1, 2006

Summary We studied the variation in critical night length for bud set in two photoperiodic ecotypes (two latitudinally distant stands) of silver birch (*Betula pendula* Roth) in three phytotron experiments. Seeds from 21 open-pollinated mother trees in a southern (Tuusula, 60° N) and a northern (Kittilä, 67° N) Finnish stand were germinated and grown for 4 weeks in a 24-h photoperiod in a greenhouse and then moved to different night length treatments at 18 °C for 4 to 6 weeks. Night lengths from 5 to 8.5 h were used for southern origin seedlings and from 1 to 4.5 h for northern origin seedlings. At the end of the treatments, apical bud set was observed and the percentage of seedlings with bud set calculated for each treatment and tree progeny. The critical night lengths (CNL) for 50% bud set were determined separately for seedlings from each mother tree by regression analysis. In both ecotypes, the mean percentage of seedlings with bud set was lowest for the shortest night lengths and increased rapidly as night lengths increased. Mean CNL with its 95% confidence interval for the southern and northern ecotypes was 6.3 ± 0.2 and 3.1 ± 0.3 h, respectively. The CNL of the two ecotypes differed significantly in three experiments. Within-ecotype variance of the CNL was significantly higher in the northern ecotype (0.484) than in the southern ecotype (0.150). Significant differences in CNL were detected between individual mother trees of the southern ecotype, but not between mother trees of the northern ecotype. The ranking of individual mother trees, based on CNL, differed in the three experiments.

Keywords: annual rhythm, climatic adaptation, critical day length, growth cessation, photoperiod.

Introduction

Well-timed development of dormancy and frost hardiness are crucial for the success of northern temperate tree species. In trees with a free growth pattern, cessation of height growth, which is the first visible sign of the frost hardening process (Weiser 1970), is predominantly triggered by changes in photoperiod (Nitsch 1957, Fuchigami et al. 1982). The critical day

length for growth cessation is defined as the maximum day length (i.e., the minimum night length) causing cessation of extension growth, but the photoperiod for 50% bud set is also used to define the critical day length (Thomas and Vince-Prue 1997). In this study, night length rather than day length was used because the effect of photoperiod is determined by the length of the unbroken dark period and not by day length (Nitsch 1957, Thomas and Vince-Prue 1997).

Tree species with a wide geographic distribution have photoperiodic ecotypes that differ in critical night length (CNL); northern ecotypes having shorter CNLs than southern ecotypes (Sylvén 1940, Vaartaja 1954, 1959, Heide 1974, Ekberg et al. 1979). Håbjørg (1972a) demonstrated the existence of photoperiodic ecotypes in *Betula pubescens* Ehrh., as has been found in other Scandinavian tree and shrub species, including *Betula pendula* Roth (Håbjørg 1978). Because of the gradual change in photoperiod with latitude and effective gene flow between birch populations (Hjelmroos 1991, Eriksson et al. 2003), the adaptive variation in timing of growth cessation among adjacent populations shows a gradual clinal pattern of change rather than differentiation into discrete ecotypes (Viherä-Aarnio et al. 2005). However, when comparing origins from distant latitudes, the concept of ecotype is commonly used.

The within-population variation in several characteristics of birch has been studied, including growth and quality traits (Johnsson 1951, Clausen 1973, 1980, Raulo and Koski 1977, Nepveu and Velling 1983, Eriksson et al. 2003), adaptive traits such as dates of bud burst (Clausen 1973), flowering (Clausen 1980), growth cessation (Clausen 1973), leaf discoloration (Eriksson et al. 2003) as well as selectively neutral isoenzyme markers (Rusanen et al. 2003, Eriksson et al. 2003). However, the variation in CNL among individual trees within birch populations has not been studied, even though it may largely explain the variation in important adaptive traits such as timing of growth cessation and development of frost hardiness. The objective of this study was to examine the CNL for 50% bud set and its variation in two photoperiodic ecotypes—a southern and a northern stand—of silver birch.

Material and methods

Seed origins

The seed material for the study was collected from two silver birch (*Betula pendula*) stands, from distant latitudes, i.e., from locations differing in photoperiodic regime. One stand was in Tuusula, southern Finland (60°27' N, 24°58' E, 50 m a.s.l.) and the other was in Kittilä, northern Finland (67°44' N, 24°51' E, 200 m a.s.l.). Day length on June 21 in Tuusula and Kittilä is 19 and 24 h, respectively. Both stands originated through natural regeneration and are regarded as representative of the local birch populations. Open-pollinated seeds from 21 mother trees were collected from the Kittilä stand in 1998 and from the Tuusula stand in 2000.

Seedlings

Seeds of the 21 mother trees from each stand were sown in separate boxes filled with a 1:1 (v/v) peat:sand mix. In Experiment 1, the seeds were germinated in a greenhouse at 21 °C and 78% relative humidity (RH) in a 24-h photoperiod for one week and then transferred to the conditions described below. In Experiments 2 and 3, the seeds were germinated for 2–3 weeks at 18 °C and 74% RH in a 24-h photoperiod (Table 1). In all experiments, seedlings at the cotyledon stage were transplanted to 12-cm diameter pots (0.72 l) filled with a 3:1 (v/v) peat:perlite mix and grown at 18 °C and 74% RH in a 24-h photoperiod for 2–3 weeks. The night length experiments were started when the plants were about 4 weeks old and 2–5 cm in height. In Experiment 1, the Kittilä seeds germinated 3–4 days later than the Tuusula seeds. Thus, for Experiments 2 and 3, the Kittilä seeds were sown 3–4 days earlier than the Tuusula seeds to diminish the difference in germination date.

Experiments

The three photoperiodic response experiments were carried out in the phytotron of the University of Tromsø (69°39' N), Norway, during autumn 2001 and spring 2002 (Table 1). Seed-

lings of both ecotypes were subjected to four (Experiment 1) or six (Experiments 2 and 3) night lengths that varied around the mean CNLs estimated according to Håbjørg (1978) for Tuusula (60° N) and Kittilä (67° N) ecotypes (about 8 and 4 h, respectively). Thus, the night lengths for the Tuusula seedlings varied from 5 to 8.5 h and the night lengths for the Kittilä seedlings ranged from 1 to 4.5 h. After completion of Experiment 1, the treatments were slightly adjusted to optimize the amplitude and division of the night lengths around the mean. The duration of the treatments varied among the experiments (Table 1).

Each half-sib progeny of 21 mother trees from each stand was represented by 10 seedlings per treatment (two pots each with five seedlings) in Experiments 1 and 2 and by nine seedlings (three pots with three seedlings) in Experiment 3.

Experiment 1 was carried out in two, Experiment 2 in three and Experiment 3 in four phytotron chambers. Each chamber was divided with curtains into four compartments in Experiments 1 and 2, and into three compartments in Experiment 3. The night length treatments were completely randomized to compartments in Experiments 1 and 2. Because of technical arrangements, randomization in Experiment 3 was partial: the neighboring day-length treatments were established in the same chamber. The locations of seedling pots of mother trees were completely randomized within compartments in all experiments. In the phytotron, temperature-controlled air entered through a perforated floor ensuring an even temperature throughout the chamber. In Experiments 1 and 2, the seedlings were illuminated for 12 h each day with a photosynthetic photon flux (PPF) of 180–200 μmol m⁻² s⁻¹ (400–750 nm) from incandescent and fluorescent lamps (Philips Fluorescent tubes, TCD 58/840) preceded and followed by a PPF of 15 μmol m⁻² s⁻¹ (400–750 nm) from incandescent lamps to give the different night length treatments. In Experiment 3, the chambers received natural daylight (0800–2000 h) and the night lengths were modified as in Experiments 1 and 2. Temperature was 18 ± 0.5 °C and relative humidity was maintained at 74 ± 3% (corresponding to 0.5 kPa water vapor pressure deficit). The plants were watered daily and fertilized weekly with

Table 1. Description of Experiments 1–3.

Trait	Experiment 1	Experiment 2	Experiment 3
Sowing date	28.8.2001	Kittilä: 12.11.2001 Tuusula: 16.11.2001	Kittilä: 18.4.2002 Tuusula: 22.4.2002
Transplanting date	10.–14.9.2001	26.–30.11.2001	6.5.2002
Age of seedlings (from sowing to start of treatments)	4 weeks	Kittilä: 4 weeks 4 days Tuusula: 4 weeks	Kittilä: 4 weeks Tuusula: 3 weeks 4 days
Start of treatments	27.9.2001	14.12.2001	16.5.2002
Duration of treatments	4 weeks	4 weeks 5 days	6 weeks 5 days
Treatments, hours	Tuusula: 6.5–7–7.5–8 Kittilä: 2.5–3–3.5–4	Tuusula: 5–6–6.5–7–7.5–8.5 Kittilä: 1–2–2.5–3–3.5–4.5	Tuusula: 5–6–6.5–7–7.5–8.5 Kittilä: 1–2–2.5–3–3.5–4.5
Lighting	artificial	artificial	natural 12 h, difference artificial
Number of pots/treatment/tree	2	2	3
Number of seedlings/pot	5	5	3
Observation date	25.–26.10.2001	17.–21.1.2002	2.–3.7.2002

a complete nutrient solution (for composition, see Junttila 1980).

Measurements

A seedling was recorded as having set bud if no leaves or only one small leaf had formed at the shoot apex during the preceding week and if the uppermost leaf differed considerably in size from that immediately below. If there was an even continuum of leaves of varying size at the top of the seedling, it was assumed to be still growing. At the end of the experiment, the number of seedlings with set buds was counted and the percentage of seedlings with set buds calculated for each treatment and mother tree.

Statistical analysis

At the end of each experiment, the proportion of seedlings with set terminal buds was calculated for each treatment and mother tree. To estimate the CNL for 50% bud set in the progeny of a particular mother tree, S-shaped regression models for each mother tree and experiment were estimated:

$$\ln\left(\frac{p}{1-p}\right) = \alpha + \beta x + \varepsilon \quad (1)$$

where x is night length and p is the proportion of seedlings with set terminal buds. The models were then used to calculate CNL values for each mother tree ($\text{CNL} = -a/b$). Five cases with unrealistic slope parameter in Equation 1 ($b \leq 0$) and two cases (distance to group mean ≥ 3.1 standard deviations) were considered outliers and omitted from the subsequent analysis.

A repeated measures mixed model analysis of variance was used to test for the differences in the mean CNL value between ecotypes and experiments:

$$y_{ijk} = \mu + \alpha_i + \tau_{k(i)} + \beta_j + \alpha\beta_{ij} + \beta\tau_{jk(i)} + \varepsilon_{ijk} \quad (2)$$

where $y = \text{CNL}$, $\alpha = \text{ecotype}$ ($i = 1, 2$; fixed), $\tau = \text{mother tree}$ ($k = 1, \dots, n_i$; random) and $\beta = \text{experiment}$ ($j = 1, \dots, 3$; fixed).

The residual variances of ecotypes were not homogeneous (Levene's test, $P < 0.001$), whereas those of experiments within ecotypes were (Levene's test, $P = 0.593$ Tuusula ecotype, $P = 0.051$ Kittilä ecotype). Thus, the inverse of the over-experiments pooled variances for ecotypes were used as case weights. In addition to the standard analysis of variance F tests, the equality of the differences between ecotypes within experiment were tested with simple contrast F tests.

The effect of individual mother trees in the three experiments was tested by two-way analyses of variance without an interaction term because of lack of replications. The interaction between mother tree and experiment was analyzed with Spearman rank correlation coefficients.

Analyses were performed with the statistical package, SPSS 13.0.1 (SPSS, Chicago, IL).

Results

Effect of photoperiod on bud set

The mean percentage of seedlings with a set terminal bud was

lowest in the shortest night length treatments and increased sharply with night length (Figure 1). Ecotypic differences were evident and consistent in all experiments: seedlings of the northern ecotype set bud with nights of shorter length than seedlings of the southern ecotype.

The effect of night length on the pattern of bud set was similar in Experiments 2 and 3, but a lower proportion of the seedlings of both ecotypes set bud in all night lengths in Experiment 1 compared to Experiments 2 and 3 (Figure 1). For the Kittilä ecotype, the mean percentage of seedlings with a set terminal bud remained below 50% even in the longest night length, so CNL values for most of the individual mother trees was based on extrapolation in Experiment 1.

Critical night length for 50% bud set

The CNL value for the progeny of each mother tree was determined by regression models (Equation 1). The mean CNL value for the Tuusula ecotype, calculated over all three experiments, was 6.3 ± 0.2 h (mean \pm 95% confidence interval) and that for the Kittilä ecotype was 3.1 ± 0.3 h (Table 2; Figure 2). When the non-overlapping confidence intervals of CNLs of ecotypes, estimated from the experiments, were converted to the calendar time scale of the mother tree locations (Figure 2), the confidence intervals of ecotypes overlapped, except in Experiment 2.

There was a slight, but significant interaction ($P < 0.001$; Equation 2; Figure 3) between ecotype and experiment. The difference in CNL values between Tuusula and Kittilä ecotypes was the same (2.9 h) in Experiments 1 and 2, but was higher (3.8 h) in Experiment 3 ($P < 0.001$; Table 2). However, in each experiment, the CNL value for the southern Tuusula ecotype was higher than for the northern Kittilä ecotype (all $P < 0.001$). In Experiment 1, in which the period of exposure to the night length treatments was the shortest, CNL values for

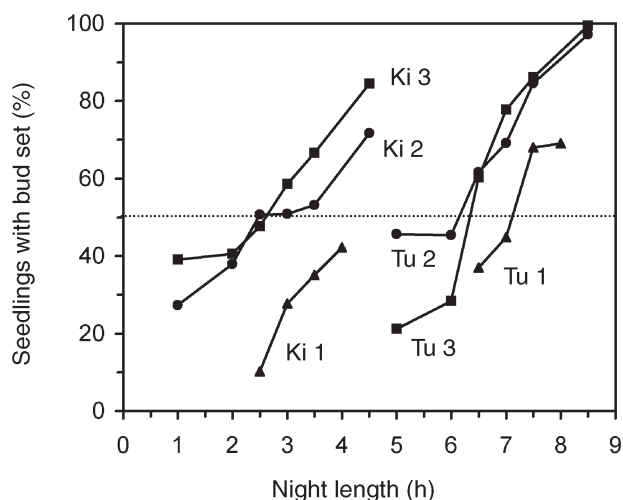


Figure 1. Mean percentage (%) of seedlings with set terminal bud in a southern (Tu = Tuusula, 60°27' N) and a northern (Ki = Kittilä, 67°44' N) Finnish silver birch ecotype in Experiments 1–3 as a function of night length.

Table 2. Critical night length (h) for 50% bud set and its variation in a southern (Tu = Tuusula, 60°27' N) and a northern (Ki = Kittilä, 67°44' N) Finnish silver birch ecotype in Experiments 1–3. An asterisk denotes pooled variance. Abbreviation: *n* = sample size; and CI = confidence interval.

Experiment	<i>n</i>		Mean		95% CI for mean		Variance		Min–Max	
	Tu	Ki	Tu	Ki	Tu	Ki	Tu	Ki	Tu	Ki
1	18	18	7.1	4.2	6.9–7.3	3.8–4.5	0.177	0.467	6.2–7.7	3.6–6.1
2	21	20	5.8	2.9	5.7–5.9	2.7–3.1	0.100	0.232	5.1–6.3	1.9–3.7
3	20	20	6.1	2.3	5.9–6.3	1.9–2.7	0.177	0.752	4.8–6.7	0.7–3.9
1–3	59	58	6.3	3.1	6.1–6.5	2.8–3.4	0.150 *	0.484 *	4.8–7.7	0.7–6.1

both Tuusula and Kittilä were higher than in Experiments 2 and 3 (all *P* < 0.001; Table 2; Figures 2 and 3).

Variation in critical night length within ecotypes

Within-ecotype variances in CNL were systematically higher for the Kittilä ecotype than for the Tuusula ecotype (Table 2); however, CNL variances within ecotypes did not differ between experiments. The pooled variance of the CNL value for the Kittilä ecotype was significantly higher than the pooled variance of the CNL for the Tuusula ecotype (0.484 versus 0.150; Levene’s *P* < 0.001).

The mean CNL value for the progeny of individual mother trees calculated over the three experiments varied between 5.5 and 6.7 h for the Tuusula ecotype and between 1.8 and 4.0 h for the Kittilä ecotype. Mean CNLs of mother trees differed significantly in Tuusula (*P* = 0.003), but not in Kittilä (*P* = 0.265). However, the ranking of CNL values for mother trees within an ecotype differed between experiments. Among the experiments, Spearman rank correlations of mother tree CNL values ranged from –0.20 to 0.45 and were not statistically significant, indicating an interaction between mother tree and experiment.

Discussion

Variation in the CNL for 50% bud set of two photoperiodic ecotypes (i.e., two latitudinally distant stands) of silver birch was studied. Significant differences in CNL were detected between the ecotypes as well as in its within-ecotypes variances (Table 2; Figure 3). Although there have been several studies on ecotypic differences in CNL (Håbjørg 1972a, 1978, Heide 1974, Ekberg et al. 1979), within-ecotype variation in birch has not been reported previously. Our results are in accordance with earlier studies on the differentiation between distant populations. Although the mean CNL of the ecotypes differed between experiments, the difference in CNL between ecotypes remained constant (Figure 3). We were able to estimate mean CNL values precisely because the confidence intervals of the means were narrow (Table 2; Figure 2). Despite the slight interaction between ecotype and experiment, evident as crossing lines for Experiments 2 and 3 in Figure 3, the main pattern was clear. This interaction may be a result of the sensitivity of northern populations to light quality, as shown in *Betula pubescens* (Håbjørg 1972b), *Salix pentandra* L. (Junttila and Kaurin 1990) and in *Picea abies* (L.) Karst. (Clapham et al. 1998).

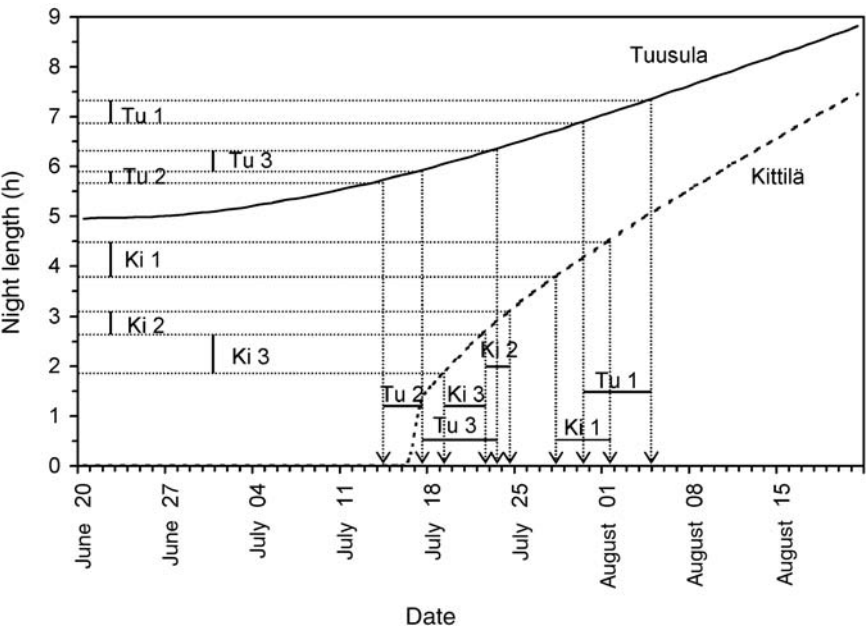


Figure 2. The 95% confidence interval of the mean critical night length for 50% bud set of a southern (Tu = Tuusula) and a northern (Ki = Kittilä) Finnish silver birch ecotype in Experiments 1–3 in relation to the seasonal change in night length at the source locations of Tuusula (solid line) and Kittilä (dash line) and associated calendar date.

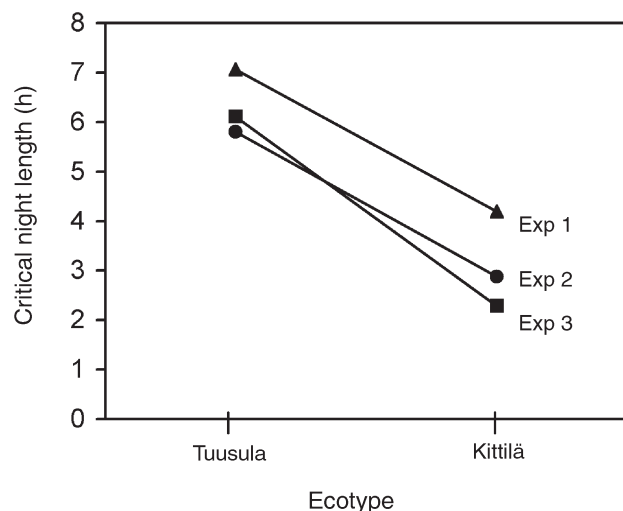


Figure 3. Mean critical night length for 50% bud set of a southern (Tuusula) and a northern (Kittilä) Finnish silver birch ecotype in Experiments 1–3.

In Experiment 3, in which seedlings were grown in natural light for 12 h, the Kittilä (lat. 67°44' N) seedlings may have benefited from the northern light conditions at Tromsø (lat. 69°39' N).

Our mean CNL values were slightly lower than those reported by Håbjørg (1978). This discrepancy may be associated with differences in experimental conditions and in methods for determining CNL. Our results were based on 50% bud set, whereas Håbjørg (1978) recorded complete cessation of apical growth. Longer nights are probably required for complete cessation of apical growth than for 50% bud set, on attainment of which half the seedlings may still be growing.

In local light regimes, the date at which the mean CNL was reached for the Tuusula and Kittilä ecotypes is July 23 and July 25, respectively. Growth cessation of northern ecotypes occurs in the middle of August (Junttila and Nilsen 1993). Considering the 1–3 weeks from the time that the CNL is achieved and the time that growth ceases (Junttila et al. 2003) and taking into account the modifying effects of temperature and other external factors on growth cessation (Håbjørg 1972a, 1972b, Heide 1974, Black-Samuelsson and Eriksson 2002, Li et al. 2002), our dates for CNL seem realistic. The broader confidence intervals of the CNL values of the northern Kittilä ecotype compared with the southern ecotype, were not apparent when converted to calendar time because of the faster change in night length at higher latitudes (Figure 2).

For both ecotypes, mean CNL was significantly longer in Experiment 1 than in Experiments 2 and 3 (Table 2). This difference might be related to the period of exposure to the night length treatments, which was shortest in Experiment 1 (Table 1). Over a shorter treatment period, a longer night length is probably needed to reach the same frequency of bud set as in treatments of longer duration. The response to photoperiod may also be modified by temperature, soil water availability, air humidity and nutrient availability (Håbjørg 1972a, 1972b,

Heide 1974, Black-Samuelsson and Eriksson 2002, Li et al. 2002). Seedling size and stage of development can also modify the response to night length (Junttila 1976, Koski and Selkäinaho 1982, Partanen 2004, Viherä-Aarnio et al. 2005). The low frequency of bud set of the Kittilä seedlings in Experiment 1 (Figure 1) may, thus, in part, be related to their lower age (Luoranen and Rikala 1997, Luoranen 2000). As a result of slower germination, the Kittilä seedlings were younger at the start of Experiment 1 and may not have been able to complete bud set within the treatment time.

The variance in CNL was significantly higher in the northern Kittilä ecotype than in the southern Tuusula ecotype (Table 2). In contrast to our results for birch, Dormling (1979) reported a lower amplitude in CNL for bud set in northern than in southern origins of *Picea abies*. It has been suggested, although not supported by results for *P. abies* (Tigerstedt 1973) and *Acer platanoides* L. (Rusanen et al. 2003), that populations near the edge of a species distribution possess less genetic variation than other populations. The Kittilä stand of silver birch that we studied contains significantly less isoenzyme variation than southern Finnish birch populations (Rusanen et al. 2003). Neutral molecular markers such as isoenzymes, are not, however, necessarily good predictors of quantitative, adaptive traits such as timing of bud set (Karhu et al. 1996). Silver birch, with a widespread distribution, outcrossing breeding system and widely dispersed seeds, would be expected to maintain a high within-population genetic diversity (Hamrick et al. 1992). Large variation within birch populations has been reported in, for example, the timing of growth cessation (Clausen 1973) and leaf discoloration (Eriksson et al. 2003).

The mean CNL values of individual mother trees varied between 5.5 and 6.7 h (1.2 h) for the Tuusula population and between 1.8 and 4 h (2.2 h) for the Kittilä population, which would occur between July 10 to July 28 at Tuusula and between July 19 to July 29 at Kittilä. Thus, the range in calendar dates corresponding to the CNL is narrower in the north than in the south.

One of our objectives was to determine whether trees with significantly shorter or longer CNL (early or late types) existed in either of the ecotypes studied. In the southern ecotype, we found some support for this hypothesis. The earliest and the latest mother trees differed in CNL significantly from each other on the average, but the trees had a different ranking in the three experiments. Ranking of the individual trees within the northern ecotype was even more irregular between experiments and no significant differences among trees were detected.

In conclusion, mean CNL values of a southern and a northern silver birch ecotype were precisely estimated. Although CNL varied according to the experimental conditions, differences between the distant ecotypes were significant and consistent in the three experiments. Variation in CNL was larger in the northern ecotype than in the southern ecotype.

Acknowledgments

The authors thank Dr. Jarle Nilsen and his excellent team at the

phytotron of the University of Tromsø for carrying out the experiments, Dr. Berhanu Abrha Tsegay for assisting in the measurements, Mrs. Tuula Viitanen for putting the data into electronic form, Prof. Katri Kärkkäinen for critical reading of the manuscript and Dr. Michael Starr for his revision of the language. This study was financed by the Finnish Academy as a part of the Life2000—Research Program on Biological Functions.

References

- Black-Samuelsson, S. and G. Eriksson. 2002. Effects of nitrogen stress on adaptive genetic variation in *Acer platanoides* L. and *Betula pendula* Roth. *For. Genet.* 9:71–86.
- Clausen, K.E. 1973. Within-provenance variation in yellow birch. *Proc. 20th NE Forest Tree Improvement Conference*, Univ. New Hampshire, Durham, pp 90–98.
- Clausen, K.E. 1980. Survival, growth, and flowering of birch progenies in an open-field test. *Silvae Genet.* 29:108–114.
- Clapham, D.H., I. Dormling, I. Ekberg, G. Eriksson, M. Qamaruddin and D. Vince-Prue. 1998. Latitudinal cline of requirement for far-red light for the photoperiodic control of budset and extension growth in *Picea abies* (Norway spruce). *Physiol. Plant.* 102:71–78.
- Dormling, I. 1979. Influence of light intensity and temperature on photoperiodic response of Norway spruce provenances. *IUFRO Norway spruce meeting*, S 2.03.11–S 2.02.11, Bucharest, pp 398–408.
- Ekberg, I., G. Eriksson and I. Dormling. 1979. Photoperiodic reactions in conifer species. *Holarct. Ecol.* 2:255–263.
- Eriksson, G., S. Black-Samuelsson, M. Jensen, T. Myking, M. Rusanen, T. Skråppa, P. Vakkari and L. Westergaard. 2003. Genetic variability in two tree species, *Acer platanoides* L. and *Betula pendula* Roth, with contrasting life-history traits. *Scand. J. For. Res.* 18:320–331.
- Fuchigami, L.H., C.J. Weiser, K. Kobayashi, R. Timmis and L.V. Gusta. 1982. A degree growth stage (°GS) model and cold acclimation in temperate woody plants. *In Plant Cold Hardiness and Freezing Stress*. Eds. P.H. Li and A. Sakai. Academic Press, New York, pp 93–116.
- Håbjørg, A. 1972a. Effects of photoperiod and temperature on growth and development of three latitudinal and three altitudinal populations of *Betula pubescens* Ehrh. *Meld. Nor. Landbrukshøgsk.* 51: 1–27.
- Håbjørg, A. 1972b. Effects of light quality, light intensity and night temperature on growth and development of three latitudinal populations of *Betula pubescens* Ehrh. *Meld. Nor. Landbrukshøgsk.* 51: 1–17.
- Håbjørg, A. 1978. Photoperiodic ecotypes in Scandinavian trees and shrubs. *Meld. Nor. Landbrukshøgsk.* 57:1–20.
- Hamrick, J.L., M.J.W. Godt and S.L. Sherman-Broyles. 1992. Factors influencing levels of genetic diversity in woody plant species. *New For.* 6:95–124.
- Heide, O.M. 1974. Growth and dormancy in Norway spruce ecotypes (*Picea abies*). I. Interaction of photoperiod and temperature. *Physiol. Plant.* 30:1–12.
- Hjelmroos, M. 1991. Evidence of long-distance transport of *Betula* pollen. *Grana* 30:215–228.
- Johnsson, H. 1951. Avkommeprövning avbjork preliminara resultat från unga försöksplanteringar. Summary: Progeny tests in birch—preliminary results from young experiments. *Sven. Papperstidn.* 54:412–426.
- Junttila, O. 1976. Apical growth cessation and shoot tip abscission in *Salix*. *Physiol. Plant.* 38:278–286.
- Junttila, O. 1980. Effect of photoperiod and temperature on apical growth cessation in two ecotypes of *Salix* and *Betula*. *Physiol. Plant.* 48:347–352.
- Junttila, O. and Å. Kaurin. 1990. Environmental control of cold acclimation in *Salix pentandra*. *Scan. J. For. Res.* 5:195–204.
- Junttila, O. and J. Nilsen. 1993. Growth and development of northern forest trees as affected by temperature and light. *In Forest Development in Cold Climates*. Eds. J. Alden, J.L. Mastrantonio and S. Ødum. Plenum Press, New York, pp 43–57.
- Junttila, O., J. Nilsen and B. Igeland. 2003. Effect of temperature on the induction of bud dormancy in ecotypes of *Betula pubescens* and *Betula pendula*. *Scand. J. For. Res.* 18:208–217.
- Karhu, A., P. Hurme, M. Karjalainen, P. Karvonen, K. Kärkkäinen, D. Neale and O. Savolainen. 1996. Do molecular markers reflect patterns of differentiation in adaptive traits of conifers? *Theor. Appl. Genet.* 93:215–221.
- Koski, V. and J. Selkäinaho. 1982. Experiments on the joint effect of heat sum and photoperiod on seedlings of *Betula pendula*. *Commun. Inst. For. Fenn.* 105:1–34.
- Li, C., T. Puhakainen, A. Welling, A. Viherä-Aarnio, A. Ernsten, O. Junttila, P. Heino and T. Palva. 2002. Cold acclimation in silver birch (*Betula pendula*). Development of freezing tolerance in different tissues and climatic ecotypes. *Physiol. Plant.* 116:478–488.
- Luoranen, J. 2000. Control of growth and frost hardening of silver birch container seedlings: growth retardants, short-day treatment and summer planting. *Academic dissertation*. The Finnish Forest Research Institute, Research Paper 777, 167 p.
- Luoranen, J. and R. Rikala. 1997. Growth regulation and cold hardening of silver birch seedlings with short-day treatment. *Tree Planters' Notes* 48:65–71.
- Nepveu, G. and P. Velling. 1983. Rauduskoivun puuaineen laadun geneettinen vaihtelu. Abstract: Individual genetic variability of wood quality in *Betula pendula*. *Folia For.* 575:1–21.
- Nitsch, J.P. 1957. Photoperiodism in woody plants. *Proc. Am. Soc. Hortic. Sci.* 70:526–544.
- Partanen, J. 2004. Dependence of photoperiodic response of growth cessation on the stage of development in *Picea abies* and *Betula pendula* seedlings. *For. Ecol. Manage.* 188:137–148.
- Raulo, J. and V. Koski. 1977. Growth of *Betula pendula* Roth progenies in southern and central Finland. *Comm. Inst. For. Fenn.* 90: 1–39.
- Rusanen, M., P. Vakkari and A. Blom. 2003. Genetic structure of *Acer platanoides* and *Betula pendula* in northern Europe. *Can. J. For. Res.* 33:1110–1115.
- Sylvén, N. 1940. Lång-och kortdagstyper av de svenska skogsträden. Long day and short day types of the Swedish forest trees. *Sven. Papperstidn.* 43:317–324, 332–342, 350–354.
- Tigerstedt, P.M.A. 1973. Studies on isozyme variation in marginal and central populations of *Picea abies*. *Hereditas* 75:47–60.
- Thomas, B. and D. Vince-Prue. 1997. Photoperiodism in plants. 2nd Edn. Academic Press, London, 428 p.
- Vaartaja, O. 1954. Photoperiodic ecotypes of trees. *Can. J. Bot.* 32: 392–399.
- Vaartaja, O. 1959. Evidence of photoperiodic ecotypes in trees. *Ecol. Monogr.* 29:91–111.
- Viherä-Aarnio, A., R. Häkkinen, J. Partanen, A. Luomajoki and V. Koski. 2005. Effects of seed origin and sowing time on timing of height growth cessation of *Betula pendula* seedlings. *Tree Physiol.* 25:101–108.
- Weiser, C.J. 1970. Cold resistance and injury in woody plants. *Science* 169:1269–1278.