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Bud burst timing in *Picea abies* seedlings as affected by temperature during dormancy induction and mild spells during chilling

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Summary In trees adapted to cold climates, conditions during autumn and winter may influence the subsequent timing of bud burst and hence tree survival during early spring frosts. We tested the effects of two temperatures during dormancy induction and mild spells (MS) during chilling on the timing of bud burst in three *Picea abies* (L.) Karst. provenances (58–66° N). One-year-old seedlings were induced to become dormant at temperatures of 12 or 21 °C applied during 9 weeks of short days (12-h photoperiod). The seedlings were then moved to cold storage and given either continuous chilling at 0.7 °C (control), or chilling interrupted by one 14-day MS at either 8 or 12 °C. Interruptions with MS were staggered throughout the 175-day chilling period, resulting in 10 MS differing in date of onset. Subsets of seedlings were moved to forcing conditions (12-h photoperiod, 12 °C) throughout the chilling period, to assess dormancy status at different timings of the MS treatment. Finally, after 175 days of chilling, timing of bud burst was assessed in a 24-h photoperiod at 12 °C (control and MS-treated seedlings). The MS treatment did not significantly affect days to bud burst when given early (after 7–35 chilling days). When MS was given after 49 chilling days or later, the seedlings burst bud earlier than the controls, and the difference increased with increasing length of the chilling period given before the MS. The 12 °C MS treatment was more effective than the 8 °C MS treatment, and the difference remained constant after the seedlings had received 66 or more chilling days before the MS treatment was applied. In all provenances, a constant temperature of 21 °C during dormancy induction resulted in more dormant seedlings (delayed bud burst) than a constant temperature of 12 °C, but this did not delay the response to the MS treatment.

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Introduction

For trees growing in cold climates, optimal synchronization of the onset and release of dormancy with the prevailing climate is crucial to avoid frost damage. In *Picea abies* (L.) Karst., the onset of dormancy is largely determined by night length (Dormling et al. 1968, Heide 1974*a*). However, a deepening of dormancy with increasing temperature during dormancy induction has been documented by Heide (1974*b*) and Søgaard et al. (2008), and this has also been reported for other species, for example, *Acer platanoides* L. (Westergaard and Eriksen 1997), *Alnus glutinosa* (L.) Moench. (Heide 2003), *Betula pendula* Roth. and *Betula pubescens* Ehrh. (Heide 2003, Junttila et al. 2003). In *P. abies*, the dormancy induction temperature had a greater effect on the seedlings of southern provenances than on the seedlings of northern provenances (Søgaard et al. 2008). After dormancy induction, bud burst occurs in response to chilling and accumulation of thermal time above a genotype-specific threshold (Nienstaedt 1967, Worrall and Mergen 1967, Hänninen 1990, Hannerz 1999). At least at the seedling stage, however, *P. abies* does not have an absolute chilling requirement to respond to forcing temperatures, provided the forcing takes place in long days (Nienstaedt 1967, Worrall and Mergen 1967, Søgaard et al. 2008). An exception to this was noted in buds that had matured at a high constant temperature (25 °C) (Dormling et al. 1968).

In several studies on boreal trees, models based on the thermal time accumulated from a fixed date in late winter or early spring provided better estimates of bud burst timing than estimates obtained with more comprehensive chilling-based models (Häkkinen et al. 1998, Hannerz 1999,

Linkosalo et al. 2000, Leinonen and Kramer 2002, Hänninen et al. 2007). Thus, a single or several growth-restraining factors seem to be unaccounted for in these models. The poorer performance of the chilling-based models compared with the thermal time models suggests that they overestimate the forcing effect of early high temperature events (mild spells, MS) occurring in late autumn or early to midwinter (Schaber and Badeck 2003, Linkosalo et al. 2006). This could be related to photoperiod or light quality (Partanen et al. 1998, Linkosalo and Lechowicz 2006). The lower accuracy of the chilling-based models may also be related to an inadequate description of the effect of air temperature during quiescence (Linkosalo et al. 2006). Few studies have explored the form of temperature response, although there is some evidence that it depends on the state of chilling (Campbell and Sugano 1975, van den Driessche 1975, Hänninen 1990). In view of the predicted global warming (Meehl et al. 2007), knowledge about the response of bud burst to spells of elevated air temperature during dormancy is a prerequisite for reliable predictions of the frost damage risk (Hänninen 2006).

We studied the effects of several temperatures during dormancy induction and chilling on time to bud burst in *P. abies* seedlings. Our hypotheses were: (1) that a high temperature during dormancy induction increases the amount of chilling needed to achieve bud burst within a given time under forcing conditions, and (2) that, with an increasing accumulation of chilling days before the MS event, an MS during chilling increasingly hastens the timing of bud burst in spring. Three provenances were studied to explore whether the responses differed among seed sources of different latitudinal origin.

Materials and methods

Seedling material and initial growing conditions

Seeds of three Norwegian *P. abies* provenances (Table 1) were sown in a 7:3 (v/v) mix of peat:perlite on May 27, 2005 in a daylight phytotron (18 °C, vapor pressure deficit 0.53 kPa) at Ås, Norway (59°40′ N and 10°51′ E). Additional light (129 ± 8 μmol m^{-2} s^{-1}) was provided by high-pressure mercury lamps (Osram Powerstar HQI-T 250 W/D, Osram GmbH, Munich, Germany) to extend the photoperiod to 24 h and to supplement the natural daylight. On June 15–17, the seedlings were transplanted to 12-cm pots (0.8 L), with two seedlings of each provenance per pot. The pots were randomly distributed among six replicates. During germination, all seedlings were watered daily with tap water. Thereafter, the seedlings were watered four times per week; once with tap water and three times with a complete nutrient solution (0.5‰ Red Superba (Yara) and 0.5‰ $(NH_4)_2SO_4$).

Table 1. Origin of the Norwegian provenances used in this study. All provenances were from an altitude of 0–149 m asl.

Provenance	Seed collection area	Latitude (N)	Longitude (E)
Northern (P)	Rana	66°25′	14°30′
Eastern (BV)	Østre Toten	60°35′	11°00′
Southern (F)	Arendal/Tvedestrand	58°35′	8°50′

Dormancy induction

Two and a half months after sowing (August 8), the seedlings were moved to growth chambers for dormancy induction treatment (DT) comprising a 12-h photoperiod at 145 ± 12 μmol m^{-2} s^{-1} and a constant temperature of either 12 or 21 °C. The light source and vapor pressure deficit were the same as in the daylight phytotron. The DT was terminated after 9 weeks (October 10), when the seedlings were moved to dark cold storage at a chilling temperature of 0.7 ± 0.7 °C.

Simulated MS and forcing treatments

The various treatments applied after termination of the DT (hereafter referred to as Day 0 of the experiment) are shown in Figure 1. During the period from Day 7 to Day 154, subsets of pots from each DT temperature were transferred from cold storage to growth chambers for a 14-day MS treatment at a constant temperature of 8 or 12 °C in a 12-h photoperiod at 180–190 μmol m^2 s^{-1} (Osram Powerstar HQI-BT 400 W/D). After the 14-day MS exposure, the potted seedlings were returned to cold storage. On Day 175 (April 3), six pots (one from each replicate) for each combination of DT, starting the day of MS treatment and MS temperature, were transferred to forcing conditions (a 12 °C constant temperature and a 24-h photoperiod). Seedlings kept continuously in cold storage for 175 days were used as controls, with one pot per replicate and DT temperature.

To assess the change in dormancy status in response to chilling, additional seedlings that had not been subjected to an MS treatment were transferred to forcing conditions comprising a 12-h photoperiod and 12 °C constant temperature (Figure 1). These transfers took place on Day 0 (no chilling) and at the onset of each MS period, with one pot per replicate for each combination of DT temperature and chilling duration.

During forcing in both the continuous light and the 12-h photoperiod, the light source, the light intensity and the vapor pressure deficit were the same as during the DT treatment. The seedlings were watered every second day during the MS treatment and up to twice in total during cold storage.

Phenological registrations

Terminal bud set was recorded three times per week on all seedlings in four pots from each replicate and DT temperature (12 and 21 °C). The recordings continued until all seedlings had formed a tiny white bud, corresponding to Stage 1 in the scheme presented by Johnsen (1989).

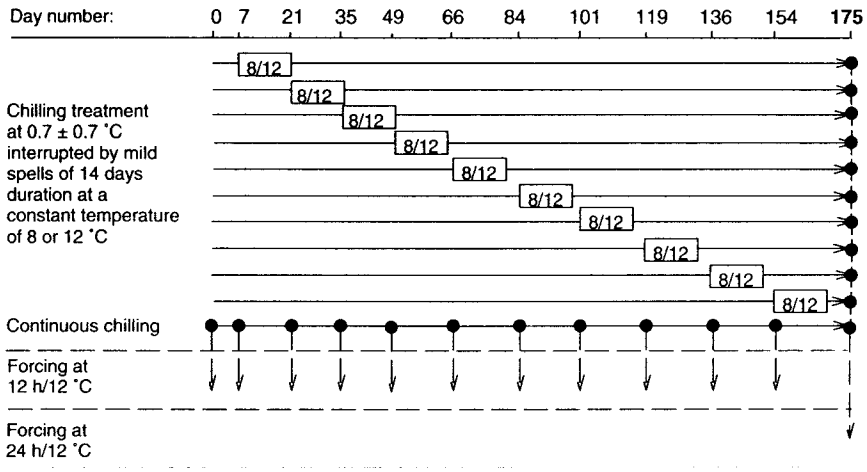

Figure 1. Schematic representation of the chilling, MS and forcing treatments that followed the dormancy induction period (9 weeks in a 12-h photoperiod at a constant temperature of 12 or 21 °C). Solid horizontal lines indicate chilling in cold storage, and the MS treatments are illustrated by boxes. Seedlings were transferred from cold storage to forcing conditions on the days marked with black dots.

The progress of bud burst was recorded at the end of each MS period, and three times per week during forcing. The following scale, modified from Krutzsch (1973), was used: (1) dormant, (2) marked swelling and gray-green bud color, (3) needle tips emerging through bud scales and (4) elongation of needles to about double bud length. A seedling was considered to have burst bud on reaching Stage 3. The bud burst recordings were terminated after 140 days. When forced in a 12-h photoperiod, bud burst did not occur in all seedlings within the 140-day period, and some seedlings failed to elongate after bud burst. A final record of whether bud burst and further shoot elongation had occurred was conducted on the seedlings that burst bud after forcing in a 12-h photoperiod.

Statistical analyses

In the analysis of variance (ANOVA) on days to bud set, a split-plot model was applied in the GLM procedure of SAS Version 9.1 (SAS Institute, Cary, NC), with DT temperature as main plot factor and provenance as subplot factor. To analyze days to bud burst (DBB) in seedlings forced in a 12-h photoperiod after continuous chilling, a three-factor model with DT temperature (main plot), chilling duration (subplot) and provenance (sub-subplot) was used. In the analysis of DBB in seedlings transferred to forcing conditions in a 24-h photoperiod on Day 175, DT temperature and provenance were the main plot and sub-subplot factors, respectively. The subplot factor, which is also referred to as dormancy release treatment (DR), included 21 treatments (two MS temperatures for each of 10 starting days plus continuous chilling). Following all ANOVA, the different treatments were compared by their least square means (lsmeans statement in SAS), provided the F test was significant. This choice was made because of unbalanced data, caused by rejection of a few damaged seedlings. A significance level of $\alpha = 0.05$ was used.

Some seedlings forced in the 12-h photoperiod following little or no chilling failed to burst bud within 140 days. These seedlings were assigned a DBB value of 150 to allow meaningful statistical treatment of the data. The bud burst data for these seedlings were not normally distributed, however, and this could not be corrected by data transformation. An additional analysis was therefore run with the nonparametric Kruskal–Wallis test (NPAR1WAY procedure in SAS). There were only small deviations in the P values with the different methods. Based on the assumption that the ANOVA requirements were satisfied when both procedures gave similar results (Montgomery 2001), we have chosen to refer only to the parametric ANOVA.

During the late MS periods, several seedlings burst bud, but they did not develop beyond Stage 3 within the 14-day treatment period. The LOGISTIC procedure in SAS was used to test for the significance of the different experimental factors and associated two-way interactions on the probability of individual seedlings reaching bud burst Stage 3 during the 14-day MS. The same procedure was also used to assess the effects of treatments and provenances on the probability of seedlings resuming growth when forced in a 12-h photoperiod after different durations of continuous chilling.

Results

Bud set

The 21 °C DT reduced time to bud set compared with the 12 °C DT (19.1 versus 24.0 days; $P = 0.0008$ for means averaged across provenances). Although time to bud set increased with decreasing latitude of seed origin ($P = 0.0001$), the difference between the most northern (P) and southern (F) provenances was < 2 days. The effect of DT temperature was consistent among provenances because no significant interaction occurred ($P = 0.517$).

Changes in dormancy status in response to chilling and DT

After 21 or more chilling days, all seedlings burst bud and started elongation growth when transferred to forcing in a 12-h photoperiod (Table 2). With only 0 or 7 days of

Table 2. Effect of temperature during dormancy induction and duration of continuous chilling at 0.7 °C in darkness on the phenological status of the terminal bud after 140 days of forcing at 12 °C in a 12-h photoperiod. The results for seedlings chilled for 21 days or longer were pooled (21 + days), because all seedlings kept in cold storage for 21 days or more burst bud and started shoot elongation under forcing conditions.

Dormancy induction temperature (°C)	Chilling duration (days)	Bud scales not opened (% of seedlings)	Bud scales open and terminal shoot not extended (% of seedlings)	Bud scales open and terminal shoot extended (% of seedlings)
12	0	36	36	28
	7	11	23	66
	21 +	0	0	100
21	0	53	28	19
	7	28	53	19
	21 +	0	0	100

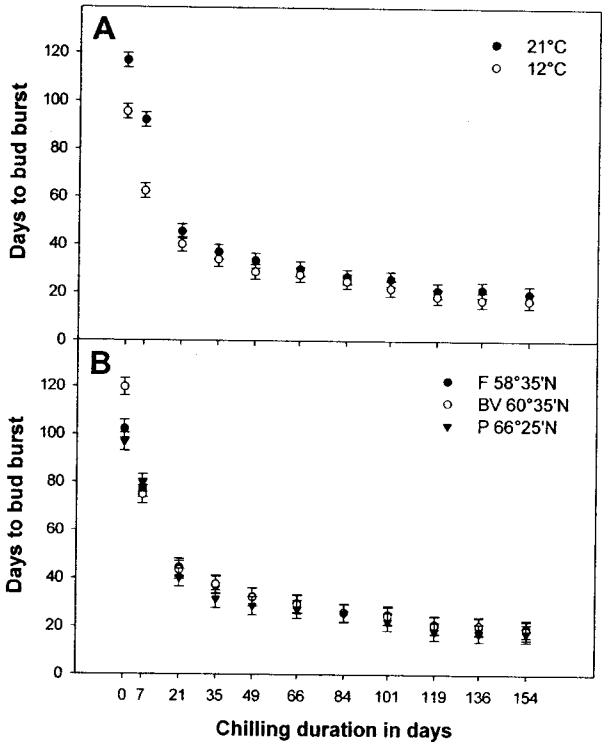

Figure 2. Effects of (A) temperature during dormancy induction and (B) provenance on DBB after transfer to forcing conditions in a 12-h photoperiod after different durations of continuous chilling. Bars = standard error.

chilling, only a fraction of the seedlings burst bud, and in several individuals further shoot extension did not occur. The higher DT temperature (21 °C) reduced the percentage of seedlings that burst bud after 0 and 7 days of chilling ($P = 0.0150$), and provenance had no significant effect ($P > 0.10$).

Days to bud burst declined with increasing duration of continuous chilling ($P < 0.0001$), to a minimum of 18 days after 154 chilling days (mean of both DT temperatures). The higher DT temperature (21 °C) delayed bud burst (Figure 2A, $P = 0.0005$). Chilling rapidly diminished this effect, causing a significant interaction between DT temperature and chilling duration ($P < 0.0001$). An effect of DT temperature was, however, evident even after 154 chilling days (separate analysis on seedlings transferred to forcing conditions on Day 154, $P = 0.0114$). The northern (P) provenance burst bud slightly earlier than the other provenances (Figure 2B, $P = 0.0002$).

Effects of MS during chilling

With the onset of MS treatment on Day 66 or later, some seedlings started to swell or burst their buds during the 14-day MS period (Table 3). The probability of a seedling reaching bud burst Stage 3 was higher with the 12 °C MS temperature than with the 8 °C MS temperature ($P < 0.0001$), whereas the higher (21 °C) DT temperature had the opposite effect ($P = 0.0004$). The probability of a seedling reaching bud burst Stage 3 increased with increasing chilling time before the MS ($P < 0.0001$). The northern (P) seedlings had a higher probability of reaching Stage 3 than the southern (F) seedlings ($P = 0.0225$), whereas the eastern (BV) seedlings did not differ significantly from the other seed sources. Interactions did not influence the probability of bud burst during the MS period ($P > 0.10$).

Days to bud burst following transfer to forcing conditions in continuous light on Day 175 was influenced by all the main experimental factors (Table 4). For seedlings given MS at 12 °C, a significant reduction in DBB, compared with continuous chilling, occurred with the onset of MS from Day 49 onward (Figure 3). When the seedlings were given MS at 8 °C, the difference became significant from Day 84. The difference in DBB between the seedlings given an MS treatment and the control seedlings increased with increasing chilling time before the MS treatment. When the MS treatment was given after 66 chilling days the difference in DBB between the 8 and 12 °C MS treatments remained almost constant, with a mean difference of 3 days.

The higher (21 °C) DT temperature delayed bud burst by 2.6 days on average. The response to the different DRs was independent of both DT temperature and provenance, as indicated by the absence of any significant interactions

Table 3. Terminal bud development on completion of the 14-day MS treatment, as affected by temperature during dormancy induction (DT: 12 or 21 °C), starting day and temperature (MS: 8 or 12 °C) of the MS and provenance (F, BV, P). Part (A) of the table gives the proportion of seedlings (%) in which the bud scales had opened (Stage 3). Part (B) of the table gives the proportions of seedlings that reached at least Stage 2 (i.e., sum of seedlings in Stage 2 or 3).

Start of MS treatment	DT 12 °C						DT 21 °C					
	MS 8 °C			MS 12 °C			MS 8 °C			MS 12 °C		
	F	BV	P	F	BV	P	F	BV	P	F	BV	P
(A) Seedlings with terminal bud in Stage 3 (%)												
Day 66	0	0	0	0	9	0	0	0	0	0	0	0
Day 84	0	0	8	0	0	17	0	0	0	0	0	8
Day 101	0	0	8	0	0	17	0	0	0	0	0	8
Day 119	0	0	0	0	17	42	0	0	0	0	0	0
Day 136	0	0	0	9	0	9	0	0	0	0	0	8
Day 154	0	0	0	17	25	33	0	0	0	0	0	17
(B) Seedlings with terminal bud in Stage 2 or 3 (%)												
Day 66	0	0	0	17	27	25	0	0	0	0	0	0
Day 84	0	0	8	50	25	25	0	0	0	0	9	17
Day 101	0	8	17	42	33	50	0	0	0	0	8	25
Day 119	8	8	8	83	83	100	0	0	0	17	33	25
Day 136	8	25	33	91	67	64	0	0	8	33	42	75
Day 154	17	33	58	100	100	100	0	17	33	83	75	67

Table 4. Summary of split-plot ANOVA on DBB following transfer to final forcing conditions on Day 175. The DRs included a control with seedlings given 175 days of continuous chilling at 0.7 °C in darkness and the MS treatment (14 days at 8 or 12 °C, 12-h photoperiod) that was given once, but at different starting dates, during the 175-day chilling period.

Source	df	*F*	*P*
Replication	5	12.57	0.0074
Dormancy induction treatment (DT)	1	737.37	<0.0001
Error A[1]	5		
Dormancy release treatment (DR)	20	86.91	<0.0001
DT × DR	20	1.32	0.1700
Error B[2]	200		
Provenance (PROV)	2	75.38	<0.0001
DT × PROV	2	2.14	0.1183
DR × PROV	40	1.15	0.2394
DT × DR × PROV	40	0.84	0.7561
Error C[3]	1159		

[1] Replication × DT; denominator for the *F* test on effects of replication and DT.
[2] DT (DR × Replication); denominator for the *F* test on effects of DR and the DT × DR interaction.
[3] Residual error; denominator for the *F* test on effects of PROV and all interactions involving PROV.

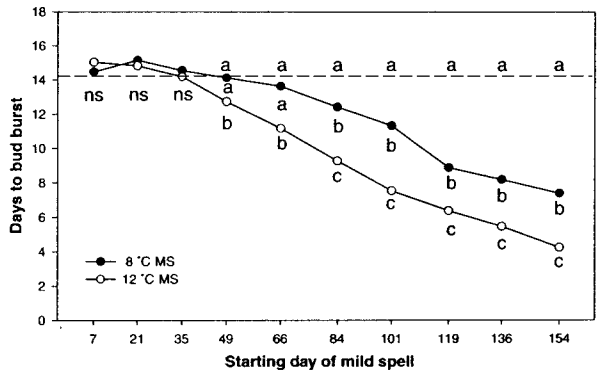

Figure 3. Days to bud burst after transfer to final forcing in continuous light on Day 175 for seedlings given a 14-day MS treatment (8 or 12 °C) at various times during the 175-day chilling period. The value for continuously chilled seedlings is shown by the dotted line. Values shown (lsmeans) were pooled across dormancy induction temperatures and provenances. Different letters within starting days of the MS indicate significant differences among seedlings receiving either the continuous chilling or the 8 or 12 °C MS treatment (ns, no significant difference).

(Table 4). Bud burst occurred earliest in the most northern (P) provenance, whereas the difference between the other two provenances was not significant. The effect of provenance on DBB was < 2 days and thus modest compared with the effects of the other treatments.

Discussion

An increase in air temperature during autumn and winter may result in severe damage to forest trees if this changes the annual growth cycle such that spring frost episodes coincide with the sensitive phase of bud burst (Sakai and Larcher 1987). A detailed understanding of the response of bud burst to periods of elevated temperature during dormancy is therefore crucial for assessing the risks of frost damage (Hänninen 2006).

Effects of temperature treatments during dormancy induction

The chilling requirement for bud burst and subsequent shoot elongation was maximally 21 days in all of our study

seedlings (Table 2). This finding corroborates other studies showing that *P. abies* seedlings have a short chilling requirement even when forced in short days (Nienstaedt 1967, Worrall and Mergen 1967), with little variation among provenances (Hannerz et al. 2003). However, in contrast to the above-mentioned studies, several unchilled seedlings burst bud in our study. This could be associated with the use of a low (12 °C) forcing temperature, because 12 °C might have a slight chilling effect (Hänninen and Pelkonen 1988). A chilling effect of our lower (12 °C) dormancy-induction temperature may also explain why this temperature treatment increased the percentage of seedlings commencing growth following no or a very short chilling.

The effects of our treatments on time to bud burst were similar to those observed by Søgaard et al. (2008), who observed a gradual delay in bud burst in *P. abies* seedlings when the dormancy induction temperature was increased from 9 to 21 °C (in increments of 3 °C). In contrast to our results, they also reported an increasing effect of dormancy induction temperature with decreasing latitude of seed origin; however, this was observed only when forcing the seedlings in a 24-h photoperiod, and the differences were greatly diminished after a 10-week chilling period. We used either a short photoperiod when forcing the seedlings, or a considerably longer chilling time, which may explain why the temperature response did not differ significantly between provenances.

The effect of dormancy induction temperature diminished with increasing chilling duration. An effect was, however, still apparent after as much as 154 and 175 days of chilling, followed by forcing in 12 h and continuous light, respectively. This supports the notion that the effect of dormancy induction temperature may also be significant under natural conditions, as shown for *B. pendula* (Heide 2003). A difference in timing of bud burst has also been observed when comparing seedlings given a short-day treatment in nurseries with seedlings forming terminal buds under natural conditions, with bud burst occurring earlier in the short-day-treated seedlings (Heide 1974*b*, Sandvik 1980), thus making them more susceptible to spring frost damage. Our results indicate that exposure to high temperature during or after short-day treatment may counteract the promoting effect of short days on DBB.

Effects of MS during chilling

The effect of a 14-day warm period during chilling on DBB depended jointly on the timing and the temperature of the MS treatment. With the onset of the MS treatment on Day 49 of chilling or later, bud burst was hastened and the effect increased with increasing length of the chilling period before the MS. From Day 66 onward, bud burst occurred about 3 days earlier following the 12 °C MS compared with the 8 °C MS (Figure 3). Our results do therefore not invalidate a simple dependency of accumulated high temperature on timing of bud burst. However, because both MS treatments became gradually more effective with increasing chilling time before the onset of the MS, there was also an increasing relative effect of the 8 °C MS treatment compared with that of the 12 °C MS treatment (cf. Figure 3). This pattern closely agrees with the conceptual model of post rest formulated by Vegis (1964), who interpreted the effect of chilling as a widening of the temperature range over which the buds can grow as dormancy is gradually released. An increasing relative effect of low forcing temperatures in response to accumulated chilling has been reported for *Pseudotsuga menziesii* (Mirb.) Franco seedlings (Campbell and Sugano 1975, van den Driessche 1975). A chilling-dependent response to different forcing temperatures was implemented in a synthesis model of bud burst by Hänninen (1990). When tested on a hypothetical dataset, this approach generated realistic predictions, including both the dormancy release ratio (per cent of seedlings commencing growth) and the exponentially declining curve of DBB versus chilling duration that has been observed in many experiments (e.g., Murray et al. 1989, Heide 1993, Myking and Heide 1995, Leinonen 1996).

In conclusion, a 14-day period of elevated temperature and short photoperiod had no effect on DBB when given after a short period of chilling, indicating a security mechanism preventing resumption of growth when temperatures conducive to growth occur in fall and winter. Later on, the effect on timing of bud burst gradually increased with increasing chilling time received before the MS treatment. Even after prolonged chilling, seedlings were more dormant when the buds had matured at 21 °C than at 12 °C. This response modified the timing of bud burst similarly in all provenances studied, and independently of the DRs applied during chilling. Thus, although the onset of mild temperatures in spring is the main driving force for bud burst, the timing can be significantly modified by the temperature conditions during bud set and bud maturation. Considering that thermoperiodic responses may be involved in the phase of terminal bud formation in *P. abies* (Fløistad and Patil 2002), it remains to be resolved whether the effect of dormancy induction temperature is solely a temperature sum response. The relevance of this effect under natural conditions and in adult trees also needs to be determined.

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