Adaptation of the Timing of Bud Burst of Norway Spruce to Temperate and Boreal Climates

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The adaptation of the annual cycle of development of boreal and temperate trees to climatic conditions has been seen as a result of stabilizing selection caused by two opposite driving forces of natural selection, i.e. the tolerance of unfavorable conditions during the frost exposed season (survival adaptation) and the effective use of growth resources during the growing season (capacity adaptation). In this study, two theories of the effects of climate on the adaptation of the timing of bud burst of trees were evaluated. This was done with computer simulations by applying a temperature sum model for predicting the timing of bud burst of different Norway spruce genotypes on the basis of air temperature data from various climatic conditions. High geographical variation in the temperature response of bud burst, typical for Norway spruce, was included in the theoretical analyses. The average timing of bud burst and the corresponding risk of occurrence of damaging frost during the susceptible period after bud burst were calculated for each genotype in each climate. Two contrasting theories of the stabilizing selection were evaluated, i.e. the overall adaptedness of each genotype was evaluated either 1) by assuming a fixed threshold for the risk of frost damage, or 2) by assuming a tradeoff between the risk of frost damage and the length of the growing season. The tradeoff assumption produced predictions of between provenance variation in bud burst which correspond more closely with empirical observations available in literature, compared to the fixed threshold assumption.

Keywords adaptation, bud burst, frost damage, modelling, phenology, stabilizing selection

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1 Introduction

Among the evolutionary forces affecting the genetic differentiation of populations, natural selection caused by macroclimatic conditions has been considered to play a major role in boreal and temperate conifers (e.g. Eriksson 1998). The adaptation of the annual cycle of development of boreal and temperate trees to prevailing climatic conditions has been seen as a result of stabilizing selection caused by two opposite driving forces of natural selection. First, protection against the unfavorable frost exposed season requires a sufficiently long dormant period, during which trees are at a frost hardened stage (survival adaptation). Second, for the effective use of growing resources, a sufficiently long growing season is needed (capacity adaptation) (Hänninen and Hari 1996).

Due to the varying climatic conditions in different geographical areas, tree species with a broad distribution range can be predicted to have clinal variation in their environmental regulation of the annual cycle of development. The variation in traits such as the timing of spring bud burst and autumn growth cessation has been studied by growing trees representing different geographical provenances in uniform growing conditions, i.e. utilizing the common garden experiments or experiments under controlled conditions in growth chambers (e.g. Burley 1966, Hänninen 1990, Beuker 1994, Hannerz 1994, Myking and Heide 1995, Leinonen 1996, Hurme et al. 1997, Oleksyn et al. 1998).

In the case of the timing of bud burst in spring, the most important driving forces of natural selection are probably the avoidance of spring frost damage, which may reduce growth, or in extreme cases kill the plant (survival adaptation), and the effective utilization of the growing season through early initiation of growth (capacity adaptation). The optimal timing (or temperature response) of bud burst in each climate can be considered to be a result of a certain combination of these driving forces. However, it should be noted that the local provenances do not necessarily represent the optimal genotypes.

It has been suggested that several climatic variables are involved in the adaptation of the timing of bud burst. For example, Sarvas (1967) found a relationship between the temperature sum required for certain phenological events and the average total length (or total temperature sum accumulation) of the growing season of the original growing site of different tree provenances. It has also been suggested that the distribution of spring temperatures (maritime vs. continental climate), which affects the risk of occurrence of spring frost damage, is related to the differences in the timing of bud burst among different geographical origins (e.g. Burley 1966).

Norway spruce (*Picea abies* (L.) Karst.) is a species with typically large geographical variation in the timing of the events of the annual cycle of development. According to the common garden experiments, a latitudinal trend has been found in the temperature response of the timing of bud burst in spring. Several results indicate that southern spruce provenances have generally much higher temperature sum requirements for bud burst than northern ones (e.g. Beuker 1994, Hannerz 1994). A similar trend has been observed also in other boreal and temperate tree species (Beuker 1994, Leinonen 1996).

In this study, meteorological data and theoretical modelling were used to study the performance of different tree genotypes under different climatic conditions. The climatic adaptation of the different genotypes was studied with reference to two contrasting theories, based on either 1) an assumption of a fixed threshold for the risk of frost damage, or 2) an assumption of a tradeoff between the risk of frost damage and the length of the growing season. The analysis was based on the timing of spring bud burst, which was predicted by applying the temperature responses previously found suitable for predictions concerning Norway spruce.

2 Material and Methods

2.1 Climatic Data

The timing of bud burst and the risk of spring frost damage of different tree genotypes were predicted in contrasting climatic conditions. Three sets of temperature data (daily minimum and mean temperatures) were used for this purpose representing southern continental (Voronez, 51°40´N, 39°13´E), southern-boreal semi-continental (Tampere, 61°28´N, 23°44´E) and northern-boreal semi-continental (Muonio, 67°58´N, 23°40´E) climates. The temperature data from each of these sites covered a period of 15 years (1966–1980).

2.2 Predictions on Timing of Bud Burst and Frost Damage Risk

To predict the timing of bud burst and the risk of spring frost damage of different genotypes in different climatic conditions, the approach used previously by Hannerz (1994) for Norway spruce was utilized.

The timing of bud burst for different tree genotypes was predicted by carrying out simulations using a temperature-based model. Among several types of phenological models (reviewed by e.g. Kramer 1994, Hänninen 1995), a simple and generally used temperature sum (or thermal time) model has been found to be most suitable for predictions concerning Norway spruce (Hannerz 1999). By using this modelling approach, the accumulation of temperature sum (day degrees or d.d.) was calculated, assuming a linear temperature response based on daily mean temperatures above a threshold temperature of +5 °C. 1st January was used as the starting date of the calculations. Bud burst was assumed to occur when a genotypically specific critical temperature sum, TScrit, was attained. In the model simulations, the genotype-specific values of the critical temperature sum ranged from 80 d.d. to 260 d.d. This range covered the variation observed in Norway spruce in common garden experiments (Leinonen, unpublished), and therefore it was assumed to include most of genotypes of Norway spruce occurring in nature.

The risk of frost damage was estimated by recording the daily minimum temperatures during the most frost sensitive period of Norway spruce, which was assumed to begin at the time of bud burst and end when 100 d.d. had accumulated after this event (Hannerz 1994). Since the temperature data were obtained by measurements from a standard height, they do not necessarily show the locally occurring frosts at the ground level, which might be critical especially for seedlings. Therefore, the daily minimum temperature of +2 °C was used as a threshold of possibly occurring frost (Hannerz 1994). The risk of frost damage for each genotype was defined as the proportion of years when temperatures below the threshold occurred during the frost sensitive period out of the total number of years involved in the calculations.

For further analyses, the mean calendar day of bud burst during the simulation period was used to represent the beginning of the growing season, thus indicating the differences in the capacity adaptation of different genotypes in different climates. This information was connected with the predicted frost damage risk of each genotype in each climate, in order to study the relationship between the capacity and survival adaptation.

3 Results and Discussion

The results showed that the patterns how the frost risk changed as a function of the timing of bud burst differed between the sites (Fig. 1). In the southern, continental site (Voronez), there was a quite constant decrease of frost risk as the temperature sum required for bud burst increased, until a constant risk level close to zero was achieved with genotypes with a rather late bud burst (about 200 d.d.). On the contrary, in the boreal semi-continental sites, such leveling occurred in genotypes with a rather early bud burst (100–150 d.d.). In general, the frost risk was higher in the northern sites compared to the southern one, especially in genotypes with late bud burst.

The relationship between survival and capacity adaptations was demonstrated graphically by plotting the predicted risk of frost damage against the mean days of bud burst (Figs. 2 and 3). In Fig. 2 it is assumed that an absolute threshold for spring frost risks identifies the optimal genotype with maximum overall adaptedness (cf. Hänninen and Hari 1996). In this case, amongst those genotypes not exceeding this threshold (sufficient survival adaptation), the maximum overall adaptedness is found in the genotypes with the earliest date of bud burst (maximum capacity adaptation). Two hypothetical threshold risk levels were consid-

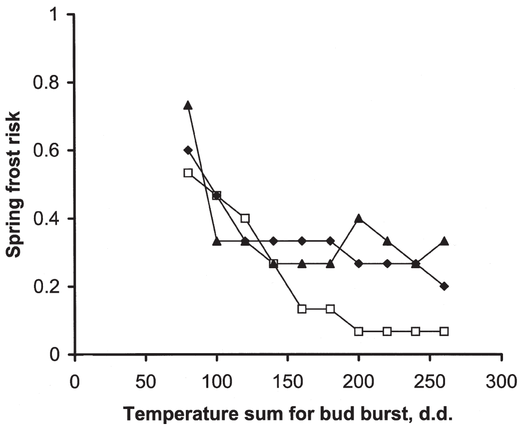

Fig. 1. Model predicted risks of occurrence of spring frost with different genotypes of Norway spruce in three different climates: Voronez (□), Tampere (▲) and Muonio (◆). Risk of frost damage is expressed as the proportion of years with damaging frost appearing during the susceptible period after bud burst. The critical temperature sums (TScrit) on x-axis specify the Norway spruce genotypes examined.

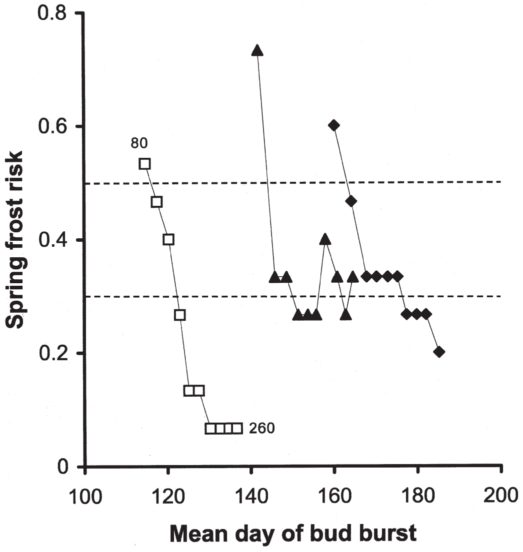

Fig. 2. Predictions of the principle of fixed risk of frost damage, for the identity of the optimal Norway spruce genotype in different climates: Voronez (□), Tampere (▲) and Muonio (◆). For each location, the curves indicate the computed combination of the spring risk of frost damage and the mean day of bud burst (Julian date) for ten Norway spruce genotypes, the critical temperature sum of bud burst (TScrit) varying at each location from 80 to 260 d.d. with an increment of 20 d.d. between two adjacent genotypes. Two arbitrary levels of the fixed risk of frost damage (0.3 and 0.5) are indicated with two corresponding horizontal dotted lines. In each case, the optimal genotype is identified as the value of TScrit where the computed line crosses the horizontal line.

ered, namely 0.3 and 0.5. In the case of the higher risk level, the genotypes with maximum overall adaptedness were nearly the same in all climatic conditions, i.e. the genotypes with TScrit between 80 an 100 d.d. At the lower risk level, the maximum overall adaptedness was found both in the southern continental and southern boreal climates in genotypes with TScrit between 120 and 140 d.d., whereas in the northern boreal climate the genotype with the maximum overall adaptedness had considerably later bud burst (TScrit between 180 and 200 d.d.).

An alternative possibility for identifying the optimal genotype with maximum overall adaptedness in a certain climate is the tradeoff principle, i.e. that both the timing of the beginning of the growing season (capacity adaptation) and the risk of occurrence of frost damage (survival adaptation) have quantitative effects which are related to each other. When the levels of overall adaptedness of two given genotypes are compared, it can be postulated that the genotype with earlier timing of bud burst always has higher adaptedness through capacity adaptation, and the genotype with lower risk of frost damage always has higher adaptedness through survival adaptation. The logical outcome is that if it were possible to decrease the frost damage risk and simultaneously accelerate the bud burst, the overall adaptedness would automatically increase. In the opposite case, increased frost risk and simultaneously delayed bud burst would always decrease the overall adaptedness. In the actual situation, however, decreased frost damage risk is generally connected with later bud burst and vice versa, if the climatic conditions remain the same. In this case, if the advance

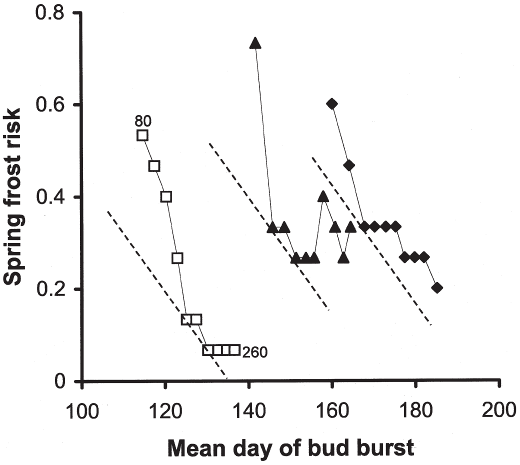

Fig. 3. As Fig. 2, but the predictions of the tradeoff principle. In each case, the optimal genotype is identified as the value of TScrit where the computed line crosses the arbitrarily selected sloping dotted preference line.

in bud burst is sufficient to compensate for the increased risk of frost damage through increased capacity adaptation, the overall adaptedness will increase or remain the same, and otherwise it will decrease.

In Fig. 3, the relationship between the length of the growing season (determined by the timing of spring bud burst) and the risk of frost damage is described by a tradeoff function. For simplicity, this function is presented by a straight line, i.e. the preference line, the slope of which has been chosen arbitrarily and is assumed to remain constant in all climatic conditions. The behavior of all genotypes which are located on this line, are assumed to represent equal adaptedness, i.e. their relationship between survival and capacity adaptation is equal. Consequently, genotypes located closer to origin, compared to the line, have higher overall adaptedness, and those located further from origin have lower overall adaptedness. Therefore, in each climate considered, the highest adaptedness can be found at a point (or points) where the preference line situated as close to origin as possible crosses the curve describing the performance of all possible genotypes in that climate. In the example described in Fig. 3, the maximum adaptedness in the southern continental climate is found in genotypes with relatively late bud burst (TScrit ≈ 160–200 d.d.). Conversely, in southern boreal and northern boreal climates, the genotypes with much earlier bud burst (TScrit ≈ 100–140 d.d.) have the maximum adaptedness.

In the examples presented above, the principles describing two contrasting theories on the climatic adaptation of the timing of bud burst are demonstrated by using arbitrarily selected threshold values or preference functions. Therefore, the examples can be considered to represent the conceptual differences between these two theories, rather than actual quantitative relationships. However, these examples can be used to indicate the qualitatively different predictions of different theories of adaptation for genetic differentiation. If the climatic adaptation of the timing of bud burst is dependent on the fixed threshold of the risk of spring frost damage, as assumed in Fig. 2, then in the northern climates the highest overall adaptedness would occur in genotypes with later bud burst (higher temperature sum threshold) compared to the southern continental climates, where the absolute frost risk is generally lower. On the contrary, if the adaptation is determined by the tradeoff between the avoidance of spring frost risk and the early beginning of the growth period (Fig. 3), then the adaptation might favor genotypes with late bud burst in the southern climates. This is due to the fact that in a continental climate, the rise of temperature in spring is relatively rapid, and therefore late bud burst is connected with low risk of frost damage. On the contrary, in more maritime climates, more variation occurs in spring temperature conditions. In this case, late bud burst does not automatically result in the avoidance of frost damage and therefore genotypes with early bud burst would be favored in adaptation, since they can better utilize the growing season without increasing their frost damage risk compared to the genotypes with later bud burst.

As stated above, the results from common garden experiments on Norway spruce have shown a general trend where the temperature sum requirement for bud burst is related to the latitude of origin, i.e. the bud burst occurs in southern provenances later than in northern ones, when grown at uniform conditions (Beuker 1994, Hannerz 1994, Leinonen, unpublished). Despite the general awareness of this trend, little attention has been paid to its evolutionary background. A general argument concerning the geographical adaptation of the bud burst of trees is that maritime origins have a high temperature sum requirement for bud burst, since the natural selection has favored genotypes which can avoid spring frost damage, the risk of which is high due to high variation in spring temperatures (Leinonen 1996). However, for example in the case of Norway spruce, the highest temperature sum requirement has been found in central and eastern European origins, which can be considered to represent a continental rather than a maritime climate (e.g. Beuker 1994, Hannerz 1994).

According to the simple climatological calculations presented above, if natural selection would only favor genotypes that minimize the risk of spring frost damage, genotypes with early bud burst would be favoured in southern (or continental) climates, not in northern, more maritime climates (Fig. 2). However, this trend is opposite to the empirical observations, at least in the case of Norway spruce. Instead, the theory of adaptation based on the tradeoff principle produces results that fit the observations more closely (Fig. 3). Thus, it seems probable that the stabilizing selection on the timing of bud burst works by following the tradeoff principle, rather than by maximizing the length of the growing season on the condition that a fixed risk of frost damage is not exceeded.

Since spring frost damage can probably not be totally prevented by the adaptation towards late bud burst, it is likely that the optimal adaptation is a compromise of reasonable frequency of the occurrence of damaging frosts and a sufficiently long growing season. The relation between these two factors is likely to be dependent on the species. In the case of species that tolerate frost damage or have good recovery potential, the length of the growing season may be a more important driving force of adaptation than the avoidance of damage. In such species, based on the analysis presented in this study, the slope of the preference line in Fig. 3 would be rather steep, thus favoring genotypes with early bud burst. Correspondingly, in species with poor tolerance of frost damage, genotypes with late bud burst would be favored. In all cases, however, the relative overall adaptedness of each genotype would be determined by the prevailing climatic conditions and would therefore lead to geographical genetic differentiation.

The theoretical analysis described in this paper can be considered to be a possible starting point in quantifying the mechanisms of climatic adaptation. In order to keep the analysis as straightforward as possible, several simplifying assumptions have been made. First, only the timing of bud burst has been taken into account in determining the length of the growing season. However, also the timing of growth cessation varies between the provenances of Norway spruce, and may also be genetically linked with the bud burst (e.g. Skrøppa et al. 1995). On the other hand, these facts do not necessarily contradict the premises of the analysis, according to which the timing of bud burst affects length of the growing season and is also a subject of climatic adaptation.

Second, in the analysis based on the tradeoff approach, the slope of the preference line is assumed to be dependent only on the tree species, and to be similar for all provenances. If this is true, there should be no between-provenance differences for example in the level of frost hardiness at the time of bud burst, or in the potential for recovery from frost damage. If such differences occur, different tradeoff functions should be used for different provenances.

Third, in the example presented in this study, the shape of the tradeoff function is assumed to be linear. However, in reality this is not necessarily the case. It is likely that when the frost risk is extremely high, it is no longer possible to compensate the growth loss caused by frost damage through prolonged growing season. In that case, the overall adaptedness of each genotype might be determined by the absolute frost risk threshold (Fig. 2) rather than by the tradeoff function. On the other hand, if the growing season is very short, early bud burst might be relatively more important than the avoidance of frost damage. Therefore, it is also possible that preferred relationship between the frost risk and the timing of the onset of the growth period varies between different climates.

The aspects discussed above should be taken into account in further development of models for climatic adaptation. In addition, more data than utilized in this study should be used in order to properly evaluate the modelling approaches. Such data should include long term climatic observations from various sites and information on phenological patterns from corresponding tree provenances.

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