Conclusions

In most cases, geographically isolated regions could be differentiated on their growth response. Localities in the main range of ssp. *globulus* on the east coast of Tasmania were relatively variable compared with the main group of Victorian and Bass Strait island localities, and could be separated into four major groups. On the basis of similarities in growth response in five Tasmanian trials and geographic consistency, 12 geographic races of ssp *globulus* were identified (*Table 4*).

Acknowledgement

We thank North Forest Products for permission to access their trials. Peter Gore, Jean Jackson, Rick Hand, Martin Wind, Ian Rogers, Peter Bramich and Andrew Crick measured the trials. Jim Reid and Carolyn Raymond provided useful comments on the manuscript. This research was assisted by a grant from the Tasmanian Forest Research Council.

References

Almeida, M. H. R. N. R.: Estudo da Variabilidade Geográfica em *Eucalyptus globulus* Labill. Unpublished PhD thesis, Universidade Técnica de Lisboa (1993). —— Borralho, N. M. G., Cotterill, P. P. and Kanowski, P. J.: Breeding objectives for pulp production of *Eucalyptus globulus* under different industrial cost structures. Can. J. For. Res. **23**: 648—656 (1993). —— Cotterill, P. P., Dean, C., Cameron, J. and Brindbergs, M.: Nucleus breeding: a new strategy for rapid improvement under clonal growth. In: Proceedings of the IUFRO Conference on Breeding Tropical Trees: Population Structure and Genetic Improvement Strategies in Clonal Growth and Seedling Forestry. Pattaya, Thailand. Gibson, G. L., Griffin, A. R. and Matheson, A. C. (eds): 39—51. Oxford Forestry Institute, Oxford, U. K. and Winrock International, Arlington, Virginia (1989). —— Gardiner, C. A., and Crawford, D. F.: 1987 Seed collections of *Eucalyptus globulus* subsp. *globulus* for tree improvement purposes. Unpublished Report, CSIRO Division of Forest Research, Canberra (1987). —— Gardiner, C. A., and Crawford, D. F.: 1988 seed collections of *Eucalyptus globulus* subsp. *globulus* Labill. for tree improvement purposes. Unpublished Report, CSIRO Division of Forestry and Forest Products, Canberra (1988). —— GENSTAT 5: Genstat 5, Release 2. Reference Manual Supplement. Oxford University Press, Oxford (1991). —— Hasan, O.: The Effect of Paclobutrazol on Flowering Activity and Gibberellin Levels in *Eucalyptus* nitens and *Eucalyptus globulus*. Unpublished PhD. thesis, University of Tasmania (1993). —— Jordan, G. J., Potts, B. M., Kirkpatrick, J. B., and Gardiner. C. A.: Variation in the *Eucalyptus globulus* complex revisited. Aust. J. Bot. **41**: 763—785 (1993). —— King, R. C. and Stansfield, W. D.: A Dictionary of Genetics. Oxford University Press, New York (1990). —— Kirkpatrick, J. B.: Geographical Variation in *Eucalyptus globulus*. Bulletin No. 47, Forestry and Timber Bureau. Australian Government Publishing Service, Canberra (1975). —— Orme, R. K.: *Eucalyptus globulus* provenances. In: Proceedings of the Third World Consultation on Forest Tree Breeding, Canberra: 207—221. CSIRO, Division of Forest Research, Canberra (1978). —— Orme, R. K.: Progress with *Eucalyptus globulus* provenance research. Silvicultura **31**: 483—486 (1988). —— Patterson, H. D. and Williams, E. R.: A new class of resolvable incomplete block designs. Biometrika **63**: 83—92 (1976). —— Phillips, B. F., Campbell, N. A. and Wilson, B. R.: A multivariate analysis of geographic variation in the welk *Dicathais*. J. Ep. Mar. Biol. Ecol. **11**: 27—69 (1973). —— Potts, B. M. and Jordan, G. J.: Variation in a base population trial of *Eucalyptus globulus* subsp. *globulus* in Tasmania. In: Research Working Group No. 1 of the Australian Forestry Council, Forest Genetics, Proceedings of Twelfth Meeting, Canberra; February 1993: 87—89. Australian Forestry Council, Canberra (1993). —— Quaas, R. L. and Pollack, E. J.: Modified equations for sire models with groups. J. Dairy Sci. **64**: 1868—1870 (1981). —— Raymond, C. A.: Developing breeding populations for temperate eucalypts in relation to natural populations. In: Proceedings of the IUFRO Conference on Breeding Tropical Trees: Population Structure and Genetic Improvement Strategies in Clonal Growth and Seedling Forestry, Pattaya, Thailand. Gibson, G. L., Griffin, A. R. and Matheson, A. C. (eds): 423—424. Oxford Forestry Institute, Oxford, U. K. and Winrock International, Arlington, Virginia (1989). —— SAS Institute Inc.: SAS/STAT User's Guide Version 6, Volume 2. SAS Institute Inc., Cary, NC (1990). —— Searle, S. R.: Linear models for unbalanced data. John Wiley and Sons, New York (1987). —— Sneath, P. H. A., and Sokal, R. R.: Numerical Taxonomy. W. H. Freeman and Co., San Francisco (1973). —— Sokal, R. R., and Rohlf, F. J.: Biometry. 2nd Edn. W. H. Freeman and Co., San Francisco (1981). —— Volker, P. W., Dean, C. A., Tibbits, W. N. and Ravenwood, I. C.: Genetic parameters and gains expected from selection in *Eucalyptus globulus* in Tasmania. Silvae Genetica **39**: 18—21 (1990). —— Volker, P. W. and Orme, R. K.: Provenance trials of *Eucalyptus globulus* and related species in Tasmania. Aust For. **51**: 257—265 (1988). —— Woolaston, R., Whiteman, P. H. and Cameron, J. N.: Genetic analyses of four year diameter measures for *Eucalyptus globulus* growing across four sites in Victoria, Australia. In: Intensive Forestry: The Role of Eucalypts. Proceedings of the IUFRO symposium, P2.02-01 Productivity of Eucalypts, 2 to 6 September 1991, Durban, South Africa. Schönau, A. P. G. (ed.): 371—381. ICFR, Durban (1991).

Effects of Sexual Reproduction at Different Latitudes on Performance of the Progeny of Picea abies

By T. Skrøppa[1]), T. Nikkanen[2]), S. Ruotsalainen[3]) and Ø. Johnsen[1])

(Received 6th June 1994)

Abstract

Controlled crosses of the same combinations were performed in a Norway spruce seed orchard in northern Finland and in 1 of 2 orchards in southern Finland. Seedlings from 11 family pairs were cultivated and cold acclimated in a phytotron together with control provenances and were frozen in artificial freezing tests at different temperatures. The seedlings from the crosses at the northern location were generally more frost hardy than their full-sibs from the southern crosses and were also taller. The controlled cross seedlings were less frost hardy than natural stand seedlings originating from the same latitude as their parents. A close relationship was found between the hardiness of the control provenances and their latitude. The results indicate that adaptive properties of Norway spruce seedlings to some extent depend on the climatic conditions at the site where the reproduction is performed.

Key words: full-sib families, frost hardiness, height growth, environmental preconditioning, adaptation.

FDC: 165.52; 165.53; 181.5; 232.11; 232.12; 174.7 *Picea abies*; (480).

Introduction

Recent results have shown that seedlings from seeds produced after controlled crosses in Norway spruce (*Picea abies* (L.) Karst.) seed orchards or clonal archives may not

---

[1]) The Norwegian Forest Research Institute, 1432 Ås, Norway

[2]) The Finnish Forest Research Institute, Punkaharju Research Station, 58450 Punkaharju, Finland

[3]) The Finnish Forest Research Institute, Kolari Research Station, 95900 Kolari, Finland

always retain the adaptational properties of their parents. Such effects are observed when the parental clones have been transferred from a northern to a southern latitude or from high to low altitudes or from outdoor climate to elevated temperature inside a greenhouse (JOHNSEN, 1989a and b; JOHNSEN and ØSTRENG, 1994; JOHNSEN et al., 1994; SKRØPPA, 1994). A more frequent and abundant flowering and better seed ripening under more favourable climatic conditions are in most cases the reasons for such transfers. This has been an important strategy in the breeding of spruce. The effects observed on the seedlings have been an extended growth season, a later bud-set and reduced frost hardiness in comparison with related seedlings from seeds produced in a northern environment. The observed differences seem similar to provenance differences in adaptive traits between provenances from different latitudes or altitudes. The effects may have practical consequences both for the cultivation of seedlings in the nurseries and later in plantations. If true genetic differences are expressed, then this may also be an important factor in the evolution of the species.

The former studies were incomplete in that only open pollinated families were available from the northern environment, thus the paternal contribution was not under control. In order to investigate these effects further identical full-sib families were generated both at a southern and a northern crossing location in Finland. The present paper reports the results from experiments with 1-year-old seedlings from these families.

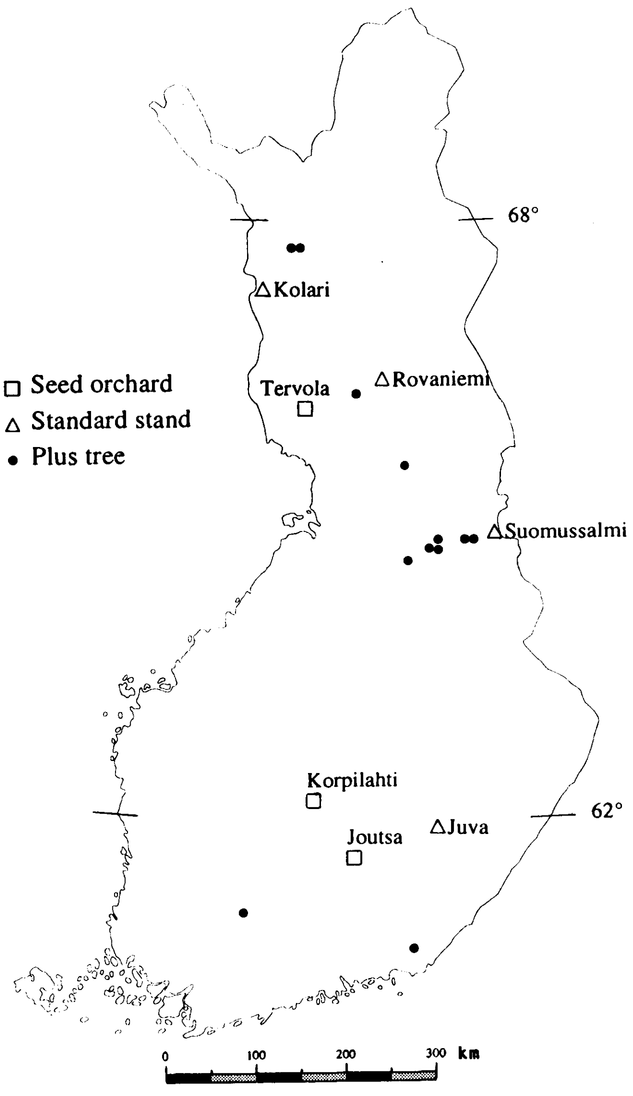

Figure 1. — Map of Finland showing the crossing locations and origins of the provenances (standard stands) and plus trees.

Table 1. — Cross combinations and families included in the experiment. The latitude of origin is given of each clone. The family numbers of 1 to 11 are those referred to in *tables 2, 3* and *4* and *figures 2* and *3*.

♀	♂	P 689 65°39'	P 1218 64°44'	P 679 64°43	P 684 64°49'	P 677 64°37'	E 137 61°05'	E 10 60°45'
P 391	66°12'	1	2					
P 275	67°44'			3				
P 532	67°44'			4	5			
P 670	64°44'					6		
P 679	64°43'		7					
P 684	64°49'					8		
P 683	64°49'					9		
P 689	65°39'						10	11

Materials and Methods

Experimental materials

Identical controlled crosses were performed in 1 Norway spruce seed orchard in northern Finland (Tervola, lat. 66°08'N), and 1 of 2 seed orchards in southern Finland (Joutsa, lat. 61°39'N and Korpilahti, 62°13'N) (*Fig. 1*). The crosses were performed in different years in the period 1987 to 1991, using pollen from the same year and location in some of them and stored pollen in others. A description of the 11 pairs of full-sib families included in the experiment and their crossing history is given in *tables 1* and *2*. Nine of the families are from crosses between northern parents (N x N families: # 1 to 9) and two from crosses between a northern clone used as female and a southern pollen parent (N x S families: # 10 to 11). The monthly mean temperatures at a southern and a northern site during pollen production, pollination and embryo and seed development are presented in *table 3*.

In addition to the 11 pairs of full-sib families, seedlots from 4 natural stands (provenances) were included as controls (Juva, lat. 61°55'N; Suomussalmi lat. 64°51'N; Rovaniemi, lat. 66°24'N and Kolari, lat. 67°17'N) (*Fig. 1*). The Juva seedlot was from 1973, while the 3 others were from 1986.

The weight of each seedlot was determined before germination.

Plant cultivation

The seeds were germinated and seedlings were grown in multipot containers in a phytotron. Each seedlot was grown in family plots in 2 replicates in each of 2 phytotron rooms. In each replicate the 2 members of each of the 11 family pairs (S and N) were grown in plots adjacent to each other. The provenance lots were likewise grown adjacent to each other, in the same replicates as the families. Cold acclimation was induced by short day and low temperatures during night according to the methods described by JOHNSEN (1989c) (Exp. 3).

The germination rate of the different seedlots varied considerably, and notes were taken of seedlots that germinated late. However, germination rates were not recorded of each individual seedlot.

Table 2. — Year and dates of crosses and year of pollen collection of the 11 full-sib families included in this experiment. S: southern location; N: northern location.

Full-sib family #	Year of cross		Date of pollination		Year of pollen collection		Location of pollen collection in N cross
	S	N	S	N	S	N	
1	1987	1989	31.5	25.5	1987	1987	N
2	1987	1989	31.5	25.5	1987	1984	S
3	1989	1988	15-16.5	5.6	1989	1987	S
4	1989	1991	15-16.5	10-11.6	1989	1989	S
5	1989	1989	15-16.5	25.5	1989	1987	S
6	1987	1989	31.5	26.5	1987	1983	S
7	1987	1989	31.5	25.5	1987	1984	S
8	1989	1989	15-16.5	26.5	1989	1983	S
9	1987	1989	31.5	26.5	1987	1983	S
10	1987	1989	31.5	25.5	1987	1983	S
11	1987	1991	31.5	10-11.6	1987	1989	S

Table 3. — Monthly mean temperatures (°C) at a southern (Jyväskylä) and a northern (Kemi) meteorological station. Information from the Finnish Meteorological Institute.

Station/ year	March	April	May	June	July	August	September
Jyväskylä							
1983	- 4.3	3.6	10.6				
1984	- 6.5	3.5	12.3				
1987	- 7.6	1.2	7.0	12.7	14.2	10.5	7.2
1989	- 0.2	3.6	9.9	15.6	15.8	13.4	9.8
Kemi							
1987		- 1.2	5.8	11.6	13.6	10.6	7.3
1988		- 1.5	6.8	14.6	18.4	13.0	9.7
1989		2.5	7.2	13.3	14.8	13.8	9.1
1991		0.8	4.7	11.1	15.7	14.8	6.7

Freezing tests

When the night length was 10 hours in the phytotron and 16 weeks after the seeds were sown, seedlings were collected for freezing tests. All seedlings had then stopped growing and most had set terminal buds. The first freezing test was performed at temperatures —8 °C, —9.5 °C, —11 °C, —12.5 °C, and —14 °C, and a second test 6 days later at —9.5 °C and —11 °C. The freezing tests were performed as reported by JOHNSEN et al. (1994).

Two chambers were used per test temperature. In each chamber the entries were replicated 4 times in plots containing 2 seedlings. These 4 replicates were arranged corresponding to the 4 replications (room, replication within room) during plant cultivation in the phytotron rooms. Two seedlings from each member of the family pairs that had grown in adjacent plots during cultivation, were therefore placed in adjacent plots also during the freezing tests.

When the freezing tests were finished, the seedlings were placed in a greenhouse at 22 °C under humid conditions and continuous light. After 3 weeks the damage on needles of each individual seedling was classified according to the following 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

Statistical analyses of damage scores were performed only for the temperatures —9.5 °C, —11 °C and —12.5 °C at the first freezing occasion, with mean damage scores 4.8, 5.9, and 8.3, respectively. This selection was due to either very low or high damage levels, making the data less suitable for statistical analyses, or few seedlings were left of many families at the second freezing occasion. All means presented are based on the average results from these 3 temperatures.

Before performing statistical analyses the mean damage score of the 2 seedlings of each plot was transformed by the transformation $y=\text{arcsine}(x/11)^{1/2}$ (JOHNSEN, 1989c).

The transformed damage scores and heights (plot means) of seedlings of the provenances were analysed in analyses of variance by the procedure GLM in Statistical Analysis System (SAS) (SAS Institute, 1987), by a model with the following effects included: provenance, temperature, provenance x temperature, freezing chamber(temperature), phytotron room and replicate(room). Provenance and temperature were considered as fixed effects.

In the 2 sets of families (N x N and N x S) the differences in transformed damage scores and seedling heights between seedlings from the southern and northern crossing location were tested by individual 2-sided t-tests within each family pair. Within each replicate the difference between the means of the 2 members of each adjacent family plot was calculated. As these seedlings had shared the same common environment during the phytotron cultivation and also in the freezing chambers, all common environmental factors vanished in these differences. A common error for the t-tests was calculated on the basis of the within-family differences in each freezing chamber and then pooled across chambers, temperatures and families.

Correlation coefficients were calculated between family means of damage scores at the northern and southern crossing location, between height measurements and seeds weights, and between these traits and the mean latitude of origin of the parents.

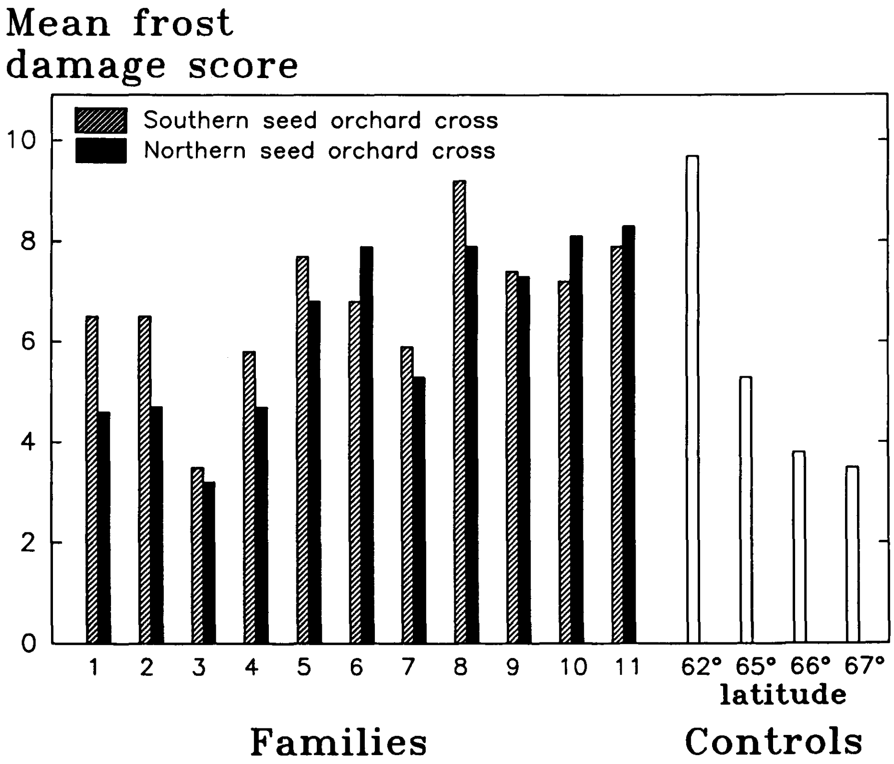

Figure 2. — Mean frost damage scores of the 11 pairs of full-sib families and the control provenances.

Results

Frost damage

The differences between the provenances were highly significant in the analysis of variance ($p<0.0001$), as is also shown in *figure 2.* The southern provenance Juva was substantially more damaged than both the other provenances and the full-sib families.

In the set of N x N families, the southern seedlings in 8 out of the 9 families were more damaged than their full-sibs from crosses at the northern locality (*Fig. 2*). The differences within family pairs were significant by individual two-sided t-tests in 6 of the 9 pairs (*Table 4*), one of these being the aberrant family 6.

Table 4. — Results of 2-sided t-tests (p-values) within family pairs to test difference in performance between crossing locations. Families are numbered as in *table 1.* The first 9 families are of type N x N, the last 2 N x S.

Family #	Transformed frost damage	Seedling height
1	< 0.0001	0.014
2	0.0001	< 0.0001
3	0.55	0.72
4	0.006	0.092
5	0.048	0.01
6	0.006	0.0001
7	0.32	0.018
8	0.011	0.84
9	0.75	0.45
10	0.078	0.58
11	0.43	0.10

For the N x S families, the seedlings from the northern crosses had more damage than their full-sibs from the southern localities (*Fig. 2*, #10 to 11). However, these differences are not significant *(Table 4).*

A considerable variation was observed among the N x N families. The most hardy family had the same low level of damage as the seedlings from the northernmost stand. On average, the seedlings from the crosses were more severely damaged than the seedlings from natural stands from the same latitudes (*Fig. 2*).

Height growth

The northernmost control provenance (Kolari, lat. 67°17'N) had the tallest seedlings, while the southern control (Juva, lat. 61°55'N) had the lowest mean height. Within the full-sib family pairs the heights of the northern seedlings were significantly taller than their southern full-sibs in 5 of the 9 families (*Fig. 3, Table 3*). Smaller and nonsignificant differences were present in the set of N x S families.

Seed weight

The mean weight of 1000 seeds from the southern crosses was 5.8 g, compared to 6.7 g for the northern ones. Within 3 family pairs the weight difference were as large as 2.7 g, the northern seedlots being the heaviest. The differences in seed weights between the provenance seed lots were negligible.

Relationships between traits

A strong relationship was present between provenance mean damage score and the latitude of origin of the parents. In a linear regression analysis the latitude accounted for 96% of the variation ($r=-0.98$, $p<0.001$) in mean damage score. A similar relationship was also pre-

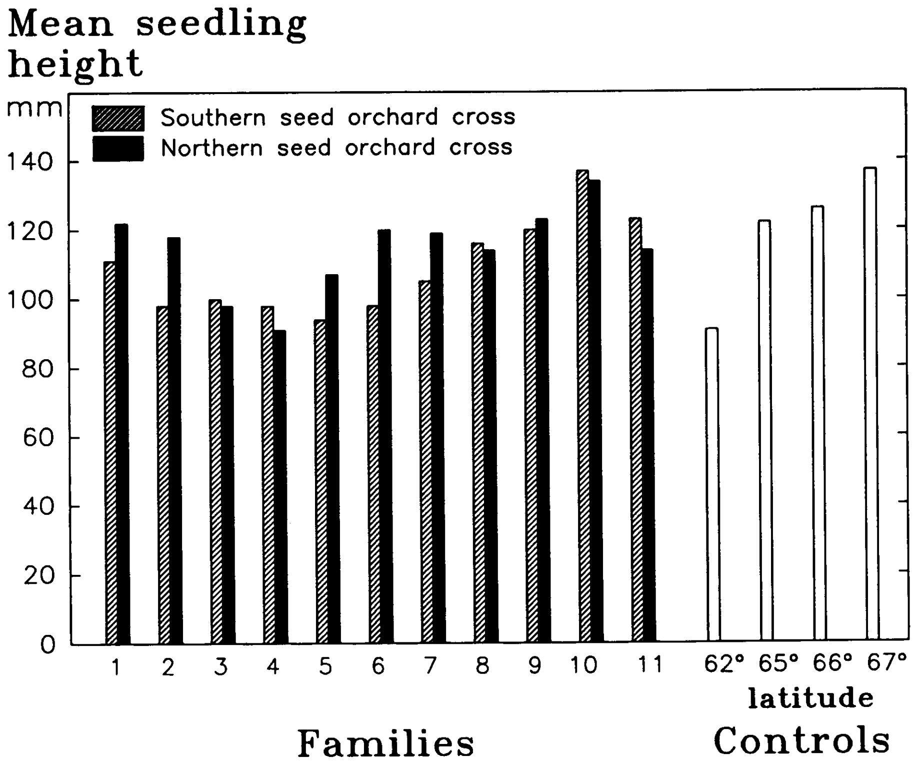

Figure 3. — Mean seedling heights of the 11 pairs of full-sib families and control provenances.

sent between the height and latitude, but with a positive correlation coefficient ($r=0.98$, $p<0.001$).

For the full-sib families, significant correlations between the mean latitude of the 2 parents and damage were found only when the N x S families were included and at the northern ($r=-0.74$, $p=0.01$), but not at the southern location ($r=-0.47$, $p=0.15$). For height growth these correlation coefficients were $r=-0.66$ ($p=0.03$) and $r=-0.80$ ($p=0.003$), respectively.

Likewise, the correlation between the difference in frost damage within family pairs and the mean latitude of the parents was significant only when the 2 N x S families were included ($r=0.62$, $p=0.04$). The correlation coefficient between mean damage of each full-sib family at the 2 crossing locations in the N x N crosses was $r=0.84$ ($p=0.005$). This indicates a low location by family interaction. For heights the correlation was $r=0.46$ ($p=0.21$).

No relationships were found between damage scores and heights at any of the crossing locations.

No relationships were present between seed weights and damage scores, nor between seed weights and height growth. Neither could the differences within family pairs be related to differences in seed weights within each pair.

No correlation coefficients could be calculated between germination rates and seedling traits. However, both short and tall families and low and high levels of damage were found among the few slowly germinating families. The seeds of the southern provenance, Juva, harvested in 1973, were among the slowest to germinate.

Discussion

Frost hardiness

The presented results show that the performance of seedlings of full-sib families of Norway spruce is not independent of the location where the crosses are performed. Seedlings from crosses performed at the northern site were generally more frost hardy than their full-sibs from seeds produced at a southern site. Similar results have been demonstrated for the same species by Bjørnstad (1981), Johnsen (1989a and b) and Johnsen and Østreng (1994). Differences in hardiness between identical crosses performed in a greenhouse and in a nearby seed orchard have also been found (Johnsen et al., 1994). In *Pinus sylvestris*, Dormling and Johnsen (1992) found that 1 year old seedlings from crosses at a northern site were more frost hardy than seedlings from the same cross at 2 southern sites, and Lindgren and Wei (1994) have shown that the same northern families have better survival and are shorter in 2 field trials than their "southern" full-sibs. Johnsen (1988) and Skrøppa (1994) have demonstrated that similar effects may be present on seedlings after crosses at low altitudes between clones that are transferred from high altitudes. The effects persist after a clonal propagation by rooted cuttings (Johnsen, 1989b) and have been observed to last at least 10 years (Skrøppa, 1994).

The reproductive process in *Picea*-species follows a 2-year cycle which can be subdivided into several stages (Owens and Blake, 1985). After a dormant period, meiosis and pollen development take place in late winter and early spring, the mature seed cone is pollinated and fertilization takes place after a few weeks. Embryo and seed development are rapid and seeds are mature in early autumn. During these stages there are several opportunities for processes to take place that may have genetic implications, either as selective events or as rapid genomic changes or epigenetic effects, see Skrøppa and Johnsen (1994) for more thorough discussions. Temperature and photoperiod are the most likely triggering factors.

The full-sib families tested in this experiment are from crosses performed in different years, some with fresh and some with stored pollen. In the 2 southern seed orchards, 7 of the 11 crosses were performed in 1987, while 8 were made in 1989 at the northern site. The climatic conditions were very different in those 2 years (*Table 3*). In 1987, the spring was late and both spring and summer temperatures were low. Two years later, in 1989, the spring was rather early, and the temperatures were high both in southern and northern Finland. Based on the monthly mean temperatures, the whole reproductive process took place in 1989 in the northern seed orchard in a warmer climate than it did in the 2 southern orchards in 1987. Five of the N x N full-sib family pairs (families 1, 2, 6, 7 and 9) were produced under these conditions. In the 4 other family pairs the crosses were made in 1989 in southern Finland under higher temperatures than in the 3 crossing years in northern Finland (1988, 1989 and 1991). Therefore no direct relationship can be found between the frost hardiness differences and the temperature conditions during pollination, fertilization and embryo and seed development. A complicating factor is that pollen for the northern crosses were produced in different years.

The photoperiod is the only climatic factor which differs systematically between the northern and southern crossing locations in all years. In mid-May the night is approximately 2 hours longer at lat. 62^0 than at lat. 66^0. The night length differences will be larger when the northern crosses are performed at later dates. It is therefore most likely that the observed differences in frost hardiness between the northern and southern crosses are related to differences in the photoperiod at some point during the reproductive process, with the possibility of interactions with the temperature. The mechanisms involved, however, are not known.

The northern clone P 677 was used as the paternal parent in 3 full-sib families. All the 3 maternal parents originate from the same latitude and within 1 degree of longitude. The 3 crosses in the northern seed orchard were all performed in 1989, with pollen collected in a southern seed orchard in 1983, and have similar damage scores (7.3, 7.9, 7.9). At the southern site, 2 of the crosses (families 6 and 9) were performed in 1987 on the last day of May, whilst the third (family 8) was performed on May 15 to 16 in 1989. All pollen was at this site collected shortly before pollination. The seedlings of the cross from 1989 were substantially more damaged (mean score 9.2) than those of the crosses from 1987 (scores 6.8 and 7.4). This may indicate effects of the climatic conditions of the dates or the year the reproduction took place. Such differences are demonstrated by Kohmann and Johnsen (1994), who found large differences in photoperiodic responses between seedlings from seed collected in the same 2 years, 1987 and 1989, in a Norwegian seed orchard.

However, it may also express genetic differences in frost hardiness among the parental clones, which were found in another freezing test based on seeds harvested in the same seed orchard and the same year (Nikkanen and Pulkkinen, unpublished).

Seed weight

Eight of the 11 northern crosses were from 1989, while 7 of the southern were from 1987. The higher seed weights of the northern families are most likely due to the more favorable temperature during seed maturation in northern Finland during the summer of 1989 (*Table 3*). Within the full-sib family pairs there are many combinations of temperatures during seed maturation, which may have caused differences in seed weights. These differences, however, can not account for the variability in frost damage and height growth.

Height growth

The southern provenance Juva produced the shortest seedlings which is contradictory to earlier results (Mikola, 1980; Pulkkinen, 1993). This result can be explained by the slow germination of this seedlot, which had been stored for 13 years longer than the seed of other provenances. The unexpectedly small size of the seedlings of this southern provenance does not seem to have any relationships to its frost hardiness, as the ranking in frost damage between the provenances are according to expectations based on their latitudes of origin.

In the families no indications were found for relationships between germination rate and seedling heights. Within each family pair the seedlings from the northern locations were generally taller than their "southern" full-sibs. This may have been caused by interactions between germination rate, seed weight and the growth conditions in the phytotron, even if no significant correlations could be shown between these traits and height growth, as have been found by other authors, e. g. Mikola (1980). Alternatively, it may be due to yet not explainable effects of the very different temperature conditions of the two years 1987 and 1989. However, these factors seem not to be related to the observed differences in frost hardiness. It has also been shown by Christerson (1975) that plant height in itself has no influence on frost hardiness development.

Concluding remarks

The growth cessation and autumn frost hardiness of families of 1-year-old Norway spruce seedlings seem under northern conditions to some extent to depend on the environmental conditions where the sexual reproduction is performed. The presented results indicate that the photoperiod is an important influencing factor.

The possible effects of the crossing environment on seedlings performance are being investigated further. Pollen have been produced under controlled conditions in factorial combinations of long and short days and high and low temperatures. These pollen lots have been used in controlled crosses in seed orchards. Seedlings from these crosses are now being tested. Other crosses have been made at different dates and under indoor and outdoor conditions. An understanding of the environmental influence during sexual reproduction on the performance of the progenies is considered to be of utmost importance, both for the production of seed in orchards and for a better understanding of the evolutionary process of our conifer species.

Acknowledgement

We thank the Nordic Forest Research Co-operation Committee for financial support of the research.

Literature

Bjørnstad, Å.: Photoperiodical after-effect of parent plant environment in Norway spruce (*Picea abies* (L.) Karst.) seedlings. Rep. Norw. For. Res. Inst. **36** (6), 1—30 (1981). —— Christerson, L.: Frost hardiness development in rapid- and slow growing Norway spruce seedlings. Can. J. For. Res. **5**, 340—343 (1975). —— Dormling, I. and Johnsen, Ø.: Effects of parent plant environment on full-sib families of *Pinus sylvestris*. Can. J. For. Res. **22**, 88—100 (1992). —— Johnsen, Ø.: After-effects on progenies from orchard clones moved to non-native environments. In: Physiology and genetics of reforestation. Eds. J. Worall, J. Loo-Dinkins and D. T. Lester.

Proc. Tenth North American Forest Biology Workshop, Vancouver, B. C., pp 1—11 (1988). —— Johnsen, Ø.: Phenotypic changes in progenies of northern clones of *Picea abies* (L.) Karst. grown in a southern seed orchard. I. Frost hardiness in a phytotron experiment. Scand. J. For. Res. **4**, 317—330 (1989a). —— Johnsen, Ø.: Phenotypic changes in progenies of northern clones of *Picea abies* (L.) Karst. grown in a southern seed orchard. II. Seasonal growth rhythm and height in field trials. Scand. J. For. Res. **4**, 331—341 (1989b). —— Johnsen, Ø.: Freeze-testing young *Picea abies* plants. A methodological study. Scand. J. For. Res. **4**, 351—367 (1989c). —— Johnsen, Ø. and Østreng, G.: Effects of plus tree selection and seed orchard environment on progenies of *Picea abies*. Can. J. For. Res. **24**, 32—38 (1994). — Johnsen, Ø., Skrøppa, T., Haug, G., Apeland, I. and Østreng, G.: Seedlings of *Picea abies* from crosses in a greenhouse were less hardy than their full-sibs from crosses in a seed orchard. Tree Physiology, (In press) (1994). —— Kohmann, K. and Johnsen, Ø.: The timing of bud set in seedlings of *Picea abies* from seed crops of a cool versus a warm spring and summer. Silvae Genet., (In press) (1994). —— Lindgren, D. and Wei, R.-P.: Effects of maternal environment on mortality and growth in young *Pinus sylvestris* field trials. Tree Physiology **14**, 323—327 (1994). —— Mikola, J.: The effect of seed size and duration of growth on the height of Scots pine (*Pinus sylvestris* L.) and Norway spruce (L.) Karst.) provenances and progenies at the nursery stage. Silva Fennica **14**, 84—94 (1980). —— Owens, J. N. and Blake, M. D.: Forest tree seed production. Information Report PI-X-53. Petawawa National Forestry Institute, Chalk River, Ontario. 161 pp. (1985). —— Pulkkinen, P.: Frost hardiness development and lignification of young Norway spruce seedlings of southern and northern Finnish origin. Silva Fennica **27**, 47—54 (1993). —— SAS Institute Inc.: SAS/STAT^{TM} Guide for personal computers. Version 6 Edition. Cary, NC (1987). —— Skrøppa, T.: Growth rhythm and hardiness of *Picea abies* progenies of high altitude parents from seed produced at low elevations. Silvae Genet. **43**, 95—100 (1994). —— Skrøppa, T. and Johnsen, Ø.: The genetic response of plant populations to a changing environment: the case for non-Mendelian processes. In: Biodiversity, Temperate Ecosystems and Global Change. Boyle, T.J.B. and Boyle, C.E.B. (eds). Springer Verlag, Heidelberg. pp. 183—200 (1994).

Time Trends for Genetic Parameters in Progeny Tests of Abies sachalinensis (Fr. Schm.) Mast.

By T. Sato

Hokkaido Forest Research Institute,
Bibai, Hokkaido 079—01, Japan

(Received 6th June 1994)

Summary

Changes of genetic parameters for tree height with stand development were examined on 21-year performance data from 4 open-pollinated progeny tests of *Abies sachalinensis* in Hokkaido, Japan. Differences in tree height among families were significant on each site, while among regions were unclear. Large genotype-environment (GE) interaction was observed. Heritability was highest at the youngest age, and showed a tendency to decrease with stand development. Genetic juvenile-mature correlation was almost always higher than phenotypic correlation. Expected genetic gain in height by early selection was comparable to that by selection at 21 years.

Key words: Heritability, juvenile-mature correlation, stand development, genetic gain, early selection.

FDC: 165.3; 165.5; 232.11; 174.7 *Abies sachalinensis.*

Introduction

Information on genetic parameters and time trends in them with stand development are important for decisions about breeding strategy and optimal selection age. Heritability and juvenile-mature correlations affect genetic gains and selection efficiency. These parameters have been estimated by many authors, and the possibility of early selection was discussed by them (Toda, 1972; Giertych, 1974; Squillace and Ganssel, 1974; Namkoong and Conkle, 1976; Franklin, 1979; Lambeth, 1980; Foster, 1986; Jiang, 1987; Cotterill and Dean, 1988; Rehfeldt, 1992; Eriksson et al., 1993). Genetic parameters at various ages are available for index selection based on assessment data at different ages (Burdon, 1989).

In progeny tests of *Abies sachalinensis* in Hokkaido, Japan, differences among progenies are obvious at an early stage for some traits. For example, susceptibility to Rhacodium-snow blight and winter desiccation damage were observed on seedlings aged 2 and 7 years from seeds respectively (Hatakeyama, 1981). However, it remains unclear whether early selection in this species is possible for growth traits. In this paper, time trends of heritability and juvenile-mature correlation of tree height are investigated and the possibility of early selection, or of an effective way of selection is discussed.

Materials and Methods

Progeny test data

Plus trees of *Abies sachalinensis* have been selected from natural stands and plantations all over Hokkaido about 1958. Open pollinated seeds were collected from these in-

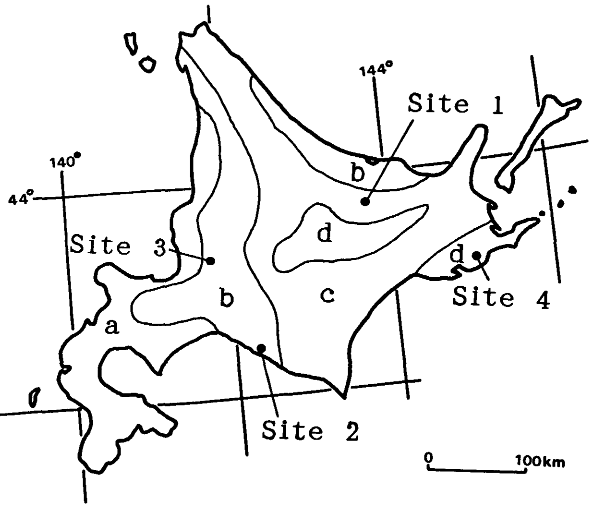

Fig. 1. — Locations of progeny test sites of *Abies sachalinensis* in Hokkaido. Four seed zones (a to d) of Yanagisawa (1965) are also indicated.