Effects of thermal model and base temperature on estimates of thermal time to bud break in white spruce seedlings

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Abstract: To improve the predictability of bud burst and growth of boreal trees under varying climate, the thermal time for bud break in white spruce (*Picea glauca* (Moench) Voss) seedlings was evaluated under a range of temperature conditions in controlled environment chambers. Thermal time requirements were calculated as the sum of growing degree days or growing degree hours above base temperatures ranging from –1 to 5 °C. The results indicated that the common modeling approach, which uses a high base temperature of 5 °C and growing degree days, may not be appropriate for future climatic conditions. Estimates of thermal time requirements using a base temperature of 5 °C varied considerably among temperature treatments and thus would reduce the predictability of bud burst under changing climate. In contrast, estimates of thermal time requirements with lower temperatures closer to 1 °C were relatively consistent among treatments. Growing degree hour models were less sensitive to base temperature than degree day models. These results should help in the selection of appropriate base temperatures and thermal time models in quantification of thermal time for bud burst modeling in other boreal trees.

Résumé : Dans le but d'améliorer la prévisibilité du débourrement et de la croissance des arbres en milieu boréal sous diverses conditions climatiques, le temps thermique nécessaire au débourrement chez l'épinette blanche (*Picea glauca* (Moench) Voss) a été évalué dans différentes conditions de température dans des chambres à environnement contrôlé. Le temps thermique requis a été calculé par le cumul des degrés-jours de croissance ou degrés-heures de croissance au-dessus de températures de base allant de –1 à 5 °C. Les résultats indiquent que l'approche commune de modélisation qui utilise une température de base élevée de 5 °C et les degrés-jours de croissance n'est peut-être pas appropriée pour les conditions climatiques futures. Les estimations du temps thermique requis en utilisant une température de base de 5 °C varient considérablement parmi les traitements de température et, par conséquent, réduiraient la prévisibilité du débourrement sous un climat qui est en train de changer. Par contre, les estimations du temps thermique requis avec des températures de base plus près de 1 °C étaient relativement consistantes parmi les traitements. Les modèles qui utilisent les degrés-heures de croissance étaient moins sensibles à la température de base que ceux qui utilisent les degrés-jours. Ces résultats devraient aider à choisir les températures de base et les modèles de temps thermique appropriés pour quantifier le temps thermique et modéliser le débourrement chez d'autres espèces boréales d'arbre.

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Introduction

The annual cycle of growth and dormancy in temperate and boreal trees is controlled by seasonal changes of the environment (Saxe et al. 2001). Termination of tree growth in late summer is thought to be induced by shortening photoperiod, while a period of chilling temperatures (–4 to 5 °C) during the subsequent fall and winter is required for buds to break dormancy (Kramer 1994; Saxe et al. 2001). Once chilling requirements are met, trees are ready to resume growth, beginning with bud burst, which occurs following a species-specific accumulation of thermal time above a base temperature (Fuchigami et al. 1982; Hänninen 1995; Hannerz 1999; Tanja et al. 2003; Søgaard et al. 2008). In

boreal regions, winter is long and chilling requirements are readily met (Heide 1993; Myking and Heide 1995; Colombo 1998; Hannerz et al. 2003; Linkosalo et al. 2006), and the start of growth therefore depends largely on the critical cumulative thermal time in the spring. The increase of temperatures with climate change will therefore affect bud burst and growth through different timing of bud break and duration of growing season

The time required for bud burst to occur decreases with increasing temperatures, following a sigmoidal response pattern between the minimum base temperature of 0 °C and a maximum at about 35 °C (Hänninen 1990; Kramer 1994). Within the dominant range of temperatures for bud burst in spring (between 10 and 25 °C), the relationship can be approximated using a linear model (Bloomberg 1978). Thus, the thermal time required for bud burst is often expressed as the sum of degree days or degree hours above a base temperature (Cannell and Smith 1983; Hannerz 1999; Bailey and Harrington 2006). The degree day model is used more commonly than the degree hour model mostly because hourly temperature data are often unavailable and bud burst data are collected over a fairly long time interval. However,

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these two models are rarely compared under different temperature regimes in the same study.

Determining species-specific thermal time requirements involves selecting base temperatures and temperature conditions under which bud burst data will be collected. Among possible base temperatures, 5 °C is most commonly used to determine the cumulative thermal time required for bud burst in studying the bud burst phenology of trees (O'Reilly and Parker 1982; Cannell and Smith 1983; Murray et al. 1989; Hunter and Lechowicz 1992; Beuker 1994; Colombo 1998; Bailey and Harrington 2006). However, base temperatures above and below 5 °C have also been used in some studies (Blum 1988; Kramer 1994; Karlsson et al. 2003; Rousi and Pusenius 2005). Where the temperature regimes under which the bud burst data are collected are similar to those affecting the bud burst to be predicted, the choice of base temperature may not matter. Chances are, however, that temperature regimes in different years and at different locations vary considerably, especially under expected climate change scenarios. The use of high base temperatures systematically underestimates thermal time requirements at low temperatures (Heide 1993; Myking 1997) and, therefore, could significantly affect the accuracy in predicting bud burst time under different or warmer temperature regimes. The evaluation of appropriate base temperatures for estimating thermal time requirements has received little attention in the published literature.

Natural fluctuating temperatures may be more conducive to bud burst than constant temperatures (Campbell and Sugano 1975; Garber 1983; Murray et al. 1989; Hänninen 1990). For example, Murray et al. (1989) found that for a number of tree species, a continuous 15–20 °C in a glasshouse provided bud burst times that were equivalent to those resulting from a mean daily outside temperature of 12.5 °C. However, Heide (1993) and Myking (1997) indicated that thermal time requirements of northern deciduous trees were not affected by temperature conditions as long as appropriate base temperatures were used. It is not known whether this also applies to trees in boreal Canada.

Bailey and Harrington (2006) suggested that freezing temperatures can change physiological processes and, therefore, delay bud burst of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Under natural conditions, frost tolerance of trees decreases with accumulation of thermal time towards bud burst (Bigras and D'Aoust 1993). The frequency of lethal freezing temperatures occurring in late spring decreases as bud development continues. Even following bud burst when they are actively growing, most boreal conifers can tolerate a short period of freezing temperatures of –3 to –5 °C without serious tissue damage (Glerum 1973; Bigras and Hébert 1996). It is not known whether conditions at or above –3 °C affect the timing or duration of bud burst in boreal tree species.

The general objective of this study was to determine the thermal time requirements for boreal conifers to break bud and to assess the effects of temperature regimes on estimates of thermal time requirements. The seedlings of white spruce (*Picea glauca* (Moench) Voss), a widely distributed boreal conifer, were used as an example. We were particularly interested in gaining insight into how the selection of base temperatures and thermal time models affected the predict-

ability of bud burst under varying temperature conditions. The lack of such knowledge restricts our effort in modeling bud burst and growth in the current and future climatic conditions and response of forest ecosystems to changing climate.

Materials and methods

White spruce seedlings and temperature regimes

White spruce seed collected from natural forests in Ontario were sown in early April 2008. Seedlings were grown in 3.8 cm × 21 cm SC-10 Super Cell tubes filled with 2:1 commercial peat moss:vermiculite (*v*/*v*) mixture. Greenhouse conditions were maintained at a temperature regime of 26 °C (day)/18 °C (night) and a 16 h photoperiod.

In early September, seedlings were moved to a polyhouse where temperatures and photoperiod followed ambient conditions (3 to 9 °C day, 1 to 8 °C night), except night temperatures were kept above freezing. Seedlings were watered regularly and fertilized with all-purpose 20–8–20 (N–P–K) fertilizer (Plant Products Co. Ltd., Brampton, Ontario) at 100 ppm N to maximize growth. In early September, fertilization rates were increased to 20–20–20 at 50 ppm N to promote seedling hardiness until mid-September when fertilization was stopped but watering continued as needed.

After the first growing season, the container seedlings were wrapped in plastic bags, boxed, and stored at –3 °C in darkness for one month (mid-December to mid-January). For the next month (mid-January to mid-February), seedlings were stored at 2 °C in darkness to continue the chilling treatment.

On February 17, seedlings were moved from cold storage to computer-controlled growth chambers and (or) growth rooms to break bud under six temperature treatments (Table 1). Treatments 1, 3, and 6 represented low, medium, and high temperature conditions common during conifer bud development in the boreal forest. Treatments 2 and 5 were chosen to examine the influence of increasing seasonal temperatures and periodic warming on bud development. Treatment 4 was used to assess the effect of periodic freezing on bud development.

A completely randomized experimental design was used, with each growth chamber as an experimental unit, i.e., temperature treatment. Each growth chamber held 121–137 seedlings and the study was repeated twice. A total of 10 computer-controlled growth chambers and two growth rooms were used. The timing of bud burst of the terminal bud was recorded for individual seedlings, at 1000 and 1500 hours daily, until all seedlings had broken bud in about 8 weeks. Following Murray et al. (1989) and Bigras and Hébert (1996), buds with broken scales and visible green foliage were considered burst. A total of 17 seedlings were dropped because of damaged or dead terminal buds.

Data analysis

The accumulation of thermal time to bud burst for individual seedlings was calculated as the summed product of degree days (Nienstaedt 1974; O'Reilly and Parker 1982; Colombo 1998) or degree hours (Bailey and Harrington 2006) above a base temperature. The base temperatures used were –1, 0, 1, 2, and 5 °C. Thermal time estimates for

Table 1. Temperature treatments used to test thermal time required for white spruce seedlings to break bud in a controlled environment.

Treatment No.	Temperature
1	0 °C (night)/10 °C (day) throughout experiment
2	Started at 0 °C (night)/10 °C (day), with a 3 °C increase in both temperatures every 6 days
3	5 °C (night)/15 °C (day) throughout experiment
4	5 °C (night)/15 °C (day), with a 4 h exposure to –2 °C every 3 days until first bud break
5	5 °C (night)/15 °C (day), interspersed with an 8 h exposure to 20 °C every 3 days until end of experiment
6	10 °C (night)/20 °C (day) throughout experiment

Note: Photoperiod remained constant at 16 h day and 8 h night.

each individual seedling within each treatment (growth chamber) were examined for normality using SAS Proc Mixed and SAS Proc Univariate Procedures (SAS Institute Inc. 2008). The analytical model was

$$Y_{ijk} = \mu + R_i + T_j + e_{ij} + w_{ijk}$$

where Y_{ijk} is the thermal time calculated for the kth seedling within the jth temperature treatment (growth chamber and (or) room) of the ith replication; μ is the grand mean of all thermal time estimates; R_i is the random effect of the ith replication ($i = 1, 2$); T_j is the fixed effect of the jth temperature treatment ($j = 1, 2, \ldots 6$); e_{ij} is the random effect of interaction between the jth temperature treatment (growth chamber) and the ith replication (experimental error); and w_{ijk} is the residual effect, representing the subsampling error within experimental units. No obvious deviation was found for all normal probability plots of the residuals.

For each of the selected base temperatures, differences among means of temperature treatments were used to assess the variation in estimating thermal time requirements for bud burst.

Results

Higher temperatures during bud development reduced the average time to bud break for 1-year-old white spruce seedlings (Fig. 1). The relationship was nearly linear, i.e., the lower the temperature, the longer it took for buds to break.

Seedlings completed bud burst in the same sequence as was found for average time to bud break (Fig. 2), with seedlings in treatment 6 completing bud burst first, followed by treatments 2, 5, 3, 4, and 1, respectively. This sequence generally reflects the temperature treatment gradient (Table 1).

The uniformity of bud burst among individual seedlings within a temperature treatment varied among growing conditions during bud burst (Fig. 2). Seedlings in treatment 2 were the most uniform in the time required to bud break. In treatment 2, bud burst lasted only 11 days, with 95% of the buds breaking within a 5 day period. The duration of bud burst in treatments 3, 4, 5, and 6 was 18–24 days, with 95% of bud burst occurring in a 12 day period. Comparatively, the bud burst in treatment 1 was longer (27 days) and less uniform, with less than 70% of seedlings completing bud burst in a 12 day period.

Estimates of thermal time requirements for seedlings varied considerably among the base temperatures examined

Fig. 1. Days to bud burst (least square means ± SE) relative to mean temperature for white spruce seedlings grown in six temperature treatments (Nos. 1–6 correspond to temperature treatments; see Table 1 for descriptions).
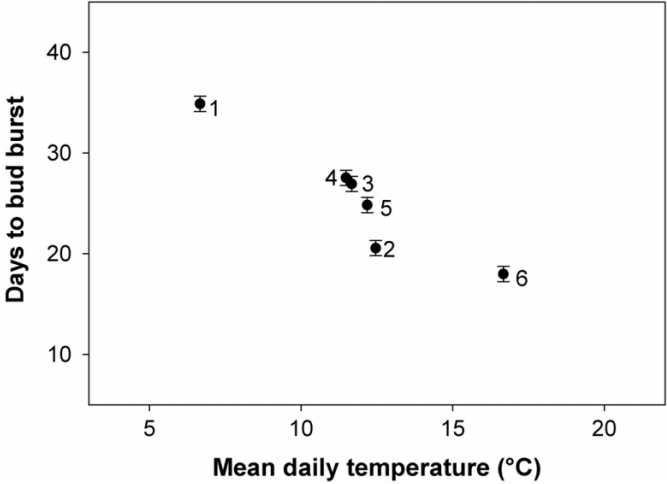
Fig. 2. Percentage of white spruce that broke bud over time by temperature treatment (Nos. 1–6 correspond to temperature treatments; see Table 1 for descriptions).
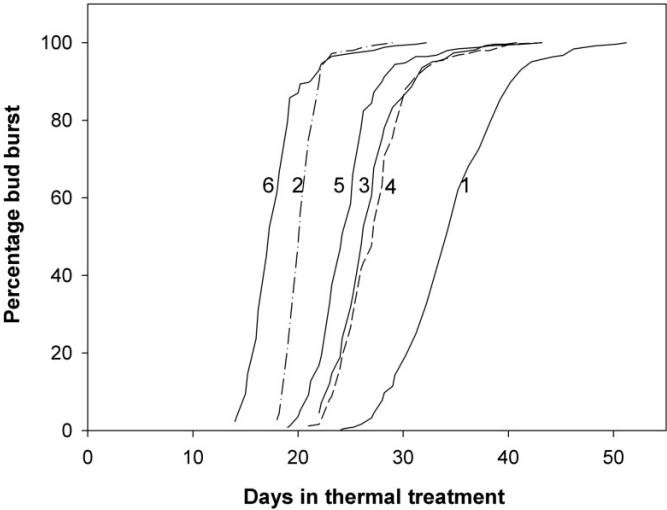
Table 2. Estimates (least square means) and variation of thermal time required for white spruce seedlings to break bud determined as growing degree hours and growing degree days above a range of base temperatures from 0 to 5 °C.

Base temperature (°C)	Temperature regime						Variation
	1	2	3	4	5	6	
Growing degree hours							
−1	6155	5613	8162	8207	7857	7632	327
0	5596	5166	7518	7568	7260	7200	133
1	5036	4720	6875	6929	6664	6769	109
2	4477	4273	6231	6291	6067	6337	80
5	2798	3030	4299	4374	4278	5042	149
Growing degree days							
−1	268	238	315	343	329	321	17
0	233	217	315	315	304	303	6
1	198	197	288	287	279	285	1
2	164	176	261	260	255	266	4
5	59	114	180	177	180	212	18

(Table 2). Higher base temperatures resulted in substantially shorter thermal time requirements for both the growing degree day (GDD) and growing degree hour (GDH) models for all temperature treatments. For example, averaged across the treatments, thermal time estimates resulting from a 5 °C base temperature were 30%–75% shorter than those from a 0 °C base temperature and 25%–70% shorter than those for a 1 °C base temperature (Table 2).

Estimates of thermal time requirements also varied substantially among temperature treatments, but the latter could be categorized into two groups. At base temperatures of 0, 1, and 2 °C, estimates of thermal time requirements for seedlings in treatments 1 and 2 were about 30%–50% shorter than those for seedlings in treatments 3, 4, 5, and 6 (Table 2). Differences among estimates within each group were not significant ($P < 0.05$). However, as base temperature increased to 5 °C differences within groups were significant ($P < 0.05$) — estimates for seedlings in treatment 1 differed from those in treatment 2 for the GDD model, and estimates for seedlings in treatment 6 differed from those in treatments 3, 4, and 5 for both the GDD and GDH models. Similar differences within groups were also found at the lower base temperature of −1 °C.

Among the base temperatures examined, the variation among treatment means in thermal time estimates was smallest at 1 °C for the GDD and at 2 °C for the GDH model (Table 2). The GDD model was more sensitive to changes in base temperature than the GDH model. When used for predicting the date of bud burst, estimates differed by less than a day for base temperatures ranging from 0 to 2 °C, regardless of temperature treatment or thermal time model (Table 3). Differences in predictions of days to bud burst increased with higher or lower base temperature, especially for the GDD model in the lower temperature treatments.

Although statistically insignificant, the thermal time required for bud burst at base temperature 1 °C appeared to be shorter for seedlings in treatment 2 than those in treatment 1, and for those in treatment 5 compared with treatment 3. Periodic exposure to freezing in an otherwise

Table 3. The uncertainty (number of days) in predicting days to bud burst for white spruce grown under three temperature regimes (treatments 1, 3, and 6), two thermal time models (growing degree hour and growing degree day), and a range of base temperatures.

Base temperature (°C)	Temperature regime		
	1	3	6
Growing degree hours			
−1	1.9	1.1	0.8
0	0.8	0.7	0.3
1	0.6	0.6	0.3
2	0.6	0.5	0.2
5	1.9	1.0	0.4
Growing degree days			
−1	2.2	1.3	0.9
0	0.9	0.5	0.3
1	0.3	0.1	0.1
2	0.9	0.4	0.3
5	10.7	2.7	1.5

Note: The night and day time temperatures were, respectively, 0 and 10 °C for treatment 1, 5 and 15 °C for treatment 3, and 10 and 20 °C for treatment 6.

constant temperature treatment (treatment 4) did not cause any obvious delay in seedling bud burst compared with results from the constant temperature (treatment 3).

Discussion

Our results suggest that the appropriate base temperature for assessing thermal time accumulation in white spruce is about 1 °C, which is similar to the findings of Myking (1997) in *Betula pubescens* Ehrh. seedlings using the GDD model. However, the associated uncertainty in the estimates of days to bud burst is relatively small and similar at base temperatures from 0 to 2 °C, regardless of thermal time

models (Table 3). Heide (1993) examined the thermal time response of six deciduous trees by using the GDD model and recommended 0 °C for convenience, even though the optimum base temperatures varied among species.

A base temperature of 5 °C is widely used for white spruce (Nienstaedt 1974; Owens et al. 1977; O'Reilly and Parker 1982; Colombo 1998) and many other tree species (Cannell and Smith 1983; Hunter and Lechowicz 1992; Beuker 1994; Hänninen 1995; Bailey and Harrington 2006). As demonstrated by Heide (1993) and Myking (1997), the choice of high base temperature discounts the contribution of thermal time to physiological processes and bud development at low temperatures and increases the variation in thermal time estimates and uncertainty in estimating days to bud burst, particularly when the GDD model is used (Tables 2 and 3). The suggestion by Bailey and Harrington (2006) to differentially weight high and low temperatures (greater weights to high temperature) when calculating thermal time estimates would further reduce the contribution of thermal time to bud burst at low temperatures. The use of high base temperatures could result in bud burst predictions that are too early when the thermal time estimates determined at low temperature conditions are applied in areas with higher temperatures or that are too late when the thermal time estimates determined at high temperature conditions are applied to areas with lower temperatures (see Table 2). This may help to explain the variation in thermal time requirements reported for bud burst among years (Nienstaedt 1974; Blum 1988; Bailey and Harrington 2006). Bud burst modeling has been reasonably accurate for current conditions but tends to result in early predictions in warmer temperatures expected in future (Hänninen 1995; Bailey and Harrington 2006).

Daytime temperatures are generally higher than those at night and, thus, contribute more to thermal time accumulation. Therefore, averages of daily maximum and minimum temperatures increase the chance of underestimating thermal time contribution at low temperatures when hourly temperatures are replaced with daily mean temperatures in thermal time calculation. As such, using a degree hour model is likely a more consistent way to estimate thermal time and reduce uncertainty in days to bud burst resulting from varying base temperatures.

In this study, a brief period of freezing temperatures during bud development did not affect thermal time estimates. Therefore, our results did not support the suggestion by Bailey and Harrington (2006) that freezing temperatures delay the bud burst process, although sustained effects by longer and more extreme freezing events (below –2 °C) were not determined in our study.

Most estimates of the thermal time requirements for white spruce have been made using the GDD model and a base temperature of 5 °C or higher, with variable results reported in the literature. O'Reilly and Parker (1982) reported a 67–114 day range of degree day requirements for white spruce seedlots from northern Ontario, which are very similar to the values we found in treatments 1 and 2. Estimates reported by Nienstaedt (1974) and Blum (1988) in Wisconsin were closer to the values reported for the other four treatments in this study. However, at base temperatures of 0 or 1 °C, the thermal time estimates found in this study were generally smaller than those reported by Owens et al. (1977) for white

spruce in northern British Columbia, but greater than those reported by Heide (1993) and Myking (1997) for hardwood trees in Norway. This is not surprising given that thermal time requirements for bud burst vary among species and provenances (O'Reilly and Parker 1982; Blum 1988; Murray et al. 1989; Heide 1993).

The lack of significant differences between temperature regimes 1 and 2 and between regimes 3 and 5 does not support our initial expectation that a gradual increase in seasonal temperatures or warming episodes during bud development reduces the thermal time needed for bud burst in white spruce. This is also different from the findings by Campbell and Sugano (1975) and Hänninen (1990) who found that fluctuating temperatures are more efficient for bud burst and reduce thermal time requirements. Myking (1997) pointed out that the studies claiming higher bud burst efficiency under fluctuating temperatures (high and low) are generally conduced before dormancy release is completed, confounding chilling requirements at low temperatures and creating an impression that bud burst is advanced by fluctuating temperatures. As was found by Myking (1997) and Bronson et al. (2009), our results indicated that thermal time requirements for bud burst do not change with temperatures in white spruce seedlings of the same chilling treatments.

It was interesting to observe that the thermal time estimates in treatments 1 and 2 were considerably less than those in the other four treatments (Table 2). The exact physiological processes were not clear. We suspect that it might relate to the fulfillment of chilling requirements of white spruce before bud burst. Treatments 1 and 2 had two additional weeks with night temperatures in the range for effective chilling in boreal trees and this might have promoted bud burst (Kramer 1994; Saxe et al. 2001). The inadequacy of chilling treatment could increase the thermal time required for bud burst but should not affect the evaluation of appropriate base temperatures and thermal time models.

In conclusion, the use of a base temperatures of 5 °C to study bud burst phenology in different temperature conditions resulted in variable thermal time estimates and uncertainty in predicting days to bud burst, as compared with 0, 1, and 2 °C. For white spruce seedlings, the use of base temperatures close to 1 °C for GDD or GDH models is recommended. Comparatively, the degree hour model is less sensitive to the choice of base temperatures than the degree day model. Seasonal temperature patterns, warming episodes, and light freezing events (–2 °C) did not affect the bud burst process for white spruce. These results should help in the selection of appropriate base temperature and thermal time model in quantification of thermal time for bud burst in other boreal trees, a key prerequisite for modeling tree phenology, growth, productivity, and forest ecosystems in current and future climactic conditions.

Acknowledgements

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