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Twilight far-red treatment advances leaf bud burst of silver birch (*Betula pendula*)

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Summary Bud development of boreal trees in spring, once initiated, is driven by ambient air temperature, but the mechanism triggering bud development remains unclear. We determined if some aspect of the diurnal or seasonal light regime influences initiation of bud burst once the chilling requirement is met. We grew 3-year-old birch plantlets cloned from a mature tree of boreal origin in light conditions realistically simulating the lengthening days of spring at 60° N. To emulate the reduction in red to far-red light (R:FR) ratio between daylight and twilight, one group of plantlets was subjected to reduced R:FR ratio in the morning and evening in addition to progressively lengthening days, whereas the other group was subjected to the same R:FR ratio throughout the day.

The reduced R:FR ratio of twilight advanced bud burst by 4 days compared with the reference group ($P = 0.04$). To assess the interplay between the fulfillment of the chilling requirement and the subsequent response to warming, we fitted a thermal time model to the data with separate parameterizations for the starting dates of heat sum accumulation in each treatment. Least-squares fitting suggested that bud development started in light regimes corresponding to late March, almost two months after the chilling requirement for dormancy release was satisfied. Therefore, shortening night length or increasing day length, or both, appears to be the cue enabling bud development in spring, with twilight quality having an effect on the photoperiodic response. If twilight alone were the cue, the difference in bud burst dates between the experimental groups would have been greater than 4 days. The result gives experimental support for the use of thermal-time models in phenological modeling.

Keywords: chilling, dormancy, light environment, phenology, phytochrome, sequential model, thermal time model.

Introduction

The timing of unfolding of new leaves in spring poses an interesting optimization problem for perennial plants at high latitudes: developmental control systems must balance productivity gains associated with the longer growing period afforded by early leafing against the risk of foliar damage or loss caused by late spring frosts (Chabot and Hicks 1982, Kikuzawa 1989, Reich et al. 1992). Although native trees in boreal and temperate growing zones occasionally incur spring frost damage (Lechowicz and St. Jacques 2000), in general there is a good coordination between plant phenology and seasonality within a particular region (Lechowicz 2001). However, some recent studies simulating the outcome of climatic warming predicted that bud development in boreal trees would be triggered too early under future climate scenarios, exposing young leaves to freezing periods (Bach 1988, Hänninen 1991, Kramer 1994). These studies utilized phenological models where temperature-driven bud development is enabled simply by sufficient previous exposure to chilling temperatures (Landsberg 1974, Sarvas 1974). These are referred to as Sequential Time (ST) models because chilling and bud development follow each other in an obligatory sequence (e.g., Hunter and Lechowicz 1992, Hänninen 1995).

Even more simplistic Thermal Time (TT) models (Hunter and Lechowicz 1992) use only a selected, specific date in spring to release bud development. Comparisons between these models (Häkkinen et al. 1998, Linkosalo et al. 2000) suggest that TT models fit observed phenological data better than any sequential model. This implies that once the chilling requirement is satisfied, it may be an environmental cue associated with the diurnal light regime that triggers the response to warming that ultimately leads to bud burst. This hypothesis has experimental support for some plant species (e.g., Heide 1993*a*, 1993*b*, Partanen et al. 1998, 2001, 2005), but the nature and importance of any cue associated with the changing light regime as high-latitude winter turns to spring has not been determined. Because simulations of bud burst under climatic warming scenarios based on TT models do not predict an increased risk of frost damage for boreal trees (Linkosalo et al. 2000), it is important to assess the role of the seasonally changing light regime in regulating bud burst phenology.

Based on previous studies (Heide 1993*b*, Vince-Prue 1994, Olsen et al. 1997, 1998, 2001, 2005, Olsen and Junttila 2002), we identified three aspects of the seasonal light regime that might function as phenological cues, either singly or in combi-

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nation: day length, night length and diurnal changes in the spectral composition of light. The effects of photoperiod on plant processes are well established, whereas the possible influence of qualitative diurnal changes in the light environment has received less attention. Given the role of phytochromes in photoperiodic responses (Vince-Prue 1994), it is reasonable to consider that latitudinal and seasonal shifts in the duration of twilight play a role in initiation of bud burst. The red to far-red light (R:FR) ratio is constant during daylight and independent of cloud cover, but is much reduced during twilight when sun elevation is low (Nilsen 1985). A reduced R:FR ratio during the twilight hours, especially in the evening, has been shown to control the cessation of internode elongation of aspen at the end of the active growing period (Olsen and Junttila 2002). Similarly, an evening far-red pulse enhances the effect of night length on initiation of flowering in some annual plants (Vince-Prue 1994). The annual variation in day, night and twilight period duration during a 24-hour cycle increases substantially at higher latitudes (Figure 1). These quantitative and qualitative aspects of light regime all have a regular seasonal progression at a given latitude (Figure 1) and thus, individually, or in combination, could be the basis for a functional response triggering initiation of bud development on a given date in accordance with the TT models as opposed to the ST models.

To assess these possibilities, we studied the onset of leaf bud development of silver birch (*Betula pendula* Roth) in a controlled environment experiment. We manipulated the light environment of cloned birch plantlets to simulate natural light conditions during the progression from winter through spring in southern Finland (60° N latitude), with increasing day length and decreasing night length as well as the normal diurnal progression of irradiance under a clear sky. To assess possible twilight effects, we included a treatment in which plantlets were subjected to a reduced R:FR ratio during the morning and evening twilight periods, whereas a reference group of plantlets received spectrally unaltered light at a similarly reduced irradiance during the twilight periods. To allow modeling of the interplay between temperature and light-dependent processes possibly involved in bud burst, we exposed subsets of the plants to varying amounts of warming to introduce some variation in the timing of bud burst in both light treatment groups. Our primary aims were to assess (1) if a change in photoperiod is involved in initiating bud development after chilling requirements are satisfied; and (2) if twilight modulates any photoperiodic response. Increased understanding in these areas will help in deciding the best approaches to modeling bud burst, which is necessary to predict potential effects of climatic warming on forest trees at high latitudes.

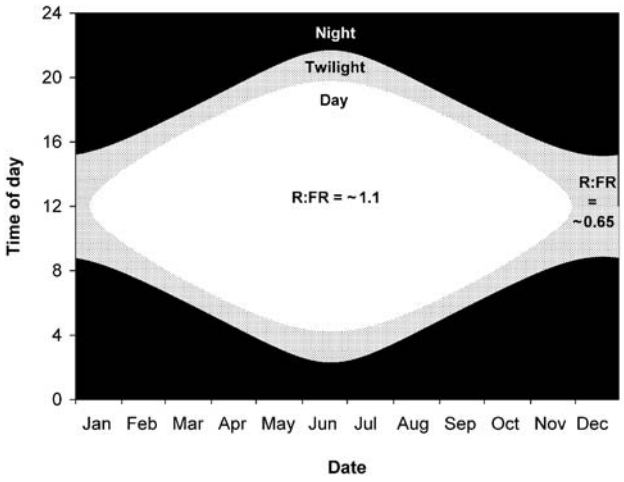

Figure 1. Natural night (black), twilight (gray) and day (white) lengths at 60° N latitude, as used in our experiment. Twilight was defined as the time when sun elevation is less than 2° below and less than 8° above the horizon. The red to far-red (R:FR) values refer to those in natural conditions.

Materials and methods

Plant material

Birch plantlets were cloned in summer 2002 at the University of Helsinki from lateral bud tissue of a mature tree. Plantlets were from clonal line JR 1/4, used as source and reference in several studies of transgenic birch ecology at the University of Helsinki (e.g., Pasonen et al. 2004). Although juvenile plants of several tree species act differently from mature trees, e.g., in their bud burst timing (Augsburger and Bartlett 2003, Partanen et al. 2005), plantlets derived from the tissue of mature trees should act as mature trees (Jones et al. 1996, Ryynänen and Aronen 2005). Thus, we expected that our results would be comparable with those from studies based on historical data for mature trees (Kramer 1994, 1995, Häkkinen et al 1998, Chuine et al. 1999, Linkosalo 1999, 2000, Schaber and Badeck 2003).

The plants were grown in tissue culture in Helsinki to about 1 cm tall and then sent to McGill University, Montreal, Canada, where they were transferred from their initial tissue culture environment to soil culture in October 2002. Some of the tissue culture stock was somewhat crowded with stems, and we could not entirely separate individuals when we transplanted the plantlets to soil culture; we ended up with some solitary plants and some small clusters of plantlets. The plantlets were grown in the McGill University phytotron in a 16-h photoperiod at a day/night temperature of 19/16 °C until December 2002, then in an 8-h photoperiod at a constant temperature of 16 °C until January 2003, and finally in an 8-h photoperiod and a day/night temperature of 8/6 °C to induce a winter resting stage. Dormancy was broken in April–May 2003 by gradually lengthening the photoperiod and increasing the temperature. Toward the end of their second growing period, the plantlets (n = 99) were about 10 cm tall. In October 2003, the plants were exposed to cool short days to encourage leaf senescence and normal winter bud development. By December 2003, the plants had developed winter buds and were exposed to chilling treatment at 0 °C in a 6-h photoperiod. Before the chilling treatment began, plantlets were labeled, their size, stem number and bud number per stem recorded as possi-

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ble covariates to be considered during data analysis. Of all the plants, the 60 most uniform in size and form were chosen for the experiment, and the remaining plants were used only to determine if the chilling requirement had been satisfied.

Day-length pattern

The day-length pattern for the experiment was based on the sun path in cloudless sky at 60° N latitude (Gates 1980). The twilight period was considered the time when the sun was between < 8° above and < 2° below the horizon. The R:FR ratio has a reduced and rather constant value between these elevations (Nilsen 1985). Daylight was considered the time when the sun was > 8° above the horizon; and night, when the sun was > 2° below the horizon.

At 60° N latitude, the annual variation in day length is large. In midwinter the days are short, whereas summer nights barely exist. Thus, in the experiment, the initial night length for the plants was 17 h and only 40 minutes of the light period was bright midday light, the rest being twilight. By the spring equinox, night length was less than 12 h and the twilight period was at its shortest duration—only about 80 minutes each morning and evening (Figure 1). By the spring equinox, the rate of change in day length was at its largest, thereafter decreasing toward the end of the experiment.

Experimental design

All treatments were applied with individual plants as experimental units. From the start of the light treatments each plant was enclosed in its own cardboard container. The containers were light-tight when the lids were closed, but constructed to allow air to flow around the plants at all times. Air and soil temperatures were similar inside and outside the containers. Each container lid incorporated a colored filter to modify the spectral composition of light reaching the interior. Within the light treatments, the plants were divided into five groups receiving different warming treatments. There were six replicates per treatment group. Plant locations in the growth chamber were randomized. All the plants were grown in one growth chamber, but were moved daily for varying time periods to a second chamber for a warming treatment during the forcing phase of the experiment. Illumination in the warming treatment chamber was the same as in the main chamber during the daytime hours.

Light treatments

Both light treatments followed the pattern of natural light conditions and changing day lengths that prevail from January through May in southern Finland (60° N). The light environment in the growth chamber simulated midday spectral conditions with a combination of fluorescent and incandescent bulbs giving an R:FR ratio of 1.3 and an irradiance of 180 μmol m^{-2} measured with a Skye SKR 110 R:FR sensor and Li-Cor LI-190SA quantum sensor, respectively. During the twilight period, the R:FR ratio of the plants in one light treatment group was reduced by translucent lilac filters; the filter, two layers of Roscolux/Supergel No. 51 "Surprise Pink" by Rosco International (www.rosco.com), reduced the R:FR ratio to 0.58, a value typical at low sun elevations, and reduced the overall irradiance to 72 μmol m^{-2}. Semi-transparent white filters consisting of two layers of onionskin paper (Product No. 21160, Hilroy, Canada) were used to create a control light environment with an overall irradiance of 85 μmol m^{-2}, but little change in the light spectrum (Figure 2). We used an Optronic Laboratories OL 754 spectroradiometer (Orlando, FL) to record the light spectrum in the growth chamber under the filters, before and after the experiment. No change in the optical properties of the filters occurred during the experiment. To start the evening twilight treatment, the filter box lids were closed in the late afternoon in accordance with the seasonal progression of twilight duration; when the growth chamber lights automatically turned off for the night, the twilight filters were still in the closed position. In the morning, when the chamber lights came on again, the twilight treatment resumed

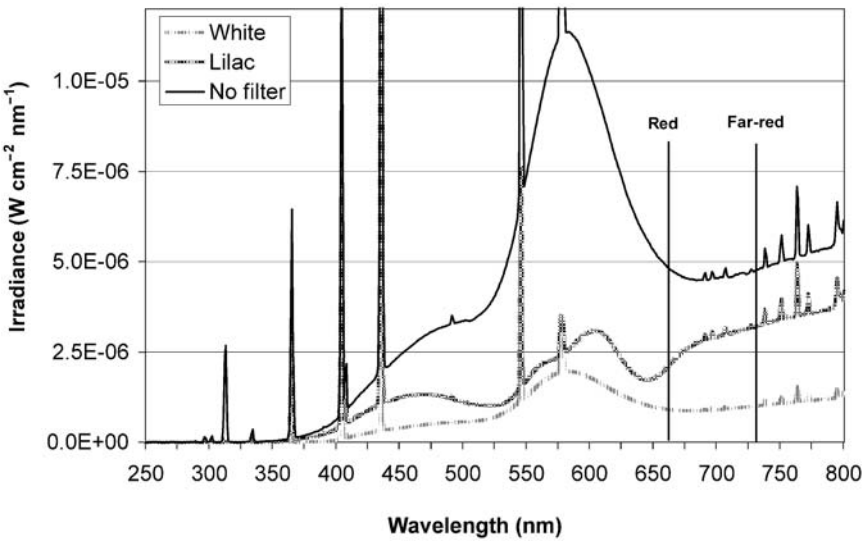

Figure 2. Irradiance spectrum in the growth chamber with and without the two filters. Spectra are for unfiltered light and light filtered with lilac and white filters (black, dark gray and light gray line respectively). Vertical lines to the right indicate the wavelengths for red and far-red light.

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until an automated command from the growth chamber timer opened the filter box lids.

Chilling

At the start of the simulated chilling period in January 2004, the growth chamber temperature was held at 0 °C (Table 1). At this temperature chilling proceeds, while forcing, should the development restraining condition of the bud be released, is still minimal. After three weeks of chilling, some test plants exposed to forcing temperatures (15 °C and 24-h light period) showed bud development in 5 days, so we concluded that the chilling requirement of the plants was met and proceeded to the next phase of the experiment.

Forcing and warming treatments

During the forcing phase, the nighttime temperature of the growth chamber was initially held at 0 °C, which is close to natural conditions in southern Finland. Starting on February 22 in the simulated season, we increased the daytime temperature to 7 °C, with a 1-h ramp at each end of the photoperiod (Table 1). This temperature, in addition to simulating the daily temperature variation in spring, would enhance the forcing if the plants were able to proceed in bud development. We used a TT model to estimate that the time to bud burst would be about 60 days in this temperature regime and a 12-h photoperiod. In the simulated season, we started our warming treatment on March 8. In this phase the plantlets were exposed to elevated temperature to enhance bud burst. The plantlets were divided into five groups that received warming treatments for 0.75, 1.5, 3, 4 or 5 hours during daylight hours. Initially, a warming treatment of 15 °C was imposed by moving the plants to an adjacent growth chamber with light conditions similar to the daytime light in the main growth chamber. After four weeks, the night temperature was increased to 3 °C and the warming treatment was increased to 19 °C. These temperatures were maintained until the end of the experiment.

Observing bud burst

The status of the leaf buds was observed at the end of the warming treatment, as the plants were then outside the filter boxes and more easily observed. We kept separate records for three phases in bud development, namely (1) the start of bud swelling, bud scales split open; (2) emergence of the first leaf from the bud; and (3) the emergence of the base and petiole of the first leaf from the bud. The number of buds in each phase was recorded daily on all plants.

After a review of the observations, we considered that bud burst was most consistently assessed as the time when at least three buds of a plant had reached Phase 3 (petiole emerging from bud). The buds observed were the first to show signs of development (Myking and Heide 1995). For most of the plants, the first buds to burst were apical and typically on the main stem.

Thermal time model and historical phenological data

The initiation of temperature-driven bud development cannot be observed from ontogenetic changes, so we fitted a thermal time (TT) model to the observed bud burst dates to estimate the date when our plants started reacting to ambient temperature. The model has two adjustable parameters—starting date of heat sum accumulation, and a threshold for bud burst. When the degree-day sum exceeds the threshold, the model predicts that bud burst will take place.

In the TT model, the rate of heat sum accumulation (r) is the amount of ambient temperature T above a threshold T_0, as shown in Equation 1:

$$r(T) = \begin{cases} T - T_0, T > T_0 \\ 0, T \le T_0 \end{cases} \quad (1)$$

Accumulated heat sum S at time t is calculated in Equation 2 as:

$$S(t) = \int_0 r\big(T(t)\big)dt = \sum_{i = t_0}^{t} r\big(T(i)\big)t_i, \quad (2)$$

where t_0 is the starting date of heat sum accumulation and t_i is the duration of the time period i. Because we hypothesized that light quality affects initiation of bud development, we used separate starting date parameters for the twilight and reference light treatment groups.

To estimate required parameter values for the TT model (t_0, threshold temperature T_0 and bud burst threshold S_{crit}) and to

Table 1. Timescale and temperatures during the experiment.

Date[1]	Comment	Day temperature (°C)	Night temperature (°C)	Warming treatment temperature (°C)
December 2003	Chilling starts	0	0	–
January 26, 2004	Chilling continues, twilight treatment starts	0	0	–
March 8, 2004	Warming treatment starts	7[2]	0[2]	15
April 9, 2004	First buds burst			
April 10, 2004	Warming treatment continues, temperatures elevated	7[2]	3[2]	19
May 18, 2004	Experiment ends			

[1] This is the date on which natural daylength corresponds with the growth chamber daylength.
[2] One-hour temperature ramp between night and day temperatures.

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compare our results, we used historical data of phenological observations collected in central and southern Finland (between 60 to 65° N and 21 to 30° E, repectively), during the period 1896 to 1955, together with temperature records for the same period from the same area (Linkosalo 1999, 2000, Linkosalo et al. 2000). The parameter values of the TT model were estimated by minimizing the Root Mean Square Error (RMSE) between the observed and model-predicted bud burst dates. The same model was applied when fitting the TT model to the bud burst data from in this study.

Results

In mid-January 2004, after three weeks of chilling, test plants exposed to forcing conditions (15 °C and a 24-h photoperiod) broke bud in 5 days. This translates to 53 degree-days of accumulated heat sum, which is in good agreement with our main result (Table 2) and suggests that the chilling requirement of the plantlets was fully met by this time. At the end of January 2004, we subjected the main group of plantlets to the twilight treatments, initially with rather low growing temperatures, as our simulated conditions were similar to those in Finland in midwinter. The first phase of the warming treatment began in early March, and the second phase of the warming treatment was initiated in early April (Table 1).

Of 60 plants in the experiment, 12 died or failed to burst buds and were omitted from the subsequent analyses. The dead plants were small and had multiple stems, indicating that they were probably derived from clusters of several individuals. We were left with 48 plants for analysis with the number of plants within each treatment regime varying from four to six.

Mean bud burst dates and standard deviation within treatment are presented in Figure 3. We compared the heat sums accumulated from a fixed and common starting date until the time of bud burst for the two light treatment groups with Student's *t* test. The test indicated that the mean accumulated heat sums differed statistically between the groups ($P = 0.05$). The starting date of the heat sum accumulation did not affect the test result. We used the accumulated heat sum as the scale on which to compare the light treatment groups because this enabled us to eliminate the effect of warming treatments on the bud burst date from the comparison and focus on the effect of the twilight treatment only.

To verify the effects of the twilight and warming treatments, we fitted a 2-way analysis of variance (ANOVA) model to the

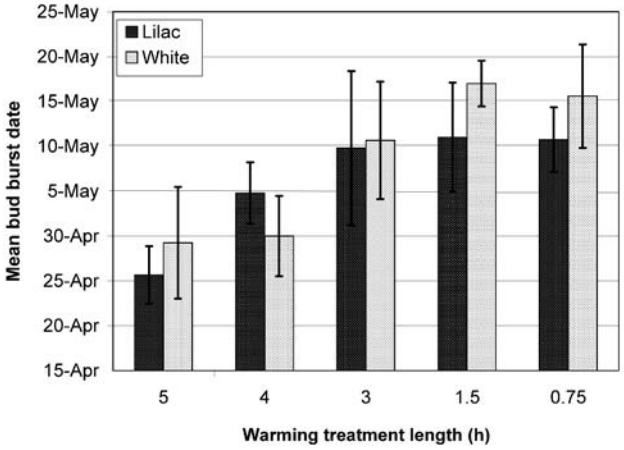

Figure 3. Mean bud burst dates for the warming and light treatments. Values on the *x*-axis refer to the length of warming treatment and bar shading to the filter colors used (light bars = white filters, dark bars = lilac filters). Error bars are ± 1 standard deviation (in days) within each treatment group.

data, with warming treatment and light treatment as fixed parameters. The warming treatment showed high significance ($P < 0.0001$), whereas the effect of light treatment was not statistically significant ($P = 0.07$). To determine if differences in plant morphology (single versus clumped stems) influenced the response of bud burst to the light treatments, we conducted an analysis of covariance as follows: to identify a morphological index that could be used as a covariate in an analysis of covariance (ANCOVA), we calculated the principal components of three variables—the number of stems, the number of branches on each plant and the logarithm of the overall number of buds on the plant. The first two principal components reflected simple correlations with plant size and total bud numbers, but the third component provided a useful index of "bud density" after the effects of plant size had been removed. This component had positive loadings for the numbers of stems and branches in the plant and negative loading for the number of buds. We used this component as a covariate in an unbalanced 2-way ANCOVA model (SAS procedure GLM). The model showed high significance of the bud-burst date on the warming treatment ($P < 0.0001$), and statistically significant dependence of the bud-burst date on the twilight treatment ($P = 0.04$), with reduced R:FR ratio advancing bud burst by 4 days (Table 3). There was no significant heterogeneity of slopes in the

Table 2. Comparison of thermal time model parameters fitted to the experimental and historical data.

	Latitude	Starting date	Bud burst threshold (Degree days)	Root mean square Error of model fit (days)
Experimental data	60° N	March 19 (Lilac filter) March 23 (White filter)	86.0	5.45
Chilling release experiment	–	–	54	–
Historical data	62° N	March 19	63.4	2.70
Historical data with fixed threshold	62° N	March 7	86.0 (fixed)	3.17

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Table 3. Summary of analysis of variance of factors influencing bud-burst date. Temperature and filter are experimentally manipulated variables; and bud density is a covariate allowing for morphological differences among the replicate plants.

Source	DF	Sum of squares	*F* value	*P* > *F*
Model	6	2255	14.32	< 0.0001
Error	41	1076		
Corrected total	47	3331		

Source	DF	Type III SS	*F* value	*P* > *F*
Temperature	4	1936	18.44	< 0.0001
Filter	1	115	4.37	0.043
Bud density	1	66	2.51	0.121

ANCOVA, or any treatment interactions.

We fitted a TT model to the observed data to determine the date when the plants started to react to the warming treatments. Fitting the model to the historical data suggested a temperature threshold of 4.4 °C, which we used also for our experimental data. Other model parameter values are in Table 2. The parameter values resulting from fitting the model with our experimental data were in good agreement with the values achieved by fitting the model to the historical data (Table 2). The starting dates show the same four days of difference that was found in the bud-burst dates between the two light treatment groups. The modeling result suggests that the experimental plants started reacting to ambient temperature only in late March, and the forcing test indicates that the chilling requirement of the plants had been met at the end of January.

Discussion

Our results confirmed that once bud development of boreal trees is initiated in spring, further bud development is driven mostly by ambient temperatures (e.g., Cannell and Smith 1983, Hänninen 1995), but we also demonstrated that plants do not necessarily respond to warming as soon as their chilling requirement is met, as is commonly assumed (Hänninen 1995, Kramer 1995, Chuine et al. 1999). As there are no visible features or generally known biochemical markers that can be used to assess the readiness of buds to respond to warming, we used a TT model to estimate the moment when bud development was initiated. Our results suggest that the initiation date for bud development was around the spring equinox, months after the fulfillment of the chilling requirement both in natural conditions and in our experiment. We conclude that satisfying the chilling requirement is a necessary, but not a sufficient condition for releasing dormancy of vegetative buds in birch. Bud development was initiated so late in the spring that dormancy release cannot be driven only by ambient temperatures.

We sought to identify the environmental cue that releases bud development once the chilling requirement is satisfied. Our experiment suggests that the major cue enabling bud development of birch in spring is photoperiodic, either the shortening night length or the increasing day length. The spectral conditions associated with twilight modulate the photoperiodic response and accounted for a four-day advance in bud burst, which is too small an effect to determine the initiation of bud burst in the absence of a quantitative contribution associated with photoperiod. A modulating influence of twilight has been reported in other photoperiodic phenomena. For example, flowering of *Pharbatis* and *Xanthium* is enhanced by an evening far-red treatment (Vince-Prue 1994). Neff et al. (2000) point out that many plant-response mechanisms appear to depend on both photoperiod and light quality.

The modulating effect of twilight on bud burst suggests that phytochromes are involved in the phenological control systems for birch. Phytochromes react to the ratio of red (660 nm) and far-red (730 nm) irradiance (Smith 1994) over a 24-h cycle, and this ratio differs between daylight and twilight (Nilsen 1985). Phytochromes are known to influence seed germination, growth and plastic adjustments of form (Smith 1994, Vince-Prue 1994). Similarly, phytochromes appear to have an essential role in controlling shoot elongation in some boreal deciduous trees (Olsen and Junttila 2002). Our results provide indirect support for the involvement of phytochromes in the activation of bud development of birch. This possible role of phytochrome in the activation of bud development could be verified directly in an experiment utilizing biochemical measurements of phytochrome activation during bud development.

Although we cannot distinguish between the influence of day length and night length in our experimental design, it is clear from our modeling analysis that the changing photoperiod in the vicinity of the vernal equinox plays a role in the release of bud development in birch. The initiation date and degree-day-sum threshold from our model fitting are in good agreement with results from model evaluations utilizing historical phenological and temperature data collected from trees growing in natural conditions (Table 2). Neither the historical data nor the effects of our experimental warming treatments can account for the timing of bud burst without invoking a fixed date at which bud development is initiated in response to warming. This fixed date occurs well after the chilling requirement has been met, supporting the conclusion that a change in light environment triggers bud development in spring, and justifying the use of simple TT-type models in phenological studies. A TT-type model seems to more accurately describe bud development of birch than an ST-type model. Therefore, we recommend using TT-type models rather than ST-type models, provided that the date of the onset of bud development is not chosen arbitrarily, but in accord with plant responses to changes in the light regime.

In the 1990s, the predictions of a large increase in the risk of frost damage to boreal trees as a result of climatic warming were based on ST-type models (Hänninen 1991, Kramer 1994). Our results suggest that the signal for the onset of spring development comes from light conditions, implying that the bud-burst date of birches will not advance as much as these earlier studies anticipated. This result has major ecological consequences. The anticipated increase in the frost damage

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risk of boreal trees is unlikely to occur even with substantial climatic warming (Linkosalo et al. 2000). Therefore the boreal birch forest is likely to continue acting as a carbon sink in the future, although the active growing period of these forests may not increase as much as the simulations based on ST-type models have predicted (Linkosalo et al. 2000).

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