

EFFECT OF SEED-MATURING CONDITIONS ON THE GROWTH AND HARDINESS OF ONE-YEAR-OLD *PINUS SYLVESTRIS* SEEDLINGS

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ABSTRACT

Identical pairs of seed lots were produced in northern and southern Finland by controlled crosses on grafts of Scots pine plus trees originating from northern Finland. Seedlings from these seedlots were grown in a greenhouse experiment. Growth and hardiness traits were measured during the first growing season. Entries from southern Finland had a slightly faster germination and were clearly taller than corresponding entries from northern Finland. No significant differences attributable to environment of seed development were detected in bud formation or in tolerance to artificial freezing. Neither did the performance of crossed entries deviate from that of natural stands of corresponding origin. All the studied traits showed significant variation between families. No sufficient evidence was obtained to corroborate the so-called after effect hypothesis on the hardiness traits studied.

Key words: *Pinus sylvestris*, germination, height, freezing tolerance, environmental preconditioning, after effect

INTRODUCTION

Seed maturing conditions are known to have a great influence on the quality of conifer seed (WIBECK 1920, KUJALA 1927, SIMAK & GUSTAFSSON 1954, MORK 1957, ANDERSSON 1965, SARVAS 1970, HENTTONEN *et al.* 1986). The properties of seed, in turn, influence the growth of seedlings (PERRY 1976, MIKOLA 1980, SORENSEN & CAMPBELL 1985). These effects – mainly mediated through seed weight – usually disappear within a few years. BJØRNSTAD (1981) was the first to show that the growth rhythm of Norway spruce (*Picea abies* (L.) Karsten) seedlings can be affected by the environment in which flowering and seed development take place (so-called after effect).

Later studies have shown that the frost hardiness of the progeny is also affected by the growing conditions of the mother trees and that the after effect persists beyond the first growing season (JOHNSEN 1989a, 1989b, JOHNSEN *et al.* 1989, SKRØPPA *et al.* 1994). Most of the work has been done with Norway spruce, although Scots pine (*Pinus sylvestris* L.), shortleaf pine (*P. echinata* Mill.) and Virginia pine (*P. virginiana* Mill.) have also been studied (LINDGREN & WANG 1986, SCHMIDTLING 1987, DORMLING & JOHNSEN 1992, ANDERSSON 1994, LINDGREN & WEI 1994). The after effect phenomenon has, in addition to being scientifically interesting, practical implications, because seed orchards have usually been established in climatic

conditions which are more favourable than those from which the plus trees originate (SARVAS 1970, WERNER 1975, DIETRICHSON *et al.* 1982, MÁTYÁS 1991). Possible explanations for the after effect have been presented earlier (BJØRNSTAD 1981, JOHNSEN 1989a, SKRØPPA & JOHNSEN 1994), and can be separated into two groups: the differences are attributed either to seed physiological factors or to genetic influences.

The objective of this study was to obtain an accurate estimate of the assumed effect of seed maturing environment on growth and hardiness. We, therefore, crossed plus tree clones of Scots pine in climatically different environments using pollen of known origin. Seed collected from natural stands was used in order to determine whether the performance of the controlled crosses deviated from that expected on the basis of the geographic origin of the parent trees.

MATERIAL AND METHODS

Material

Grafts of five Scots pine plus trees from northern Finland were pollinated in isolation bags with pollen from three plus trees and two unselected trees at four locations to produce the seed material for this study (Table 1, Fig. 1). Two of the locations were in southern and two in northern Finland. These two geographically distant pairs of locations are hereon referred to as seed

maturing environments (or in short, environments). The reference material originated from 12 natural stands covering the whole range of Scots pine in Finland (Fig. 1). Most of the stands were represented by a sample of 20 trees.

The effective temperature sum (+ 5 °C threshold) was used to describe the environment of seed development and the original sites of the plus trees and reference stands. The temperature sum of the seed maturing year was measured in Kolari and Punkaharju, but estimated for the other seed maturing locations using a computer program developed by OJANSUU and HENTTONEN (1983). This program was also used to estimate the average annual temperature sums (mean from 1951–1980) for the original growing sites of the plus trees and reference stands.

Crosses were performed during the period 1987–1990. The maturing conditions of the seed were always colder in the north than those in the south, as a certain cross was regarded. The pollen was collected one to three years prior to the crossing. In the case of one cross, one graft in Kolari was enclosed in the green-

house during the summer of seed maturation. Thus the seed from this cross were subjected to three different maturing conditions.

The cones were extracted and the seed were stored at Kolari and Punkaharju research stations. The storage temperature was –5 °C at Punkaharju and +4 °C at Kolari. The age and storage conditions of the reference stand seed varied considerably. The majority of the seed lots were less than ten years old, but the seed lots from the four southern stands were more than 20 years old.

The seedlings were grown in a greenhouse experiment at the Punkaharju Research Station (61° 48' N, 29° 19' E, 90 m asl). Sowing was done on seedling trays filled with pre-fertilized peat on May 25–27, 1992. The crossed entries were sown using a split plot design (main plot: family, sub-plot: seed maturing environment), whereas the reference seed lots were sown at random. The number of blocks was 10. Each sub-plot consisted of 20 pots.

The seedlings were grown without any artificial heating or illumination. The temperature in the greenhouse varied from +15 to +30 °C in the daytime, with maxima above +30 °C. The night temperature was normally above +10 °C during the summer and decreased towards the end of the growing season with minima below 0 °C. The seedlings were irrigated 2–3 times a week when needed and fertilized twice during the growing season.

Measurements

1000-seed weight was estimated from all the seed lots. Germination percentage was assessed 14 and 26 days after sowing. The presence of at least one germinated seed per pot was recorded as a positive result. No attention was paid to the number of germinating seeds. Thus, the values obtained are not true germination percentages, but rough estimates.

Total height and hypocotyl length were measured at the end of the growing season on ten seedlings per plot in five blocks. The presence of a terminal bud was recorded on each seedling in these same five blocks. This was done three times in September.

Freezing tests were performed using all the material from the remaining five blocks not used for measuring height. Each block was subjected to a separate freezing test. The tests were performed on the following dates (freezing temperature in parentheses): August 26 (–6 °C), August 27 (–9 °C), September 3 (–5 °C), September 10 (–8 °C) and September 17 (–10 °C).

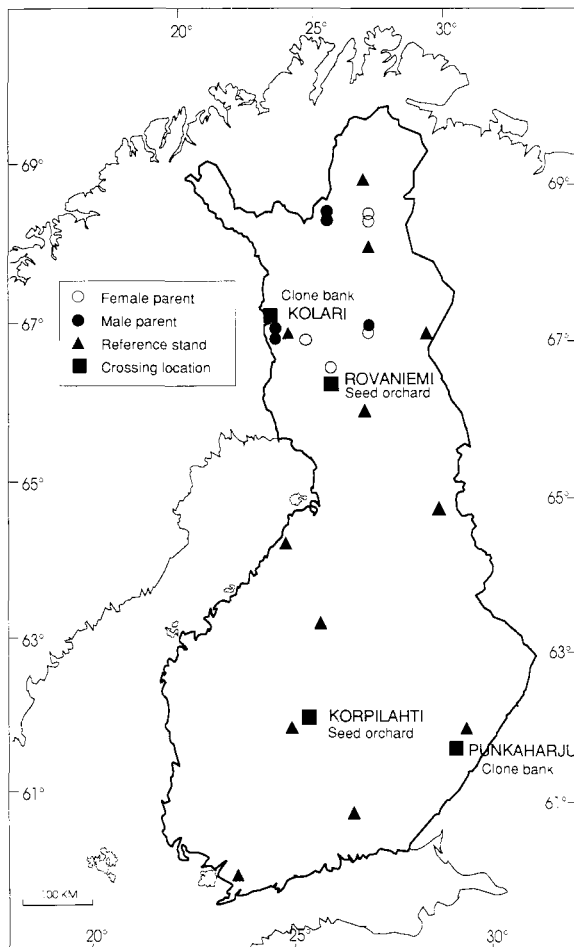


Figure 1 Origin of trees used in the crosses, crossing locations and origins of reference stands used in experiment

Table 1 Description of the crossings and the seed maturing locations

	Crossing (female × male)				
	P602 × P563	P577 × P560	P75 × P74	P115 × St6/tree 111	P218 × St6/tree 107
Southern seed maturing location	Punkaharju	Punkaharju	Punkaharju	Punkaharju	Korpilahti
Seed maturing year and temperature sum, d.d.	1988 1444	1988 1444	1990 1226	1987 1023	1990 1084
Northern seed maturing location	Rovaniemi	Rovaniemi	Kolari	Kolari	Kolari
Seed maturing year and temperature sum, d.d.	1988 1044	1988 1044	1988 956	1990 810	1988 956 1192 ¹⁾

¹⁾ Temperature sum during seed maturing in the greenhouse

Table 2 The split-plot, mixed-model analysis of variance for the crossed material. The variance components of the random effects are denoted by σ^2 and those of the fixed effects by κ^2 (see SNEDECOR & COCHRAN 1968)

Source of variation	Degrees of freedom	Expected mean squares
Family	$f-1$	$\sigma_e^2 + e\sigma_{FB}^2 + eb\sigma_F^2$
Block	$b-1$	$\sigma_e^2 + e\sigma_{FB}^2 + fe\sigma_B^2$
Family × block	$(f-1)(b-1)$	$\sigma_e^2 + e\sigma_{FB}^2$
Environment	$e-1$	$\sigma_e^2 + b\sigma_{FE}^2 + fb\kappa_E^2$
Family × environment	$(f-1)(e-1)$	$\sigma_e^2 + b\sigma_{FE}^2$
Error	$f(b-1)(e-1)$	σ_e^2

The seedlings were transferred to a freezing chamber about six to nine hours before the start of the freezing treatment. In the freezing tests, the temperature was decreased from 10 °C to the desired freezing temperature at a rate of about 3 °C·h⁻¹. The minimum temperature was maintained for two hours, after which the temperature was raised (again at a rate of 3 °C·h⁻¹). The second freezing treatment killed most of the seedlings. These seedlings were not used in the analyses, so the results of freezing damage are based on four blocks.

The seedlings were subsequently moved outdoors and kept there for about two weeks before the freezing damage was assessed. The seedlings were classified into seven damage classes (0–6), which corresponded to the proportion of damaged primary needles (0 = no damage, 1 = 10 % , 2 = 30 % ... 5 = 90 % , 6 = all needles damaged). In the analyses of the data the per cent values were used.

Statistical analyses

The analysis of variance was based on a split-plot design, using the following linear model for the sub-plot mean:

$$Y_{ijk} = \mu + F_i + B_j + FB_{ij} + E_k + (FE)_{ik} + \epsilon_{ijk}$$

where: Y_{ijk} = mean of sub-plot ijk , μ = grand mean, F_i = effect of family i , B_j = effect of block j , FB_{ij} = effect of main plot ij , E_k = effect of environment k , $(FE)_{ik}$ = effect of sub-plot ik and ϵ_{ijk} = variation among sub-plots. The seed maturing environment was regarded as a fixed effect, and all the other effects as random. The mean square partitioning is shown in Table 2.

The analyses of variance were computed using PROC GLM of the SAS statistical package (SAS INSTITUTE 1989). In addition, some of the growth rhythm traits were regressed to climatic and seed character variables using SAS procedures CORR and REG.

RESULTS

Differences between seed maturing environments

The average 1000-seed weight in the southern and northern environment was 5.9 and 4.1 g, respectively. The seed lot which had developed in the greenhouse had the heaviest seed (7.5 g). The 1000-seed weight of the reference stands was lower (3.7 g) than that of the crosses.

The seed of the southern environment germinated faster than that of the northern (Fig. 2). This difference in germination (14 days after sowing) was statistically nearly significant ($p = 0.056$) (Table 3). The family effect was highly significant ($p = 0.0001$). The reference material generally showed poor germination, although the variation between stands was large. The

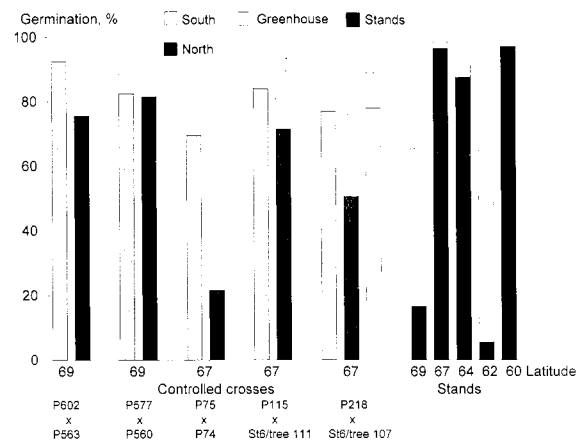


Figure 2 Germination of the crossed material and some reference stands 14 (lower part of the bar) and 26 (total bar) days after sowing. Percentage refers to the proportion of germinated sowing spots. Latitude of origin and identity of the crosses is given under the bars

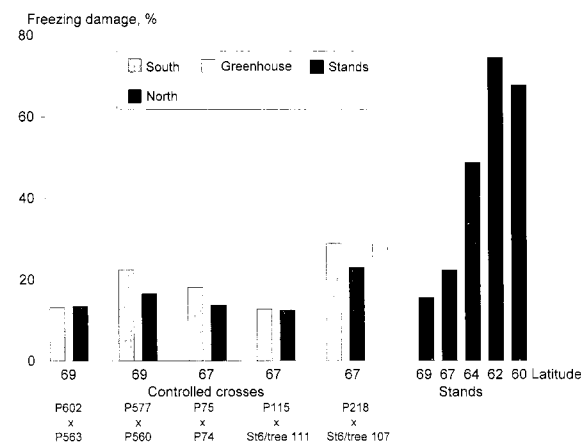


Figure 4 Damage to needles after the artificial freezing test in August-September of crossed material and some reference stands. Latitude of origin and identity of crosses is given under the bars

germination of the northern seed lot matured in the plastic greenhouse corresponded to that obtained in the southern environment. However, the differences in germination between the different groups of material subsequently diminished (26 days after sowing) and even partly disappeared.

The seedlings from the southern environment had a longer hypocotyl and also greater total height than their northern counterparts. The difference in total height was 17 mm (Fig. 3). These differences in growth traits between the seed maturing environments were statistically significant (Table 3). The effect of the environment on the epicotyl length was the least significant ($p = 0.012$). The differences between families were statistically highly significant in all growth traits. The northern greenhouse entry resembled the southern material in height growth.

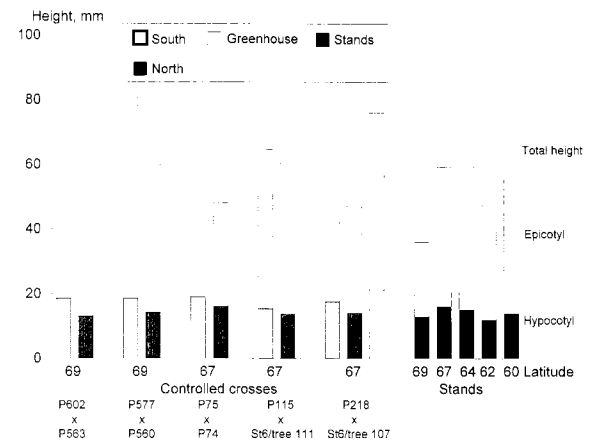


Figure 3 The total height of the crossed material and some reference stands divided into hypocotyl and epicotyl. Latitude of origin and identity of the crosses is given under bars.

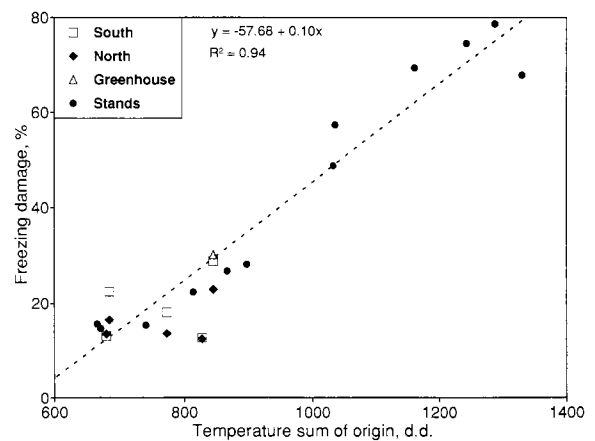


Figure 5 Dependence of freezing damage on the seedlings on the temperature sum of the origin in the reference stand material. Crossed entries are also shown.

Table 3 Split-plot analysis of variance for the crosses (see Table 2 for the model)

Character		Environment	Family	Block	Family × environment	Family × block	Error
Germination in 14 days	d.f.	1	4	9	4	36	45
	F	7.07	23.90	1.13	8.12	1.13	
	p	0.0565	0.0001	0.3705	0.0001	0.3451	
Hypocotyl length	d.f.	1	4	4	4	16	20
	F	33.04	13.38	0.35	7.53	1.41	
	p	0.0045	0.0001	0.8426	0.0007	0.2305	
Epicotyl length	d.f.	1	4	4	4	16	20
	F	19.27	14.33	1.69	5.21	2.21	
	p	0.0118	0.0001	0.2015	0.0048	0.0472	
Total height	d.f.	1	4	4	4	16	20
	F	24.89	10.19	1.30	5.71	2.32	
	p	0.0075	0.0002	0.3131	0.0031	0.0385	
Bud set percentage (September 3)	d.f.	1	4	4	4	16	20
	F	1.31	11.40	2.13	2.64	2.85	
	p	0.3165	0.0001	0.1243	0.0642	0.0142	
Freezing damage	d.f.	1	4	3	4	12	15
	F	2.32 ¹⁾	3.42	47.54	0.43	1.55	
	p	0.1485	0.0437	0.0001	0.7867	0.2090	

¹⁾ Note: The error variance was used as denominator in this F-test quotient instead of the family × environment mean square because $MS_{F \times E} < MS_{error}$

The difference between the two environments in bud formation was not statistically significant, but highly significant differences existed between the families (Table 3).

The seedlings from the southern environment were slightly more damaged (19 %) in the freezing test than those from the north (16 %) ($p = 0.148$). The level of significance for the between-family differences was 0.044, which was not as high as that of the other traits (Table 3). The northern greenhouse entry showed the same amount of freezing damage as the corresponding southern entry (Fig. 4).

Performance of the reference material

Clear geographic trends were observed in bud formation and freezing damage in the reference material. A decrease in the temperature sum of the origin by 100 degree days decreased the freezing damage by 10 % (Fig. 5). The respective regression between temperature sum and bud formation was also significant (bud form. Sep 9 = $159.85 - 0.11$ (temp. sum), $R^2 = 0.79$). Seed weight increased from north to south ($r_{seed\ weight, temp.\ sum} = 0.85^{***}$). Germination and seedling height had no clear relationship with the latitude or the temperature sum of

the origin.

Bud formation and freezing damage were not influenced by seed physiology or germination. The tallest seedlings were from stands with the fastest seed germination ($r_{germ\ 14\ days, total\ height} = 0.78^{**}$). The age of the seed had an effect on hypocotyl length ($r = -0.80^{**}$), but not on the epicotyl length ($r = -0.12$) or total height ($r = -0.24$).

Deviation of the crosses from the geographic trend

The crosses had a higher percentage of bud forming seedlings (22 %) in the early stage of bud formation (September 3) than was expected on the basis of their geographic origin (10 %) ($t = 3.13$, $p = 0.011$). Later on (September 9), this deviation diminished and became non-significant (80 % vs. 73 %, $t = 1.33$, $p = 0.220$). The respective deviation for freezing damages was not statistically significant (19 % vs. 22 %, $t = -1.33$, $p = 0.214$).

DISCUSSION

Seed weight, germination and height growth

The existence of variation on the population and family level has been confirmed in several studies for all traits studied here (WRIGHT & BULL 1963, MIKOLA 1980, 1982, BRAMLETT *et al.* 1983, HENTTONEN *et al.* 1986, NILSSON & ANDERSSON 1987, DORMLING & JOHNSEN 1992, AHO 1994). The greater seed weight and better germination in the material from the southern environment compared to the northern environment obviously resulted from the higher seed maturing temperature in the south (WIBECK 1920, KUJALA 1927, SIMAK & GUSTAFSSON 1954, HENTTONEN *et al.* 1986, DORMLING & JOHNSEN 1992). In the reference material, seed weight decreased towards the north, as has earlier been reported by *e.g.* KUJALA (1927), WRIGHT & BULL (1963) and REICH *et al.* (1994). However, there was no clinal variation in germination in the reference material, which is contrary to earlier findings (WIBECK 1920, WRIGHT & BULL 1963) and probably caused by several interfering factors like seed age and seed storage conditions (HUSS 1967, HARRINGTON 1972).

The clear differences between families in germination indicate that it is possible to improve seed maturation by selecting for seed maturation. Differences in seed maturing ability between trees have been reported in natural stands (*e.g.*, EHRENBORG *et al.* 1955, RYNNÄNEN 1982), but the genetic background of these differences has not been investigated.

The one-year-old seedlings from the southern environment were taller than those from the northern environment, owing to their considerably greater seed weight and faster germination (PERRY 1976, MIKOLA 1980, BOOTH & MORGAN 1993, REICH *et al.* 1994). In our study, the difference between the environments was greater in the hypocotyl length than in the epicotyl length. This is best explained by the temporary effect of seed weight (MIKOLA 1980). According to MIKOLA (1980), the effect of seed weight on height gradually diminishes during the first growing season. DORMLING and JOHNSEN (1992) observed that during the first weeks of development, differences between the heights of seedlings resulting from three seed maturing environments were associated with seed weight. Later on this correlation disappeared. It should be noted that LINDGREN and WANG (1986) and DORMLING and JOHNSEN (1992) found that differences in height between different seed maturing environments increased during the development, which is contrary to our results.

Growth rhythm and hardiness

The material from the southern environment was, on the average, slightly more susceptible to freezing damage than the corresponding northern material. A similar result was also obtained by DORMLING and JOHNSEN (1992) and by ANDERSSON (1994). The difference in

our study was not statistically significant ($p = 0.15$). However, although this result does not confirm the existence of the after effect phenomenon, it does not fully exclude it. DORMLING and JOHNSEN (1992) observed that there were no differences in freezing hardiness during the second growing season between seedlings from different seed maturing environments. Variation between families in freezing tolerance was greater than the variation between the seed maturing environments, which is in accordance with earlier results (DORMLING & JOHNSEN 1992, ANDERSSON 1994).

No differences were found between the environments as regards bud formation, but there were great differences between the families. These results are similar to those reported by DORMLING and JOHNSEN (1992).

In the reference material the northern stands showed earlier growth cessation and a higher tolerance to freezing than the southern ones, as has also been reported in other studies (WRIGHT & BULL 1963, MIKOLA 1982, NILSSON & ERIKSSON 1986, ANDERSSON & WESTIN 1990, AHO 1994).

The great differences in freezing damage and bud formation between the families are in accordance with earlier results (NORELL *et al.* 1986, NILSSON & ANDERSSON 1987, NILSSON 1988, DORMLING & JOHNSEN 1992, AHO 1994).

The crossed entries were more tolerant than expected on the basis of the regression in which temperature sum was related to bud formation or freezing damage. This can be partly explained by the better physiological status of the crossed seed, but the results do not support the assumption of an after effect of seed maturing environment on hardiness. On the other hand, AHO (1994) found that controlled crosses behaved in freezing tests as if their parents had originated from locations more than 100 km to the south than the actual ones.

The northern greenhouse entry closely resembled the respective entry matured in the southern environment. These two entries, again, differed from the one which had matured in the open only a few metres away from the greenhouse. The observed effects of environment on seed development were presumably caused by the different temperature conditions during seed maturing, because the greenhouse was erected around the graft during the summer when the seed matured. JOHNSEN *et al.* (1995) observed that progenies of Norway spruce originating from crosses made in a greenhouse were less hardy than their full-sibs from an outdoor seed orchard. In their study grafts were moved out after flowering, so the effect could not be due to different seed maturing conditions. The positive effect of increased greenhouse temperature on seed quality and

germination has also been demonstrated with larger material (EERONHEIMO & RUOTSALAINEN 1991), and is in good agreement with the well-known relationships between temperature and seed development (WIBECK 1920, KUJALA 1927, SIMAK & GUSTAFSSON 1954, SORENSEN & CAMPBELL 1985, HENTTONEN *et al.* 1986).

No clear evidence of a decrease in hardiness or change in growth rhythm due to the southern seed maturing environment was observed. Neither was the hardiness decreased compared to the seedlings from natural stands of corresponding origin. It is probable that the seedlings were not exposed to low enough temperatures in the freezing test, resulting in weakened manifestation of the differences between environments and families (CHRISTERSSON 1978, AHO 1994). Furthermore, since freezing damage was assessed on a categorical scale, the significance levels of the analysis of variance are likely to be approximate ones only.

Earlier studies (DORMLING & JOHNSEN 1992, ANDERSSON 1994, LINDGREN & WEI 1994) have shown that the effect of seed maturing environment can change in either direction over time. Thus it is too early to conclude whether the results obtained at the juvenile age will remain valid over the years. At least indirect effects caused by seedling size and vigour can be expected, since the southern seed maturing environment clearly increased height growth. The observed slight decrease in freezing tolerance of material from the southern environment was opposite to that expected on the basis of differences in germination speed (*c.f.* NILSSON & WALFRIDSSON 1990). Thus there seem to be several maternally determined factors which influence the hardiness in different directions. The variation between families as regards hardiness was, however, great enough to counteract the possible after effects caused by the seed maturing environment.

Our results obtained with Scots pine clearly differed from those with Norway spruce (BJØRNSTAD 1981, JOHNSEN 1989a, SKRØPPA 1994, SKRØPPA *et al.* 1994), but are in quite good agreement with earlier work on Scots pine (DORMLING & JOHNSEN 1992). In Norway spruce the after effect in growth and hardiness was connected both to the light and temperature climate. In Scots pine, again, the temperature during seed maturation seems to be the most important factor. This is in accordance with the greater photoperiodical sensitivity of Norway spruce compared to Scots pine (DORMLING 1975, EKBERG *et al.* 1979, KOSKI & SIEVÄNEN 1985).

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