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Variation in Temperature Sum Requirement for Flushing of Beech Provenances

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Dedicated to G. H. MELCHIOR to his 70th birthday

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Summary

The time of bud-burst of provenances of beech (Fagus sylvatica L.) is important especially on sites with frequently occurring late frosts. On a field trial in the nursery of the Institute of Forest Genetics at Grosshansdorf, Germany, the time of budburst was scored in 2 different ways on 158 3 year old provenances representing most part of the natural distribution of beech. Also the air temperatures were logged to calculate temperature sums at the time of bud-burst. A cline became evident with provenances from the east and south-eastern part of the range of distribution to flush early and provenances of the western part of the range to flush late. Also provenances from higher elevations tend to burst bud earlier than those from lower elevations. At a base temperature of 5 °C starting from January 1st early flushing provenances require 8,500 degree hours for bud-burst whereas late flushing provenances require 11,000 degree hours. Averagely 9,750 degree hours were required for bud-burst. The first single trees to flush required 7,600, the last 14,750 degree hours before bursting bud. According to the local risk of late frost occurrence during the period when the freshly flushing beech leaves are prone to frost it can be predicted which provenances could be potentially planted without late frost risk at a certain site and for which the late frost risk is too high.

Key words: Fagus sylvatica L., bud-burst, flushing, temperature sum, provenance variation, phenology.

FDC: 165.53; 181.22; 181.8; 232.12; 176.1 Fagus sylvatica.

Introduction

Many studies of temperate tree species have shown that the character "bud-burst" is highly heritable and the time of flushing of populations relative to another between years is highly correlated (e.g. Worrall, 1983, 1993; von Wuehlisch et al., 1995). This results from the adaptation to the local climate allowing the trees to flush early enough to profit from the favourable spring and early summer growing conditions but flushing late enough not to be at too high a risk of late frost damage. Also beech (Fagus sylvatica L.), a species covering large areas in Central, Western, and Southern Europe is known to flush differently in the different regions (BORGHETTI and Giannini, 1982; Muhs, 1985; Reck, 1972; Šindelář, 1985; SITTLER, 1982; Teissier du Cros et al., 1988; Thomasius and GÄRTNER, 1985). Generally, provenances from higher elevations and more eastern origin flush earlier than populations from lower elevations or atlantically influenced areas (Muhs, 1985; MADSEN, 1995; VON WUEHLISCH et al., 1993, 1995). This adap-

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tive behaviour corresponds to that found in other temperate and northern tree species. The timing of bud-burst is controlled by night length and more important by temperature. High correlations between time of bud-burst and temperature sums (degree-days; e.g. Sarvas, 1974; Cannell and Smith, 1983; Campbell, 1974, 1980; Eriksson et al., 1978; Hannerz, 1994; Heide, 1993a; Owens et al., 1977). Hunter and Lechowitz (1992) demonstrated for a number of species and Heide (1993b) for beech that bud-burst timing is influenced also by the amount of chilling during the dormant period preceding bud-burst.

Aim of the study is to estimate the variation in temperature sum requirement for bud-burst in three year old provenances of beech covering most part of the natural distribution range of beech in Europe.

Material and Methods

Seed samples of 158 stands throughout Europe were collected and seeded in a nursery at the institute in Grosshansdorf. After one growing period the plants were transplanted at a spacing of 20 cm in the rows and 60 cm between the rows in 2 replications 1 each on 2 nursery fields lying about 400 m apart. After letting the plants adjust to the site for 1 growing period and 2 winters the time of bud-burst was scored in 2 ways. In daily (sometimes 2 days) intervals, the day of bud-burst (score 3) was recorded on each of maximally 20 trees of the 2 replications. In the other method the same set of trees was scored by a 5-step scale on 1 specific day only. This was the presumed day on which most plants had reached the score of "3".

The following scale was applied which is the same as in earlier scorings (VON WUEHLISCH et al., 1993, 1995). In each case the earliest flushing buds were scored irrespective of their position:

- 1 = Dormant winterbud
- 2 = Buds expanding
- 3 = Bud-burst (first green is visible)
- 4 = Leaves are flushing
- 5 = Leaves are fully expanded

On 1 of the 2 nursery fields a weather station was installed which recorded air temperatures 5 cm above ground electronically and calculated half-hour-means. The temperature sums were calculated as the sum of only the differences of the half-hour temperatures above a base temperature of 0 °C, 4 °C, 5 °C, and 6 °C. Because as base temperature often 5 °C is given, this has been done here too. By dividing the half-hour-means by 2, degree hours were calculated which is the unit used frequently in phenological data. During 1 week in March the weather station had a technical defect and the missing data had to be interpolated. For statistical analysis, SAS Procedures (1990) were used.

Results

After a winter with more or less "normal" temperatures, the spring temperatures were lower than average until 20th of April. Afterwards temperatures increased sharply resulting in a strong increase of degree hours (Figure 1). First trees burst buds (score 3) on April, 25th, last trees 28 days later on May, 23rd. Provenance means ranged from April, 30th to May, 9th spanning only 9 days which may be the result of the strongly increasing temperatures after 20th of April. Average day of all provenances to burst bud was May, 5th. The WALLER-DUNCAN multiple range test shows that provenances breaking bud with more than about 2 days difference differ significantly at

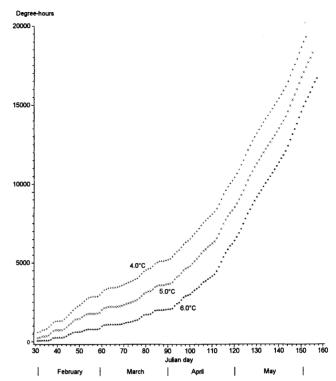


Figure 1. – Development of temperature sums at base temperatures of $4\,^{\circ}\mathrm{C},\,5\,^{\circ}\mathrm{C},$ and $6\,^{\circ}\mathrm{C}$ at the nursery in Grosshansdorf 1995.

 $p < 0.001 \ (not \ presented), \ bud-burst on the field with a shallow slope being earlier.$

In terms of degree hours the first trees that burst bud had a temperature sum requirement of 7,600, the last trees one of 14,750 degree hours at a base temperature of 5 $^{\circ}$ C (*Figure 1*). The first provenance to break bud had a temperature sum requirement of 8,500, the last provenance one of 11,000 degree hours. The average of all provenances was reached at a temperature sum of 9,750 degree hours.

The values of the 2 replications growing on 2 nursery fields compared very well and gave a high correlation (not presented). The one field is located on a flat part of land retaining cold air whereas the other field is located on shallow slope allowing cold air to flow off. Although the fields are at the same elevation and only 400 m apart this small topographical difference causes a difference in bud-burst of one day which is statistically highly significant, the bud-burst on the field with a shallow slope being earlier.

Correlations between the 2 ways of recording bud-burst gave a close relationship $(Table\ 1)$ showing that scoring of provenances just on 1 day with a 5-step scoring system gives a relatively precise result. This is important in provenance testing where frequently a test site is located at a distant place which cannot be observed continuously over the period from

Table 1. - Correlations.

	BB-Scoring*	TempSum 0°C	Longitude	Latitude	Elevation
BB-Day*	-0.91***	0.91***	-0.45***	0.30***	-0.32***
BB-Scoring			0.44***	-0.19*	0.30***
TempSum 0°C			-0.43***	0.32***	-0.36***
Longitude				-0.08	0.15
Latitude					-0.72***

 \overline{n} =158, *)p<0.05, ***)p<0.001; BB-scoring=according to the 5-step-scale, BB-day=the day when a plant has reached bud-burst (score 3 of the 5-step-scale) ¹) the relationship of BB-Day and BB-Scoring is inverse, a low BB-Day is related to a high BB-Score and vice versa.

the flushing of the first to the last trees (28 days difference in this trial).

Correlations of bud-burst with the geographical parameters longitude, latitude, and elevation give differing correlation coefficients (Table 1; Figure 2). Relatively close is the correlation with longitude, showing that provenances from eastern regions generally flush earlier than those from the west. Both latitude and elevation have an effect on bud-burst but it is lower than longitude. Provenances from higher elevations tend to flush earlier than those from lower elevations. These results prove results from many earlier findings. However, the correlation between bud-burst and latitude is not expected in this way. It shows that provenances from lower latitudes (south) tend to flush earlier than those from higher latitudes (north).

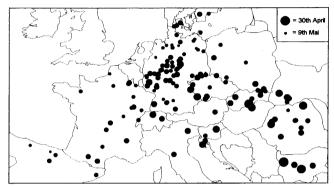


Figure 2. – Time of bud-burst of 3year old plants of 158 provenances at Grosshansdorf 1995. The size of the dots indicates the time of bud-burst. Large dots represent early flushing and low temperature sums, small dots represent late flushing provenances with higher temperature sum requirement.

Since temperature sum is closely related to the recorded day of bud-burst (BB-day), correlations between temperature sum and geographical parameters (longitude, latitude, and elevation) correspond well (*Table 1*).

The regression of the mean Julian day of bud-burst on longitude, latitude, and elevation is significant (R^2 =0.28). Longitude east has a positive sign, longitude west is negative.

Expected BB-day = 121.5-0.13 (degrees longitude E) + 0.12 (degrees latitude N) -0.1 (elevation in units of 100 m)

This regression equation shows that provenances originating from one degree more east have bud-burst 0.13 days earlier and per one degree latitude north 0.12 days later. Each 100 m increase in elevation of a provenance results in an earlier bud-burst of 0.1 day.

The regression of the temperature sums reached at the mean Julian day of bud-burst on the same regressor variables as above is also significant (R2=0.28).

Expected degree-hour=67-292 (degrees longitude E) + 249 (degrees latitude N) -320 (elevation in units of 100 m)

Provenances originating further east require 292 degree hours less per one degree longitude in order to flush. Provenances originating further north require 249 degree hours more before they can flush and 100 m increase in elevation of a provenance results in lower temperature sum requirement of 320 degree hours. The regression equations are valid only within the range of the material investigated.

Discussion

The distribution of the day of bud-burst of the different provenances shows the general east-west trend which has been found in earlier studies (Muhs, 1985; Madsen, 1995; von Wuehlisch et al., 1993, 1995). Very early flushing provenances occur at the eastern edge of the distribution, very late flushing provenances occur at the oceanically influenced western edge. In the central part of the distribution there is not always such a clear clinal distribution which might be the result of different influences, probably mainly the variability of local climatic conditions and the different elevations at which beech occurs.

The correlation analysis as well as the regression analysis show an unexpected relationship between bud-burst and latitude, demonstrating that southern provenances flush earlier than those from the north which is the reverse of what is usually found in other species (CAMPBELL, 1974, 1980; ERIKSSON et al., 1978; HANNERZ, 1994; WORRALL, 1983). The reason for this is probably the distribution of beech extending in a north-west to south-east direction from a mild oceanic climate in the north west (high temperature sum requirement) to a continental climate in the south east (low temperature sum requirement). The adaptation process during migration after the ice age seems to be different from other species. However, in 34 Quercus petraea provenances LIEPE (1993) found a trend similar to that in this study.

The variation in temperature sum requirement for bud-burst is very large with about twice the number of degree hours between the first (7,600) and the last trees to flush (14,750 degree hours). Also between the provenances large differences were found (range 8,500 to 11,000 degree hours). The values given here have been recorded on three year old plants which are known to flush earlier (e.g. in *Picea abies* von Wuehlisch and Muhs, 1986) and thus have a smaller temperature sum requirement than older plants. The temperature sums given might therefore be low. Also by scoring the first buds to burst irrespective of their position on the plant might lead to slightly lower temperature sum values.

The calculation of temperature sums gives comparable values which are expected to be independent of the year to year variation in weather and the local conditions. Thus predictions of the risk of late frosts become possible if a record of the weather at a certain place exists and the temperature sum requirement of a provenance is known (Cannell and Smith, 1983; Campbell, 1974, 1980; Hannerz, 1994; Hunter and Lechowitz, 1992).

The character "bud-burst" is known as a character with a high heritability. It is also a highly adaptive character. Because it is so relatively easy to score, it has been widely recorded and used as a reference for adaptedness. It may be assumed that when a provenance is frequently struck by late frosts because it flushes too early (too low temperature sum requirement for bud-burst) it is probably also not adapted to that site in other characters.

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Investigations on the Genetic Variation of Beech (Fagus sylvatica L.) in Bavaria

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Summary

Using isozyme analysis the microgeographic genetic variation of beech in Bavaria is evaluated. Justification, goals and methods of this study are presented. For 20 populations (old beech stands) allele frequencies, genetic multiplicity and diversity values and genetic differentiation values are presented. The mean number of alleles per locus was 2.51, the gene pool diversity, v, varied from 1.27 to 1.35. The genetic variation within the stands is quite large and the variation between populations low. Less than 2% of the total diversity can be attributed to genetic differences among populations of beech. The vast majority of allelic variation (98%) resides within individual stands.

Key words: Beech (Fagus sylvatica L.), Bavaria, isozyme analysis, genetic variation.

FDC: 165.3; 165.5; 176.1 Fagus sylvatica; (430).

Introduction

Polymorphic isoenzymes, whose genetic control is known, are increasingly being used to describe and quantify the genetic variation of forest tree populations (BERGMANN, 1991; MÜLLER-

STARCK, 1991; MÜLLER-STARCK et al., 1992). This is also true for beech where the genetic control of numerous enzyme systems has been clarified (MÜLLER-STARCK and STARKE, 1993) and which can be implemented for a genetic inventory.

Up to now little differentiation between beech stands in central Europe has been found, however there is considerable variation within stands (see summary in MÜLLER-STARCK et al., 1992; PAULE, 1992; HATTEMER et al., 1994). In the southern distribution range of beech in Europe Comps et al. (1991a and b) found a higher degree of differentiation than in the northern part. The authors suggested that this was due to more heterogeneous ecological conditions and an older age of the investigated stands. At 2 gene loci selection was found to correlate to climatic factors. Further correlation between genetic structure and provenance location could not be found. Selection processes, gene flow, mating system, historical factors are suggested as possible causes for the differentiation, although it was not possible to rank this factors according to their significance (COMPS et al., 1991a; PAULE, 1992). Little information on the pattern of variation within smaller, but heterogeneous regions is available. An inventory study on the variation of

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