High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming

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Summary   The effect of temperature during short-day (SD) dormancy induction was examined in three boreal tree species in a controlled environment. Saplings of *Betula pendula* Roth, *B. pubescens* Ehrh. and *Alnus glutinosa* (L.) Moench. were exposed to 5 weeks of 10-h SD induction at 9, 15 and 21 °C followed by chilling at 5 °C for 40, 70, 100 and 130 days and subsequent forcing at 15 °C in a 24-h photoperiod for 60 days. In all species and with all chilling periods, high temperature during SD dormancy induction significantly delayed bud burst during subsequent flushing at 15 °C. In *A. glutinosa*, high temperature during SD dormancy induction also significantly increased the chilling requirement for dormancy release. Field experiments at 60° N with a range of latitudinal birch populations revealed a highly significant correlation between autumn temperature and days to bud burst in the subsequent spring. September temperature alone explained 20% of the variation between years in time of bud burst. In birch populations from 69 and 71° N, which ceased growing and shed their leaves in August when the mean temperature was 15 °C, bud burst occurred later than expected compared with lower latitude populations (56° N) in which dormancy induction took place more than 2 months later at a mean temperature of about 6 °C. It is concluded that this autumn temperature response may be important for counterbalancing the potentially adverse effects of higher winter temperatures on dormancy stability of boreal trees during climate warming.

Keywords: alder, birch, chilling requirement, dormancy induction, phenology, photoperiod.

Introduction

Winter dormancy is an essential adaptive mechanism for winter survival in cold climates. It is well documented that, in most temperate woody species, growth cessation and bud dormancy are induced by short photoperiods (SD) in late summer and autumn (Downs and Borthwick 1956, Wareing 1956, Nitsch 1957, Heide 1974*a*). Temperatures within the normal range (12–24 °C) have little effect on SD dormancy induction (Heide 1974*a*), whereas near-freezing temperatures (4 °C) induce growth cessation even in a 24-h photoperiod (LD) (Heide 1974*a*, Li et al. 2002). Low temperature (chilling) is also the main environmental factor required for dormancy release (Vegis 1964, Hänninen 1990, Heide 1993*a*). However, in many species, long photoperiods can at least partially substitute for lack of chilling (Wareing 1956, Campbell and Sugano 1975, Heide 1993*a*, Myking and Heide 1995). In some species, like European beech (*Fagus sylvatica* L.), both chilling and subsequent long photoperiods are required for spring bud burst (Heide 1993*b*).

With the anticipated global warming predicted by General Circulation Models (IPCC 1990) and observed over the last decades (Serreze et al. 2000), terrestrial high-latitude areas will experience the largest relative changes in climate worldwide, with the greatest effect on winter temperature (IPCC 1990, 1997). The potential consequences for winter survival of boreal trees and shrubs could be substantial. It has been suspected that, in species with a large chilling requirement, milder winters might result in inadequate chilling and hence delayed and erratic bud burst in the spring (Cannell and Smith 1986). However, the upper temperature limit for breaking of bud dormancy has been found to be as high as 12 °C in both Norway spruce (Hänninen 1990) and two species of birch (Myking and Heide 1995). Therefore, even with several degrees of warming, the natural winter chilling capacity of boreal climates greatly exceeds the requirement for complete dormancy release in boreal trees (Murray et al. 1989, Heide 1993*a*). The main effect of higher winter temperatures in these regions is, therefore, earlier (and not later) bud burst in the spring and an associated increased risk of frost damage in late spring (Cannell and Smith 1986, Murray et al. 1989, Heide 1993*a*, Myking and Heide 1995). Extensive damage to forest trees as a result of early spring bud burst followed by severe late-spring frost has been widely documented. The large-scale birch die-back in the late 1930s in which more than 490,000 km^2 of white and yellow birch forest in eastern Canada and northeastern USA were damaged as a result of late winter thaws followed by spring frost is a dramatic example (Balch 1953, Braathe 1995). In boreal climates, the frequency and probability of such incidences are likely to increase with climatic warming.

An important question related to the potential effects of climatic warming on boreal trees is whether increased autumn temperature will interfere with the dormancy-inducing effect of short days (SD) in autumn, resulting in an incomplete or shallow dormancy state that might render the trees even more

vulnerable to winter damage. To answer this question, I examined the effect of temperature during SD dormancy induction on the duration and stability of bud dormancy in three boreal tree species grown in a controlled environment. The phenology of a latitudinal range of birch populations was also studied in the field, and the relationship between spring bud burst and autumn and spring temperatures was examined by correlation and regression analyses.

Materials and methods

Controlled environment experiment

The experiment was performed in the Ås phytotron. Seeds of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) and alder (*Alnus glutinosa* (L.) Moench.) were sown on May 10 and germinated at 21 °C in a 24-h photoperiod. All seed sources were of South Norwegian origin (60–61° N and 100–150 m a.s.l.). On June 13, seedlings were transplanted to multipot containers and the plants raised at 15 °C in continuous light (10 h of natural summer daylight plus day length extension to 24 h with incandescent lamps providing about 10 µmol m^{-2} s^{-1} of photosynthetically active radiation (PAR)) to ensure continuous plant growth. On August 29, when the plants were about 40 cm tall, they were randomly distributed among daylight phytotron compartments set at temperatures of 9, 15 and 21 °C and exposed to short days (SD; 10-h photoperiod) for 5 weeks for induction of growth cessation and bud dormancy. Growth cessation occurred within 8–12 days in all species in order of decreasing temperature. On October 3, when the plants had fully developed winter buds and senescent leaves, all plants were transferred to a growth room and chilled at 5 °C. The growth room was maintained at a 10-h photoperiod with a PAR of 70 µmol m^{-2} s^{-1} from a combination of Philips HPI-T 400-W high-pressure mercury lamps and incandescent lamps. All temperatures were maintained within ± 0.5 °C, and a water vapor pressure deficit of 530 Pa was maintained at temperatures above 9 °C. For further details on plant cultivation, see Myking and Heide (1995).

After 40, 70, 100 and 130 days of chilling, samples of 10 seedlings of each species and temperature treatment were transplanted to 10-cm plastic pots and moved to another growth room maintained at 15 °C with a 24-h photoperiod (10 h with Philips HPI-T 400-W lamps giving 190 µmol m^{-2} s^{-1} PAR plus 14 h with 10 µmol m^{-2} s^{-1} PAR from incandescent lamps) for flushing. Dates of bud burst were recorded for the terminal and upper lateral buds every second day based on the criterion for bud burst defined as Stage 3 of Murray et al. (1989) (green foliage showing). The experiment was a split-plot design with dormancy induction temperature as the main plot factor and species and chilling time as sub-plots. The bud burst data were subjected to analysis of variance (ANOVA) according to standard procedures using the SYSTAT program (Version 5.0). Because the experiment was not replicated in time, the 10 plants per treatment and species combination were treated as replicates in the analysis. Buds that failed to burst after 60 days were recorded as flushing after 60 days for the purpose of the statistical analysis. Because the variance was not constant, variance-stabilizing transformation was performed before ANOVA analysis, using the square root of number of days to bud burst (Myking and Heide 1995). Only data for the terminal buds are presented because of close agreement between terminal and lateral bud responses.

Field experiment

One-year-old trees of each of the birch populations listed in Table 1 were planted in a field nursery at Ås (60° N) in May 1994. Except for the Hammerfest population of *B. pubescens*, the populations are the same as those used by Myking and Heide (1995) in their controlled environment experiments. Ten trees (50–60 cm tall) of each population were randomly distributed into two blocks of five trees of each population at a spacing of 1 × 3 m. Weeds were controlled mechanically 2–3 times per year. No fertilizers were applied during the experiment. During the years 1996–2002, date of bud burst (green foliage showing) and date of 50% leaf shedding were recorded for all trees. Length of the active growing season was calculated from these data. Tree height and stem base circumference were also measured in the autumn of 2002 after completion of nine growing seasons. The phenological and plant size data were subjected to ANOVA as described previously, and regressions and correlations with temperature data (monthly mean temperatures determined from the daily averages) were calculated by standard methods (Snedecor and Cochran 1967). Temperature data are from the Ås weather station (Agricultural University of Norway) located about 1 km from the tree nursery.

Results

Controlled environment experiment

In all species and at all chilling times, the plants maintained at 9 °C during the 5-week SD dormancy induction period were the earliest to reach bud burst, whereas plants grown at 21 °C during the SD dormancy induction period were the last to reach bud burst (Figures 1 and 2). The thermal time (heat-sum) requirement for attainment of bud burst was strongly reduced

Table 1. Geographic origin of birch populations used in the field experiment.

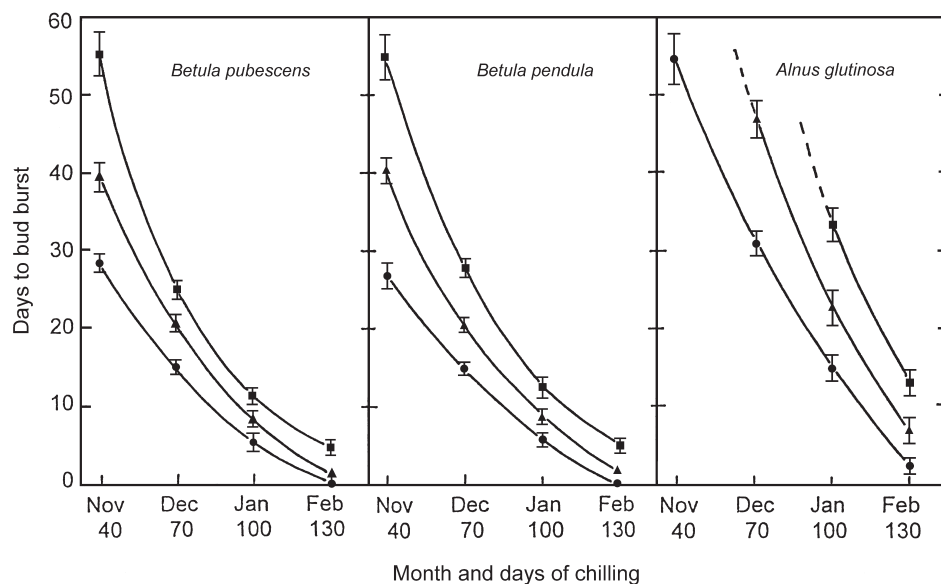| Species and origin	Latitude (° N)	Longitude (° E)	Altitude (m a.s.l.)
B. pubescens			
Hammerfest, Norway	70°40′	23°30′	20
Målselv, Norway	69°	18°30′	40
Steinkjer, Norway	64°	11°30′	90
Silkeborg, Denmark	56°10′	9°40′	50
B. pendula			
Pasvik, Norway	69°15′	29°20′	50
Steinkjer, Norway	63°50′	11°20′	80
Hillerød, Denmark	56°	12°20′	50

Figure 1. Effects of temperature during dormancy induction and length of chilling period on days to bud burst at 15 °C in saplings of three boreal tree species. Values are means ± SE for the terminal bud of 10 plants per treatment group. Symbols: ● = 9 °C; ▲ = 15 °C; and ■ = 21 °C.

with increasing degree of chilling in all species. However, in all chilling treatments, birch saplings kept at 21 °C during the SD dormancy induction period took about twice as many days at 15 °C to reach bud burst as saplings kept at 9 °C during the SD dormancy induction period, whereas plants induced to dormancy at 15 °C were intermediate in time to bud burst. After 130 days of chilling, many of the plants induced at 9 °C had burst their buds at 5 °C before transfer to the flushing temperature. There was no significant difference in the response of the two birch species.

The effect of temperature during SD dormancy induction was even larger in alder saplings than in the *Betula* species (Figure 1). Alder has a larger chilling requirement than birch (cf. Heide 1993a), and after 40 days of chilling only those
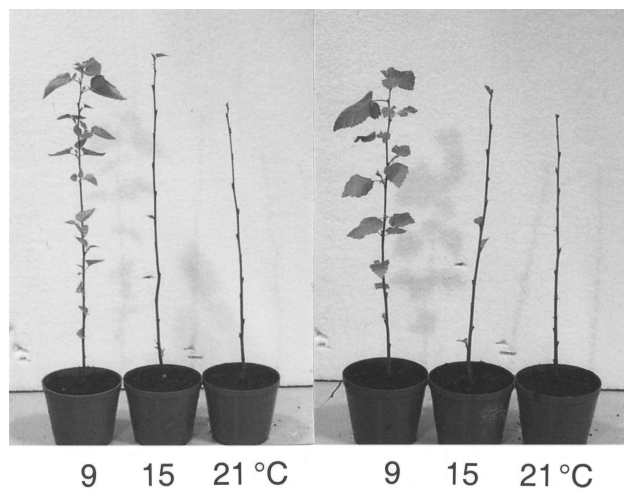

Figure 2. Stages of bud growth in saplings of *Betula pubescens* (left) and *Betula pendula* (right) as affected by temperatures during short-day dormancy induction followed by 70 days of chilling at 5 °C. Photograph was taken after 20 days of forcing at 15 °C.

plants induced to dormancy at 9 °C burst bud within 60 days of forcing at 15 °C. In alder plants grown at 15 and 21 °C during SD dormancy induction, 70 and 100 days of chilling, respectively, were required for bud burst. For all species, ANOVA of the bud burst data revealed highly significant main effects ($P < 0.001$) of both SD induction temperature and days of chilling as well as their interaction.

Field experiment

There were large differences in the length of the active growth period among the birch populations (Table 2), mainly because of large differences in time of growth cessation and leaf shedding. The high-latitude populations from 69 and 71° N shed their leaves by late August, whereas the Danish populations from 56° N grew for two more months and did not shed leaves until late October or early November. Populations from mid-Norway (64° N) were intermediate between the high-latitude and Danish populations and shed their leaves by the end of September.

In contrast, time of bud burst varied among populations by only a few days, although the variation among years was considerable and highly significant (Figure 3). However, populations from 64° N consistently had the earliest bud burst and those from 56° N consistently had the latest bud burst, with the high-latitude populations in between (Table 2, Figure 3), even though previous controlled-environment experiments have shown that the inherent dormancy period of these populations decreases with increasing latitude of population origin (Myking and Heide 1995). Because temperature during SD dormancy induction varied with earliness of growth cessation (cf. Table 2), it was suspected that temperature during SD dormancy induction might have influenced the time of bud burst in the subsequent spring. Accordingly, a regression and correlation analysis was performed on the relationship between time of bud burst and both spring and previous autumn temperature regimes (Table 3). The results revealed a highly signifi-

Table 2. Mean dates of bud burst and 50% leaf fall and the length of the active growth period in a selection of latitudinal birch populations grown at Ås (60° N) and observed over a 7-year period. Numbers in parenthesis indicate difference in time of the events between the earliest and latest years.

Species	Population	Mean date of bud burst	Mean date of 50% leaf fall	Growth period (days)
Betula pubescens	Hammerfest (71° N)	April 28 (22 days)	August 26 (16 days)	119 ± 4.0
	Målselv (69° N)	April 29 (22 days)	August 28 (16 days)	122 ± 4.2
	Steinkjer (64° N)	April 26 (22 days)	September 28 (24 days)	154 ± 5.3
	Silkeborg (56° N)	May 1 (20 days)	November 3 (7 days)	186 ± 3.6
Betula pendula	Pasvik (69° N)	April 30 (24 days)	September 3 (32 days)	126 ± 5.9
	Steinkjer (64° N)	April 25 (25 days)	September 30 (33 days)	158 ± 7.4
	Hillerød (56° N)	May 1 (22 days)	November 9 (15 days)	192 ± 4.4

cant delaying effect of high autumn temperature on time of bud burst in the subsequent spring (Figure 3, Table 3). September temperature alone accounted for 20% of the variation in days to bud burst among the years as a mean of all populations, whereas the mean temperature for September and October and the period August–October accounted for 26 and 29% of the variation, respectively. As expected, high spring temperatures advanced bud burst, but the March–April temperature explained no more than 10% of the variation in time of bud burst of these trees.

The large variation among populations in the length of the active growth period (Table 2) resulted in large variations in tree height and diameter growth (Figure 4). After nine growing seasons at 60 °N, *B. pubescens* trees of the Danish population

(56° N) were more than twice as tall as trees of the Hammerfest population (71° N), whereas the heights of the other populations were intermediate and in proportion to their latitude of origin. Also in *B. pendula*, there was a large difference in height between the north Norwegian and the Danish populations, whereas trees of the vigorous Steinkjer population (64° N) were nearly as tall as those of the Danish population (Figure 4). Stem girth decreased with increasing latitude of origin of the populations, and again the latitudinal trend was not as steep in *B. pendula* as in *B. pubescens*. All population effects, and the height difference between the two species, were statistically significant ($P < 0.01$).

Discussion

The results presented in Figures 1 and 2 demonstrate that high temperature during SD dormancy induction enhanced the state of bud dormancy and increased the chilling requirement for bud burst in birch and alder saplings. This effect of temperature on SD dormancy induction has parallels in other plant processes. For example, relatively high night temperatures also enhance the effect of SD on the induction of flowering and other photoperiodically controlled processes in SD plants (Lang 1965, Thomas and Vince-Prue 1997). The effect may
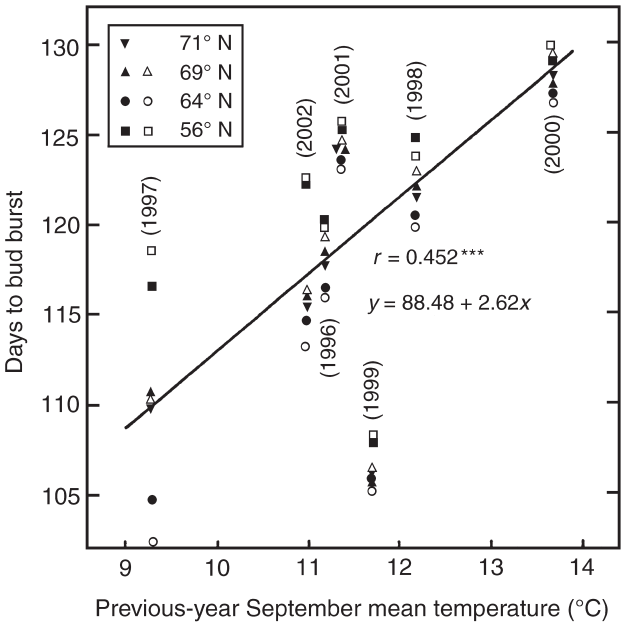

Figure 3. Correlation between September temperature (mean monthly temperature for the various years) and days to bud burst (after January 1) in the following spring in a selection of latitudinal birch populations grown at 60° N and observed during a 7-year period. Open symbols denote *B. pendula* populations and solid symbols denote *B. pubescens* populations.

Table 3. Correlation coefficients between mean monthly temperatures and days to bud burst (after January 1) in a selection of latitudinal populations of birch grown at Ås (60° N) over a 7-year period.

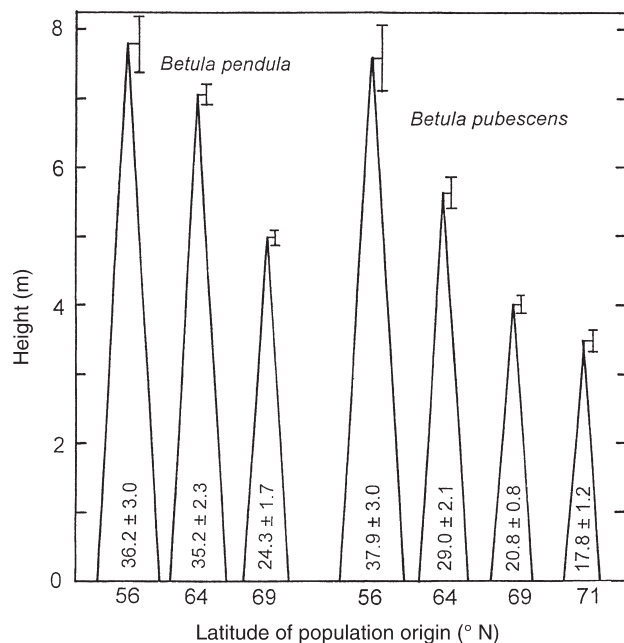| Temperature	r	P
Previous-year temperature		
August	0.128	0.382
September	0.452	0.001
October	0.092	0.528
August–September	0.385	0.006
September–October	0.512	> 0.001
August–October	0.542	> 0.001
Current-year temperature		
April	−0.264	0.067
March–April	−0.316	0.027

Figure 4. Tree height and stem base circumference in a selection of latitudinal birch ecotypes after nine growing seasons at Ås (60° N) as affected by latitude of population origin. Stem circumference ± SE (cm) is represented by the numbers at the base of each column. Values are means ± SE for 10 trees per population.

thus be a manifestation of a general synergism between high temperature and SD in photoperiodic processes. Furthermore, prolonged dormancy after high-temperature SD induction has also been previously reported for Norway spruce (Heide 1974*b*) and maple (*Acer platanoides* L.) saplings (Westergaard and Eriksen 1997). The present results with three additional boreal tree species indicate that this is an adaptive mechanism common to boreal trees. Low temperature, which is the main dormancy-breaking factor, may even start to take effect before dormancy is fully established. In other words, the buds may start accumulating chilling hours at 9 °C during the dormancy-inducing SD period. However, because temperatures above 12 °C have no chilling effect (Hänninen 1990, Myking and Heide 1995), this does not explain the different effects of the 15 and 21 °C treatments during the SD dormancy induction period (Figure 1).

Although the difference in days to bud burst between the temperature treatments diminished with increasing degree of chilling (Figure 1), the difference was still present after 130 days of chilling at 5 °C and would also be noticeable under natural conditions in the spring. Thus, trees of a range of birch populations grown in the field at Ås (60° N) demonstrated a highly significant correlation between autumn temperature and days to bud burst (Figure 3, Table 3). Furthermore, high-latitude Norwegian birch ecotypes from 69 and 71° N, which went dormant and shed their leaves in August when the mean monthly temperature at Ås is about 15 °C, exhibited a much later than expected leafing out in the spring (cf. Myking and Heide 1995) compared with Danish ecotypes from 56° N in

which dormancy induction occurred 2 months later at a mean temperature of about 6 °C (Table 3). There is thus no doubt that relatively high autumn temperatures also increase bud dormancy and delay bud burst in the following spring in larger trees under natural conditions.

Autumn temperature explained more of the variation in date of bud burst among years than did spring temperature. However, in some years, spring temperature obviously modified the effect of autumn temperature. For example, high temperatures in April 1999 (2 °C above normal) were apparently responsible for much of that year's deviation from the September temperature regression line in Figure 3. On the other hand, unusually high temperatures in October and November 2000 (3 and 5 °C above normal, respectively) may also explain the relatively late bud burst in spring of 2001 (Figure 3). However, these observations covered a period of only 7 years; a longer time series is desirable for such a correlation analysis.

In conclusion, high temperatures during SD dormancy induction in the autumn delayed bud burst in the following spring in both controlled and natural environments. Rising autumn temperatures may thus counterbalance the advancing effect on spring bud burst that would otherwise occur in response to higher winter temperatures caused by climate warming (Murray et al. 1989, Heide 1993*a*). This autumn temperature response may be important for reducing the potentially adverse effects of higher winter temperatures on dormancy stability of boreal trees during climate warming.

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