

Rapid change in adaptive performance from one generation to the next in *Picea abies*—Central European trees in a Nordic environment

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Abstract Seedlings of open-pollinated *Picea abies* families from Norwegian and Central European parent trees standing at three sites in Norway were tested for timing of bud set at the end of the first growth season together with seedlings from control provenances producing seeds at their geographical origin. The parental origins were confirmed with a maternally inherited mitochondrial marker that distinguishes trees of the Northern European range from those of the Central European range. The seedlings from the families of Central European mother trees producing seeds in Norway had on average a bud set more similar to the families of local Norwegian origin producing seeds at the same site than the provenance of the same Central European origin. It is argued that the rapid change in this adaptive trait from one generation to the next can be explained by recent research results demonstrating that day length and temperature conditions during embryo formation and maturation can influence the phenotypic performance of seedlings in Norway spruce. This effect may influence the fitness of naturally regenerated plants produced in plantations of Central European trees in Norway.

Keywords *Picea abies* · Adaptive performance · Provenance transfer · Reproductive environment

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Introduction

Norway spruce (*Picea abies* (L.) Karst.) is an important commercial tree species that has been intensively planted across Europe for centuries. Plantations have been established with seedlings of both local and nonlocal seed sources. In Southern Scandinavia, provenances from Central Europe have been an important component of the commercial seed supply for the last century. In Norway, e.g., several tons of Norway spruce seeds were imported from Central Europe, and recommendations were given for the use of these provenances in the southern parts of Norway (Skogdirektøren 1960). The present spruce forests are in Southern Scandinavia mixtures of naturally regenerated forests and plantations of both native and nonnative origins.

Planted trees originating from southern latitudes are more prone to frost damage on exposed sites in Southern Scandinavia than trees of local provenances (e.g., Persson and Persson 1992; Skrøppa and Dietrichson 1986). Such damage has caused a reduction in the timber quality of the plantations with Central European spruce provenances (Skrøppa et al. 1993). It has, therefore, been a growing concern that natural regenerations and plantations established with seedlings from seeds collected in forests of mixed origins will have a reduced adaptability to the climatic conditions in the northern forests. Recent results, however, have demonstrated that the climatic conditions during the sexual reproductive process may influence adaptive properties of the next generation, in particular when the maternal parents are transferred from cold to warmer conditions where they produce seeds (Johnsen et al. 2005a, b). The question has been raised as to whether similar effects may influence adaptive properties of the first generation offspring of Central European trees in Scandinavia, making them better adapted to the northern climatic conditions.

Skrøppa and Kohmann (1997) thought they had answered this question. They tested the timing of terminal bud set in progenies from trees supposedly of German origin growing in Norway. Norway spruce, as other temperate and boreal forest trees, shows a strong latitudinal cline in growth cessation and bud set (e.g., Dormling 1973; Holzer 1975; Krutzsch 1986). This variation is thought to be determined by a genetically controlled response to photoperiod and is understood as an adaptation to climatic conditions along latitudinal and altitudinal clines (Vaartaja 1959; Ekberg et al. 1979; Savolainen et al. 2004). Skrøppa and Kohmann (1997) found that seedlings grown from seeds produced in Norway by mother trees believed to be of German origin had a much earlier terminal bud set in the autumn than seedlings grown from seeds produced in Germany by German mother trees. Indeed, the seedlings seemed to form terminal buds almost as early as seedlings of the Norwegian provenances, demonstrating a considerable change in bud set only after one generation.

We later tested the origin of the material used in the study of Skrøppa and Kohmann (1997) with the maternally inherited mitochondrial (mt) marker *nad1* (unpublished data). In the second intron of the *nad1* gene, a 33-bp insertion/deletion characterises and unequivocally distinguishes Northern European populations from Central European populations (Sperisen et al. 1998, 2001; Tollefsrud et al. 2008). Using this marker on the material from the 1997 publication, we discovered that all 15 trees that we were told to be of German origin, in fact, showed a Northern European mitochondrial profile. The seed samples from these trees then most likely had to be of local Norwegian origin, since no other Northern European provenances have been used in these plantations. Regrettably, the conclusions presented by Skrøppa and Kohmann (1997) were based on major flaws in the data and can, therefore, not be considered valid. The aim of this study is to investigate the same questions based on a larger number of families, with origins of the mother trees identified with the mtDNA marker *nad1* (Sperisen et al. 1998, 2001) and seeds produced at several sites.

We, thus, investigated the timing of terminal bud set of seedlings grown from seeds produced by (1) Central European mothers in different locations in Norway and (2) Norwegian and German controls setting seeds at their origin. As timing of terminal bud set is a heritable trait with mainly additive inheritance (Eriksson et al. 1978), we would expect the seedlings grown from seeds produced by Central European mothers in Norway to have an intermediate timing of the terminal bud set, if they were pollinated by Norwegian pollen only, as compared to seedlings from Norwegian and German controls producing their seeds at their respective origin. Results are presented by assessments of the terminal bud set at the end of the first growth season in a greenhouse test.

Material and methods

DNA analyses

To select the families used to assess the timing of bud set, we identified the origin of the open-pollinated families (seed lots) to be of northern or central European origin by using the *nad1* marker. We screened the seed lots for the presence or absence of 33 bp which differentiate between trees from Northern and Central Europe. Each seed lot contained seeds from one mother tree only. For each seed lot screened, DNA was extracted from three to six seeds, using the DNeasy Plant Mini Kit (Qiagen). We amplified the second intron of the *nad1* gene using the primers *nad1b* and *nad1c* (Demesure et al. 1995). The samples were amplified in 20 µl containing 1× PCR buffer (Qiagen), 1.6 mM MgCl₂, 0.1 mM of each dNTP, 0.4 µM of each primer, 1.5 U of HotStar *Taq* DNA polymerase (Qiagen) and 30 ng DNA template using a Gene Amp PCR 9700 (Applied Biosystems) with the profile 15 min denaturation at 95°C followed by 31 cycles of 1 min denaturation at 94°C, 1 min annealing at 57°C, 2 min extension at 72°C and a final extension for 7 min at 72°C. The PCR products were digested with the restriction enzyme *RsaI* to screen for 33 bp insertion/deletion. The presence of 33 bp, indicating a Central European origin, or the absence, indicating Northern European origin, was visually inspected on a 1.8% agarose gel. The gel was run together with two controls and a marker.

Seed lots

Forty seed lots (families after open pollination) which the *nad1* marker identified to be of either central or northern European origin were selected. The seed lots had been collected in the autumn of 1998 at three different locations; each of the locations had plantations of Norwegian and Central European trees of known origin. In Hurdal, southern Norway (lat. 60°20' N, alt. 450 m), the seed lots came from seven trees of Austrian (Tirol) origin and six trees of local Southern Norwegian origin. In Steinkjer, Central Norway (lat. 64°01' N, alt. 320 m), the seed lots came from eight trees of German (Harz) origin and seven trees of local central Norwegian (L1) origin. In Verdalen, Central Norway (lat. 63°50' N, alt. 120 m), the seed lots came from six trees of German (Harz) origin and six trees of local Norwegian (L1) origin. The plantation at Steinkjer was a provenance trial planted with seedlings of the same seed lots that were used in the Verdalen plantation.

From available commercial seed lots we selected control samples. These seed lots had been harvested from trees growing and producing seeds at their geographical origin, harvested in different seed years. These seed lots were:

Southern Norway (lat. 59–61° N, alt. 0–150 m) (C1); Southern Norway (lat. 59–61° N, alt. 350–450 m) (C4); Germany (lat. 51°40' N, alt. 700 m) (Harz); and Austria (lat. 47° N, alt. 900 m) (Tirol). The commercial seed lots typically contain seeds from more than 100 mother trees. The information about the different seed lots is summarised in Table 1, and the seed production sites and origins of mother trees are shown in Fig. 1.

Experiment, assessments and calculations

Seeds from each of the 40 families and four control seed lots were germinated in the spring in a greenhouse located on the experimental farm Hoxmark, Ås, Norway, lat. 59°45' N. The seedlings were grown in the greenhouse under natural night conditions following standard routines as regards watering and fertilisation routines (Skrøppa 1991; Johnsen et al. 2005a). A randomised block design with four replicates was used. Each block contained one plot with 45 seedlings from each of the 44 genetic entries, giving 180 siblings from each family, altogether 7,920 seedlings.

Terminal bud set was assessed at the end of the growth season. From August 7, when already more than 50% of the seedlings of the northernmost provenance had set terminal bud, and every fifth, sixth or seventh day until September 24, each seedling was classified as having set bud or not. At each date, the proportion of seedlings with terminal buds was calculated for each plot. The transformed plot proportions by the arcsine transformation were subject to analyses of variance. For the families from seeds produced at the Southern Norwegian site the transformed bud set proportions on August 17 and August 22 were analysed according to the model

$$Y_{jkl} = \mu + O_j + F_{jk} + B_l + e_{jkl}$$

where μ is the general mean, O_j is the fixed effect of the origin of the mother tree, F_{jk} and B_l are the random effects

of family within origin and block, respectively, and e_{jkl} is the random residual error. The random effects are assumed to be independent and with expectations zero and respective variances.

For the families grown from seeds produced at the two sites in Central Norway, the transformed bud set proportions on August 15 were analysed according to the model

$$Y_{ijkl} = \mu + P_i + O_j + PO_{ij} + F_{ijk} + B_l + e_{ijkl}$$

where μ is the general mean, P_i is the fixed effect of the seed production site, O_j is the fixed effect of the origin of the mother tree, PO_{ij} is the fixed interaction between seed production site and origin, F_{ijk} and B_l are the random effects of family within seed production site and origin and block, respectively, and e_{ijkl} is the random residual error.

The analyses were done by the procedure PROC GLM in SAS (SAS Institute 2003), using the test statement to assure that proper denominators are used in the F tests.

To test whether or not the timing of the terminal bud set for central European trees setting seeds in south Norway was intermediate between seedlings from Norwegian and central European provenances, t tests were performed on the transformed bud set percentages at August 29 for seeds produced at the south Norwegian site and at August 28 for seeds produced at the two central Norwegian sites.

Results

As expected, there were striking differences between the timing of terminal bud set in the seedlings from seeds produced at more northern latitudes and higher altitudes and the seedlings from seeds collected at lower latitudes (Figs. 2 and 3). At the first day of assessment, August 7, 60% of the seedlings of the families of the local provenance from latitude 64° N had set visible terminal buds. The same bud set percentage was obtained on August 29, September

Table 1 Seed lots of Norway spruce included in the greenhouse experiment

Seed production site	Origin	Type of material
Southern Norway, Hurdal, Lat. 60°20' N, alt. 450 m	Southern Norway (Hurdal) Lat. 60° N, alt. 450 m	6 families
	Austria (Tirol) Lat. 47° N, alt. 1,000 m	7 families
Central Norway, Verdal, Lat. 63°50' N, alt. 120 m	Central Norway (L1) Lat. 63° to 64° N, alt. 0–150 m	6 families
	Germany (Harz) Lat. 51° to 52° N, alt. 850 m	6 families
Central Norway, Steinkjer, Lat. 64°01' N, alt. 320 m	Central Norway (L1) Lat. 63° to 64° N, alt. 0–150 m	7 families
	Germany (Harz) Lat. 51° to 52° N, alt. 850 m	8 families
Southern Norway (C1) Lat. 59–61° N, alt. 0–150 m	Same as site	Commercial seed lot
Southern Norway (C4) Lat. 59–61° N, alt. 350–450 m	Same as site	Commercial seed lot
Germany (Harz) Lat. 51° 40' N, alt. 700 m	Same as site	Commercial seed lot
Austria (Tirol) Lat. 47° N, alt. 900 m	Same as site	Commercial seed lot

Seed production site is the location where the trees produced their seeds; origin is where the seed mothers originally came from

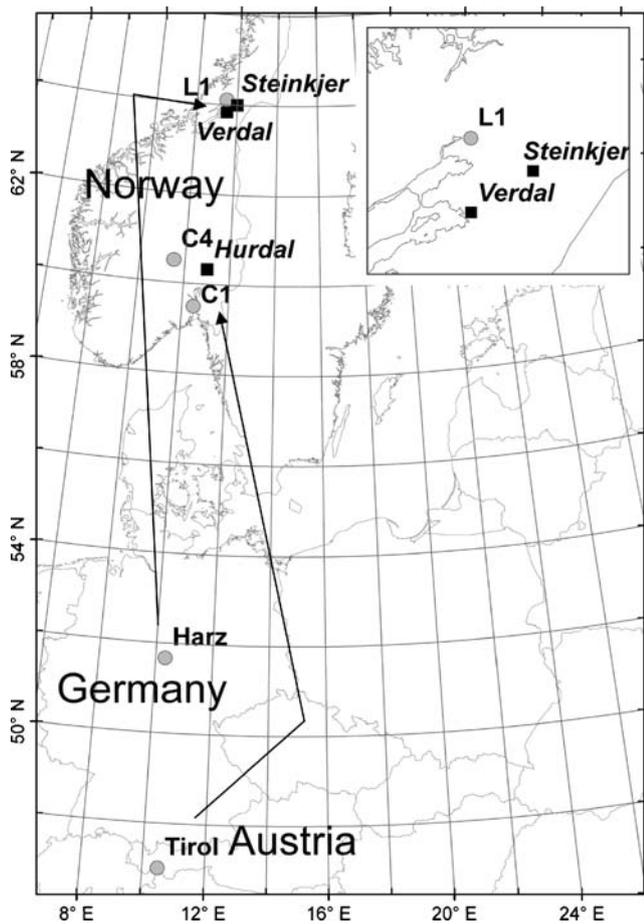


Fig. 1 Map showing the origins and seed production sites of the populations studied. Grey circles indicate the geographical origin of populations and black squares the seed production sites of families. For Norwegian families at Hurdal, the population origin and seed production sites are identical

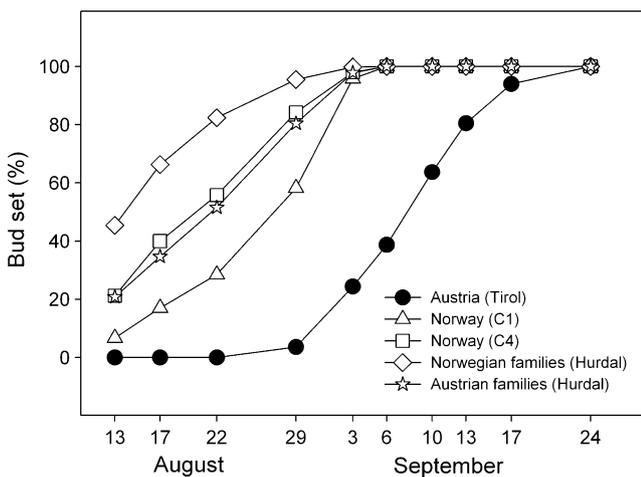


Fig. 2 Timing of bud set at the end of the first growth season for seedlings from seeds collected at three sites in Southern Norway (C1, lat. 59–61° N, alt. 0–150 m; C4, lat. 59–61° N, alt. 350–450 m; and Hurdal, lat. 60°20' N, alt. 450 m) and one site in Central Europe (Austria (Tirol) lat. 47° N, alt. 900 m)

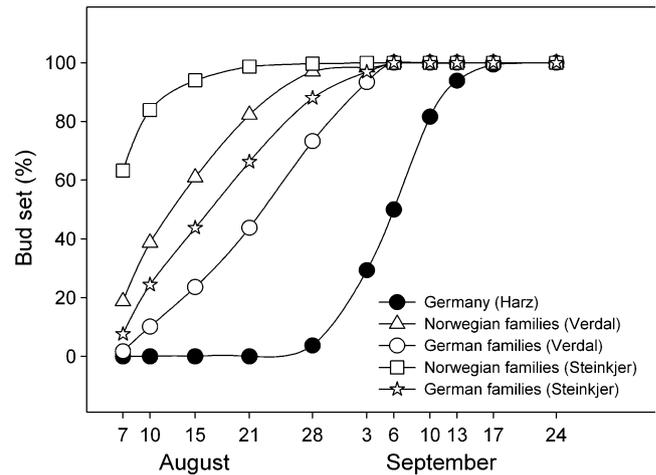


Fig. 3 Timing of bud set at the end of the first growth season for seedlings from seeds collected at two sites in Central Norway (Verdal, lat. 63°50' N, alt. 120 m; and Steinkjer, lat. 64°01' N, alt. 320 m) and one site in Central Europe (Germany (Harz), lat. 51°40' N, alt. 700 m). The parent trees at Verdal and Steinkjer originate from the same seed lots, either central Norway (L1) (lat. 63° to 64° N, alt. 0–150 m) or Germany (Harz) (lat. 51° to 52° N, alt. 850 m)

8 and September 10 for the provenances from latitudes 60°, 51°40' and 47° N, respectively.

Seedlings from the local families at Hurdal, south Norway, had an average bud set of 82% on August 22, while the families of Austrian mother trees producing seeds at Hurdal had 52% bud set on the same date ($p=0.003$; Fig. 2, Table 2). The families of Austrian mother trees had a bud set similar to the south Norwegian control provenance C4 from altitude 400 m but were earlier than the other Norwegian control provenance C1 from altitude 100 m. Significant variation ($p<0.001$, Table 2) was present on August 22 between families within both origins, varying between 71% and 95% bud set for the Hurdal families and between 31% and 71% for the Austrian families. The

Table 2 Analysis of variance of the transformed bud set percentages on August 22 and August 15, respectively, of (a) families from seeds produced at Hurdal, southern Norway and (b) families produced at Verdal and Steinkjer, central Norway

Source	df	F value	p value
Families from seeds produced at Hurdal, Southern Norway			
Origin	1	14.01	0.003
Family (origin)	11	10.58	<0.0001
Block	3	14.95	<0.0001
Families produced at Verdal and Steinkjer, Central Norway			
Seed production site	1	66.74	<0.0001
Origin	1	27.15	<0.0001
Seed production site × origin	1	3.25	0.08
Family(seed production site, origin)	23	10.98	<0.0001
Block	3	5.93	0.0011

Austrian control provenance initiated bud set more than 20 days later than the families of Austrian mother trees from seed set in south Norway and reached 95 % bud set 16 days later than these families.

The families from seeds collected at Steinkjer had on average an earlier timing of bud set than those from seeds collected at Verdal, with bud set percentages of 67% and 42%, respectively, on August 15 ($p < 0.0001$; Fig. 3, Table 2). The families of local Norwegian origin (L1) had on average a bud set percentage of 78% on August 15 compared to 34% for the families from mothers of German (Harz) origin ($p < 0.0001$, Table 2). Significant variation ($p < 0.001$) was present between families.

The bud set curve of progenies from Central European trees setting seeds in Norway is skewed towards the local Norwegian performance compared to the midpoint curve. The Austrian families producing their seeds in South Norway had on average a bud set percentage that is 31% higher ($p < 0.001$) than the midpoint value (49% on August 29) between the local Norwegian and the Austrian control provenance (Fig. 2). The seedlings of the German (Harz) control provenance started to form terminal buds at the end of August when the Harz families from the two central Norwegian sites already had obtained bud set percentages of 74% (Verdal) and 88% (Steinkjer). The bud set of these families occurred therefore far earlier ($p < 0.001$) than the midpoint value between the Harz control and the central Norwegian local provenance (Fig. 3).

Discussion

The present experiment demonstrated a latitudinal cline in the timing of bud set of Norway spruce seedlings. A difference in bud set of more than 4 weeks was revealed between seedlings from the northernmost and southernmost origin. Such latitudinal clines have been interpreted as adaptive population differentiation, triggered by changes in photoperiod and temperature conditions (e.g., Eriksson 1995; Howe et al. 2003; Savolainen et al. 2004; Ingvarsson et al. 2006). Such responses allow the individuals of northern populations to cease growth and attain hardiness before the occurrence of the first autumn frost which may be a main selective factor. Another factor contributing to the observed differences is that the seedlings from Central European provenances growing at northern latitude experience their critical night length for bud set at a later date than they do at their native latitude due to the shorter nights in the north. This fact will generally delay their growth cessation and enhance provenance differences (e.g., Skråppa and Magnussen 1993).

As the mother trees of Central European origin at all three sites to a large extent were surrounded by spruce trees

of local origin, it is most likely that the majority of their offspring have Norwegian fathers. Due to the additive inheritance of the trait studied (Eriksson et al. 1978; Skråppa unpublished) such hybrids should have a terminal bud set intermediate that of their parents. In this experiment, the parental performance is represented by the offspring of the local parents and by the seedlings of the German (Harz) and Austrian (Tirol) provenances, respectively. However, the bud set curves of the progenies of the mother trees of Central European origin were much closer to the performance of the local Norwegian seedlings than they were to the midpoint curve. A bud set percentage similar to the midpoint value of August 29 between the Austrian control provenance and the native families was attained by the families of Austrian origin on August 21. These families, therefore, set bud 8 days earlier than should be expected. This approximately corresponds to the differences in bud set between the two commercial provenances C1 and C4, which have an altitudinal differences of 300 m. Additional factors must, therefore, contribute to the observed variation patterns.

A selective factor that relates to early growth cessation in Norway spruce is early autumn frost (Langlet 1960; Dietrichson 1964). We do not have any information about injury from frost events occurring in the nursery where seedlings for these plantations were produced. Selection in the plantations is also unlikely as a large portion of the planted trees are still standing.

It has recently been shown that the temperature during maternal reproduction affects adaptive traits in Norway spruce progenies. In particular, seed production in a cold environment advances bud set and cold acclimation in the autumn (Johnsen et al. 2005a, b; Webber et al. 2005). Compared to outdoor conditions, seed production of the same full-sib families under higher temperatures in a greenhouse delayed the bud set for several days. Progeny performance was strongly associated with the degree-days from proembryo to mature seeds. It has been suggested that when mother trees of central European provenances produce seeds under Norwegian temperature and photoperiodic conditions, a memory is programmed in the developing embryo (Johnsen et al. 2005a; Kvaalen and Johnsen 2008). This memory later influences the phenotypic performance of the seedlings. A northern, but not too cold, seed-producing environment will influence the seedlings to have a more northern like and early bud set (Johnsen et al. 2005b). Based on knowledge about the intermediate inheritance of the quantitative trait in question (Eriksson et al. 1978), the seedlings in our experiment terminate growth and form terminal buds earlier than we should expect from progenies of mother trees of southern origin (Figs. 2 and 3). Our results are, therefore, consistent with the recent findings that there is a mechanism in

Norway spruce that operates during embryo development to adjust the timing of bud set in accordance with the prevailing temperature conditions during seed production in the mother tree. This mechanism could be important for adaptation to new and unstable environments (Rohde and Junttila 2008) as it can influence bud phenology and frost hardiness. Furthermore, the change in adaptive traits may enhance early survival and competitive ability during the important 10–15 first years of the young trees' life (Skrøppa et al. 2007).

In addition, our results demonstrate that plantations in relative proximity, which are planted with trees of the same origin, may produce offspring with quite large differences in an adaptive trait like terminal bud set. The two sites at which the seeds were produced in Central Norway, Verdalen and Steinkjer, are approximately 35 km apart and have a difference in altitude of 200 m. On average, the mean temperature decreases by 0.6°/100 m increase in altitude (Lindgren 1994). Ignoring local temperature conditions, this should give a difference of about 140 degree-days between the two sites for the 4 months June–September, using 5°C as the threshold value (Sarvas 1968). Based on the results from Johnsen et al. (2005a, Fig. 6), such a difference in degree-days could imply a difference in bud set of 7% to 8%. The observed differences between the mean bud set percentages of all progenies from each of the two sites were considerably higher. They varied between 19% and 29% for the different dates of registration (Fig. 2), most likely due to larger differences in local climatic conditions than predicted by the altitudinal differences alone.

Differences in adaptive traits may be present between seedlings from seeds produced in the same plantation in different years (Kohmann and Johnsen 1994; Skrøppa et al. 2007). Such effects may also influence the results of our study. The seed lots of the two provenances from southern Norway, C1 and C4, were collected in 1983, a year with temperatures above the long term average for the months July, August and September. The general difference in degree-days between the provenances from altitude 100 and 400 m amounts to 205 degree-days, while the differences in bud set between seedlings from the provenances C1 and C4 were in the range 23% to 26%, depending on date of assessment. Again, these observations may be influenced by the local temperature conditions. This may also be the case for the family seed lots collected at an altitude of 450 m in Hurdal in 1998 compared with the provenance seed lot collected in 1983. In 1998, the accumulated temperature sum for the months June–September, with 5°C as the threshold value, was 948 degree-days at the closest meteorological station Gardermoen at altitude 200 m above sea level, while it was 1,116 degree-days at the same station in 1983. The differences we have observed

in bud set between the seedlings from the seed lots collected in Norway can, therefore, be influenced by annual temperature variations, by differences in altitude and local climatic conditions and differences in allelic frequencies of structural genes caused by differential climatic adaptation (see discussion in Skrøppa et al. (2007)).

Our results are different from those of Langlet (1941), who compared seedlings from seeds produced in southern Sweden by German and Swedish mother trees with seedlings from seeds collected in Germany. He found similar seed size and dry weight of the two types of seedlings of German origin and that they were significantly different from those of Swedish origin. He, therefore, concluded that no effects of the seed production site were present in the offspring of German mother trees producing seeds in Sweden. However, his results are not comparable to ours as he studied different traits. In addition, the differences in temperature conditions during the seed production period are in general less likely to differ considerably between the seed-production sites in Germany and in Southern Sweden.

The mitochondrial DNA marker in our study will make it possible to identify Norway spruce plantations of Central European origin. It is our experience that many forest owners are not sufficiently informed about the origins of the seedlings that were used to establish their spruce plantations. In several cases in which climatic damage has occurred and the spruce plantations were claimed to be of Central European origin based on phenotypic performance alone, the trees possess a marker profile that is characteristic for Norway spruce of northern Europe. The use of this marker to verify origin is therefore important, as it helps to avoid drawing erroneous conclusions in such cases. It can also be used to exclude unwanted seed lots in cases where seed lot identification is important and to avoid establishing gene conservation stands of mixed Nordic and Central European origin.

Conclusions

The observed results can be explained by the recent research demonstrating the effects of temperature during maternal reproduction on adaptive traits in Norway spruce progenies. The conclusions from an earlier publication (Skrøppa and Kohmann 1997) are, therefore, confirmed and extended, but this time, based on proper plant materials with origin confirmed by an informative molecular marker. Our data indicate that the memory from embryo development can influence bud phenology of young Norway spruce trees (Skrøppa et al. 2007); thus, a rapid change in adaptive performance may take place from one generation to the next. This could diminish the expected reduction in fitness of naturally regenerated plants produced in plantations with

alien nonadapted provenances of Norway spruce compared to that of seedlings of local provenances. These results should be taken into consideration when interpreting differences in adaptive traits in genetic tests of trees from seed lots produced in different years and at different sites.

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