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Growth Rhythm and Hardiness of Picea abies Progenies of High Altitude Parents from Seed Produced at Low Elevations

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Abstract

A complete diallel was performed by crossing Norway spruce grafts of high altitude parents at a low elevation site. The families were planted in a short term field trial. Freezing tests were performed with ten controlled cross families and comparable controls.

Measurements were made of the annual shoot elongation patterns at ages 9 and 10 years from seed in the field trial and final tree heights at age 10 years. The trees of the diallel full-sib families did not have the timing and duration of shoot elongation that is to be expected of high altitude Norway spruce trees and performed similarly to trees of low altitude provenances. In diallel analyses of variance, significant reciprocal effects were found for the shoot elongation characteristics and height growth, indicating a non-symmetric genetic contribution from the 2 parents. In the freezing tests, high altitude families from crosses at low elevation sites were significantly more damaged than control provenances from the same or lower altitudes as the origins of the parents.

The present results confirm earlier observations that progenies of high altitude parents do not retain the annual growth rhythm of their parents when the parents have been grown at a low altitude site. The results are similar to observations after transfer of clones from a northern to a southern location where crosses are made.

Key words: diallel cross, sexual reproduction, environmental preconditioning, adaptation.

FDC: 165.3; 165.4; 174.7 *Picea abies.*

Introduction

Seed orchards intended to produce seed for northern latitudes or high altitudes are often located in a more favourable climate in order to enhance seed production. After transfers of parent clones from northern to southern Norway, seedlings from seeds produced in a Norway spruce (*Picea abies* (L.) KARST.) seed orchard after controlled crosses did not have the adaptational properties of the parents (JOHNSEN, 1989a and b; JOHNSEN et al., 1989). They had in particular an extended growth season and

later bud-set and were more damaged in freezing tests than related seedlings from seeds produced in the northern environment. Later similar effects have been demonstrated in the same species after identical crosses performed both in southern and northern Finland (SKRØPPA et al., 1994) and inside and outside a greenhouse (JOHNSEN et al., 1994). Effects of different crossing locations have also been demonstated in Scots pine (DORMLING and JOHNSEN, 1992; LINDGREN and WEI, 1994).

Clones from high altitudes grafted at a lowland site experience climatic changes similar to the north-south transfers (JOHNSEN, 1988). Results from experiments with families after controlled crosses under such conditions are reported in this study. The crosses and a field trial were planned for other purposes, but are here utilized to study the performance of progenies produced after altitudinal tranfers of the parents.

Materials and Methods

Experimental material

In the spring of 1970, controlled crosses were performed in a grafted clonal archive of Norway spruce at Haga, southeastern Norway, altitude 100 m. The crossing design was a complete diallel involving 5 parents and included both self-fertilized and reciprocal cross families. In addition, each parent was crossed with a mixture of pollen from 5 other clones in the archive. Pollen for the crosses was produced in the clonal archive the same year. Sufficient seed for experiments was obtained from 18 outcrossed and 4 self-fertilized families from the diallels.

The 5 parent trees in the diallel originated from altitudes ranging between 620 m and 850 m in southern Norway. The parents contributing pollen to the pollen mix originated from altitudes between 680 m and 720 m in the same area. All the parents had been grafted in the clonal archive in 1964 with scions collected from plus trees in natural stands. They had been phenotypically selected

for outstanding height growth and high branch and stem quality and were included in a breeding population intended to produce seeds for the marginal areas at high altitudes in southern Norway.

In 1987, controlled crosses were performed at Stein Norway Spruce Seed Orchard in southern Norway, altitude 70 m. This seed orchard contains clones selected in natural stands between altitudes 500 m and 1000 m in southern Norway. Thirty clones in the orchard were pollinated with mixed pollen from 12 other clones originating from altitudes between 680 m and 900 m. The pollen was from the same year, produced partly in the Stein orchard and partly in a clonal archive at Ås, altitude 130 m.

Field trial. Measurements

The seeds from the Haga crosses were sown in the spring of 1971, and 4 year old seedlings were planted in 1975 in a short-term field trial at Ås, altitude 130 m. The experimental design was randomized blocks with 12 replicates of 4-tree family plots at 1 m spacing. The trial was planted on an agricultural field.

The trial also included seedlings from a commercial seedlot, B4, originating from the same geographic area as the parental clones. It contained a mixture of seeds from several natural stands from altitudes between 350 m and 450 m. The seedlings from this control lot were planted in 3 4-tree plots in each replicate. In an adjacent trial a family test was planted at the same time, consisting of full-sib families after controlled crosses performed in a clonal archive between selected trees from altitudes between 100 m and 400 m in southern Norway.

In the 9th (1979) and 10th (1980) growth season weekly measurements were made of the elongation of the terminal shoot of all trees in 8 replicates of the diallel trial. The measurements were made in millimeters from a fixed base point to the tip of the shoot. In 1979, the dates of measurement were June 1, 7, 13, 20, 28 and July 3 and 15 and August 15. The next year, measurements were made on May 27, June 2, 9, 16, 23, 30, July 4, 15 and with the final measurement of the terminal shoot on August 20. The elongation from a 2nd flush after the termination of normal growth (lammas growth) was not included in the measurements. Similar measurements were also made on the same dates in 1980 in the adjacent test of low altitude full-sib families. The mean shoot growth characteristics of 19 full-sib families in the replicates closest to to the measured replicates of the Haga test will be used for comparisons. Twelve parents were involved in these crosses.

Tree heights were measured at age 10 years from seed when the diallel experiment was terminated in 1980.

Freezing tests

An artificial freezing test was performed in 1992 with seedlings from 5 of the diallel full-sib and 2 pollen mix families from the Haga crosses. The experiment also included 3 families from the crosses at Stein and seedlings from commercial seed lots originating from altitudes 600 m (B6) and 800 m (B8) in southern Norway. The seedlings were cultivated in 2 replicates in each of 2 phytotron rooms, and the freezing tests were performed after cold acclimation was induced by short day and low temperatures during night according to the methods described by JOHNSEN (1989c) (Exp. 3). The freezing was performed at 5 temperatures (—8 °C, —9.5 °C, —11 °C, —12.5 °C and —14 °C) with 2 freezing chambers each with 4 replicates of 2-seedling plots at each temperature. A balanced distribution of seedlings from the phytotron rooms and replicates was attempted when distributing seedlings to the freezing test, keeping track of rooms and replicates. More details of plant cultivation and freezing tests are given by JOHNSEN et al. (1994).

Visual damages on individual seedlings were classified 6 weeks after the freezing test following the scale (JOHNSEN, 1989c):

0 = no visible damage, needles green;
1 to 10 = brown or discoloured needles in 10 % classes;
11 = all needles completely brown, seedling dead.

Statistical methods

The elongation at each day of measurement was calculated in percentage of final shoot length for each individual tree. Weibull distribution functions were fitted to each plot based on the relative elongation measurements of the 4 trees on the plot by the method described by SKRØPPA and MAGNUSSEN (1993).

From each estimated Weibull curve the following characteristics were calculated:

DAY1 = day of completion of 1st 20 mm elongation (growth start day);
DAY2 = day when last 20 mm of total elongation is to be completed (growth cessation day);
DAYS = DAY2 — DAY1 (duration of the elongation period);
RSE = average rate of shoot elongation (mm/day) during period between DAY1 and DAY2.

April 1 is set equal to day 1.

Differences in shoot elongation characteristics between the diallel full-sib families and the B4 provenance were tested by calculating the contrast between the 2 groups for each replicate and year and then testing its deviation from 0 by t-test. The error was calculated from the variation between the replicates pooled over the 2 years.

Analyses of variance of the outcrossed families from the diallel were performed for the 4 elongation characteristics, annual shoot length (ASL) and tree heights at age 10 years (H10). All analyses were based on plot mean values using the computer program DIALL (SCHAFFER and USANIS, 1969), following the model (COCKERHAM and WEIR, 1977):

$$Y_{tijk} = \mu + A_t + G_i + G_j + S_{ij} + M_i - M_j + R_{ij} + AF_{t'ij} + B_k + E_{tijk}$$

where

Y_{tijk} is the plot mean value year t of full-sib family between parents i and j in block k, μ is a constant, A_t is the year effect, G_i and G_j are general combining ability effects, S_{ij} specific combining ability effect, B_k block effect, M_i and M_j maternal effects, R_{ij} reciprocal effect, $AF_{t'ij}$ interaction between year and family and E_{tijk} is the residual error. All effects, except μ, are considered as random with expectations 0 and appropriate variances. For H10, the year (A_t) and interaction ($AF_{t'ij}$) effect were not included in the model.

The significance of the variance components were tested by F-tests. The SCA mean square was used for testing the GCA component and the reciprocal mean square for testing the maternal component. Reciprocal, SCA and the interaction components were tested against the error term. No genetic variance components or correlations were estimated due to the small number of parents involved.

The mean damage score of the 2 seedlings in each plot was transformed by the transformation y=arcsin (sqrt
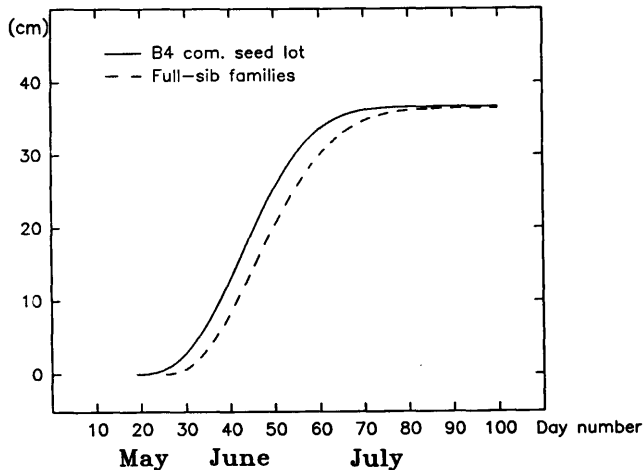
Shoot elongation

Figure 1. — Estimated mean shoot elongation curves for the full-sib families and the B4 control provenance.

(x/11) (JOHNSEN, 1989c). Analyses of variance were performed on these transformed means to test differences between the Haga family means, ignoring family relationships, to test differences between the Haga families and the two control seed lots and between the Stein families and the controls. A high damage level at the 2 lowest temperatures made the data from these tests unsuitable for statistical analyses, which were performed only for the 3 freezing temperatures —8 °C, —9.5 °C and —11 °C for the Stein families. As the Haga families had a very unbalanced number of seedlings at —8 °C, that temperature was also deleted in their analysis. The model for the analyses of variance included the effects: locality (seed orchard or natural stand), family within locality, temperature, chamber within temperature, phytotron room and replicates within rooms. The 2 natural stand controls were in the analyses treated as 2 families.

Correlation coefficients were calculated between frost injury means and shoot elongation traits for the 7 families that were included in both types of tests.

Results

Diallel experiment

The means of the estimated shoot elongation curves from 1980 for the outcrossed full-sib families from the diallel and the B4 control are shown in *figure 1*. The curve of the low altitude full-sib families is very close to the diallel curve. The B4 provenance trees started their shoot growth earlier than the 2 other groups and had the earliest growth termination. The growth curves from 1979 show similar differences between the diallel and B4 group. The differences are quantified in *table 1*, which shows the mean values of the 3 groups for DAY1, DAY2, DAYS, RSE and ASL in 1980. The means of the diallel and the low altitude full-sib families are very similar for all characteristics, while the B4 group had a significantly earlier initiation and cessation of growth and a shorter growth period (*Table 1*).

The p-values of F-tests for testing the GCA, SCA, maternal and reciprocal variance components are shown in *table 2*. No interactions were found between families and years (p>0.50 for all traits). Significant GCA components were present for all traits, except ASL, and SCA was significant for DAY1 and RSE. No maternal components were present, but there was a remarkably strong significant reciprocal component for DAY2, DAYS, RSE and ASL, which indicates a non-symmetric contribution from the 2 parents to the progenies of at least one pair of full-sib families. The reciprocal contribution can not be systematically related to either of the sexes, as no maternal components were observed. A similar non-symmetric contribution from the maternal and paternal parents has earlier been observed in the same material for filled seed percentages (SKRØPPA and THO, 1990). The full-sib family means for DAY1 and DAY2 for both years are shown in *table 3*. Rather small variations are observed for DAY1. The variation in the day of shoot growth cessation was considerably larger in 1980 than in 1979, expressed by standard deviations of family means of 2.7 days in 1979 and 4.3 in 1980. Two pairs of families (3 x 4 and 4 x 3, 3 x 5 and 5 x 3) showed the same consistent deviations in both years, although more strongly expressed in 1980. The families 2 x 5 and 5 x 2 deviated for the 1980 measurements, but not in 1979.

Table 1. — Mean values of shoot growth characteristics in 1980 for 3 groups of trees and p-values for testing the difference between diallel families and the B4 provenance.

Characteristic/ unit	Diallel families	Low altitude families	B4 provenance	p- value
DAY1 day number	60.4	60.5	56.3	<0.001
DAY2 day number	97.7	98.9	91.1	<0.001
DAYS days	37.3	38.4	34.9	0.003
RSE mm/day	9.2	10.1	10.7	0.02
ASL mm	383	430	414	0.20

Table 2. — Results (p-values) of F-tests for testing variance components in the diallel analyses of variance.

Source of variation	DAY1	DAY2	DAYS	RSE	ASL	H10
GCA	0.025	0.013	0.013	0.025	0.065	0.01
SCA	0.006	0.36	0.73	0.002	0.05	0.35
Maternal	0.33	0.73	0.69	0.17	0.37	0.45
Reciprocal	0.20	0.019	0.004	0.014	0.001	0.005

Table 3. — Mean day number (after April 1) for growth start (DAY1) and growth cessation (DAY2) of diallel full-sib families for the 2 years 1979 and 1980.

DAY1 1979

♀\♂	1	2	3	4	5
1	–	–	67	65	65
2	66	–	65	65	66
3	66	66	–	67	66
4	64	63	67	–	65
5	66	65	67	–	–

DAY1 1980

♀\♂	1	2	3	4	5
1	–	–	60	60	60
2	60	–	60	59	60
3	60	59	–	63	62
4	59	59	62	–	61
5	61	59	64	–	–

DAY2 1979

♀\♂	1	2	3	4	5
1	–	–	105	105	99
2	101	–	101	101	96
3	104	101	–	104	102
4	103	101	107	–	101
5	100	96	99	–	–

DAY2 1980

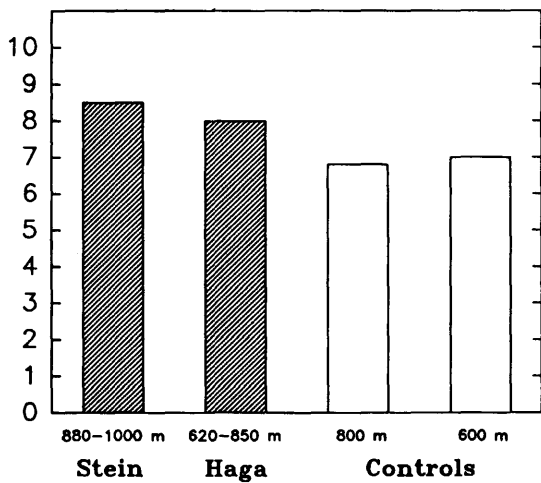| ♀\♂	1	2	3	4	5
1	–	–	99	102	97
2	93	–	96	96	94
3	99	94	–	100	103
4	100	94	106	–	97
5	97	90	97	–	–

Frost damage

Figure 2. — Mean damage scores of controlled cross families and commercial control provenances

Freezing tests

The controlled cross families were more severely damaged than tne commercial provenances A6 and A8 (*Fig. 2*). Both the Stein and Haga families had a significantly higher level of damage than the mean of the 2 controls, as shown by the analyses of variance of the transformed damage scores (*Table 4*).

The differences in damage scores within the Haga set of controlled cross families were not significant (p=0.13). However, the maternal progenies from Stein that originated from 1000 m altitude had a mean score of 7.7 compared to 8.7 and 9.2 for the 2 other families, and these differences were significant (p=0.01).

The mean height of the seedlings in the freezing tests was 115 mm for the Haga families, 138 mm for the Stein families and 110 mm for the 2 control provenances. The last 2 means were significantly different (p=0.03).

No relationships were found between mean damage scores and the shoot elongation characteristics of the 7 Haga families that were included in both tests.

Table 4. — Results from F-tests (p-values) from analyses of variance of transformed damage scores for comparing the Haga and the Stein families with the 2 control provenances.

Source	Haga		Stein	
	df	p	df	p
Locality	1	0.01	1	0.05
Family(locality)	7	0.55	3	0.02
Temperature	1	0.27	2	<0.001
Chamber(temperature)	2	0.15	3	0.18
Phytotron room	1	0.74	1	0.75
Replicate(room)	2	0.74	1	0.46

Discussion

The Haga diallel families did not have the timing and duration of shoot elongation that is to be expected of high altitude Norway spruce trees. Normally, trees of high altitude provenances will have an early cessation of shoot growth and a rather short elongation period, even when they are planted at low elevations. The families in this experiment had a shoot elongation rhythm very similar to the low altitude families and terminated their growth considerably later than the B4 control provenance in both years.

The results from the freezing tests show that the Haga families had a later development of autumn frost hardiness than comparable provenances from 600 m and 800 m. Similar effects were expressed by the 3 Stein families. They also had a better height growth than the provenance seedlings. These results agree with the data of JOHNSEN (1988) and JOHNSEN and APELAND (1988), who showed that seedlings from Kaupanger Seed Orchard, containing selected clones from altitudes between 600 m and 800 m and located at sea level, had the same autumn frost hardiness as provenances originating from altitudes 200 m to 400 m.

The present results indicate that progenies of high altitude clones do not retain the annual growth rhythm of their parents when sexual reproduction occurs at low altitude. They rather perform as if they were adapted to a considerably lower altitude, in particular regarding growth cessation and development of autumn frost hardiness. Similar results have been observed after transfer of parents from a northern to a southern latitude, when the sexual reproduction is performed at the southern latitude (BJØRNSTAD, 1981; JOHNSEN, 1989a and b; SKRØPPA et al., 1994); progenies of parents of northern and hardy provenances express growth rhythm traits similar to those of populations originating from a more southern latitude.

In contrast to earlier results which in most cases were based on the performance of 1 or 2 year old seedlings, parts of the present data are from measurements of 9 and 10 year old trees. This shows that the effects of the crossing environment may be long-lasting, as was indicated by JOHNSEN (1989b), who made his observations on seedlings of age 4 to 7 years.

The factors causing these effects are not yet known. Physiological effects due to a higher weight of seeds produced in a better climate and genetic effects due to the selection of plus trees have been disproved (JOHNSEN and

ØSTRENG, 1994; JOHNSEN et al., 1994). One possible explanation might be directed selection during the sexual reproductive process, either at the haploid pollen or postzygotic diploid level. The present results indicate an unbalanced genetic contribution from the 2 sexes in the diallel families, as shown by the significant reciprocal effects. Similar reciprocal effects were found for traits measured in the 2nd growth period in Scots pine after crosses made at 3 different latitudes (DORMLING and JOHNSEN, 1992). In other diallels performed in natural Norway spruce stands, reciprocal effects have not been found for any seedling traits (SKRØPPA, unpublished).

A possible male gametophytic selection could also explain the large paternal effects on filled seed percentages in these diallel families (SKRØPPA and THO, 1990). Evidence of pollen selection have been found in several plant species (HORMAZA and HERRERO, 1992). In Norway spruce, there are indications of non-random events taking place during sexual reproduction (SKRØPPA and LINDGREN et al., 1994). However, evidence of directed selection has not yet been shown, nor of any relationships between selective factors during the reproductive process and the phenotypic expressions of growth rhythm in the seedlings. Other types of genetic effects of permanent (rapid genomic changes) or less permanent (epigenetic effects) type are also possible; see JOHNSEN et al. (1994) for a more thorough discussion. So far, however, no conclusive evidence is available that favours any of these explanations. More studies are needed to identify the causal factors.

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Frequency of Seedlings from Natural Self-Fertilization in Pacific Northwest Ponderosa Pine (Pinus ponderosa Dougl. ex Laws.)

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Summary

Phenotypic mutant markers were used to estimate natural selfing (Ŝ) in 112 trees in 4 regions of the Pacific Northwest: 1) Siskiyou Mountains in southwest Oregon, 2) east side of the Cascade Range in Oregon, 3) Ochoco Mountains east of the Cascades in Oregon, and 4) east side of the Cascades near Wenatchee, Washington. In region 2, stands were classified by whether they were part of the main distribution, part of the forest-high desert ecotone, or disjunct populations. Estimated selfing was also related to filled seed percent in a sample of trees from regions 2 and 3 and to seed survival after several months of storage at room temperature in trees from region 1. Effects of crown position were examined in 6 trees. Mean Ŝ was 0.091 and 0.076 if trees were excluded that were in disjunct stands and in stands with ponderosa pine as a minor component. Median Ŝ was 0.056. Difference among regions was not significant; difference among stand types was. Heterogeneity among trees-in-regions was large and significant in all regions. Ŝ was significantly, but weakly and inversely, correlated with filled seed percent and with seed storability. Seeds from upper crown had lower estimates of selfing than seeds from mid and lower crown, but the difference was not significant.

Key words: Self-pollination, selfing rate, outcrossing rate, mating system, inbreeding, seed yield, seed storability, stand structure, geographic variation, crown level.
FDC: 165.3; 181.521; 174.7 Pinus ponderosa.

Introduction

Several reports of controlled and natural inbreeding of ponderosa pine have been published. Sorensen (1970) self- and cross-pollinated 19 trees in 2 stands in the Oregon Cascade Range. Mean percentages of round, normal-appearing seeds that were filled were 23.7 after self-pollination and 66.5 after cross-pollination giving a mean relative self-fertility of 0.367. Wang (1970) reports that germination of sound seeds from selfing was about 45 % that of

sound seed from wind-pollination. Using isozyme gene markers, Mitton et al. (1981) estimated the mean proportion of outcrossed offspring at the viable seed stage to be 0.96 (0.04 self-seed) but found no significant difference among 31 trees in a stand near Boulder, Colorado. Farris and Mitton (1984) reported an outcrossing rate of about 81 % (19 % self-seed) in a scattered stand at the forest-grassland ecotone. Sorensen and Miles (1974) estimate 11.3 % self seedlings in wind-pollination families of 17 ponderosa seed parents based on seedling mortality in self-, cross-, and wind-pollination families.

In the present study, phenotypic mutant markers were used to estimate natural selfing over a broad area in Oregon and Washington. Specific purposes were to 1) obtain a general estimate of natural selfing in Pacific Northwest ponderosa pine; 2) test for geographic, stand type, and individual tree variation in rates of selfing; 3) examine crown level effects on natural selfing; and 4) relate the magnitude of natural selfing to filled seed percent and to seed storability.

Materials and Methods

Distribution of marker-carrying trees

From controlled inbreeding (Sorensen, 1970) and 4 large common garden tests (unpublished), 112 seed parents were identified that carried readily detectable mutant markers (Table 1). Seed parent locations for the original common garden studies were distributed at a frequency of about 1 parent per half township (4700 h) to 1 parent per 2 townships (18 500 h) over the sampled area. In about 25% of the sample locations, cones were collected from 2 parents in the same stand; elsewhere from 1 tree per stand. In 2 cases, both trees in a stand carried a mutant marker but not the same one. Seed trees carrying mutant markers constituted about 8 % of the original tested population and were well distributed throughout the sample area.