

Variations in phenology and growth of European white birch (*Betula pendula*) clones

MATTI ROUSI^{1,2} and JYRKI PUSENIUS^{2,3}

¹ The Finnish Forest Research Institute, Finlandiantie 18, Fin-58450 Punkaharju, Finland

² Corresponding author (matti.rousu@metla.fi)

³ Department of Biology, University of Joensuu, PO Box 111, Fin-80101 Joensuu, Finland

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Summary Phenology can have a profound effect on growth and climatic adaptability of northern tree species. Although the large interannual variations in dates of bud burst and growth termination have been widely discussed, little is known about the genotypic and spatial variations in phenology and how these sources of variation are related to temporal variation. We measured bud burst of eight white birch (*Betula pendula* Roth) clones in two field experiments daily over 6 years, and determined the termination of growth for the same clones over 2 years. We also measured yearly height growth. We found considerable genetic variation in phenological characteristics among the birch clones. There was large interannual variation in the date of bud burst and especially in the termination of growth, indicating that, in addition to genetic effects, environmental factors have a strong influence on both bud burst and growth termination. Height growth was correlated with timing of growth termination, length of growth period and bud burst, but the relationships were weak and varied among years. We accurately predicted the date of bud burst from the temperature accumulation after January 1, and base temperatures between +2 and –1 °C. There was large clonal variation in the duration of bud burst. Interannual variation in bud burst may have important consequences for insect herbivory of birches.

Keywords: abiotic resistance, bud burst, climatic adaptability, growth termination, length of growth period.

Introduction

Trees at northern latitudes have survived several major climatic changes including glaciations in the Pleistocene epoch (e.g., Wright 1977), indicating good adaptability to climatic variations. The survival of northern trees depends on correct timing of both release of winter dormancy in spring and growth termination in autumn. For light-demanding pioneer species, such as white birch (*Betula pendula* Roth), rapid shoot growth is of fundamental importance. A delay in canopy development can lead to large losses in growth, because peak solar radiation receipt precedes the peak in mean daily temperatures (Cannell 1989). Both theoretical considerations (Can-

nell 1989) and some empirical results (e.g., Rönnerberg-Wästlund and Gullberg 1999) indicate that differences in timing of bud burst are more important determinants of tree growth than differences in timing of growth termination.

The rate of global warming since 1976 has been greater than at any time during the last 1000 years (IPCC 2001). Recent meta-analyses suggest that a significant impact of global warming is already evident in some plant populations and that the events of spring phenology of trees have been brought forward by 3 days (Root et al. 2003). In addition to this trend, long time series have revealed large annual fluctuations in date of bud burst. For example, Häkkinen (1999) studied a 38-year time series of bud burst and found yearly variation in the range of 40 days for birch. Although the effects of environmental factors on the breaking of dormancy and on bud burst have been studied intensively, modeling bud burst has proved difficult. Because weather is mostly unpredictable (Lorenz 1993), a light signal may be needed to prevent premature breaking of winter dormancy. Recent models of bud development in boreal trees suggest the need to incorporate a specific date, usually March 21, after which the accumulation of heat sum determines the onset of growth (Häkkinen et al. 1998, Linkosalo et al. 2000). However, Leinonen (1996) concluded that absolute timing of rest completion cannot be determined, because the timing of growth initiation depends partly on dormant period chilling and partly on spring temperature accumulation. Suggested base temperatures for degree day (d.d.) temperature sums for birch ontogenesis cover the range of +5 (e.g., Sarvas 1972) to 0 °C (Heide 1993). In autumn, night length regulation of growth cessation is the most important factor according to computer simulations (Hänninen et al. 1990), although temperature may have a modifying effect (Koski and Sievänen 1985).

Flushing leaves provide high-quality food for herbivores, because young foliage is rich in nutrients and poor in defensive compounds (Bernays and Chapman 1994, Kauser et al. 1999, Laitinen et al. 2002b). Therefore, spring emergence of many tree-defoliating insects is closely synchronized with bud burst of their host trees (e.g., Quiring 1994, Tikkanen and Julkunen-Tiitto 2003). Consequently, the extent of variation in bud burst among individual trees and stochasticity of weather-re-

lated variation in bud burst among years influences the extent of colonization and larval densities on trees. In addition to insect herbivores, deer damage in young broadleaf trees may be associated with timing of bud opening (Moore et al. 2000). Prolonged growth in the autumn may also influence the timing of bud burst next spring (Koski and Siev nen 1985), thereby affecting the rate of emergence of insect herbivores.

Different genotypes may vary in their reactions to the challenges imposed by variations in physical growing conditions and occurrence of natural enemies. Pronounced spatial variation in growing conditions may also modify phenology. However, little is known about genotypic and spatial variations in phenology and how these sources of variation are related to temporal variation. In two field experiments, we monitored bud burst of European white birch (*Betula pendula* Roth) clones daily for 6 years, recorded the termination of growth over 2 years and made yearly height growth measurements. We used these measurements to determine: (1) interannual variation among individual birch genotypes (clones) in bud burst, termination of growth and length of growth period; (2) the effect of environmental heterogeneity (temporal variation in temperature and spatial edaphic variation) on bud burst, growth termination and length of growth period; and (3) the relationship between growth and phenology. We briefly discuss variation among genotypes in relation to global temperature change and insect herbivore resistance.

Materials and methods

Plant material

The ortet trees for micropropagated plantlets used in this study are phenotypically selected white birches (*B. pendula*), representing different generations of the breeding programs. They are either plus trees, or F₁- or F₂-generation progenies produced from either controlled crossings or open-pollinations. The geographic origin of the ortet trees is southern Finland (60°20'–62°45' N). As a result of effective gene flow, there is limited genetic variation among birch forests in southern Finland (Rusanen et al. 2003). Consequently, potential specific heat sum or photoperiod requirement based on geographic origin of the clones is unlikely to impact our measurements; however, if the phenotypic selection was successful and growth rate is related to phenology, then the variation in this material may be more limited than in nature. Given that the tallest clone was 40% taller than the shortest clone at 8 years (Ylioja et al. 2000), the phenotypic selection for these clones may have been inefficient.

Micropropagated plantlets were transplanted from laboratory cultures to 0.28-l pots during the second week of June 1990. In spring 1991, an experiment with eight clones was established on an abandoned field at Yhteislaidun. The site has sandy soil and is poor in nutrients (Laitinen et al. 2002a). Another experiment was established in 1992 on a fertile field at Common Garden, about 1 km from the first experiment. Eight clones were used at Common Garden, of which four clones were the same as those used at Yhteislaidun (Clones 36, 5952,

5818 and 5832). Both experiments were located in Punkaharju (61°48' N), in south-eastern Finland.

Bud burst, growth termination and growth

In both experiments, a randomized complete block design was used. Plantlets of each clone were randomized among eight plots within a block, such that nine plantlets per clone were planted in the same plot. The distance between plantlets was 1.5 m. At Yhteislaidun, there were five replicate blocks, and at Common Garden, there were four replicate blocks.

To evaluate bud burst and growth termination at Yhteislaidun, a random sample of three plantlets per clone in each of the five blocks was monitored, i.e., the observations are based on 15 plantlets per clone. At Common Garden, four plantlets per clone in each of the four blocks were observed, i.e., 16 plantlets per clone. For each plantlet, we monitored five buds from the top of the main shoot (the topmost bud not included). The bud was determined as open when the protective bud scales were open and the emerging first leaf was clearly visible (Figure 1). The observations were made on a daily basis during 1992–1997 at Yhteislaidun, and during 1993–1996 at Common Garden. Observations started each year before any of the buds were open and continued until all the buds were open. For each plant, bud burst was considered to have occurred when four buds were open. Otherwise, when the means of clones in replicate blocks were used, bud burst was considered to have occurred when 90% of buds, pooled across the replicate individuals of each clone, were open.

Termination of growth was determined at Yhteislaidun for 2 years (15 plantlets per clone in 1992 and 20 plantlets per clone in 1993) and at Common Garden for 1 year (16 plantlets per clone in 1993). Starting on July 16 (July 28 in 1992), we measured the height of the plantlets every third day until growth ceased (three successive measurements with the same value). Measurements were made 10 times in 1992 and 14 times in 1993. Growth was considered terminated when 95% of the final height increment was reached (to determine the exact date, the growth increment was considered to be similar between measurement dates). For each year, heights of all the plantlets were separately measured in late autumn after leaf fall, for use in growth correlations.

Temperature and statistics

Temperature was recorded at a height of 2 m with standard meteorological screens. The thermometers were located about 2 km from the experimental fields. Degree day values indicate the sum of differences between mean diurnal temperatures and the baseline temperatures (+5, +4, +2, +1, 0, –1 and –2 °C).

Annual variation in timing of bud burst was measured as the number of days from the beginning of a calendar year until bud burst. The mean of the sampled plantlets in each combination of year, clone and block was then used as a dependent variable. Analysis of variance was performed with the SPSS Version 11.0 software package (SPSS, Chicago, IL). The design was a split plot with clones as a main plot factor and time as a subplot factor. Clone and year were considered as fixed effects. Block and clone × block effects were included as random factors in

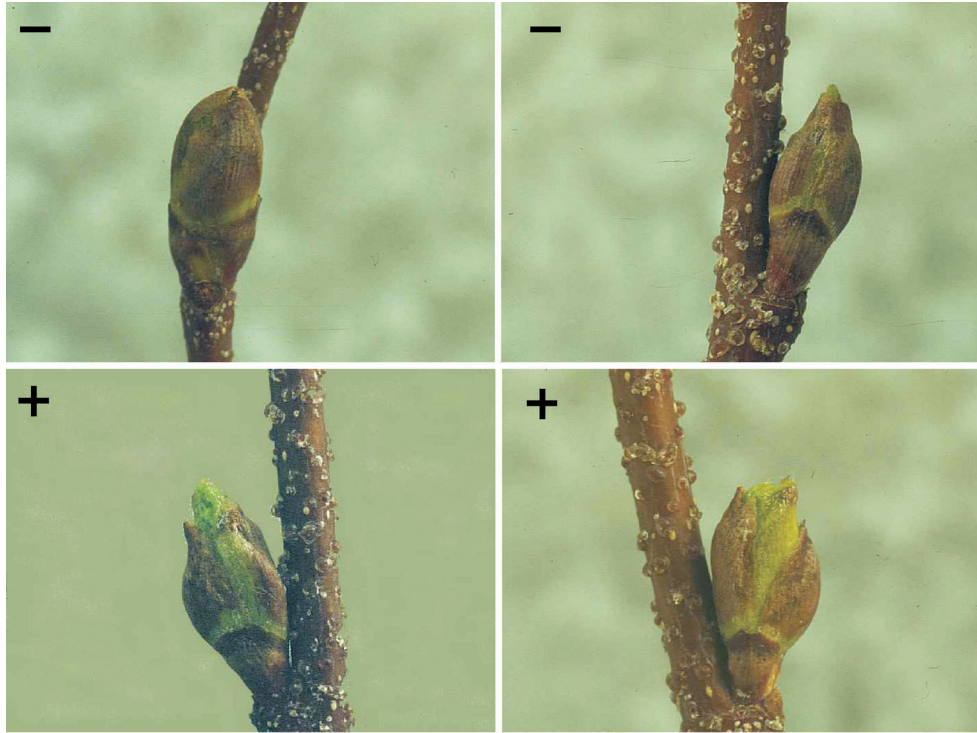


Figure 1. Bud burst of birch. Buds in the upper panels are considered closed (–) and buds in the lower panels are considered open (+).

the model and the corresponding covariance parameters were estimated by the restricted maximum likelihood method. Covariance parameters not different from zero (nonsignificant according to the Wald test ($P > 0.50$) or with a negative estimate) were omitted from the final model. Therefore, the error term for the tests of fixed effects (Type III sum of squares) depended on the observed covariance structure. The observations in different years were deemed repeated measures and different covariance structures (scaled identity and first-order autoregressive) were fitted and compared with likelihood ratio tests. The goodness of fit of the scaled identity structure suggesting non-dependence between consecutive years was always at least as good as that of the first-order autoregressive model ($P > 0.05$). The analysis comparing bud burst at the different study sites proceeded in a similar way but block was nested within study site. The random effect part of the model therefore included block (site) and clone \times block (site) terms. The fixed effects part of the model included site, clone and year and all their interactions. Annual variation in the duration of bud burst was analyzed as described for annual variation in bud burst.

Effects of clone and spatial variation on the termination of growth and duration of growth period were tested separately for different sites and years according to a randomized complete block design. The analysis of variance model included clone as a fixed factor and block as a random factor. Both were tested against the clone \times block interaction. Data were clone means in replicate blocks.

Results

During the 6-year experiment, the earliest date of bud burst at

Yhteislaidun (all clones had buds open) occurred on May 5, 1993, and the latest date of bud burst was May 18, 1995, the mean date being May 11 (Table 1, Figure 2). At Yhteislaidun, the mean temperature sums required for bud burst were d.d. 33 (threshold temperature $+5^{\circ}\text{C}$), 47 (4°C), 87 (2°C), 116 (1°C), 157 (0°C), 210 (-1°C) and 274 (-2°C). At Common Garden, the mean temperature sum needed for bud burst over the years was slightly lower (Table 1). If the temperature sum calculations were started on March 21, the d.d. values were less than if the calculations were started at the beginning of the year, especially when the lower temperature thresholds were used. When the date of bud burst was predicted as the mean date of the six experimental years, the maximum interannual error was 1 week (1995). The lowest mean yearly errors (1 day) were obtained with temperature thresholds between $+2$ and -1°C (Table 1). The interannual variation in bud burst was statistically significant (Tables 2–4).

Clonal differences in bud burst

The results of mixed effect models (Tables 2–4) indicated a significant clonal variation in date of bud burst. Moreover, clonal differences varied between years (a significant year \times clone interaction). Among clones, variation in date of bud burst was small in some years, but large in other years, e.g., it was only 2 days in 1993, whereas it was 2 weeks in 1995 (Figures 2 and 3). At Yhteislaidun in every year studied, Clone 2674 was the first to start growth, and Clone JR/1 was the second to start growth (except in year 1992). At Common Garden, these two clones were absent and Clone 40 (absent in Yhteislaidun) started growth first. This clonal variation in timing of bud burst indicates that the clones differed in their temperature requirements for bud burst (Tables 2 and 3, Figures 2 and 3).

Table 1. Mean date and the degree day (d.d.) temperature sums at the time of bud burst, and the yearly deviations (days) between the observed and predicted time of bud burst in Yhteislaidun and Common Garden. The base temperatures for d.d. sum calculations were +5, +4, +2, +1, 0, -1 and -2 °C (denoted dd5, dd4, dd2, dd1, dd0, dd-1 and dd-2, respectively). The temperatures were summed from January 1 (a) and March 21 (b). For example, if 0 °C is the base temperature, the mean temperature sum needed for bud burst in Yhteislaidun is d.d. 157 (counted from January 1) or 140 (counted from March 21). The d.d. 157 was reached 4 days after bud burst in 1996, but in 1993, 1994 and 1997 it was reached on the day of bud burst. Each value is the mean of replicate blocks (dates may differ from Figures 2 and 3), and 1992 and 1996 were bissextile years.

Year	Date	dd5(a)	dd5(b)	dd4(a)	dd4(b)	dd2(a)	dd2(b)	ddl(a)	ddl(b)	dd0(a)	dd0(b)	dd-1(a)	dd-1(b)	dd-2(a)	dd-2(b)
<i>Yhteislaidun</i>															
Mean 1992–1997	May 11	33.3	33.3	47.0	46.8	86.6	84.3	115.7	109.1	157.0	140.0	210.3	175.8	274.2	215.5
1997	+2	0	0	0	-1	0	-1	0	-1	0	-1	0	-1	0	-1
1996	-1	-3	-3	-3	-3	-2	-2	-3	-2	-4	-2	-5	-2	-8	-2
1995	+7	-2	-2	-2	-2	-2	-2	-2	-1	-1	-1	+1	0	+3	0
1994	-5	-1	-1	-1	-1	0	0	0	+1	0	+1	0	+1	-1	+1
1993	-6	+3	+3	+3	+3	+1	+1	0	0	0	-1	0	-1	0	-2
1992	+5	0	0	0	0	+1	+1	+1	+1	+1	+1	+1	+1	+2	0
Mean deviation	4.3	1.5	1.5	1.5	1.7	1.0	1.2	1.0	1.0	1.0	1.2	1.2	1.0	2.3	1.0
<i>Common Garden</i>															
Mean 1993–1996	May 10	31.8	31.8	45.3	45.2	83.4	82.2	110.4	106.9	150.1	137.8	202.4	173.7	264.6	213.7
1996	+3	0	0	0	0	+1	+1	+1	+1	0	+1	-1	+1	-3	+1
1995	+6	-4	-4	-4	-4	-4	-3	-3	-3	-2	-3	0	-2	+3	-2
1994	-4	0	0	0	0	0	0	+1	+1	+1	+1	0	+1	-1	+1
1993	-4	+2	+2	+2	+2	+1	0	0	-1	-1	-1	-1	-2	0	-3
Mean deviation	4.8	1.5	1.5	1.5	1.5	1.5	1.0	1.3	1.5	1.0	1.5	0.5	1.5	1.8	1.8

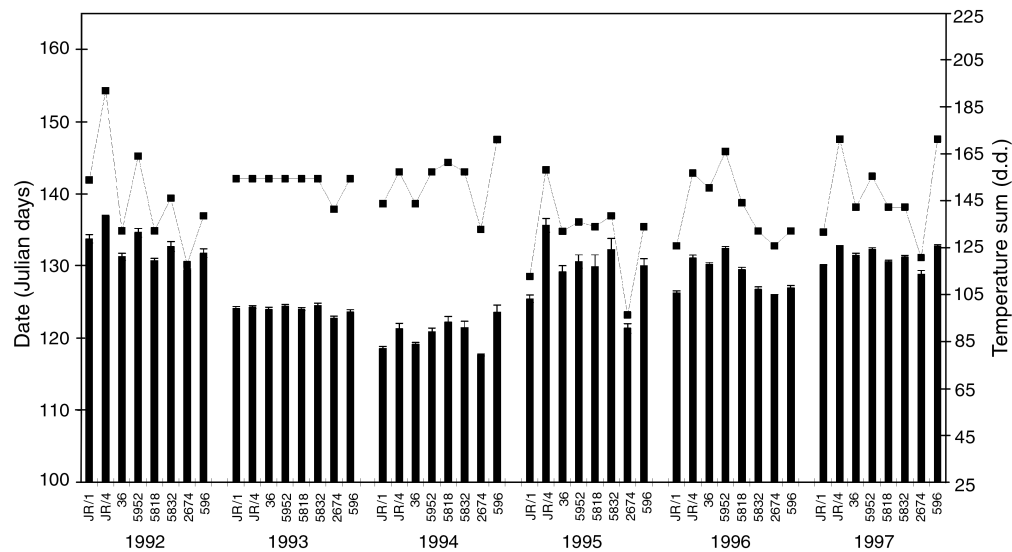


Figure 2. Bud burst of eight birch clones during 1992–1997 at Yhteislaidun. We monitored buds daily on 15 plantlets per clone and five buds per plantlet. Left y-axis and columns indicate mean date + SE (Julian days) when 90% of buds are open. Right y-axis and symbols connected with lines indicate the degree day (d.d.) temperature sum (-1°C as a threshold) required for bud burst of each clone.

Although the same clones were generally the first to break bud each year, the order of bud burst among clones differed among years (Tables 2 and 3). For example, in 1996, Clone 5832 at Yhteislaidun started growth earlier than expected based on its previous dates of bud burst (Figure 2).

The distance between the Yhteislaidun and Common Garden experiments was 1 km. Although the sites did not differ in their timing of bud burst during the four experimental years (Table 4), the yearly variation in bud burst differed between sites, as indicated by the site \times year interaction. In 1993 and 1995, bud burst was 2 and 3 days earlier at Common Garden than at Yhteislaidun, respectively, whereas in 1994 and 1996, Yhteislaidun plantlets opened their buds 0.5 and 1 day earlier, respectively.

The time it took for the clones to complete bud burst differed among years ($P < 0.0005$) and clones ($P < 0.0005$). For Clones 2674 and JR/1, at Yhteislaidun, it took, on average, 4.3 and 4.4 days, respectively, for all of the observed buds to open, whereas it took Clones 5952 and 596 more than 50% longer (6.6 and 6.7 days, respectively). Similar results were obtained at Common Garden: Clone 40 completed bud burst in 4.3 days, whereas Clones 5832 and 5938 took almost twice as long

(7.6 and 8.1 days, respectively) to complete bud burst. The relative duration of bud burst among the studied clones also varied among years, as indicated by the year \times clone interaction ($P = 0.003$).

Growth, bud burst, termination of growth and growth period

There was a clear tendency for growth rates of the plantlets to increase during the study, even when results for the planting year were excluded because of possible planting stress. A lengthy period of growth improvement may be associated with root establishment and build up of the photosynthetic apparatus, especially at the less fertile site (Yhteislaidun), where annual height growth increased from 24 cm in 1992 to 148 cm in 1997 (Table 5). Generally, with the exception of year 1994 at Yhteislaidun, plantlets exhibiting early bud burst tended to grow more quickly, as indicated by a negative correlation between number of days until bud burst and height growth (Table 5). This relationship was statistically significant in five cases out of ten and it did not change, even in 1995 when freezing temperatures (below -2°C) interrupted the ongoing bud burst; however, the low correlation coefficients ($r^2 < 0.13$ for all years) indicate that this relationship was weak even in years when there was a 2- to 3-week difference in date of bud burst among plantlets (e.g., 1994 and 1995, Table 5).

There was significant clonal variation in date of growth termination in years for which data were available (Yhteislaidun

Table 2. Summary of split-plot analysis of yearly variation in bud burst (days) at Yhteislaidun. Clone and year and their interaction were entered into the model as fixed effects and block and clone \times block as random effects.

Fixed effect	Hypothesis df	Error df	F	P
Clone	7	22.81	17.37	< 0.0005
Year	5	160.00	265.94	< 0.0005
Clone \times year	35	160.00	5.37	< 0.0005

Covariance parameter	Estimate	SE	Wald Z	P
Block	0.429	0.386	1.11	0.267
Clone \times block	0.397	0.254	1.56	0.118

Table 3. Summary of split-plot analysis of yearly variation in bud burst (days) at Common Garden. Clone, year and their interaction were entered into the model as fixed effects and block and clone \times block as random effects. Random effects with a zero variance component (block, clone \times block) were dropped from the final model.

Fixed effect	Hypothesis df	Error df	F	P
Clone	7	96	113.05	< 0.0005
Year	3	96	554.54	< 0.0005
Clone \times year	21	96	32.59	< 0.0005

Table 4. Summary of split-plot analysis of variation in bud burst (days) at Yhteislaidun and Common Garden. Site, clone, year and all their interactions were entered into the model as fixed effects and block (site) and clone × block (site) as random effects.

Fixed effect	Hypothesis df	Error df	F	P
Site	1	6.90	1.24	0.303
Clone	3	15.27	4.15	0.025
Year	3	84.00	212.94	< 0.0005
Site × clone	3	15.27	0.92	0.454
Site × year	3	84.00	10.85	< 0.0005
Clone × year	9	84.00	7.51	< 0.0005
Site × clone × year	9	84.00	1.80	0.080
Covariance parameter	Estimate	SE	Wald Z	P
Block (site)	0.642	0.527	1.22	0.223
Clone × block (site)	0.505	0.421	1.20	0.230

1992 ($P = 0.034$), 1993 ($P < 0.0005$), Common Garden 1993 ($P < 0.0005$)). For example, Clones 36 and 2674 stopped growth earlier than Clone 5818 (Figures 4 and 5). There were also differences of up to 2 weeks in date of growth termination among clones that opened buds on the same date (cf. Clones 36 and 596 in 1993, Figures 2 and 4). At Yhteislaidun, spatial variation (replicate block) had an effect on growth termination in 1993 ($P = 0.019$), but not in 1992 ($P = 0.386$). Spatial variation had no significant effect on growth termination at Common Garden in 1993 ($P = 0.117$).

The duration of the growth period varied among clones at Yhteislaidun ($P = 0.014$ in 1992 and $P < 0.0005$ in 1993) and Common Garden ($P = 0.001$). At both sites, plantlets of Clone 36 had a particularly short growth period (Figures 6 and 7). There was spatial variation (i.e., a significant block effect) in the length of the growing period at Yhteislaidun in 1993 ($P = 0.002$) but not in 1992 ($P = 0.588$). Spatial variation had no

Table 5. Variation in timing of bud burst (BB) of saplings from eight clones (difference between earliest and latest sapling in days), mean growth of saplings and the correlation between date of bud burst and growth. At Yhteislaidun, $n = 119$ –120 and at Common Garden, $n = 121$ –126.

Year	Difference in BB (day)	Mean growth (cm)	r	P
<i>Yhteislaidun</i>				
1992	9	24	−0.116	0.207
1993	8	50	−0.358	< 0.001
1994	11	75	0.063	0.494
1995	23	87	−0.258	0.005
1996	7	116	−0.129	0.159
1997	7	148	−0.101	0.273
<i>Common Garden</i>				
1993	8	84	−0.143	0.111
1994	14	84	−0.247	0.006
1995	24	101	−0.285	0.001
1996	8	143	−0.224	0.012

significant effect on duration of growth period at Common Garden in 1993 ($P = 0.174$).

The date of growth termination was more variable than the date of bud burst: e.g., at Yhteislaidun in 1992 and 1993, the range between the earliest and latest date of bud burst was 9 and 8 days, but 23 and 47 days, respectively, for growth termination. Growth period (GP) increased with decreasing date of bud burst in 1992 at Yhteislaidun (not measured at Common Garden), but no such relationship was found in 1993 at either site, despite large variations in date of bud burst (Table 6). The maximum difference in length of GP among plantlets at Yhteislaidun in 1992 and 1993 was 30 and 49 days, respectively, and the length of the GP was positively related to total growth at both sites in 1993. During 1992 and 1993, the coefficients of determination (r^2) between growth and bud burst (0.01 and 0.13, respectively) were lower than those between

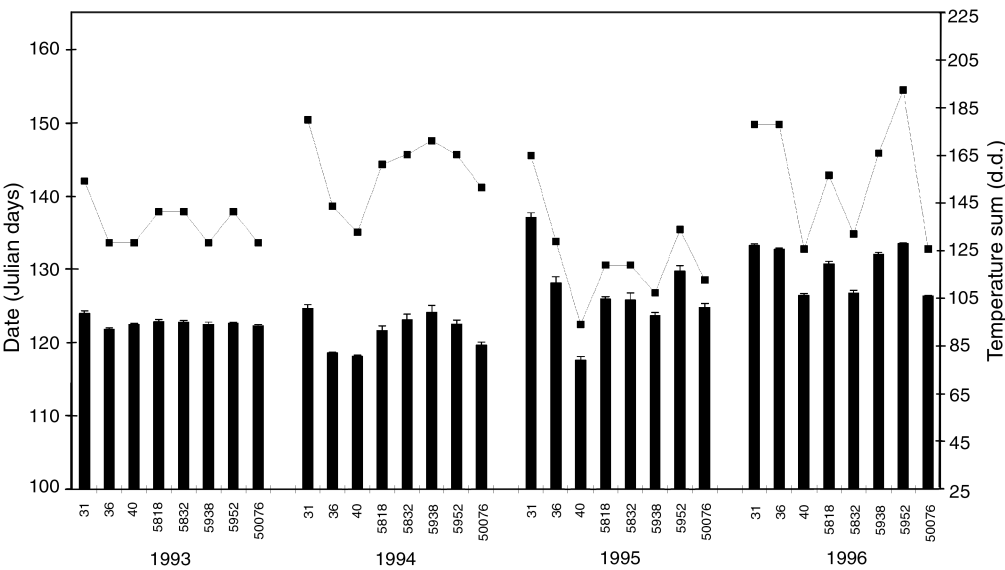


Figure 3. Bud burst of eight birch clones during 1993–1996 at Common Garden. We monitored buds daily on 16 plantlets per clone and five buds per plantlet. Left y-axis and columns indicate mean date + SE when 90% of buds are open. Right y-axis and symbols connected with lines indicate the degree day (d.d.) temperature sum (−1 °C as a threshold) required for bud burst of each clone.

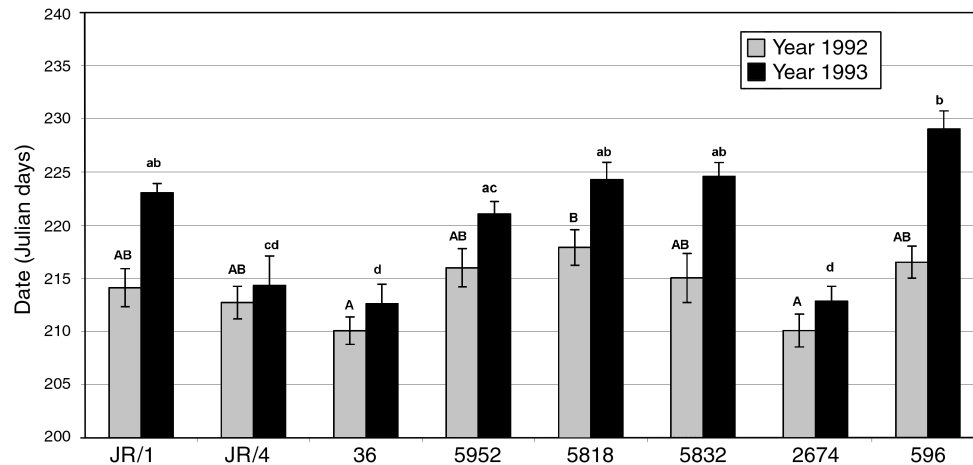


Figure 4. Mean date of growth termination of eight birch clones at Yhteislaidun in 1992 and 1993. Data are for the same plantlets as in Figure 2. Within a year, columns with different letters are significantly different at $P < 0.05$ (Tukey t -test).

growth and growth termination (0.01 and 0.20, respectively) and growth and length of GP (0.01 and 0.30, respectively), suggesting that date of growth termination and length of GP may be more important determinants of growth than date of bud burst (Tables 5 and 6).

Discussion

Determinants of phenology

The maximum interannual difference in date of bud burst of European white birch in one stand was 10 days over the 6-year study period. Longer time series (Sarvas 1952, Häkkinen 1999) have indicated much larger interannual variation: the smaller variation in our study was expected because none of the experimental years had extreme spring temperatures. Daily observations of bud burst may also have decreased the variation because several potential sources of systematic errors, such as differences in genotypes of observed trees, observers, sites observed and the impact of weather on accuracy of observation (see Häkkinen 1999) were avoided.

The main determinant for bud burst seemed to be accumula-

tion of heat sum. It has been suggested that a specific light signal is needed for the start of ontogenetic bud development to ensure that the winter dormancy is not broken too early (Wareing 1956), and the proposed threshold date for this critical photoperiod is the Vernal Equinox (March 21) (Häkkinen 1999). Before March 21, daily temperatures above 1 °C are rare under present climatic conditions in boreal forests. Longer time series from larger geographic areas are clearly needed to rule out the effect of specific threshold dates, but precise long-term data on bud burst under natural conditions is hard to obtain. Heide (2003) concluded that high autumn temperatures may delay spring bud burst of boreal trees. In our study, the autumns of 1992 and 1993 were cooler than the mean; however, the early bud burst in the following springs (Figure 2) seemed to be dependent, as in other years, on warm spring conditions (Table 1, cf. Junttila et al. 2003). Thus, we conclude that spring temperatures determine the timing of bud burst of northern birches, and temperatures between +2 and -1 °C are the most suitable threshold values for calculating temperature sums.

The finding that the birch clones differed in their bud burst temperature requirements (Tables 2 and 3) indicates a genetic basis for determination of bud burst (for poplars, see Pellis et al. 2004). The maximum difference in date of bud burst among our micropropagated birch genotypes (clones) was large (15 days), and the mean yearly difference was 1 week. The same clones opened buds earliest and latest in each year, although the order of clones was not exactly the same over the years. Billington and Pelham (1991) suggested large variation in heritability of bud burst of *B. pendula* populations in north Scotland ($h^2 = 0.06 - 0.63$) based on observations made on a few dates over 2 years. Although caution is needed when interpreting results obtained from short-term observations, our results confirm the general observation that there is a strong genetic basis underlying determination of bud burst that probably allows natural birch forests to evolve in response to climatic changes.

Based on pooled data across years, the study sites did not differ in timing of bud burst, although the difference in timing between sites varied among years, as indicated by the year \times

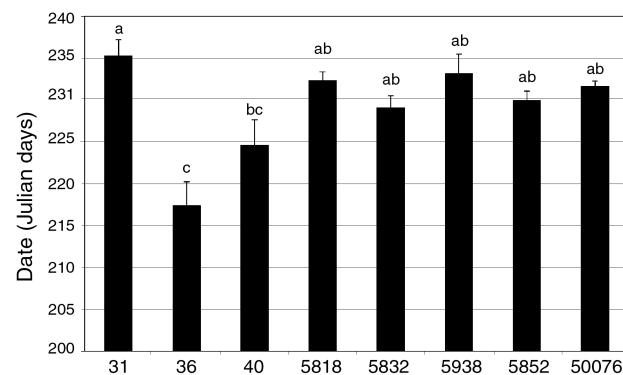


Figure 5. Mean date of growth termination of eight birch clones at Common Garden in 1993. Data are for the same plantlets as in Figure 3. Columns with different letters are significantly different at $P < 0.05$ (Tukey t -test).

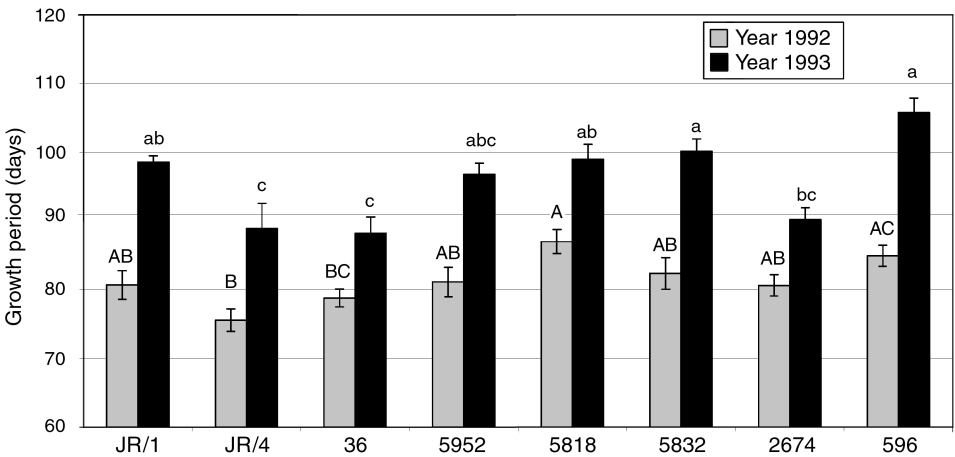


Figure 6. Mean length of growth period of eight birch clones at Yhteislaidun. Columns and bars indicate mean duration of growth period \pm SE, respectively, for 15 plantlets per clone (see Figures 2 and 4). Within a year, columns with different letters are significantly different at $P < 0.05$ (Tukey t -test).

site interaction (Table 4). These results indicate the need for caution when interpreting bud burst results from tree stands growing in heterogeneous (natural) environments.

Phenology and growth

Based on 47-year phenological data, satellite data, common garden experiments and meta-analyses, Root et al. (2003) concluded that, in response to recent climatic changes, the spring phenology of forest trees has advanced 3 days in a decade, 4.5 days in the past decade (Fitter et al. 1995, Fitter and Fitter 2002), 8 days in 8 years (Myneni et al. 1997) or 3.5 days in a decade (Chimielewski and Rötzer 2001). Foliar phenology can influence photosynthetic productivity and therefore alter the amounts of photosynthate available for growth and reproduction (Lechowicz 1995). Myneni et al. (1997) concluded that early greening of forest canopies is critical for ecosystem net primary production, and that a difference of a few days in canopy development can account for more than 20% of the inter-annual change in net photosynthetic production of a northeastern North American forest. Consequently, especially for pioneer species like white birches, producing genotypes that open buds early should be feasible, especially if such genotypes

have higher growth rates than genotypes that open buds later in the spring. However, although we found a tendency for clones that open buds early to have high growth rates, the relationship was generally weak (Table 5). Thus, factors other than genotypic variation in bud burst may be key determinants for growth. Moreover, we found large inter-annual variation in date of bud burst indicating that a 6-year study is too short to reveal an advancing trend in bud burst (Figure 2).

Unlike the effects of timing of bud burst on early canopy development, small (e.g., 1-week) differences in the timing of leaf fall are insignificant for plant growth (Cannell 1989). The variation in growth termination at the clonal and especially at the plantlet level in white birch can, however, be substantially larger than the variation in bud burst. Because of the unpredictability of weather, the relative impacts of spring and autumn phenology on growth can only be determined by long-term measurements. We found that the best predictor of growth was length of the growth period (Table 6), and the main

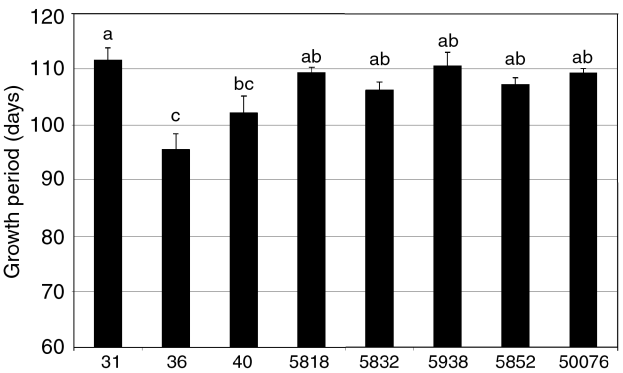


Figure 7. Mean length of growth period of eight birch clones at Common Garden. Columns and bars indicate mean duration of growth period \pm SE, respectively, for 16 plantlets per clone (see legends for Figures 3 and 5). Columns with different letters are significantly different at $P < 0.05$ (Tukey t -test).

Table 6. Correlations between timing of bud burst (BB), length of growth period (LGP), growth termination (GT) and growth (G) measured in 1992 (92) and 1993 (93). All measurements were made on the same plantlets. At Yhteislaidun, $n = 114-118$, except for GT 93 vs. G 93, where $n = 158$, and for G 92 vs. G 93, LGP 92 vs. LGP 93 and BB 92 vs. BB 93 where $n = 95$. At Common Garden, $n = 125$ or 126.

Correlation	Yhteislaidun		Common Garden	
	r	P	r	P
BB 92 vs. LGP 92	-0.357	< 0.001		
BB 93 vs. LGP 93	-0.155	0.096	0.039	0.669
GT 92 vs. LGP 92	0.919	< 0.001		
GT 93 vs. LGP 93	0.992	< 0.001	0.994	< 0.001
GT 92 vs. G 92	0.085	0.359		
GT 93 vs. G 93	0.444	< 0.001	0.409	< 0.001
LGP 92 vs. G 92	0.119	0.206		
LGP 93 vs. G 93	0.552	< 0.001	0.431	< 0.001
BB 92 vs. GT 92	0.040	0.673		
BB 93 vs. GT 93	-0.032	0.733	0.151	0.093
G 92 vs. G 93	0.176	0.088		
LGP 92 vs. LGP 93	0.116	0.265		
BB 92 vs. BB 93	0.335	0.001		

source of variation in plantlet growth period was the date of growth termination. Similarly, earlier observations have suggested the importance of timing of growth cessation on total growth of hardwoods (Pichot and Teissier du Cros 1988, Ceulemans et al. 1992, DeBell et al. 1997, but see Rönnberg-Wästlund and Gullberg 1999). We found that bud burst, growth termination and length of growth period had no effect on the phenology of the same seedlings in the following spring (Table 6). We conclude that bud burst, growth termination and length of growth period explain only a small part of the observed variation in growth.

In addition to variation in the timing of bud burst among clones, years and sites, the duration of bud burst varied between years and between clones ($P < 0.0005$ in both cases). This raises the question of why there is such large variation in timing of bud burst when it seems to be only weakly correlated with growth and when too early a start imposes a risk of frost damage. One explanation may be associated with the finding that the secondary chemical composition of European white birch leaves changes rapidly during leaf expansion; the flavonoid glycosides in particular increase during leaf development (Laitinen et al. 2002b), and, at the same time, nutritive leaf traits decrease (Haukioja 2003). The importance of perfect synchrony between bud burst of deciduous tree species and insect herbivore hatch has been shown with many species especially with Lepidopteran species (Witter and Waisanen 1978, Du Merle 1988, Raupp et al. 1988, Hunter and Elkinton 2000, Tikkanen and Julkunen-Tiitto 2003). Hatch before bud burst leads to starvation, and late emergence leads to difficulties with rapidly deteriorating leaf quality. In addition, duration of bud burst can be negatively correlated with mean caterpillar (*Tortrix viridiana* and *Operopthera brumata*) densities on trees (Hunter 1992, but see Quiring 1993). It should be easy for insect herbivores to adapt their hatch to simple heat sum accumulation, but the difficulty that insects encounter is the unpredictability in timing and duration of bud burst created by genetic variation, which is further amplified by variable reaction norms among genotypes.

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