

PHENOLOGY OF NATURAL SWEDISH POPULATIONS OF *PICEA ABIES* AS COMPARED WITH INTRODUCED SEED SOURCES

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ABSTRACT

The phenology of 108 Swedish and 16 north-eastern and central European Norway spruce provenances was studied in a short-term field experiment in central Sweden. Spring frost injury was strongly related to bud flushing stage. With increasing latitude and altitude, bud set and bud flushing started earlier, while early height growth and the proportion of trees having proleptic growth decreased. Based on multivariate analysis, three major provenance zones were distinguished: central European, Swedish south of latitude 60 ° together with the Baltic States and Belarus, and northern Swedish. In northern Sweden, phenology varied more among populations and was more attributed to clinal latitudinal variation than in southern Sweden. The transitional point between the two different patterns was at approximately latitude 60 °. We interpret this divergence as effects of immigration history and differences in gene flow and natural selection intensity within Sweden. A gene conservation programme should include more populations from northern than from southern Sweden.

Key words: *Picea abies*, phenology, clinal variation, adaptation.

INTRODUCTION

It is currently being debated whether gene conservation should be performed in situ or ex situ via breeding (ERIKSSON 1994). In both gene conservation and breeding it is important to capture existing adaptedness and create good opportunities for adaptation to future conditions and for future evolution. To enable this, it is important to know the amount of variation within and among populations in adaptive traits. Studies of growth rhythm, *i.e.* the timing of the period of active growth, are particularly important. It is important that plants are in active growth only when the risk for frost is low, and that plants are hardy when the risk for frost is high.

As Norway spruce (*Picea abies* (L.) Karst.) is in nature a climax species but is artificially regenerated as a pioneer species, growth rhythm is particularly critical. Whereas bud flushing and shoot elongation require a certain accumulated temperature sum (SARVAS 1973), growth cessation and hardening are initiated by the photoperiod and are influenced by temperature and light intensity (DORMLING 1973, 1979; KOSKI & SIEVÖNEN 1985). Phenological traits in Norway spruce exhibit a clinal pattern with latitude and altitude as the major determinants (EKBERG *ET AL.* 1979, WEISGERBER 1979, GIERTYCH 1979, PERSSON & PERSSON 1992). However, there is a large variation within provenances in growth rhythm, which is often larger than the varia-

tion among populations (*e.g.* EKBERG *ET AL.* 1982, SKRØPPA 1982, EKBERG *ET AL.* 1985). Growth rhythm and its variation among and within populations change dramatically with age during the seedling stage (EKBERG *ET AL.* 1985, VON WUEHLISCH & MUHS 1986).

The common opinion is that Norway spruce has spread from a few refugia to its vast European distribution after the glacial period (SCHMIDT-VOGT 1977, LAGERCRANTZ & RYMAN 1990). The species invaded into Scandinavia from north-east after having passed a bottleneck point in northern Sweden (SCHMIDT-VOGT 1977). Additional immigration could have occurred across the Bothnian Bay or the Bothnian Sea in the northern part of the Baltic (PERSSON 1975, HUNTLEY & BIRKS 1983, KRUTZSCH 1986, SEGERSTRÖM 1990). Nevertheless, the Baltic has prevented gene flow from Eastern-European populations and facilitated differentiation from these populations. The natural invasion of the species has not yet reached the southernmost parts of Scandinavia.

In Sweden introduced provenances of Norway spruce have been used on a massive scale during the last century. It was early acknowledged that considerable gains in yield could be obtained from using Norway spruce of foreign origin, and from the middle of the 19th century spruce originating from the mountainous parts of Germany was widely used in southern Sweden (KIELLANDER 1953). Later, provenances from

Romania and Belarus were imported on a large scale (LANGLET 1960, PERSSON & PERSSON 1992). Consequently, successive generations of the indigenous spruce have gradually become more scarce and influenced by foreign pollen. Thus, a gene-bank project was initiated in 1983 consisting of 73 evenly distributed, presumably indigenous stands, from which seed lots were harvested. The material offers a unique possibility to obtain a fine-grained grid of the variation of Norway spruce in Sweden. The material was used to study the provenance variation in bud set (KRUTZSCH 1986, 1988). Now we present more data on growth rhythm and early growth capacity in the gene-bank material.

The objectives were to find how growth rhythm, with emphasis on bud-flushing phenology and growth capacity varies among indigenous Swedish populations of Norway spruce. Based on this variation, discrete provenance zones should be delineated. The relationship between bud-flushing phenology and susceptibility to late spring frosts was also to be elucidated. The pattern of variation within Sweden was compared with the performance of provenances from eastern Europe.

MATERIAL AND METHODS

A total of 107 Swedish Norway spruce seed sources were studied along with 16 provenances representing four zones (FOTTLAND & SKRØPPA 1989) of the species' distribution in Europe: the North-eastern continental (eight Belarussian, one Latvian, two Estonian provenances), the Tatra Mountains (one Slovak provenance), the Carpathian Mountains (two Romanian provenances) and the central Alps (two Austrian provenances) (Fig. 1). The main category of the experimental entries was a seed mixture from a natural stand. Thirty four of the Swedish seed sources were from the Swedish Forest Gene Bank collections, five were seed mixtures from seed orchards containing clones of southern Swedish origin and 69 were samples from commercial harvests in natural stands.

Swedish provenances, except the southern ones, were pooled into regions of approximately 1° of latitude wide. In southern Sweden a region corresponds to a seed collection area, which approximately covers a municipal district. For the non-Swedish origins, regions are averaging the location of the experimental entries in a corresponding part of a country.

The seed sources and the seedlings were part of the material that was used for studying bud set in the nursery of Trekanten (latitude 56°43') by KRUTZSCH (1986, 1988). The sowing into 50 ml 'Hiko' containers took place in spring 1985 and bud set was assessed during May 15 to September 21. In spring 1987 the selected seedlings were planted in a fenced short-term

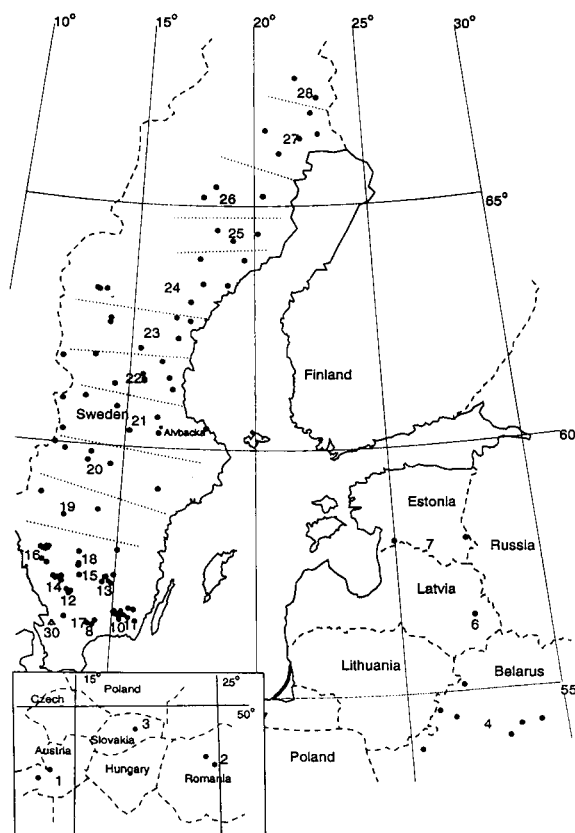


Figure 1. Location of the provenances. Numbers represent regions of provenances, dots - provenance location. Region borders within Sweden are delineated by dot line. Location of the nursery trial in Ålvbacka, central Sweden is marked by an asterisk. Provenances from region 30 in southern Sweden (marked by triangle) are second generation western German populations.

trial in the Ålvbacka experimental nursery (60°15' N, 16°01' E, 110 m a.s.l.). The experimental site was situated in a slope on silty arable land. The trial was designed as five randomised complete blocks with single-tree plots spaced at 1 × 0.5 m. Five seedlings per provenance were randomly allocated within a block. A provenance was represented by 25 seedlings. The trial was neither thinned nor fertilised.

The trial was measured in spring and summer of 1989, spring of 1990 and summer of 1994, when the seedlings were 4-, 5- and 9-years-old, respectively. In spring and summer of 1989 terminal bud flushing of the leader, seedling height and occurrence of prolepsis were assessed in all five blocks. Observations on bud flushing were made according to the scale developed by KRUTZSCH (1973) on May 30 and June 17. The class 3 was considered as corresponding to bud burst, *i.e.* with the tips of the needles emerging from the bud.

Occurrence of prolepsis and seedling height were

Table 1. Description of the variables.

| Variable | Abbreviation | Assessed | Transformation |
|---|--------------|------------|----------------------|
| Bud flushing stage (0–7) | BUDF89–1 | 1989.05.30 | $\arcsin(x/6)^{1/2}$ |
| Bud flushing stage (0–7) | BUDF89–2 | 1989.06.17 | $\arcsin(x/6)^{1/2}$ |
| Bud flushing stage (0–7) | BUDF90a | 1990.05.08 | $\arcsin(x/6)^{1/2}$ |
| Provenance proportion of seedlings with prolepsis | proIEP | 1989.08.25 | none |
| Seedling height | h89 | 1989.08.25 | $\log(x)$ |
| Seedling height | H94 | 1994.07.14 | $\log(x)$ |
| Natural spring frost injury | fROST90 a | 1990.05.21 | $\arcsin(x/5)^{1/2}$ |
| Vitality | VIT | 1994.07.14 | $\arcsin(x/4)^{1/2}$ |
| Proportion of seedlings with double stem, double top or spike knot | dDOUBLE94 | 1994.07.14 | none |
| Days from the 1st of April till 75% of seedlings per provenance set bud (KRUTZSCH 1986) | BUDSET85 | 1985 | none |

assessed on August 25, 1989. Height was measured from the root collar to the top bud.

The bud flushing assessment was repeated on May 8, 1990. Immediately after this assessment a severe natural spring frost occurred. On May 21, frost injury was scored using the following scale:

- 0 – no injury;
 - 1 – lateral shoots injured, terminal not;
 - 2 – slightly injured terminal shoot, laterals not;
 - 3 – moderately injured terminal, laterals also injured;
 - 4 – severely injured terminal, laterals also injured;
- All the measurements in 1990 were made on 3 blocks only.

On July 14, 1994 seedling height, vitality and presence of defects were assessed. The vitality was estimated according to the following scale:

- 0 – healthy seedling;
- 1 – brown needles on the top shoot (the shoot alive);
- 2 – top shoot dead;
- 3 – whole seedling severely damaged;
- 4 – dead seedling;

Seedlings with double stem, double top or spike knot were classified as 1, undamaged as 0.

A variable reflecting bud set of the 1-year-old provenance seedlings from KRUTZSCH's (1986) study was used together with the new data in multivariate analysis of the provenance variation pattern.

For the variable reference and transformations made see Table 1.

Statistical analysis

Statistical analysis were performed using the SAS statistical package (SAS Institute Inc. 1987).

Provenance mean value in each replicate was used as the unit of observation in the mixed model analysis of variance (ANOVA) for bud flushing, frost injury

and seedling height. The following model was used:

$$Y_{ijk} = \mu + B_i + R_j + P_{k(j)} + e_{ijk}$$

where: Y_{ijk} is an observation, μ is total mean, B_i is fixed block effect, R_j is fixed region effect, $P_{k(j)}$ is random effect of provenance within a region, e_{ijk} is random error. The provenance mean values of the scoring variables in each replicate were arcsine square root transformed to normalise the residuals and homogenise the variances. For seedling height a logarithmic transformation was used (Table 1).

Linear regression analysis was used to study the relationship between frost injury and bud flushing stage at the provenance level by the following model:

$$\text{FROST90} = b_0 + b_1 \text{BUDF90} + e$$

where: b_0 is intercept, b_1 is regression coefficient. Residuals from this model were normally distributed. Residual plot against the predicted values did not indicate any trend, which shows that the model was linear at the provenance level.

Canonical Correlation Analysis (CCA) (for theory see MANLY, 1994) was used to assess geographical variation of the provenances in the set of phenological traits. Longitude was not used in the CCA. We think it is of minor influence to the variation of the sample provenances in this study. Variables that were not normally distributed were transformed (Table 1). CCA was used to delineate provenance zones. To obtain more fine-grained subdivision, cluster analysis by Wards minimum variance method was employed followed by Discriminant Function Analysis (DFA), at the provenance level to see how well it is possible to separate the sub-zones that were emerging from the clustering. DFA calculates Mahalanobis distances,

Table 2. Result of the mixed model ANOVAS with the Swedish provenances. The F-values were calculated by selecting appropriate error terms for fixed and random effects. The p-values of the F-tests are given.

| Source | d.f. | BUDF90 Pr>F | FROST90 Pr>F | d.f. | BUDF89-1 Pr>F | BUDF89-2 Pr>F | H89 Pr>F | H94 Pr>F |
|-----------|------|----------------|-----------------|------|------------------|------------------|-------------|-------------|
| Region | 20 | 0.0001 | 0.0001 | 20 | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| Prov(Reg) | 84 | 0.0001 | 0.0246 | 84 | 0.0001 | 0.0001 | 0.0001 | 0.1961 |
| Block | 2 | 0.2312 | 0.0003 | 4 | 0.0001 | 0.0001 | 0.0003 | 0.0001 |
| Error | 204 | | | 394 | | | | |

which takes into account population variances and among-variable covariances, for each individual (provenance mean) to the class centre (cluster centre) and assigns it to the class that was the closest. Canonical Discriminant Functions (CDF) provide useful information on variable contribution to among class (cluster) variation. The first CDF1 gives the maximum possible F ratio on a one-way ANOVA of the between and within group variation. The second CDF2 gives the maximum possible F-ratio subject to the condition that it is not correlated with CDF1.

RESULTS

Analysis of variance and correlations

Analysis of variance of Swedish provenances revealed that the provenance phenological variation was attributable in high degree to region of origin (Table 2). The effects of provenance within region and replication were significant for most of the traits. Analysis of all provenances yielded very similar results as the ANOVA of Swedish provenances only.

Correlation coefficients among the properties and between the properties and the geographical variables, based on provenance means, are presented in Table 3. Provenance ranking in bud flushing at 1989 and 1990 was stable. Bud set at the year of sowing (DAT75PBS) predicts the further phenological performance well.

Relationship of provenance bud flushing with natural spring frost injury.

At the provenance level, frost injury class was strongly linearly dependent on bud flushing stage ($R^2=0.69$, the regression function is $FROST90 = -0.25 + 0.85 BUDF90$). The earlier the flushing, the more severe the injury. According to the regression function, an increase of the bud flushing stage by 0.5 led to an increase in frost injury class by 0.24.

The plot of region means against the bud flushing and frost injury (Fig. 2) shows that the early flushing northern Swedish regions from latitude 61° to 68°

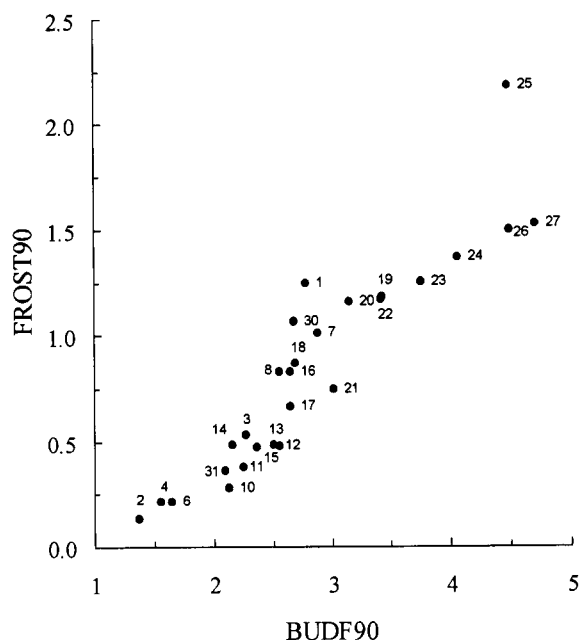


Figure 2. Relationship between natural spring frost injury class (FROST90) and bud flushing stage (BUDF90). The dots represent region means labelled by region numbers.

(regions from 23 to 27) exhibited the heaviest frost injury. In contrast to the southern zones, the origins in this zone were relatively uniform in frost injury, but varied much in bud flushing. Hardiness does not vary much once bud flushing stage three or four is reached. The provenances from Belarus, Latvia and Romania (regions 4, 6, 2 respectively) had the latest flushing and the lowest injury. The intermediate zone included the origins from Slovakia, Austria, Estonia (regions 3, 1, 7 respectively) southern and central Sweden (regions from 8 to 22) and the seed lots from Swedish seed orchards (31), which flushed earlier, what resulted in heavier injury than that of the Belarussian, Latvian and variation in frost injury with a non-linear dependence of the injury class on the flushing stage. However, when all the material was used in the regression analysis, the statistical tests on residuals proved a linear relationship.

Table 3. Pearson correlation coefficients among the traits based on provenance means ($n = 121$). The critical values for the significance levels with d.f. = 119 are the following: 0.179 ($p = 0.05$), 0.233 ($p = 0.01$), 0.296 ($p = 0.001$).

| Variable | BUDF 89-1 | BUDF 89-2 | BUDF90 | FROST90 | H94 | H89 | BUDSET 85 | PROLEP | VIT |
|-------------------|--------------|--------------|--------|---------|-------|-------|--------------|--------|-------|
| BUDF89-2 | 0.97 | | | | | | | | |
| BUDF90 | 0.90 | 0.91 | | | | | | | |
| FROST90 | 0.85 | 0.83 | 0.83 | | | | | | |
| H94 | -0.60 | -0.60 | -0.64 | -0.51 | | | | | |
| H89 | -0.64 | -0.66 | -0.68 | -0.55 | 0.75 | | | | |
| BUDSET85 | -0.74 | -0.74 | -0.78 | -0.57 | 0.71 | 0.75 | | | |
| PROLEP | -0.23 | -0.25 | -0.29 | -0.13 | 0.28 | 0.31 | 0.43 | | |
| VIT | 0.26 | 0.24 | 0.28 | 0.21 | -0.42 | -0.31 | -0.37 | -0.17 | |
| DOUBLE94 | 0.01 | 0.05 | 0.01 | 0.04 | 0.08 | -0.01 | 0.07 | -0.02 | -0.20 |
| LAT ¹⁾ | 0.81 | 0.82 | 0.82 | 0.64 | -0.66 | -0.72 | -0.92 | -0.41 | 0.37 |
| ALT ¹⁾ | 0.30 | 0.35 | 0.31 | 0.22 | -0.33 | -0.44 | -0.47 | -0.18 | 0.26 |

¹⁾ Correlation with Swedish provenances only ($n = 100$). The critical values for the significance levels with d.f. = 98 are the following: 0.197 ($p = 0.05$), 0.256 ($p = 0.01$), 0.324 ($p = 0.001$).

Table 4. Description of the canonical variables for phenological traits (PHEN1) and geographical variables (LOC1) from Canonical Correlation Analysis.

| Variable | Standardised canonical coefficients | | Canonical correlations | |
|----------|-------------------------------------|-------|------------------------|-------|
| | PHEN1 | PHEN2 | PHEN1 | PHEN2 |
| BUDF89-1 | -0.19 | | 0.84 | |
| BUDF89-2 | 0.44 | | 0.86 | |
| BUDF90 | 0.08 | | 0.86 | |
| FROST90 | -0.01 | | 0.67 | |
| H94 | -0.07 | | -0.76 | |
| H89 | -0.16 | | -0.85 | |
| BUDSET85 | -0.78 | | -0.97 | |
| PROLEP | -0.06 | | -0.43 | |
| | | | LOC1 | LOC2 |
| LAT | | | 1.07 | 0.92 |
| ALT | | | 0.42 | 0.05 |

Geographical variation of the provenances in the set of phenological traits

Correlation (Table 3) and Canonical Correlation Analysis (CCA) revealed that the relationship between the two sets of phenological and geographical variables was significant. The first canonical correlation (between the first two canonical variables of phenological and geographical variables) was 0.95 ± 0.01 . The first canonical variable for the phenological traits (PHEN1) mainly reflects provenance variation in bud flushing and bud set in 1985 (Table 4). PHEN1 contains the most important factors for provenance performance: variation in growth cessation and initiation. Standard-

ised coefficients for the first canonical variable of the location variables LOC1 mainly reflects latitude and to a lesser extent altitude. The geographical variables were positively correlated with their canonical variable (LOC1). As the first canonical correlation between LOC1 and PHEN1 was positive, an increase in latitude and altitude resulted in an increase in PHEN1.

Three major region zones are emerging from the plot of region means of PHEN1 against the canonical variables from CCA (Fig. 3). The lower region zone (labelled as 'I' on the plot) contains central European high altitudinal provenances from Austria, Slovakia and Romania. The southern Swedish together with Baltic

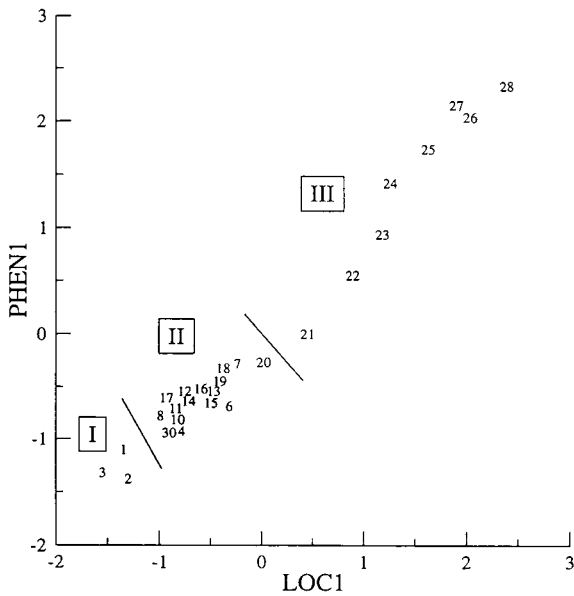


Figure 3. Region variation in the first pair of geographical (LOC1) and phenological (PHEN1) canonical variables from CCA. The numbers represent regions. According to the between regional variation pattern three major groups may be distinguished: the northern (III), the central (II) and southern (I).

and Belarussian origins comprise the largest intermediate zone (II), with a relatively low variation between regions in PHEN1. The northern zone (III) from the latitude 60° (PHEN1 > 0) and northwards, was distinguished by showing strong influence of PHEN1. The clinal pattern with latitude of the provenance variation in PHEN1 is shown in Fig. 4. The altitudinal effect is also obvious in the figure when considering that the altitude in northern Sweden generally increases from east to west.

The clustering followed by discriminant function analysis (DFA) on provenances in the intermediate zone II in the CCA estimated relatively low error variance of the multivariate data matrix; the first two canonical discriminant functions (CDF) describe 92% of the total variation. CDF1 reflects most of the differences between the sub-zones. The canonical coefficients influencing CDF1 were particularly high for bud-flushing variables (Table 5). This means that bud flushing is an important trait for distinguishing provenance sub-zones. The higher the value of the CDF1, the earlier the bud flushing and the bud set, the shorter the seedlings and the higher the spring frost injury. CDF2 is more influenced by seedling height and proleptic growth and was of minor importance for the cluster differentiation. To find a further subdivision within the zone II, the provenances having a value of PHEN1 < 1, except the origins in the zone I from central Europe,

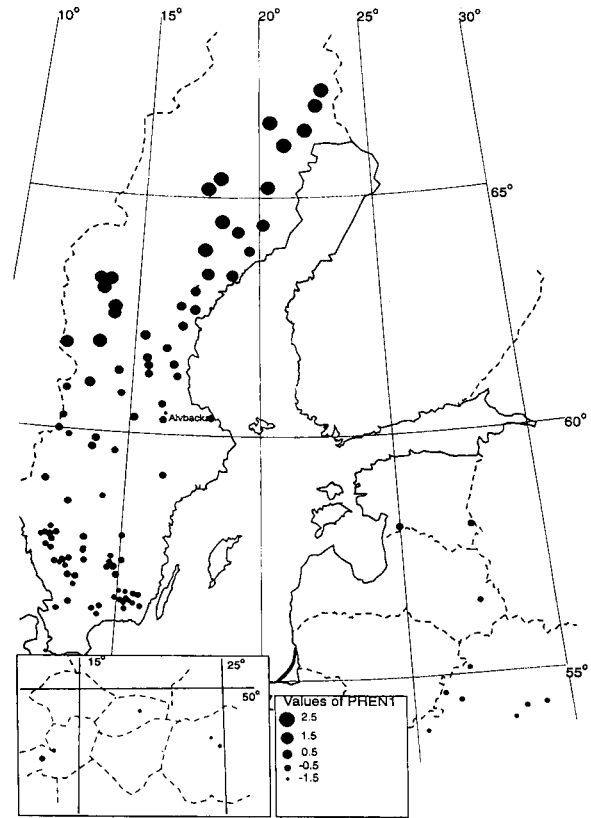


Figure 4. Provenance variation in the phenological performance summarised by the first canonical variable of the phenological traits (PHEN1) from the CCA. Provenance location is represented by dots scaled by the value of PHEN1. High values of PHEN1 basically reflect early bud flushing and set as well as low natural spring frost injury.

were taken for the clustering and DFA. Four new provenance sub-zones emerged (Fig. 5, Table 6):

II.1 – North-Eastern Continental sub-zone represented by origins from north-western Belarus and eastern Latvia, which had the latest bud flushing and set, were little injured by spring frost and had the highest growth capacity of origins in region zone II. The provenances from Estonia performed more like Swedish origins (II.2, II.3).

II.2 – Southern Swedish origins up to latitude 58°, which flushed and set buds earlier and grew somewhat slower than provenances in the sub-zone II.1, as could be expected from the latitudinal cline. The coastal origin from Estonia was assigned to this sub-zone, whereas the continental Estonian one performed similarly to the central Swedish provenances (II.3).

II.3 – Central Swedish provenances behaved as the most northern ones in the region zone II. Bud set was on average later and growth capacity higher than in the southern part of the northern Swedish region zone III (Fig. 5, Table 6).

Table 5. Description of the Canonical Discriminant Functions from Discriminant Function Analysis used for distinguishing provenance zones among origins from the Baltic states, Belarus and Sweden south to latitude 61° N. Eigen value of CDF1 = 5.1, proportion = 0.76.

| Variable | CDF1 | CDF2 |
|----------|-------|-------|
| BUDF89-1 | 0.93 | 0.09 |
| BUDF89-2 | 0.96 | 0.05 |
| BUDF90 | 0.95 | -0.13 |
| FROST90 | 0.87 | 0.14 |
| H94 | -0.36 | 0.48 |
| H89 | -0.41 | 0.73 |
| BUDSET85 | -0.61 | 0.63 |
| PROLEP | -0.10 | 0.26 |

DISCUSSION

Relationships among the traits

Relationships among the phenological traits at the provenance level were strong (Table 3). As being components of the growth rhythm controlled by photo-period and temperature, these traits are strongly intercorrelated (*e.g.* STÅHL & PERSSON 1992, SKRØPPA & MAGNUSSEN 1993, SABOR 1988). Provenance ranking in bud set at the end of the first and in bud flushing as well as final height at the beginning of the sixth growth period under outdoor conditions remained stable. This implies that provenance rank tests for desirable growth rhythm are efficient already at the end of the first growth period. Strong age-to-age correlations at the provenance level in growth rhythm traits of Norway spruce were shown by NANSON (1969, 1987), EKBERG *et al.* (1994), MIKOLA (1988). As shown by DFA, provenance bud flushing and set, together with frost injury class, were the most important traits for

differentiating the provenance sub-zones.

Interpreting provenance variation

Differentiation of the three major region zones (Fig. 3) is in concordance with studies on provenance performance (*e.g.* PERSSON & PERSSON 1992, GIERTYCH 1984, KRUTZSCH 1974, DIETRICHSON 1979) and genetic markers (LAGERCANTZ & RYMAN 1990, SPERISEN *et al.* in press). It also supports the commonly accepted Norway spruce postglacial migration pattern: Slovak, Romanian and Austrian Norway spruce, originating from two refugia in the Carpathians and the Dinaric Alps, performed differently than the northern and north-eastern European populations, which all originate from a common refugium in central Russia (SCHMIDT-VOGT 1977). Owing to late bud flushing, Romanian, Latvian and Belarussian provenances were significantly less frost-injured than the other origins, as was shown by PRESCHER (1982) and VINŠ (1967). In comparison with Romanian and Slovak provenances, Austrian origins from high altitudes resumed growth earlier, which led to severe spring frost injury, and had a large amount of prolepsis, resulting in similar timing of growth cessation as in Romanian and Slovak origins (Fig. 2, Table 6).

Geographical variation of Swedish Norway spruce provenances in phenological traits is essentially clinal over latitude (Fig. 4), in agreement with DORMLING (1973) and EKBERG *et al.* (1979). Provenance seedlings that flush and set buds late were tall and not very susceptible to spring frost injury. North to latitude 60° both bud flushing and bud set changes more markedly with increasing latitude than south to latitude 60° (Fig.3). Similarly in Scots pine, EICHE (1966) and ERIKSSON *et al.* (1980) observed a steep clinal variation in tree survival in northern Sweden. According to DORMLING (1979) above the latitude 60° the critical night length for bud set in Norway spruce also mark-

Table 6. Mean values in original units of provenance zones. Groups No. I, II and III were recognised using Canonical Correlation Analysis, groups II.1, II.2 and II.3 were separated using Discriminant Function Analysis.

| Zone | # of Name prov | BUDF89-1 Mean±s.e. | BUDF89-2 Mean±s.e. | BUDF90 Mean±s.e. | FROST90 Mean±s.e. | H94 Mean±s.e. | H89 Mean±s.e. | BUDSET85 Mean±s.e. | PROLEP Mean±s.e. |
|------|----------------|--------------------|--------------------|------------------|-------------------|---------------|---------------|--------------------|------------------|
| I | 2 Austria | 1.93±0.13 | 4.82±0.12 | 2.78±0.38 | 1.25±0.08 | 164.5±0.5 | 48.2±0.6 | 194.5±4.5 | 0.17±0.03 |
| | 2 Romania | 0.54±0.30 | 3.2±0.29 | 1.37±0.23 | 0.13±0.13 | 186.4±1.8 | 64.3±3.5 | 199.0±3.0 | 0.04±0.04 |
| | 1 Slovakia | 0.96 | 3.71 | 2.27 | 0.53 | 195.0 | 66.0 | 198.0 | 0.12 |
| II.1 | 14 Baltic | 0.74±0.05 | 3.44±0.09 | 1.92±0.05 | 0.25±0.03 | 177.7±4.2 | 56.1±1.1 | 181.0±0.9 | 0.07±0.01 |
| II.2 | 36 Southern | 1.41±0.05 | 4.28±0.05 | 2.35±0.05 | 0.58±0.05 | 162.5±1.8 | 53.0±0.6 | 177.4±0.8 | 0.05±0.01 |
| II.3 | 33 Central | 1.74±0.07 | 4.62±0.06 | 3.13±0.07 | 1.03±0.07 | 173.8±2.4 | 56.2±0.9 | 174.6±1.3 | 0.08±0.01 |
| III | 9 Northerly | 2.07±0.21 | 4.85±0.19 | 3.69±0.28 | 1.20±0.26 | 143.4±5.90 | 42.4±3.0 | 150.1±2.5 | 0.04±0.02 |

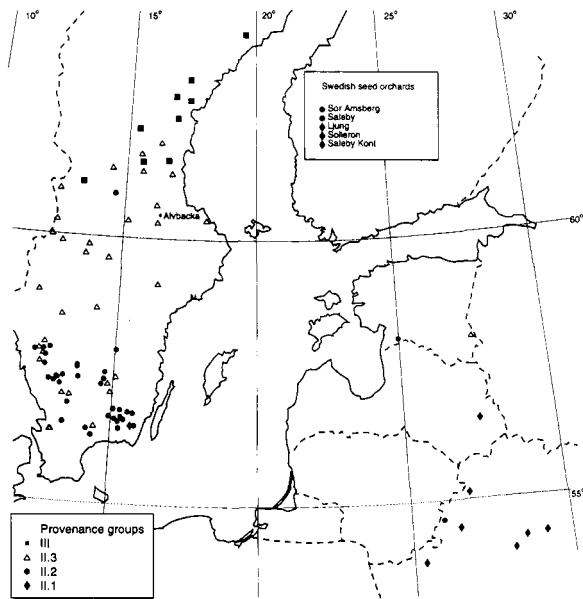


Figure 5. Subdivision of the intermediate (II) region group that was distinguished by Canonical Correlation Analysis (Fig. 3) by using clustering followed by Discriminant Function Analysis. Four major zones were emerging: northern (III), central (II.3), southern (II.2) Sweden and north-eastern continental Latvia and Belarus (II.1). Estonian origins were similar to southern and central Swedish ones. The box in the upper right corner of the figure is showing to which of the groups the Swedish seed orchards were assigned.

edly decreases. Presumably, selection intensity within populations is increasing while gene flow among populations decreases in response to increasing severity of climatic conditions northwards. This may explain higher among-population differentiation in northern than in southern Sweden, even though these populations had common immigration history. Origins from the south to approximately latitude 60° were much more phenologically uniform than the northern provenances (Fig. 3). The selective environmental neighbourhood (SEN) concept (BRANDON 1991) is useful in interpreting the provenance variation. Owing to environmental homogeneity within a SEN there is no significant change in rank among genotypes with respect to fitness. Whether a population in a SEN will be genetically different from a neighbouring population depends on the strength of the gene flow between the SENs (cf. ERIKSSON 1997). For wind pollinated species, the strength and direction of gene flow will be affected by ecological gradients within a region.

Considering that Sweden has a pronounced climatic gradient from south to north, strength of the gene flow between SENs is expected to decrease northwards owing to gradually stronger natural selection. Consequently, in northern Sweden variation within popula-

tions should be lower than in southern Sweden, as experienced by EKBERG et al. (1985). In a gene conservation programme, population sampling should not be based on geographic distance, rather on the degree of differentiation among populations.

Another important factor is the direction or pattern of the gene flow between SENs. Protogeny is a factor that directs gene flow in Sweden northwards, since pollen dispersal is earlier in a mild climate. At approximately 1000 day degrees temperature sum (latitude 60°), gene flow is gradually counteracted by strong natural selection, causing large variation among populations observed in our experiment, as in case of Scots pine discussed by ERIKSSON (1997). Assuming high variation within populations, southern Swedish origins would have a higher probability for adaptation to northern conditions, than vice versa. An example may be the spring frost injury in our study. Northern populations were relatively uniform in early bud flushing and subsequently were uniformly damaged. The relatively similar performance of the Baltic and southern Swedish origins (Fig. 3, HANNERZ 1993, PRESCHER 1982) could be effects of intense gene flow across the Baltics or the large scale introduction of continental Norway spruce in southern Sweden as discussed by LINES (1979), KRUTZSCH (1986), PERSSON (1975). Alternatively, natural selection may have resulted in similar genotypes in southern Sweden and in north-eastern Europe.

Origins from high altitude in north-western Sweden (most prominently in regions 22–24, Fig.1) perform like lowland provenances of considerably much more northern origin (Fig.4). Differentiation with altitude for phenological traits has previously been found at the provenance level by DORMLING (1973), HEIDE (1974), MODRZYNSKI (1995), CORRIVEAU et al. (1989) among others.

In conclusion, our experiment shows that clinal variation among provenances is stronger in northern Sweden than in southern Sweden. The transitional point between the two different patterns is approximately at latitude 60°. We interpret this divergence as being caused by immigration history as well as variation in selection pressure and strength of gene flow in Norway spruce. Presumably, the major pattern of gene flow in Sweden is northwards. North-eastern European Norway spruce may contribute to the genetic variation of southern Swedish populations through pollen migration across the Baltics or from plantations in southern Sweden with continental provenances. A gene conservation programme should include more populations from northern than from southern Sweden, since genetic variation in northern Sweden is substantially higher.

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