

Predicting spring phenology and frost damage risk of *Betula* spp. under climatic warming: a comparison of two models

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Received October 20, 1999

Summary Timing of bud burst and frost damage risk for leaves of *Betula* spp. in response to climatic warming in Finland was examined with two models. In the first model, ontogenetic development in spring was triggered by an accumulation of chilling temperatures. The second model assumed an additional signal from the light climate. The two models gave radically different estimates of frost damage risk in response to climate warming. The chilling-triggered model forecast a significant and increasing risk with increased warming, whereas the light-climate-triggered model predicted little or no risk.

The chilling-triggered model is widely applied in phenological research; however, there is increasing experimental evidence that light conditions play a role in the timing of spring phenology. Although it is not clear if the light response mechanisms are appropriately represented in our model, the results imply that reliance on a light signal for spring development would afford a degree of protection against possible frost damage under climate warming that would not be present if chilling were the sole determinant. Further experimental tests are required to ascertain the light-related mechanisms controlling phenological timing, so that credible model extrapolations can be undertaken.

Keywords: boreal forest, bud burst, climate change, light response.

Introduction

The boreal zone is characterized by a long, cold winter, often with several months of subzero temperatures. The summer is quite short, but the days are long, providing plenty of sunlight for photosynthesis. At the start of the growing season in spring, the probability of night frosts diminishes and the days are generally warm and favorable for growth. Thus the mechanisms regulating the start of the active growth period in perennial species represent a compromise between ensuring the maximum period for photosynthesis and growth and minimizing the risk of frost damage.

The effect of global climate change on spring phenology of trees has been widely studied. Cannell and Smith (1986) con-

cluded that the frost damage risk to *Malus pumila* Mill. would increase with a climatic warming of 2 °C, but that the risk to *Picea sitchensis* (Bong.) Carr would be unchanged. From data obtained using the dormancy-based model presented by Sarvas (1972, 1974) for boreal-zone trees and a scenario of uneven climatic warming (Bach 1988), Hänninen (1991) concluded that hardwoods in the boreal zone will suffer substantial frost damage with only slight climatic warming.

Kramer (1994) presented evidence to support Hänninen's (1991) conclusion for boreal-zone trees, but found no increase in frost damage risk of temperate-zone *Fagus sylvatica* L. with climatic warming. He concluded that differences among species in response to climate warming arise because temperate-zone species are in a different state of chilling toward the end of the winter than boreal-zone species, and thus react in a different manner to climatic warming. Moreover, studies with *Pinus sylvestris* L. (Hänninen 1995, Repo et al. 1996, Leinonen et al. 1997) and *Betula pendula* Roth (Leinonen 1996a) have shown that the advance in the date of bud burst of boreal trees in response to warming, and hence the possible increase in frost damage risk, is less than that predicted by models.

Most elements of phenological control are well known. Dormancy in autumn and early winter, driven mostly by accumulation of chilling temperatures, hinders the start of ontogenetic development. In spring, ontogenetic development is strongly temperature-dependent. There is evidence that light climate plays a role in the start of ontogenetic development (e.g., Myking and Heide 1995, Häkkinen et al. 1998, Partanen et al. 1998, Häkkinen 1999). However, it is still unclear how these elements interact. Because various modeling studies have used alternative interpretations of phenological phenomena, this may have had a considerable effect on the results obtained from simulations of phenology in response to climatic warming.

The aim of this study was to analyze the uncertainty of phenological predictions and estimated frost damage risk under climatic warming attributable to differences in model structure. Two existing models of phenological timing of boreal trees were used to forecast the timing and frost damage

risk of newly unfolded leaves of *Betula* spp. in central Finland, for two scenarios of future climatic warming.

Materials

A combined time series for bud burst of leaves of *Betula* spp. and temperature records were used to estimate the parameter values of the phenological models. The combined phenological time series was constructed from 44 observation series, collected by amateur observers during the years 1896 to 1955, based on an iterative method described by Häkkinen et al. (1995) and Linkosalo et al. (1996) (see Appendix).

The combination procedure reduces systematic biases caused by climatic and genetic variation between the observation sites. Further, it enables combination of multiple, fragmentary but partly overlapping observation series collected from a large area into a single, reliable combined series. Although the observation series (see Häkkinen et al. 1995 for a list of original publications) cover a large area of Finland (550 km in both a north–south and east–west direction), the peripheral observations fit the combined time series as well as the more central observations (Linkosalo 1999) (Figure 1). Because the data collection area is quite flat in topography, with observation sites located from 5 to 120 m a.s.l., the position of the site in the north–south direction is the major geographical feature causing systematic variation in phenological timing (Linkosalo 1999).

In the late 19th and early 20th century the two most common species of *Betula* in Finland, namely *B. pendula* and *B. pubescens* Ehrn., were not known to be different, but were specified as *Betula alba* L. in historical observation series. Because *B. pendula* is the more common species on mineral soil growing sites, and unfolds its leaves earlier than *B. pubescens*, it is probable that most observations are of the *B. pendula* species.

The center of the phenological data collection area falls near the city of Jyväskylä, and observations from locations around Jyväskylä correspond closely to those of the combined time series. This indicates that the combined phenological time se-

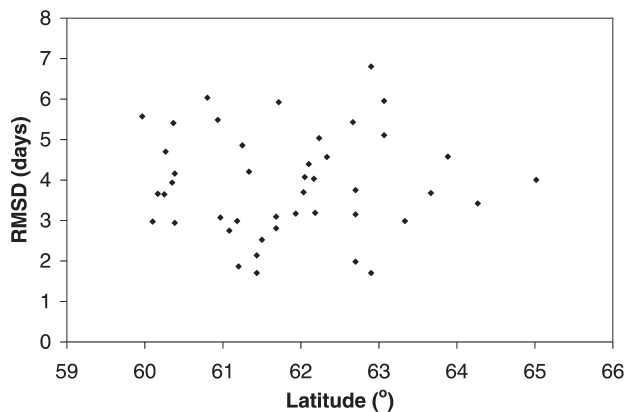


Figure 1. Root mean square deviation (RMSD) of the 44 adjusted phenological observation series from the combined time series as a function of latitude.

ries can be used to describe the phenological timing in the vicinity of Jyväskylä. Air temperature data in the city of Jyväskylä, for the period July 1883 to June 1981, were obtained from the Finnish Meteorological Institute. Four temperature measurements per day were used: morning, early afternoon, evening, and the daily minimum, with each measurement taken to represent a period of 6 h. Missing values of daily minimum temperature for 1883–1901 were estimated from the morning observations by regression analysis. Because of missing temperature observations, the period 1912–1916 was omitted from the analysis.

Methods

Bud burst models

We compared two models of bud burst timing. The first, referred to as the chilling-triggered model, is based on the classical work by Sarvas (1972, 1974). The model describes a chilling requirement during dormancy that must be fulfilled before ontogenetic development toward bud burst can commence, regardless of ambient conditions. Such a requirement prevents premature development during warm spells in the autumn and early winter. The chilling requirement, which is considered to be the only mechanism maintaining dormancy, is assumed to develop cumulatively, as a function of temperature, T , from a fixed date each year such that the stage of dormancy, S_D , at time t is:

$$S_D(t) = \int_{A_{crit}}^t f_D(T(t)) dt. \quad (1)$$

Rate of dormancy development, f_D , was determined empirically as a function of chilling temperatures by Sarvas (1974). Original tabulated values of the rate function were used. Dormancy develops when the air temperature is between -3.5 and 10.2 °C, and attains its highest rate at 3.5 °C (Figure 2).

Once S_D reaches a threshold value, D_{crit} , dormancy is completed, and ontogenetic development of buds can proceed when temperatures are favorable. The stage of ontogenetic development, S_O , at time t is:

$$S_O(t) = \int_{t_{dr}}^t f_O(T(t)) dt, \quad (2)$$

where f_O is rate of ontogenetic development as a function of temperature, T , also empirically determined by Sarvas (1972) and depicted in Figure 2. The starting date of development, t_{dr} , corresponds to the release of dormancy, and varies from year to year. Bud burst occurs when S_O exceeds a threshold value, O_{crit} (Figure 3).

The second model, referred to as the light-climate-triggered model, assumes that once the chilling requirement is met, plants do not immediately acquire the ability for ontogenetic development. Instead, another regulatory mechanism connected to light conditions further hinders ontogenetic develop-

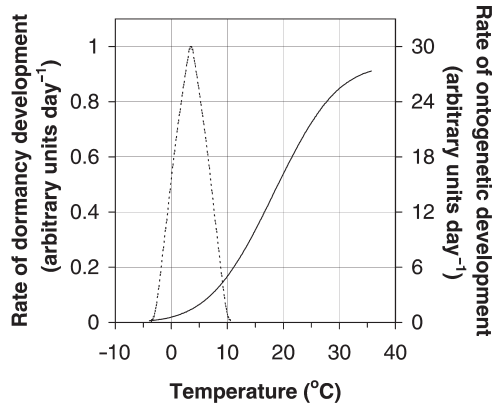


Figure 2. Rate of dormancy development, f_D , (dotted line, scale to the left) and rate of ontogenetic development, f_O , (solid line, scale to the right) as a function of temperature, as presented and tabulated by Sarvas (1972, 1974).

ment until spring. In the model, this mechanism is represented by calendar date; i.e., ontogenetic development in the model is assumed to start at a constant, parameterized date, t_{crit} . The stage of ontogenetic development, S_O^* , is again described with a temperature sum type model, with the rate, f_O , identical to that in the chilling-triggered model (Figure 2):

$$S_O^*(t) = \int_{t_{crit}}^t f_O(T(t)) dt. \quad (3)$$

Bud burst takes place once ontogenetic development reaches a threshold value O_{crit}^* (Figure 3).

Parameter values of the two models (A_{crit} , D_{crit} and O_{crit} for

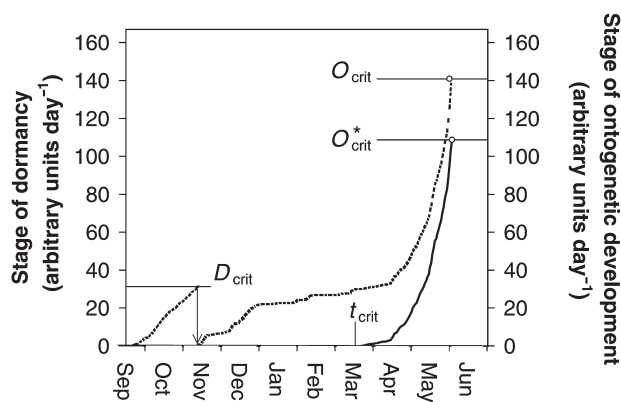


Figure 3. Comparison of the chilling-triggered model (dotted line) and the light-climate-triggered model (solid line) using 1955 as an example year. Dormancy accumulates until November, when the critical threshold value, D_{crit} , is reached and dormancy is completed. This triggers ontogenetic development, which proceeds somewhat during a warm spell in December, starts again in April, and finally reaches the critical threshold value for bud burst, O_{crit}^* , in May. Ontogenetic development according to the light-climate-triggered model starts at the threshold date, t_{crit} , and reaches the threshold value for bud burst, O_{crit} , in May.

the chilling-triggered model, t_{crit} and O_{crit}^* for the light-climate-triggered model) were estimated by minimizing iteratively the root mean square error (RMSE) of predicted bud burst dates:

$$RMSE = \sqrt{\frac{\sum_i (z_i - \hat{z}_i)^2}{n}}, \quad (4)$$

where z_i denotes observed bud burst date and \hat{z}_i denotes predicted bud burst date in year i . The number of years, n , was 55, representing the periods 1896–1911 and 1917–1955 (Table 1).

Climate change scenarios

The two models were each run for two scenarios of future temperature change. The first scenario assumed a uniform increase in temperature throughout the year, a convenient device for exploring model sensitivity, but unrealistic climatologically. The second scenario assumed a seasonal pattern of temperature increase by ratios relative to the annual mean increase of 1.41 (December to February), 0.94 (March to May), 0.71 (June to August) and 0.94 (September to November). This pattern of warming, greater in the winter months than in the summer months, is based on the central scenario of the Finnish Research Programme on Climate Change (SILMU), where temperature changes over Finland were projected to 2100 based on simulations from global climate models (Carter et al. 1996).

Climatic warming was simulated by increasing, in 0.5 °C increments of mean annual temperature up to +10 °C, the daily air temperature observations (four per day) at Jyväskylä throughout the 92 years of recorded temperature data according to the scenario pattern of temperature change. In this way, model behavior was examined over 92 increments of mean warming for each of the two scenarios. All other features of the 92-year observed time series were assumed to remain unchanged (e.g., interannual, daily and diurnal temperature variability). We note that a mean annual warming of 10 °C is at the high end of climate model estimates of century-scale warming in Finland, and well in excess of the warming described in the SILMU central scenario (about 4.7 °C by 2100).

Bud burst timing and frost damage risk analysis

The parameter values estimated from the combined time series were fixed when the models were used with the changed climate data to predict the change in timing of bud burst. Both models were applied to the 20 increments of mean warming in each climate change scenario. The mean change in bud burst date was calculated by subtracting the mean date of bud burst in a given warming scenario from the mean date of bud burst obtained with the same model run with unmodified climatic data.

Frost damage risk was estimated as the percentage of years having one or more occurrences of minimum temperatures below a threshold of -5 °C (Braathe 1995, 1996) between the occurrence of bud burst and June 30 (Cannell and Smith 1986, Häkkinen and Hari 1988).

Table 1. Parameters and root mean square error of the models.

	Symbol	Units	Chilling-triggered model	Light-climate-triggered model
Start of dormancy	A_{crit}	Day	September 10	–
Start of ontogenetic development	t_{crit}	Day	–	April 10
Dormancy release threshold	D_{crit}	Arbitrary	33.3	–
Bud burst threshold	$O_{\text{crit}}, O_{\text{crit}}^*$	Arbitrary	140.7	100.8
Root mean square error	RMSE	Day	3.9	2.5

The accuracy of the estimate of the starting date of ontogenetic development, t_{crit} , in the light-climate-triggered model was examined by varying the starting date parameter from January 1 to May 1, and finding corresponding values of the bud burst threshold, O_{crit}^* , and RMSE (Figure 4). The RMSE decreased gradually as t_{crit} was moved from January to a local minimum of 2.4 days on March 3 (Figure 4). There were two other local minima of RMSE on March 23 and April 10 (both also 2.4 days). For starting dates later than April 10, RMSE increased rapidly. Therefore, we concluded that the optimum value of t_{crit} lies somewhere between March 1 and April 15, because in this range RMSE was practically the same (Figure 4). Consequently, the light-climate-triggered model was tested with each of the three local minima (March 3, March 23 and April 10).

Results

Timing of bud burst

With a starting date, t_{crit} , between March 1 and April 15, the light-climate-triggered model predicted bud burst to occur in all scenario temperatures before the end of May. The SILMU scenario assumes a uniform increase in temperature during spring (March–May) that is only slightly lower than the annual mean. Because the other climate scenario assumes a uniform annual mean increase, the two scenarios had a similar effect on

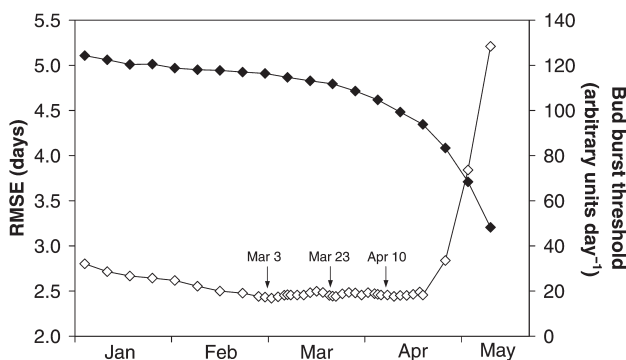


Figure 4. Root mean square error (RMSE) of bud burst dates predicted by the light-climate-triggered model (\diamond) and corresponding values of bud burst threshold of ontogenetic development (\blacklozenge) as a function of the threshold date of ontogenetic development, t_{crit} . The arrows indicate three local minima of RMSE.

bud burst predictions with this model.

The behavior of the light-climate-triggered model with climatic warming depended somewhat on the value of t_{crit} . With the late starting date, April 10, mean bud burst occurred about 2.6 days earlier per 1°C warming, whereas the interannual variability in bud burst dates was reduced to less than half with a warming of 10°C . For values of t_{crit} in March, the sensitivity of bud burst date to warming was larger (up to $4.1\text{ days }^\circ\text{C}^{-1}$), whereas the change in variability was negligible (Figure 5).

For the chilling-triggered model, the two climate change scenarios produced different results. Under both scenarios, the mean date of dormancy release moved earlier with warming of up to 2°C . For higher temperature increases, dormancy release began to shift from winter toward spring at an increasing rate (Figure 6). Regardless of this, the simulated bud burst dates occurred much earlier in spring in response to elevated temperatures (up to $5.2\text{ days }^\circ\text{C}^{-1}$ of warming). This change was especially marked in the SILMU scenario, where winter temperatures increase by more than the annual mean (Figure 6). Climatic warming decreased the interannual variability in dates of dormancy release, whereas it increased the corresponding variability in bud burst dates.

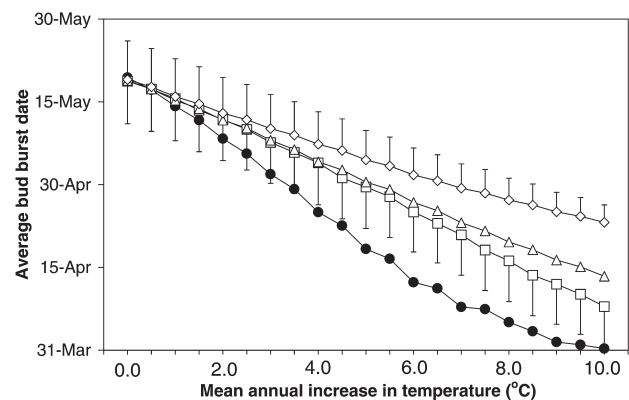


Figure 5. Mean bud burst date according to the light-climate-triggered model as a function of temperature increase, based on three values of the threshold date of ontogenetic development, t_{crit} . Symbols: $\square = t_{\text{crit}}$ of March 3, $\triangle = t_{\text{crit}}$ of March 23, and $\diamond = t_{\text{crit}}$ of April 10 (cf. Figure 4). Vertical bars show the standard deviation of bud burst dates. $\bullet =$ bud burst dates according to the chilling-triggered model for the scenario of uniform warming (cf. Figure 6). From March to May the two climatic scenarios are essentially the same, so the results from the light-climate-triggered model are similar for both scenarios.

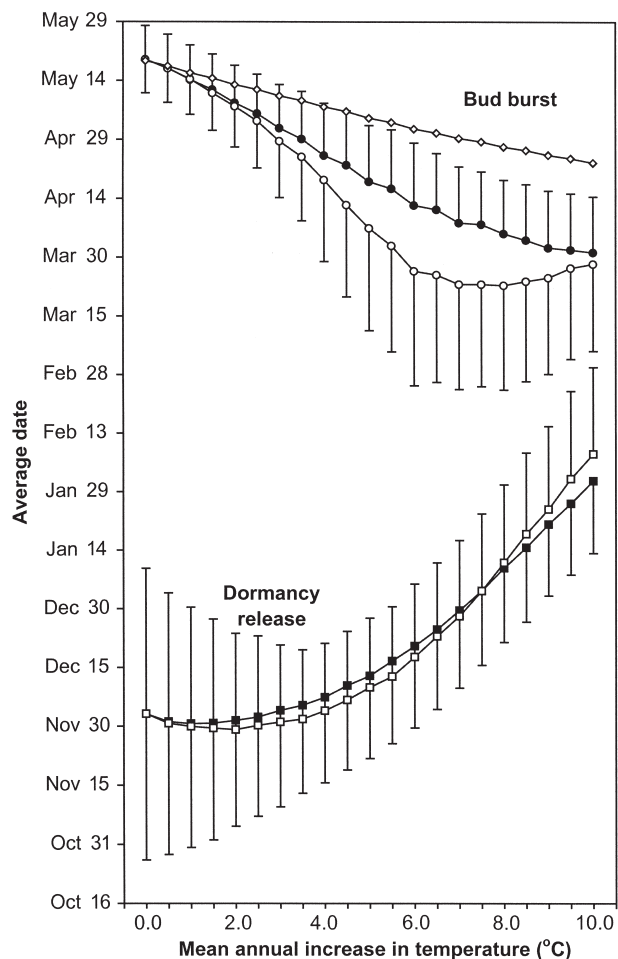


Figure 6. Dependence of timing of dormancy release and bud burst on mean annual temperature increase according to the chilling-triggered model. Symbols: (■, □) = date of dormancy release; (●, ○) = mean bud burst date; solid symbols = the scenario of uniform warming; open symbols = the SILMU scenario (see text for explanation). Vertical bars show standard deviation of the respective date. ◇ = bud burst dates according to the light-climate-triggered model starting on April 10 (cf. Figure 5).

Frost damage risk

The strongest disagreement in outcome of the two phenological models was observed for estimated risk of frost damage (Figure 7). The chilling-triggered model predicted no risk up to a mean warming of around 2 °C, which is projected to occur in about five decades in the central SILMU scenario (Carter et al. 1996). For higher temperature increases, the risk of frost damage increased, reaching a peak with a warming of 7 °C. Above that temperature, the risk started to decline in the SILMU scenario, but remained fairly constant in the uniform warming scenario. The maximum level of risk differed between the two scenarios, reaching 25% in the uniform temperature increase scenario but peaking at 52% in the SILMU scenario (Figure 7).

The light-climate-triggered model gave quite different results. For a start date of ontogenetic development, t_{crit} , of

April 10, frost damage risk was zero in both warming scenarios (Figure 7). Even with a start date of March 3, there was no risk of frost damage until warming exceeded 6 °C, the risk peaking at only 7% (Figure 7). This amount of warming is toward the high end of projections for the boreal zone by 2100 (Johannesson et al. 1995, Carter et al. 1996).

The probability of frost damage is closely related to the difference between daily mean temperature (which, when favorable, drives the ontogenetic development) and daily minimum temperature (which can cause frost damage) and how this may change with climatic warming. Under current climatic conditions, the difference varies seasonally, increasing as solar radiation and mean temperature increase in spring, but with a temporary reduction around mid-April (Figure 8). This reduction is likely to be associated with an observed increase in cloudiness in April (Sarkkula 1987), as well as daytime melting and nocturnal refreezing of surface snow and ice cover, mechanisms that suppress diurnal temperature variations. It is notable that this period of attenuated daily temperature variation coincides with the calculated optimum for the start of ontogenetic development in the light-climate-triggered model (Figure 4), implying that the plants would be able to develop in an environment that reduces the risk of frost damage.

Discussion

A strengthening of the greenhouse effect is thought to be discernible globally, based on observations of surface air temperature (IPCC 1996). The 10 globally warmest years in the 20th century have all occurred since 1980, with 1997 and 1998 being the two warmest years on record (Hadley Centre, 1998). In Finland the trends are less clear, but there is evidence for an increase in spring temperatures in the late 20th century (Heino 1994) along with a systematic lengthening of the thermal growing season, the period with mean daily temperatures exceeding 5 °C (Carter 1998).

There was substantial divergence in the predictions of phenological timing with climatic warming between the two models. The chilling-triggered model has been widely used in studies of the response of phenology of boreal trees to climate change (Hänninen 1990, 1991, 1995, Kramer 1994, Leinonen 1996b), and the results of these studies are similar to those reported here. Furthermore, the estimated advance of the start of the active growing period is consistent with observations from phenological gardens in the temperate zone (Menzel and Fabian 1999). However, these studies were based on small increments in warming compared with the warming assumed in our scenarios.

Several studies have examined the impact of climate change on phenological timing in the boreal zone by enclosing young *Pinus sylvestris* trees in transparent growing chambers that have been artificially warmed above the ambient temperature (Hänninen 1995, Repo et al. 1996, Leinonen 1996b, Leinonen et al. 1997). Results from these studies suggest that the change in phenological timing in response to warming in the boreal zone is not as strong as suggested either by the chilling-triggered

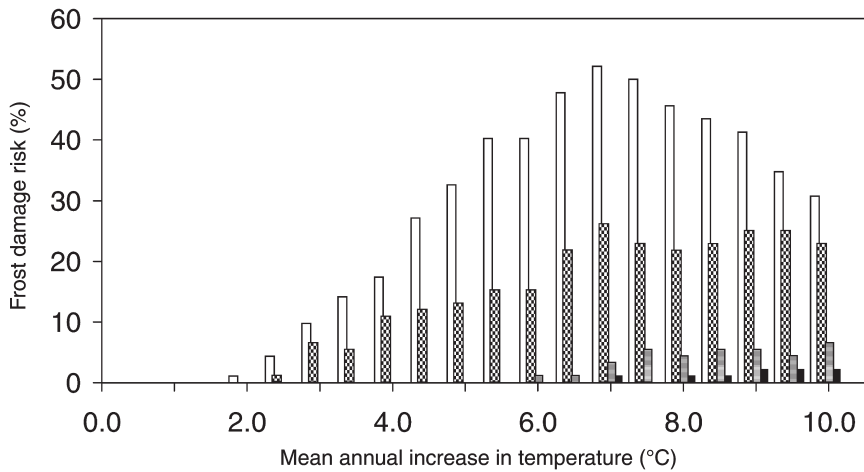


Figure 7. Frost damage risk as a function of mean annual increase in temperature, according to the two phenological models and two warming scenarios. Symbols: open bars = chilling-triggered model and SILMU scenario; crosshatched bars = chilling-triggered model and uniform warming scenario. Horizontally striped bars = light-climate-triggered model with starting date of March 3, and filled bars = light-climate-triggered model with starting date of March 23. With starting date April 10, the risk equals zero for all increments of annual warming. Because the simulated climatic warming from March to May was the same for both climate change scenarios, results for the light-climate-triggered model were similar.

gered model, or by recent temperate-zone observations.

Chilling may not be the only mechanism preventing ontogenetic development during winter; the light-climate-triggered model assumes that a light-related signal is required to trigger ontogenetic development, in addition to the chilling requirement. Studies on *Salix* (Olsen et al. 1997), *Fagus* (Heide 1993a) and *Picea* (Partanen et al. 1998), as well as *Betula pendula* and *B. pubescens* (Myking and Heide 1995, Häkkinen et al. 1998, Häkkinen 1999), have shown that daylength plays a role in the timing of bud burst. Linkosalo (2000) tested the two models described here with seven phenological time series of bud burst and flowering of boreal trees and concluded that the light-climate-triggered model estimated phenological timing better than the chilling-triggered model for each of the phenological time series. Although none of these studies indicate what the signal from the light climate might be, or what mechanism the plants utilize to detect it, the results strongly suggest that light climate should be taken into account in models predicting phenological timing in the boreal zone.

For the unmodified temperature conditions (for the period 1883–1981), the chilling-triggered model estimated dorm-

ancy release to occur on average at the end of November, although the variation between years was large. This agrees well with the empirical results of Sarvas (1974), Heide (1993b) and Leinonen (1996a). According to this model, ontogenetic development is possible during warm spells at any time following dormancy release (Figure 3). Such warm spells are rare under current climate conditions, but it is likely that they would become more frequent if climatic warming proceeds, causing bud burst to occur earlier than at present, hence possibly exposing the newly unfolded leaves to frost damage (Hänninen 1991). According to the light-climate-triggered model, ontogenetic development is hindered until spring, and thus the trees do not react to warm spells during the winter months. This explains why the estimates of frost damage risk with simulated climate change differed so radically between the two models tested.

In our simulations, only the magnitude of temperature was changed; the diurnal variation was not. However, there is evidence that the diurnal temperature range (DTR = difference between maximum and minimum daily air temperature), a measure closely correlated to the range displayed in Figure 8,

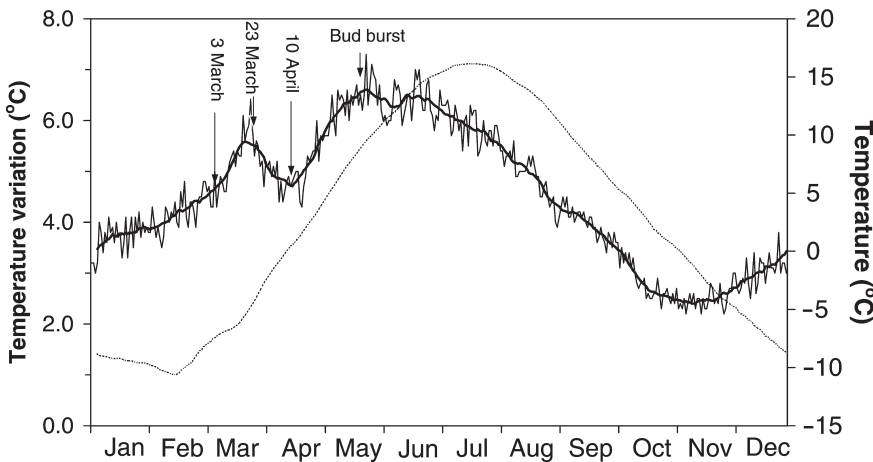


Figure 8. Mean daily temperature variation (afternoon observation minus daily minimum) and mean daily average temperature (1883–1981) as a function of date. The thin solid line shows daily observations of the temperature variation, the thick solid line indicates the 14-day moving average, and the dotted line indicates the 14-day moving average of daily average temperature. The rightmost arrow indicates the mean date of bud burst; the other arrows show the three threshold dates of ontogenetic development, t_{crit} , according to the light-climate-triggered model.

has been decreasing in recent decades at sites in the Nordic region (Heino 1994, Kaas and Frich 1995) and in many other parts of the world (Karl et al. 1991). Furthermore, a reduction in the DTR with climate warming is also projected by most climate models (IPCC 1996). Clearly, such changes in DTR could have a major effect on spring phenology and frost damage risk of boreal plants.

The threshold temperature for damage in newly unfolded leaves of *Betula* is not well established. In a study of historical frost damage to *Betula alleghaniensis* Britton in Canada and associated laboratory tests, Braathe (1995, 1996) inferred a threshold air temperature of around -5°C . The same temperature was used in this study. Observations of minimum temperatures at Jyväskylä after the recorded bud burst dates during the periods 1896–1911 and 1917–1955 indicate that the minimum temperature never fell below -5°C , the absolute minimum being -4.1°C . This, together with the observation that extensive spring frost damage of birch seldom occurs in Finland, offers some substantiation for the -5°C threshold adopted here.

The divergent estimates of bud burst and frost damage risk in response to warming climate from the two phenological models demonstrate that our current knowledge of spring phenology is not a sufficient basis for reliable forecasts. Aside from mechanisms omitted or poorly represented in the models, acclimation and adaptation of plants may greatly reduce the potentially harmful effects of climatic warming. Experiments with exotic species, and their successful introduction to foreign growing sites, demonstrates the great acclimation capacity of many perennial plants for survival under climatic conditions that vary considerably from year to year. An improved understanding and experimental testing of the climatic factors and biochemical mechanisms that may be involved and of their many interactions are required as a basis for developing robust models that are amenable to extrapolation.

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Appendix

The data combination procedure

The combination algorithm is presented as a flow chart of the algorithm in Figure A1. First, mean deviations of each observation series, c_j , were initialized to zero (A), thus the initial adjusted observations, x'_{ij} , were equal to original observations, x_{ij} (C). The values of the combined time series, t_i , were calculated as an annual mean of adjusted observations (D), and the fit of the adjusted observation series to the combined time series was estimated by calculating the sum of squared deviations of the two (E). A Hooke-Jeeves minimizing algorithm (Hooke and Jeeves 1961) was used to choose a new set of mean deviations, c_j (B). The process of choosing mean deviations, adjust-

ing the observations and calculating the combined time series was repeated until a set of mean deviations c_j that minimizes the squared deviation was found. The mean deviation was added to each observation, and the combined time series was calculated as the annual means of the adjusted observations.

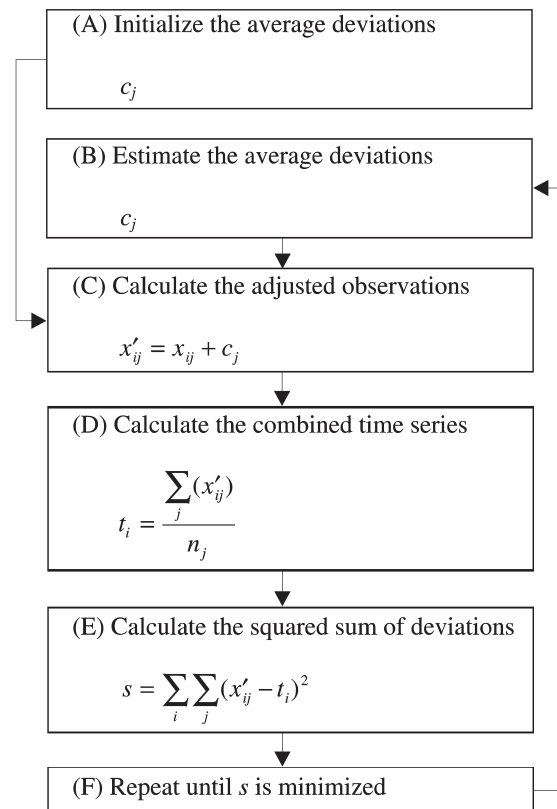


Figure A1. Flowchart illustrating the combination algorithm.