

Evaluation of temperature models for predicting bud burst in Norway spruce

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Abstract: Spring bud development was assessed on cuttings of 17 Norway spruce (*Picea abies* (L.) Karst.) clones for up to 7 years at two sites in southern and central Sweden. The ability of various temperature models to predict bud-burst timing was analysed. All temperature-based models resulted in significantly better predictions than the null model, day number. Temperature sum (TS) based on a linear response to temperature above a defined threshold, gave a more precise prediction than forcing units based on a logistic response to temperature. The most precise model could predict bud burst to within 2 days, and it included TS with a threshold of 5°C and a start day arbitrarily chosen between January and March. The models were not improved by incorporating chilling, in terms of chilling days (number of days with mean temperature <5°C) or chilling units. It is suggested that chilling requirement is fulfilled already in December under normal winter conditions in southern and central Sweden. Ranking of clones in bud-burst timing was stable over years and sites. For routine measurements of phenology in applied breeding programmes, it is proposed that standard reference material is thoroughly tested for temperature reactions and that this reference material be used each time new material is tested. With this procedure, an accurate estimate of required temperature sum for bud burst can be obtained from a 1-year assessment.

Résumé : L'auteur a étudié le développement printanier des bourgeons chez des boutures de 17 clones de l'épinette de Norvège (*Picea abies* (L.) Karst.) afin d'évaluer l'aptitude de différents modèles basés sur la température à prédire la date de débourrement des bourgeons. Les boutures étaient établies sur deux sites dans le sud et le centre de la Suède et les observations furent prises pendant une période allant jusqu'à 7 ans. Tous les modèles basés sur la température ont permis d'obtenir des prédictions significativement meilleures que le modèle de référence basé sur le nombre de jours. La somme des températures (ST), établie à partir de la réponse linéaire à la température au-delà d'un seuil critique prédéfini, a résulté en une prédiction plus précise que le nombre d'unités de forçage qui lui, était basé sur une réponse logistique à la température. Le modèle le plus précis pouvait prédire le débourrement des bourgeons à deux jours près. Ce modèle impliquait ST avec un seuil critique de 5°C et une journée de début de décompte choisie arbitrairement entre janvier et mars. Les modèles ne s'amélioraient pas lorsque le temps froid était pris en compte, que ce soit en termes de jours froids (nombre de jours avec température moyenne < 5°C) ou d'unités de froid. L'auteur suggère que l'endurcissement au froid est satisfaisant dès décembre pour les conditions hivernales normales rencontrées au sud et au centre de la Suède. Le rang des clones quant à leur date de débourrement des bourgeons est demeuré stable d'un site à l'autre et d'une année à l'autre. Pour les mesures routinières de la phénologie dans le cadre des programmes d'amélioration, l'auteur propose qu'un matériel de référence standard soit caractérisé parfaitement quant à ses normes de réaction à la température, et que ce matériel de référence soit utilisé à chaque fois que de nouvelles sources de matériel doivent être évaluées. Selon cette procédure, une estimation précise de la somme de température requise pour le débourrement des bourgeons pourra être obtenue à partir d'une seule année d'évaluation.

[Traduit par la rédaction]

Introduction

Bud burst is one of the most precise events of the annual cycle of Norway spruce (*Picea abies* (L.) Karst). It marks the completion of an irreversible process of bud development that also expresses the onset of the growing season (Sarvas 1972; Fuchigami et al. 1982). During bud burst, the new shoots become highly susceptible to low temperatures (Dormling 1982; Cannell and Sheppard 1982; Christersson and von Fircks 1988; Hannerz 1994a). Hence, bud-burst timing determines the probability of spring frost damage, and selection for genetic entries with late bud burst is widely

suggested as a tool to reduce the risk of spring frost damage (Nienstaedt and King 1969; Dietrichson 1969; Cannell and Smith 1983; Hannerz 1994a). Spring frost is occasionally a serious threat to survival, growth, and quality of Norway spruce plantations, particularly in southern and central Sweden, and reduced frost risk is defined as one of the main goals for the Swedish spruce breeding programme (Karlsson and Rosvall 1993).

Timing of bud burst is triggered by environmental factors, and this response is under strong genetic control (e.g., Langlet 1960; Worrall and Mergen 1967; Ekberg et al. 1991). Since bud burst is precise and easily observed in springtime, it is useful for screening clones and progenies in tree breeding programs. If bud-burst timing and other phenological events can be properly predicted by environmental parameters, e.g., temperature or photoperiod, material assessed in different environmental conditions can be

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compared. Proper models are also necessary tools for predicting the risk of frost injury. In the perspective of global warming, understanding the factors governing phenological events becomes increasingly important. Several studies concerning the effects of an increased temperature depict an increased risk of spring frost injury if bud-burst date is advanced (Murray et al. 1989; Kramer 1995; Hänninen 1996; Menzel 1997).

Studies of the effect of temperature on growth have a long history. According to Wielgolaski (1974), Reamur was the first (in 1735) to mathematically relate temperature sums and biological processes. Temperature sums, or accumulation of degree-days, have wide applications for predicting phenological events in agriculture (Arnold 1959). In forestry, temperature sums help to predict outbreaks of insects (Ives 1973), flowering time (Boyer 1978), and consequences of climate warming (Murray et al. 1989; Cannell and Smith 1986; Hänninen 1996; Kramer 1995; Menzel 1997). One of the most widely used applications of the calculation of heat sums in boreal conifers, is prediction of bud burst and the attendant risk of frost injury. Cannell et al. (1985) and Cannell (1985) predicted bud-burst date and mapped the risk of late spring frost on Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in Scotland. Timmis et al. (1994) used a similar approach to predict the frost risk for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and from the temperature-dependent functions also drew frost-risk maps. Hannerz (1994b) derived frost risk predictions for Norway spruce provenances at various sites in Sweden.

The annual rhythm of bud development in forest trees includes several stages that must be jointly considered when modelling phenological events in one of the stages. The active growth period starts with bud break and ends with growth cessation and bud set (Sarvas 1974). Bud set is followed by the buildup of bud dormancy (Qamaruddin et al. 1995), the period of no visible growth. Dormancy is commonly divided into a first period of rest, under which buds remain dormant even if they are exposed to growing conditions, and quiescence, when rest has been broken and favourable temperatures solely can release dormancy (review in Hänninen 1990). Bud burst thus results from a period of chilling to break rest, which usually involves temperatures about or below 5°C for some weeks, and a subsequent period of forcing temperatures, usually above 5°C (Sarvas 1972; Cannell and Smith 1983). Several studies have been made on the relation between chilling and forcing temperatures on dormancy release in trees. Cannell (1989) described four concepts for modelling dormancy release. In the first and most simple, bud burst occurs when a fixed temperature sum is achieved, regardless of other factors. In the second, a fixed chilling requirement must be fulfilled before forcing temperatures have any effect. In the third, chilling and forcing are interrelated and parallel, i.e., a short chilling period must be compensated with higher temperature sums and vice versa. In the fourth concept, models may also include photoperiod and conditions affecting the hardening in autumn. The first concept, a pure temperature sum model, was applied on Norway spruce by Lindgren and Eriksson (1976) and Hannerz (1994b), and on Douglas-fir by Campbell (1974), Thomson and Moncrieff (1982), and Timmis et al. (1994). The second concept with a fixed value of chilling

units is maintained by Sarvas (1974) and Hänninen (1990). The third concept, the interrelation between chilling and forcing have been demonstrated in many studies, e.g., Cannell and Smith (1983), Worrall and Mergen (1967), Nienstaedt (1967), Nelson and Lavender (1979), and Campbell and Sugano (1975). The fourth concept involves the impact on dormancy release of photoperiod (e.g., Campbell and Sugano 1975; Qamaruddin et al. 1993), soil temperature (Sorensen and Campbell 1978), and autumn hardening (Malcolm and Pymar 1975; Dormling 1982). Applied models for northern conifers that involve both chilling and forcing, were generated by Cannell and Smith (1983) and by Hänninen (1990). Further, response to high temperatures can be regarded as linear or logistic (see below).

The applicability of the different models depends on their intended use. Most of the studies cited above were conducted in artificial conditions (climate chambers or greenhouses), often representing unnatural combinations of constant temperatures, artificial daylengths, etc. These controlled, detailed experiments are prerequisites for the basic understanding of the biological responses to environmental cues and also provide valuable guidelines for nursery operations on how storage temperature, light, etc., affect dormancy and hardiness of the seedlings. However, when the concepts are applied on outdoor conditions, the actual response may deviate from that which was predicted. Fluctuating temperatures, frost injuries to buds, moisture, soil temperatures etc., are all part of the uncontrolled seasonal variation. In conifers, there are very few studies exploring the year-to-year variation in bud burst in outdoor conditions. Empirical data used by Cannell and Smith (1983) on Sitka spruce and by White et al. (1979) and Thomson and Moncrieff (1982) on Douglas-fir are exceptions. Worrall and Mergen (1967) and Worrall (1975) studied bud burst of Norway spruce in field conditions over 2 years. The most long-term series of phenological data for Norway spruce probably derives from the International Phenological Gardens network in Europe. The data, covering three clones of Norway spruce, have recently been analysed with the purpose of estimating effects of climate warming (Kramer 1995; Menzel 1997).

In this study, spring bud development was assessed on cuttings from 17 Norway spruce clones for 7 years at two locations in south and central Sweden. The purpose of the study was to evaluate how well temperature models can predict the timing of bud burst in Norway spruce in different years and sites. A linear temperature sum model with different thresholds and start days will be compared with a logistic forcing unit model, and the concepts of fixed and parallel chilling will be evaluated. Variation between clones will also be analysed.

Material and methods

The 17 clones used in this experiment belong to a set of clones denoted the "phenological standard set." The clones in the standard set were all selected within seedlings from commercial seedlots, most of which originated from Czechoslovakia and Belorussia. Clones were selected and initially propagated by cuttings in 1976. The clone set has thereafter been re-propagated each third or fourth year. The purpose of the clone set was to use it as a standard in clonal trials and in selection experiments in the nurseries. It was selected to represent the broad variation from early flushing to

Table 1. Bud development stages used in the study (adapted from Krutzsch (1973)).

Stage	Description
0	Dormant buds
10	Buds slightly swollen, needles below buds bent backwards and outwards
20	Buds swollen, green to grey-green in colour, bud scales still closed
30	Burst of bud scales, tips of needles emerging
40	First elongation of needles to about double bud length
50	First spread of needles, buds have now the appearance of a painter's brush
60	Elongation of shoot, basal needles not yet spread
70	Differentiation of shoot, basal needles spread
80	All needles more or less spread, new buds developing

Note: Observations refers to the average of terminal buds on the uppermost whorl of branches. Intermediate stages (5, 15, 25, etc.) were also registered. Bud burst is defined as reaching bud-stage 30.

late-flushing clones. In this experiment, 3-year-old bare-root cuttings from the fourth vegetative cycle were planted at two nursery sites in spring 1990. The sites were Ekebo in southern Sweden (55°58'N, 13°54'E) and Vipängen, Uppsala in central Sweden (59°48'N, 17°38'E). Ten ramets per clone, randomized over 10 blocks, were planted at each site.

With start in 1991, bud development was recorded yearly until 1997 at Vipängen and until 1993 at Ekebo. An additional assessment of new cuttings (fifth cycle) from the same clones was made in 1997 at Ekebo. Bud development stages were recorded following a modified scheme by Krutzsch (1973) (Table 1). Bud burst was defined as the point when bud development stage 30 was reached. Recordings were made two or three times per week during the bud-burst period in May and June. Terminal buds on the uppermost lateral branches were used for the assessment, as recommended by Krutzsch. For a comparison, the bud development of the leader apical bud was assessed in two successive years at Vipängen.

At Vipängen, temperatures were collected from the SMHI station Ultuna, located 300 m from the experiment. Temperatures were recorded in ventilated screens at meteorological standard height (1.6 m), and presented as mean, minimum, and maximum daily temperatures. At Ekebo, temperatures were collected within the nursery area with a temperature logger. The data series were not complete for the whole period, and to fill in the missing values, temperatures from the SMHI station Lund (55°43'N, 13°12'E) were used. These temperatures were adjusted to fit the Ekebo temperatures with a regression function $T_{Ek} = -0.251 + 0.954T_{Lu}$.

Temperature computations

Daily mean temperatures were used to estimate chilling and temperature sums needed to initiate bud burst. The main influences of temperature on timing of bud burst are (i) a chilling requirement for rest break and (ii) high (forcing) temperatures to release quiescence and promote bud burst. Cannell and Smith (1983) registered the number of chilling days, days with $T < 5^{\circ}\text{C}$, from November 1 until bud burst for Sitka spruce in Scotland. Hänninen (1990) calculated chilling units, under the assumption that chilling has its peak effect around 3.5°C , and gradually declines towards higher and lower temperatures. According to this model, temperatures below -3.5°C and above 10.4°C have no chilling effect. The daily number of chilling units (CUs) is calculated according to the following equations, developed by Hänninen (1990) for Finnish forest tree species:

$$\begin{aligned}
 [1a] \quad \text{CU} &= 0 & \text{if } T \leq -3.4^{\circ}\text{C} \\
 [1b] \quad \text{CU} &= 0.159T + 0.506 & \text{if } -3.4^{\circ}\text{C} < T \leq 3.5^{\circ}\text{C} \\
 [1c] \quad \text{CU} &= -0.159T + 1.621 & \text{if } 3.5^{\circ}\text{C} < T \leq 10.4^{\circ}\text{C}
 \end{aligned}$$

$$[1d] \quad \text{CU} = 0 \quad \text{if } T > 10.4^{\circ}\text{C}$$

where T is daily mean temperature. Other models for chilling assume that high temperatures could have a reverse effect on rest break (e.g., Richardson et al. 1974). These models have not been included in this study.

Temperature sums have usually been calculated as an accumulation of daily mean temperatures above a certain threshold value:

$$[2] \quad \text{TS}(t) = \sum_{t_0}^t [\text{TS}(t) - T_b]$$

where $\text{TS}(t)$ is the temperature sum on day t , in degree-days, $T(t)$ is the daily mean temperature ($^{\circ}\text{C}$) on day t , T_b is the threshold temperature ($^{\circ}\text{C}$), t is the day after t_0 , t_0 is the start day when temperature sum begins accumulation. A common threshold value is 5°C (Cannell and Smith 1983; Sarvas 1972). Start days that have been used are January 1 (Beuker 1994a), February 1, (Cannell and Smith 1983), or the first day in spring after three consecutive days with temperatures above the threshold value (Prescher 1982; Hannerz 1994b).

Cannell and Smith (1983) integrated chilling and TS into the following logistic model:

$$[3] \quad \text{TS} = a + b^{-rC}$$

where C is the number of chilling days and a , b , and r are coefficients. An evolution of the strictly linear temperature sum model is Hänninen's (1990) forcing units (FUs), which takes into account that the influence of temperature varies like a logistic function. The daily accumulation of FUs is calculated with the following formula:

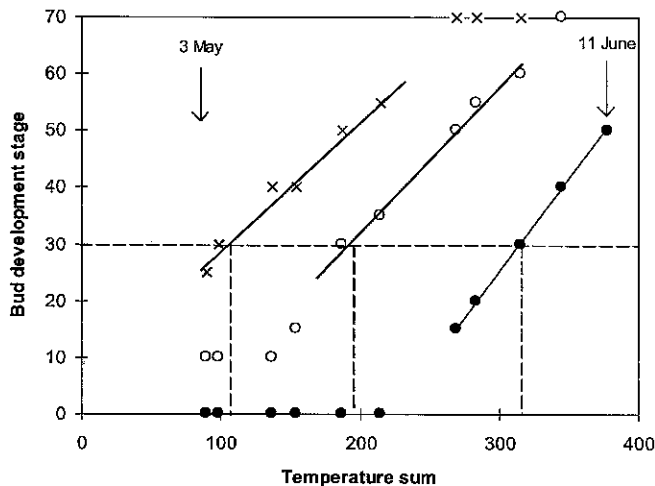
$$\begin{aligned}
 [4a] \quad \text{FU} &= 0 & \text{if } T \leq 0^{\circ}\text{C} \\
 [4b] \quad \text{FU} &= \frac{28.361}{1 + \exp[-0.185(T - 18.431)]} & \text{if } T > 0^{\circ}\text{C}
 \end{aligned}$$

According to Hänninen (1990), FUs are accumulated from the moment when a certain genotype-specific CU requirement is met. When a genotype-specific critical value of FUs is attained, bud burst occurs. With this model, one has to know the CU_{crit} before it is possible to calculate the FU_{crit} for each genotype.

In this study, the following temperature models were compared.

- (1) Linear temperature sum (TS; eq. 2), with thresholds 2, 3.5, 5, 6.5, and 8°C (denoted TS_2 , $\text{TS}_{3.5}$, etc.) and fixed start days on the first of January, February, March, April, and May. (model 1).
- (2) Forcing units (eqs. 4a and 4b), with fixed start days as above (model 2).

Fig. 1. Example of how point of bud burst (bud-stage = 30) was determined in one ramet each from an early, an intermediate and a late clone. Scoring was made on 11 occasions between May 3 and June 11, 1993 as indicated in the figure. Each scoring occasion was interpreted into temperature sum accumulated from January 1 with threshold 5°C. The fit of bud development stage scores between 20 and 60 and temperature sum is close to linear. The temperature sum at bud-stage 30 can be read from the figure, and later be converted into day of bud burst, forcing units, etc.



- (3) Forcing units (eqs. 4a and 4b) with start days after achieving CUs (eqs. 1a–1d), of 20, 50, 80, and 100, i.e., fixed chilling. Chilling units start to accumulate on September 1 (model 3).
- (4) Linear temperature sums and forcing units with starting day January 1 in relation to number of chilling days (CD) or CUs until bud burst to try to find relations similar to eq. 3, i.e., parallel chilling. Number of CDs and CUs were added from September 1 (model 4).

The temperature models were compared with the null model, predictions based on the day of the year for bud burst.

Determination of bud-burst point

The bud development stages between approximately 20 and 60 did fit well to a straight line if they are plotted against TS. Plots of bud scores for each ramet and year were used to determine bud burst, i.e., when the bud scales were opened and the new needles were visible (stage 30; Fig. 1). The data obtained expressed bud-burst point in TS_5 values, which was then converted to temperature sums with alternative start days and thresholds, FUs, CUs, CDs, and day for bud burst. The conversion was based on daily temperature development for each year and site.

Statistical evaluation

A preliminary analysis showed that there were no block effects. Analysis were thereafter based on mean values for each clone in one site and one year. The effects of year, clone, site, and their interactions on time for bud burst were analysed with the following linear model in SAS (general linear model procedure):

$$[5] \quad y_{ijk} = \mu + C_i + S_j + Y_k + (C \times Y)_{ik} + (C \times S)_{ij} + e_{ijk}$$

where y_{ijk} is the temperature sum for bud burst (TS_5) in clone i in site j in year k , C_i is the fixed effect of clone i ($i = 1, 2, \dots, 17$), S_j is the fixed effect of site j ($j = 1, 2$), Y_k is the fixed effect of year k ($k = 1, 2, 3, 4$ at Ekebo, $1, 2, \dots, 7$ at Vipängen), $C \times Y$ is the effect of the interaction between clone and year, $C \times S$ is the effect of interaction between clone and site, and e_{ijk} is the random residual.

Table 2. Date (day/month) and temperature sum (TS_5 , start day January 1) for bud burst over years and sites.

Site and year	Date			TS_5		
	Mean	Earliest clone	Latest clone	Mean	Earliest clone	Latest clone
Ekebo						
1991	26/5	14/5	15/6	155	101	273
1992	21/5	13/5	1/6	177	95	294
1993	10/5	29/4	22/5	175	90	290
1997	31/5	16/5	12/6	182	120	320
Vipängen						
1991	13/6	30/5	28/6	211	136	334
1992	27/5	18/5	10/6	212	106	385
1993	17/5	7/5	3/6	197	111	316
1994	1/6	14/5	16/6	183	110	295
1995	3/6	27/5	19/6	182	86	333
1996	3/6	26/5	12/6	162	112	260
1997	3/6	24/5	14/6	180	111	295

Differences between clones, years, and sites were tested with Tukey's test, with a significance level of 0.05. To compare the relative importance of the variance components for bud burst, eq. 5 was also run assuming all independent variables as random.

The temperature models were compared using the mean over all clones. For each temperature model, a mean value was computed, which was used to predict date of bud burst for each of the 11 combinations of site and year. Precision of the models was described with the standard deviation of differences between the observed and the predicted date for bud burst, as described by Hickin and Vittum (1976) and also applied by Hunter and Lechowicz (1992). The models were also subject to t tests on absolute values of the differences mentioned above.

Clonal variation in stability

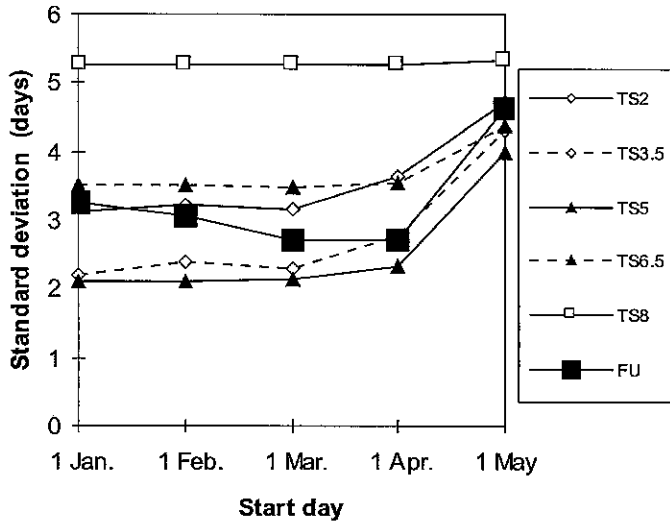
Stability in bud-burst timing among clones over site and years was examined according to the method of Finlay and Wilkinson (1963). TS_5 values (start day January 1) for bud burst for each clone, year, and site were expressed on a logarithmic scale to induce a higher degree of linearity. Yearly bud-burst scores for individual clones were regressed on the mean for all clones. The slopes of the regression lines can be considered as an index of phenotypic plasticity (e.g., Bradshaw 1965; Via 1993) and express how responsive particular clones are to year-to-year variation in temperature.

Results

General

Year-to-year variation in temperature was large during the 7 years of data collection. The mean date for bud burst over all clones varied up to 3 weeks (Ekebo) and 4 weeks (Vipängen) between years (Table 2). At Ekebo, bud burst occurred on average on May 20 and, at Vipängen, on May 31. Analysis of variance on TS_5 (start day January 1) according to eq. 5 resulted in a significant effect ($p < 0.001$) of clone, site, and year but not of the interactions clone \times year and clone \times site. Ekebo had a significantly lower TS_5 value (172 degree-days) than Vipängen (190 degree-days). The difference between sites was most pronounced in the first years. The effect of year was attributed only to the year 1996, which was significantly distinguished from the years 1991,

Fig. 2. Precision of linear temperature sum (TS) models with threshold temperatures 2, 3.5, 5, 6.5, and 8°C (TS₂, TS_{3.5}, etc.), and with start days for accumulation of temperatures from the first of January, February, March, April, and May. Comparison with forcing units (FUs) is also made. Precision is expressed in standard deviation of differences between predicted and observed date for bud burst. Standard deviation for the null model (day of the year) was 9.5 days.

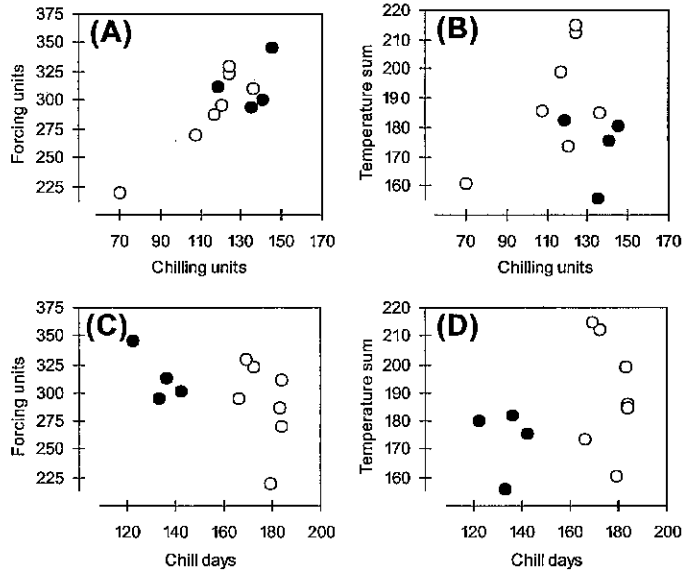


1992, 1993, and 1997. Variance components for TS₅, calculated from eq. 5 with the independent variables assumed as random, illustrate the major role of clone in the model. Variance components expressed as part of total variation (intra-class correlation) were for clone, 78%; site, 9%; year, 5%; and error, 9%. Contradictory to the TS values, forcing units were higher at Ekebo (312 units) than at Vipängen (290 units). Vipängen had more chilling days than Ekebo, 177 compared with 133 days, but chilling expressed as CUs was stronger at Ekebo than at Vipängen (135 compared with 114 units).

Precision of models

All models based on temperature gave a significantly ($p < 0.0001$) better prediction of bud-burst date than the null model (day of the year). The standard deviation between the mean bud-burst date May 28 and observed days was 9.5 days. The precision of the various temperature models with fixed start days is illustrated in Fig. 2. The deviation between observed and predicted date of bud burst was lowest (2.1 days), with a linear temperature sum model (model 1) with threshold 5°C. Start day could be chosen arbitrarily within the first 3 months, mainly because this period contributes very little to the temperature sum. Precision decreased at all thresholds with a May 1 start day. Threshold temperatures lower or higher than 5°C also decreased the precision of the model. The precision of FUs (model 2) was comparable with TSs with threshold 2°C but improved with later start days. However, none of the temperature models were significantly different, and a closer analysis showed that individual years had a large impact on the result. For example, 1991 at Ekebo was characterized by a warm period in first half of April followed by low temperatures until

Fig. 3. Forcing units or temperature sum (TS₅) required for bud burst, combined with chilling units and chill days. Chill days and chilling units are cumulative from September 1 until bud burst. Temperature sum and forcing units are cumulative from January 1 until bud burst. Each dot represents the mean for all clones at one site and one year. Solid circles are from Ekebo, and open circles are from Vipängen.



mid-May, when TS started to rise again. If this year was excluded from the calculations, precision increased for higher threshold temperatures (8 and 6.5°C) but decreased for low thresholds (2 and 3.5°C). Threshold 5°C was however still optimum.

A FU model based on a fixed amount of CUs (model 3) was less precise than the models with fixed start days. Standard deviation of differences between predicted and observed date were 5.2 and 4.1 days, with 20 and 50 chilling units, respectively. In the cold year (1996), the total amount of chilling units reached only 70 from September until the time of bud burst. Hence, models with chilling units 80 and 100 were not possible to calculate. If this particular year were excluded, standard deviation for the various chilling levels would be 3.5, 2.6, 2.5, and 3.1 days for models based on 20, 50, 80, and 100 chilling units respectively.

The hypothesized inverse relationship between chilling and TS (model 4) could not be found (Fig. 3). A weak tendency is shown in Fig. 3C. However, it is not strong enough to make any curve-fitting meaningful. Figure 3D expresses the variables used by Cannell and Smith (1983) for Sitka spruce. The cold winter in 1996 resulted in the lowest level of FUs despite the low amount of CUs. The number of CDs that winter were however high.

Clonal variation

There was considerable variation in bud-burst date among clones, with almost 4 weeks between clones with the earliest and the latest bud burst (Table 2). The ranking between clones remained very stable between years and sites (Table 3). The only pronounced shift was in the cold year of 1996. Clonal stability in achieved TS to bud burst over years and sites, according to the technique described by Finlay and Wilkinson

Table 3. Clonal average temperature sums (TS₅, start day January 1) to bud burst and ranking for each year and site.

Clone No.*	TS ₅ to bud burst			Ranking in bud burst										
				Ekebo				Vipängen						
	Ekebo	Vipängen	Mean	1991	1992	1993	1997	1991	1992	1993	1994	1995	1996	1997
2582a	96	118	107	2	1	1	1	1	1	2	1	1	5	2
1130a	106	117	112	1	3	2	2	2	2	1	2	2	1	1
2093ab	112	132	122	3	4	4	4	6	3	3	3	4	3	3
1115ab	114	139	127	6	2	3	3	3	4	4	8	3	2	4
2656ab	120	146	133	4	5	5	6	5	6	5	5	5	7	5
1274ab	128	144	136	5	6	6	5	4	5	7	4	6	6	6
2897b	137	157	147	8	7	7	7	7	7	8	7	7	8	8
2098b	143	156	150	7	8	8	8	8	8	6	6	8	4	7
1377c	178	190	184	10	9	9	9	10	9	9	10	9	11	10
2750cd	185	205	195	9	11	12	11	9	10	11	9	10	12	12
2920cde	186	218	202	12	12	10	10	12	14	10	11	11	10	11
3302cde	188	224	206	11	10	11	12	14	11	12	12	12	9	9
2365def	204	239	221	13	13	13	14	11	12	13	15	13	16	15
1298ef	221	252	236	14	14	16	13	15	16	15	14	14	14	13
2020ef	234	244	239	15	15	14	15	13	13	14	13	16	13	14
1114f	237	261	249	16	16	15	16	16	15	16	16	15	15	16
2428g	287	324	305	17	17	17	17	17	17	17	17	17	17	17

Note: Rank 1 is the earliest, rank 17 is the latest clone each year and site respectively.

*Clones with the same letter cannot be distinguished at the 0.05 level with Tukey's test.

(1963), is shown in Fig. 4. Clones with indices above 1 are less stable than average, and those with indices below 1 are more stable than average, i.e., they respond less to year-to-year variation in temperature. Most clones have values from 0.8 to 1.2, indicating a similar reaction to year-to-year variation in TS and a low clone × site or clone × year-effect (these were earlier shown to be insignificant). Clones with high indices can also be regarded as expressing a high level of phenotypic plasticity. Clones 2920 and 3302 were the most plastic clones, with index values of almost 1.5. These clones were intermediate flushers, and the high values were mainly explained by a relatively higher temperature sum requirement in the "late" years 1991 and 1992 at Vipängen.

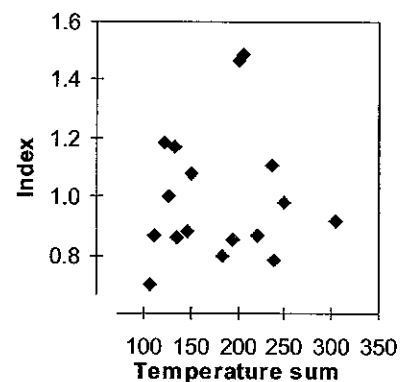
Apical bud of the leader

The development of the leader's apical bud was recorded in 1993 and 1995. The mean TS₅ for reaching bud burst was 46 (1993) and 42 (1995) degree-days above that of the buds on lateral branches. This lag corresponds to 5 and 4 days for the respective years. Classification of the apical bud was difficult compared with lateral buds, as it tended to start elongation before the bud scales were open. Consequently the scheme according to Krutzsch (1973) required modification.

Discussion

The mean dates for bud burst for the two sites and 7 years varied between May 10 and June 13, i.e., over 1 month (see Table 2), and it was evident that predictions based on day of the year alone gave poor results. All temperature-based models with thresholds between 2 and 6°C, as well as the FU model, could predict bud burst to within 3.5 days. The most precise model turned out to be TS₅, which was able to predict bud burst to within 2 days. However, precision of the

models with varying thresholds and start days were not significantly different, and further refinements would probably be masked by uncontrolled seasonal variation. This variation will also mask the difference between logistic FU and linear TS models. In practise, the logistic FU function is close to linear in its most effective interval between 10 and 20°C, and temperatures below 5°C will have small effects on the total FUs in normal years. Thomson and Moncrieff (1982) and Hunter and Lechowicz (1992) also found that start day and thresholds can be varied considerably without influencing the precision of the predictions. Menzel (1997) tested several temperature models for predicting bud burst, based



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on data from the International phenological gardens network in Europe. All models included chilling, thus it is not possible to draw any conclusions about a pure temperature sum model. The differences between models were small in Menzel's (1997) study, however it was possible to derive genotypic values for chilling and forcing thresholds.

The predictions were not improved when the chilling component was added. The concept of fixed chilling requirements still has an appeal as being theoretically more correct than fixed start days. Owens et al. (1977) found, on white spruce (*Picea glauca* (Moench) Voss), an almost exact fit between flushing time and heat sum if temperatures were accumulated from the time when bud dormancy was released. Dormancy release was in their study identified as the stage when mitosis could be observed in bud apices. The concept of fixed chilling also avoids the dilemma with simultaneous chilling and forcing in how to treat temperatures in the interval where they have both forcing and chilling effects. Hänninen's (1990) definitions of chilling and forcing units, stretches this interval to cover 0–10°C, which also explain why simultaneous accumulation of the two measures results in a positive relationship (as in Fig. 3A). The lack of precision with fixed chilling levels in this study could partly be explained by the use of daily mean temperatures instead of hourly temperatures. Chilling hours are used in many studies, including Kriebel and Wang (1962), Sarvas (1974), and Hunter and Lechowicz (1992), and it can be expected to give a better estimate of the actual level of chilling. Further considerations may also be implemented in modelling chilling requirement. Hänninen and Backman (1994) suggested that the threshold temperatures for chilling may be dynamic and shift from higher to lower temperatures during the process of rest break. However, the aim of this study was to find a robust model, which fits many conditions and which could be applied without too detailed temperature recordings. In this respect, an input of daily mean temperatures, and linear TS accumulations with a fixed start day is the most appealing.

The absence of a relation between chilling and forcing in the present study indicates that the tests did not include conditions where chilling was limiting. In this study, the number of CDs until bud burst varied between 122 and 184, and CUs, from 70 to 145. Other studies made on Norway spruce found that the effect of chilling treatment diminished after 2–4 weeks (Nienstaedt 1967), 8 weeks (Worrall and Mergen 1967), and 6 weeks (Hänninen and Pelkonen 1989), and Nienstaedt (1967) stresses that the first 2 weeks of chilling are the most important. All these studies were made in controlled conditions with a constant chilling temperature. Hänninen (1990) suggested that chilling is more efficient in natural conditions, with fluctuating temperatures. Contrarily, Nelson and Lavender (1979) claimed that fluctuating temperatures were less efficient for chilling than constant temperatures. They found that western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) needed 6–8 weeks at constant 5°C for satisfying chilling needs. In normal Pacific Northwest conditions, chilling requirement was expected to be fulfilled after 8–10 weeks around 3–5°C, concerning that daytime high temperatures may have a reversal effect of the chilling. Nevertheless, in Sweden, chilling requirement in Norway spruce should probably have been met after 6 weeks, or 40

CDs, in outdoor conditions. This requirement is already met by early December at Vipängen and by mid-December at Ekebo. On the basis of experiences from greenhouse experiments and field conditions, Hänninen (1996) proposes that the normal range for Norway spruce in Finnish conditions is between 20 and 40 CUs, which is approximately the same as number of days in the experiments performed with constant chilling temperature of 4°C. Also this level is met by the beginning of December (Vipängen and Ekebo). Based on these assumptions, chilling should have an effect on the predictions only in extreme winters in south and central Sweden. One winter, 1996 at Vipängen, was much colder than normal, with long periods when daily temperatures were far below 0°C. The level of 40 chilling units was not reached until the end of March. In spite of this, the requirement of forcing temperatures was not higher this year, if anything lower. This provides additional support for the hypothesis that chilling is seldom a limiting factor during the conditions naturally occurring in southern Sweden.

Campbell (1974) evaluated the effects of provenance transfer on the spring frost risk of Douglas-fir in Washington and Oregon, using a pure TS model. The author argued that chilling requirement of Douglas-fir is less than 80 days of temperatures below 10°C, a demand that is met in almost all winters in the region. Myking and Heide (1995) suggested that chilling deficit is unlikely to occur for *Betula* in Scandinavia, also in the view of climate warming. A true effect of natural seasonal variation in chilling on bud burst was found by Cannell and Smith (1983). An increased number of chilling days up till 200 days influenced the required TS; however, the relationship levelled out at approximately 110 days. Their study was made on Sitka spruce, a species adapted to coastal conditions with an assumed high demand for chilling. Higher chilling requirement for coastal populations than for inland was found in Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth.) (Leinonen 1996) and in Douglas-fir (Campbell and Sugano 1979). Van der Kamp and Worrall (1990) observed severe winter damage in interior conifer species but not in coastal species in British Columbia, and they attributed the difference to a lower chilling requirement in interior species, making them more susceptible to dehardening during warm spells in winter.

The threshold 5°C is frequently employed for temperature sum calculations in Finland and Sweden. Supported by extensive experience in Finland, Sarvas (1965) suggested a 5°C threshold to best explain phenological events. The threshold is used in Finland to predict bud burst (Sarvas 1974; Beuker 1994a) and to describe the temperature conditions of a site (Beuker 1994b). In Sweden, a threshold of 6°C was commonly used for describing the forest climate (Odin et al. 1983). Langlet (1936) found a good correlation between the length of growing season, calculated as the period with mean temperature above 6°C, and dry matter content in Scots pine provenances. The threshold of 6°C was also used to calculate timing of bud burst and initiation of shoot elongation (Jonsson 1969; Prescher 1982). Mainly from a pragmatic viewpoint, to better adapt to international standards, Sweden changed to using 5°C as a standard for describing temperature climate in forestry (Odin et al. 1983). This study supports the use of 5°C as a threshold for bud burst predictions. The threshold has been frequently used

internationally, which permit comparisons with studies on, for example, Norway spruce in Finland (Beuker 1994b), Sitka spruce (Cannell and Smith 1983), and white spruce (O'Reilly and Parker 1982; Owens et al. 1977).

The results confirm earlier studies that there is a strong clonal effect on TS requirement for bud burst and that ranking is stable over years (e.g., Morris et al. 1957; Worrall 1975; White et al. 1979). Clonal variation may also be expected in chilling requirement and threshold temperatures. Varying threshold temperatures between provenances have been shown in many species. Worrall (1983) demonstrated that threshold temperature decreased with increased elevation of alpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and amabilis fir (*Abies amabilis* (Dougl.) Forbes) seed sources. The high-elevation species, alpine larch (*Larix lyallii* Parl.), was also shown to have a low temperature threshold (Worrall 1993). Northern, early flushing provenances of Norway spruce were suggested by Worrall (1975) to have lower threshold temperatures. Variation in chilling requirement was demonstrated between inland and coastal populations of Douglas-fir, Scots pine, and silver birch (Campbell and Sugano 1979; Leinonen 1996). Höytyä and Hänninen (1991) found, however, that light intensity during chilling affected the variance in chilling requirement. Experiments in low light intensity could thus have overestimated genetic variation in chilling requirement, compared with what is expected in outdoor light conditions. Cannell et al. (1985) demonstrated in Sitka spruce that clonal differences in TS were the same, regardless of chilling level. It can thus be assumed that bud-burst variation in Norway spruce from within a limited region, is explained mainly by the TS requirement.

Many factors other than chilling and forcing may influence the seasonal variation in bud flushing time. Long photoperiod has been found to compensate for unsatisfied chilling in Douglas-fir (Irgens-Moller 1957; Campbell and Sugano 1975) and in Norway spruce (Worrall and Mergen 1967; Qamaruddin et al. 1995). Soil temperature can in some conditions affect timing of bud burst (Lavender et al. 1973, Sorensen and Campbell 1978). An important source of seasonal variation can be conditions during growth cessation and hardening. Dormling (1982) found that well-hardened Norway spruce seedlings flushed earlier than less hardy ones. Low temperatures during growth cessation advanced flushing dates in Sitka spruce seedlings (Malcolm and Pymar 1975). Hardening in autumn also affects the frost hardiness after bud burst in Norway spruce (Dormling 1982; Rostad 1988). Variation among years in fall conditions could help explain the variation in bud burst date in this study.

Age of the ramets was not considered in the analysis, despite being reported to be important for growth rhythm. Ununger et al. (1988) found that number of days to bud break in Norway spruce increased with age of the seedling, and days to bud set decreased. The actual period of shoot elongation was reduced from 31 days in 2-year-old seedlings to 16 days in 6-year-old seedlings. The largest reduction was between the second and fourth growth period. In contrast to the latter study, Ekberg et al. (1991) found no reduction in growth period duration from the fourth to the eighth growth period. Büsgen and Münch (1929) reported gradually delayed bud flushing in Norway spruce up to age 18 years. In this study, the ramets were cuttings from the fourth vegeta-

tive cycle, i.e., they were 18 years from seed at the time of planting, and therefore, they were expected to display characteristics of more mature material than seedlings of corresponding size. Cutting propagation causes some rejuvenation during the first growing periods of the cuttings (Ununger and Ekberg 1987). In the present study, the rejuvenation effect had probably disappeared several years previously. If ramet age had any effect on the variation, one would expect temperature sum for bud burst to increase with age. In this study, the trend was almost the opposite (see Table 2), at least for the Vipången site.

The time lag between lateral and terminal leader bud burst was above 40 degree-days, or 4 or 5 days, in this study. Later bud burst in the apical buds was found also in Sitka spruce (25 degree-days; Cannell et al. 1985) and in Douglas-fir (3–10 days, White et al. 1979; 1–23 days, Sweet 1965). Sweet (1965) found a correlation between the time lag and climatic parameters of the origin of the provenances in the study.

Practical implications

The TS model can be used in central and southern Sweden to establish genotype bud-burst values that are independent of site and test conditions. This makes it possible to compare and rank genotypes assessed in different studies if the TS can be accurately estimated. This study suggests that an estimate based on 11 repeated observations can predict bud-burst time within 2 days. In large-scale screening for tree breeding, repeated assessments are often too laborious and expensive. Single-year observations involve an error that may be too large, depending on the purpose of the estimate. Standard deviation of TS₅ estimates were 18 degree-days, and the most extreme observations varied from 155 to 212 degree-days. An alternative strategy is to use well-known material as standard references, e.g., controlled crossings with a broad variation in phenology, or natural populations representing a clinal trend. The standard references may be examined in controlled conditions for their values of chilling and forcing. The highly consistent ranking of genotypes at different sites and in different years suggests that this strategy is the most efficient. Natural populations as standards are presently used for routine assessment of winter frost hardiness in Scots pine material in Sweden (Sundblad and Andersson 1995). Hardiness of the tested genotypes can then be expressed as e.g., "hardy as natural populations originating from latitude 65°N."

Single-year estimates of TS may however be accurate enough for predicting frost risk or for culling extremely early or late material. Within the range of year-to-year variation for individual clones, the predicted frost risk is only slightly changed, according to frost risk calculations presented in Hannerz (1994b). The clones in the study varied substantially in TS₅ requirement, from 107 to 305 degree-days. This variation will result in a large variation in frost risk. In central Sweden, a seedling that flushed at 120 degree-days faced almost twice as high risk for sustaining frost temperatures, as a seedling that flushed at 180 degree-days (Hannerz 1994b). Provenance seedlings from Finland flushed at 100 degree-days, central Sweden at 120, Belorussia at 180 and Jugoslavia at 195 degree-days (Hannerz 1994b). Beuker (1994a) found a provenance variation

between 125 and 250 degree-days for mature trees, originating from northern Finland to Romania.

Some other practical implications from this study may also be mentioned. The average standard error of means for assessing TS for clone within site and year was 5.9 degree-days, or 3.4%. This indicates that when clonal material is used, 10 ramets per clone are sufficient to assess TS accurately. The results also demonstrate that scoring shall be made on lateral branches. The assessments in this study involved repeated scoring of bud stages, to find the bud-burst point by interpolation. However, it was found that the regression line of bud stages on TS (model bud stage = $a + bTS_5$) had approximately the same slope for all clones and years ($b \approx 0.25 \pm 0.05$ (mean \pm SE), see Fig. 1). This slope can be used to roughly estimate TS_5 at bud burst by extrapolation from a single observation, as long as the observed stages are between 20 and 60.

It must be stressed that this study was made on chronologically old clones, with an expected mature performance. The results cannot be directly applied on tests with young seedlings. Juvenile features such as a high proportion of free growth, an earlier bud burst and a presumed higher risk of frost injury to buds may influence how well temperature can be used to predict bud burst. Further studies in field and controlled conditions are needed to address this question.

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