Phenotypic and Genetic Variation in the Seed Maturity of Scots Pine

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Summary

Scots pine (*Pinus sylvestris* L.) seed matures poorly in northern areas, which causes great problems for forest regeneration. Variation in anatomical seed maturity between individuals and years was studied in 2 natural northern populations (67 °N and 68 °N), one of which was a timber line population. The amount of genetic variation in anatomical seed maturity was estimated in 2 test sites at different latitudes (62 °N and 66 °N) for 2 years. The test sites had identical genotypes cloned by grafting. The variation in the seed maturity between individuals in the timber line population was consistent over the years (correlations between years 0.61 to 0.67). Genetic variation was most clearly expressed in northern conditions (broad-sense heritability, H = 0.79, SD = 0.06; H = 0.73, SD = 0.08) where problems caused by poor seed maturity are the most severe. In the southern test site, the heritabilities were lower due to almost complete seed maturity. High broad-sense heritabilities suggest that seed-maturing ability should be regarded as an important character in selecting clones for seed production in northern conditions.

Key words: seed maturity, expected germination, timber line, seed orchard, broad-sense heritability.

FDC: 165.3; 165.5; 181.525; 232.311; 318; 174.7 *Pinus sylvestris.*

Introduction

Quantitatively and qualitatively good seed crops are rare in conifers in northern forests and at high altitude stands because of the short, cool growing season (Kujala, 1927; Mork, 1957; Sarvas, 1962, 1970, 1972; Koski and Tallquist, 1978; Henttonen *et al.*, 1986). Although the quantity of the seed crop is important, its quality is of equal importance. The poor quality of northern seed is caused by incomplete maturity, which leads to low germination. The temperature dependence of the maturation of Scots pine seed has been well documented in several studies (Heikinheimo, 1921; Kujala, 1927; Sarvas, 1962, 1970, 1972; Henttonen *et al.*, 1986).

The area where Scots pine does not reach 50% seed maturity at least every second year covers about 25% (5 million hectares) of the forest land in Finland (Henttonen *et al.*, 1986; Aarne, 1994). At the polar timber line (lat. 68 °N to 69 °N), the probability of achieving 50% seed maturity is 0.02, which means 2 good seed maturation years every century (Henttonen *et al.*, 1986). Thus poor seed maturity is an economically important problem not only in Finland, but also in other countries where forestry is practiced in cold climates.

To solve the problem of poor seed maturity, seed orchards of northern origin have been established at warmer southern latitudes (Sarvas, 1970; Werner, 1975; Mátyás, 1991). With regard to the seed maturation, the transfer was very successful (Bhumibhamon, 1978). Unfortunately the high level of background pollination from southern origins (Harju and Muona, 1989; Pakkanen and Pulkkinen, 1991; Wang *et al.*, 1991) makes the seed crops poorly adapted for the forest regeneration areas in the north (Nikkanen, 1982; Rousi, 1983; Ericsson, 1988). Thus forest regeneration is still dependent on the irregular seed crops collected from natural stands. For example, the last high quality seed crop in northern Finland was collected in 1972, and forest regeneration is presently suffering from a local shortage of Scots pine seed.

In order to decrease the harmful effects of background pollination, the seed orchards of northern origin should be established closer to the area where the seeds are to be used (Rusanen, 1992). Ehrenberg *et al.* (1955) and Mork (1957) have suggested the possibility of selecting for the seed-maturing ability. In natural stands seed maturity varies between years, between trees within a stand, and within the crown of a tree. It has been suggested that the between-tree variation is partly caused by genetic differences (Ehrenberg *et al.*, 1955;

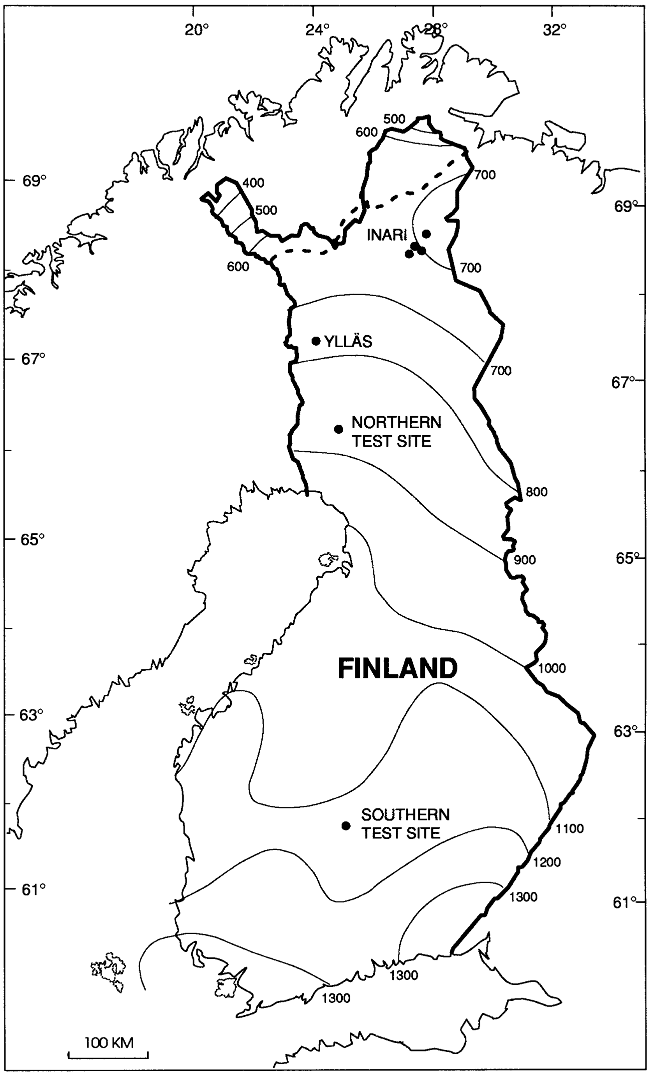

Figure 1. – Study sites and mean annual temperature sum (threshold value +5 °C) during 1931 to 1960 (Kolkki, 1966). Inari and Ylläs are natural stands of Scots pine. The northern Scots pine timber line in Finland is also shown (- - -).

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Table 1. – Location, altitude and the estimated mean effective temperature sum (in degree days, +5 °C threshold, years 1951 to 1980) of the Scots pine study sites. The number of trees or clones are also presented.

Population	lat. N	long. E	alt m	Temp. sum/ year (d.d.)	Number of trees/clones
Timber line stand					
Ylläs	67°34'	24°11'	400	656	44
Plus tree population in Inari					
Alalompolo	68°35'	27°30'	180	692	8
Pasasjoki	68°40'	27°35'	150	709	3
Menesvaara	68°45'	27°51'	150	718	2
Tolosjoki	68°33'	27°15'	140	712	2
Test sites					
Northern	66°30'	25°04'	195	857	15
Southern	62°01'	25°20'	140	1133	14

Mork, 1957; Bergmann, 1976; Hagner, 1982; Ryynänen, 1982). If differences between trees have a strong genetic component, seed orchards at higher latitudes could be established with clones that have genetically high seed-maturing capacity.

In this paper, we document ample phenotypic variation in the seed maturity within a natural population of Scots pine. Furthermore, we show that a high proportion of this variation is genetic in the 2 test sites where it is possible to separate environmental and genetic variation. To our knowledge, this study provides the first estimates of the genetic component in seed maturity in conifers.

Material and Methods

Study sites and seed samples

We studied seed maturity in a natural population at the altitudinal timber line on the northern slope of Ylläs fell (*Figure 1*). The cones were collected from 44 individually marked trees on Ylläs in 1972, 1979, 1980, 1981, 1982, 1988, and 1991. Due to the limited and variable cone production of the trees, we were not able to obtain seed samples from all the trees every year; the average number of trees studied per year was 24 (11 to 44, *Table 1*). When possible, more than 100 seeds per tree (100 to 400) were analyzed.

In 1968 to 1971, experimental populations were established at northern and southern test sites (*Figure 1*) as clonal seed orchards with grafts from same plus trees selected for good growth and stem quality. The grafts of each clone were randomized across the seed orchards. The 15 plus tree clones studied originated from a geographically limited area in Inari (*Figure 1*). The distance to the tree limit from Inari is about 80 km. The mean annual temperature sum (+5 °C threshold) in Inari is slightly higher than that in the altitudinal timber line population on Ylläs (*Table 1*). In 1990 and 1991, cones were collected from 15 clones at the northern and 14 clones at the southern test sites. We also collected cones from 9 original plus trees still growing in Inari in 1990 and 1991. On the average 4.8 grafts (3 to 6) per clone, and about 400 (90 to 437) seeds per graft or plus tree were analyzed.

Estimating seed maturity

All the cones on the trees were collected by tree or by graft in late autumn, and the seeds were extracted. Random seed samples were X-rayed and classified into seed maturity classes. The X-ray radiographs were used to classify the seeds into 5 classes (I, IIA, IIB, III, and IV) according to the sizes of their embryos (Ryynänen, 1980; Simak, 1980).

Seed maturity was estimated using 2 parameters:

1) proportion of the class III and IV seeds combined (embryo ≥ 1/2 of the embryo cavity) in seeds with an embryo, and
2) the expected germination percentage in the sound, filled seeds.

Expected germination percentage was based on the proportions of the seed classes. Percentages of germination in classes I, IIA, IIB, III, and IV were assumed to be 0, 5, 30, 88, and 100, respectively. Expected germination percentage was estimated as a weighted average across seed classes with weights determined by seed class proportions (Ryynänen, 1980). Empty, broken, and insect damaged seeds were excluded from the analyses.

Annual temperature sums with threshold value +5 °C (*Tables 1* and *2*) were estimated using the program developed by Ojansuu and Henttonen (1983). When latitude, longitude, and altitude of the site were known, the temperature sum for each particular site could be interpolated from meteorological observations published by the Finnish Meteorological Institute.

In the natural population on Ylläs, we estimated the influence of shading on the seed maturity by measuring the distance between the nearest tree growing in the southwest to southeast sector from the study tree.

Table 2. – Seed collection year, estimated effective temperature sum (TS) of the seed maturing year, means and standard deviations (sd) of expected germination percentage (EG), and of the percentage of seeds having class III and IV embryos. N = number of trees or clones.

Study site	Year	TS	N	EG		III+IV	
				mean	sd	mean	sd
Timber line stand	1972	846	44	82.2	12.9	82.3	14.5
	1979	774	11	14.4	7.8	4.7	4.9
	1980	829	16	62.0	13.7	57.3	17.3
	1981	571	20	0.5	0.5	0.0	0.0
	1982	546	21	0.0	0.1	0.0	0.0
	1988	813	18	31.6	14.6	22.0	15.0
	1991	692	40	0.7	1.4	0.3	0.8
Original plus trees	1990	708	9	22.8	12.0	17.6	11.0
in Inari	1991	688	9	6.2	2.5	1.0	1.3
Northern test site	1990	856	15	77.8	8.5	79.3	10.3
	1991	809	15	61.5	10.8	56.7	14.0
Southern test site	1990	1098	12	94.3	4.5	97.6	1.8
	1991	1117	14	97.4	1.9	99.1	0.9

Statistical analyses

Pearson's product moment correlation coefficients were estimated for expected germination percentages between different years in the material collected from the timber line population and in the plus tree material growing at 3 latitudes.

Broad-sense heritabilities (H) were determined at each test site and each study year separately on an individual graft basis (coefficient of intraclass correlation, Sokal and Rohlf, 1981, p. 216). The variances for the broad-sense heritabilities were estimated according to Kempthorne (1973).

Repeated measures, mixed-model analysis of variance was performed for expected germination percentage. Expected germination percentage in different years in the same grafts were treated as repeated measures. The test site was regarded as a fixed effect, and clone and year as random effects (*Table 6*). Variance components for random effects were calculated using the mean squares of type III estimated by the GLM procedure of SAS and the model given in *table 6*.

The expected germination percentage was arcsine squareroot transformed in order to make the distribution of residuals normal and variances equal.

GLM and CORR procedures of SAS were used for the statistical analyses (SAS Institute Inc., 1989).

Results

Timber line population

Seed maturity varied greatly between years in the timber line population (*Table 2*), and was clearly dependent on the temperature sum of the growing season (*Figure 2*). There was high variation between the trees in seed maturity during those summers when the temperature sum was between 700 and 850 degree days. When the temperature sum was lower than 700 degree days, the percentage of embryos in classes III and IV did not exceed 1% (*Table 2*).

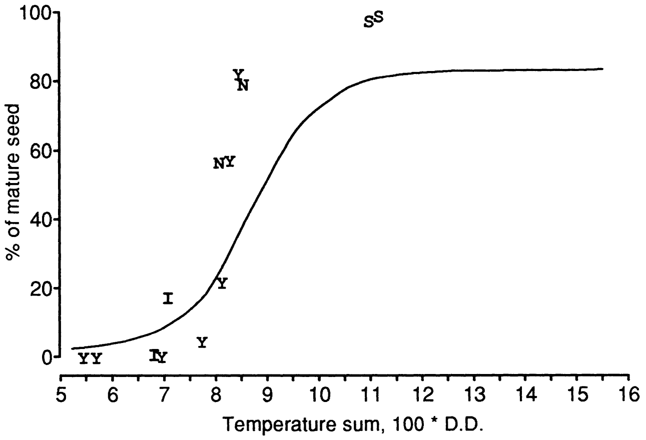

Figure 2. – Dependence of seed maturity in Scots pine on the temperature sum of the growing season. The curve is from Henttonen *et al.* (1986), I = Inari, natural stand, N = northern test site, S = southern test site, Y = Ylläs, timber line stand.

The expected germination percentage of individual trees in the timber line population was positively correlated between the years 1972, 1980, and 1988, *i.e.* during the same years when there was high variation between the individuals in seed maturity (*Table 2*). The considerable differences in the expected seed germination percentages between neighbouring trees are demonstrated in *figure 3*. No correlation was found between the expected germination percentage and the distance to the nearest shading tree in our material (*Table 3*).

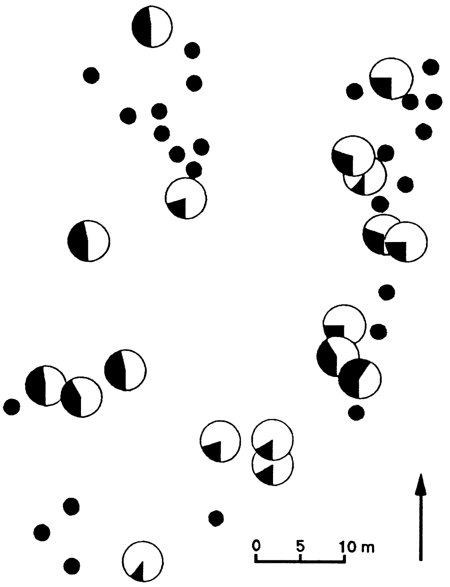

Figure 3. – Expected germination percentage (black sector in pie chart) of Scots pine seeds from the Ylläs timber line stand. Smaller closed circles are Scots pines not included in the study. Filled pie chart equals to 100% of expected germination percentage.

Experimental populations

When the genetically identical populations growing at 3 latitudes were compared, expected germination percentage of the seeds clearly increased from the north to the south (*Table 2*). Correlations between the years within test sites were positive, but statistically significant only at the northern test

Table 3. – Correlations between the expected germination percentage of Scots pine seeds in different years and the degree of shading by surrounding trees in Ylläs natural stand (for explantations, see text). Statistical significance level (p) of correlation coefficients and sample sizes (n) are also given. Data were arcsin $\sqrt{x}$ transformed prior to analysis.

	Expected germination percentage		Distance to shading tree
	1980	1988	
1972	0.672	0.665	-0.166
p	0.004	0.007	0.306
n	16	15	40
1980		0.606	0.050
p		0.202	0.853
n		6	16
1988			0.471
p			0.104
n			13

site (*Table 4*). Correlations between the northern and southern test sites were usually positive, but statistically significant only in 1990. The correlations between the original site in Inari and the test sites varied greatly and were statistically non-significant (*Table 4*).

Separate analysis of the test sites and years indicated genetic determination of seed maturity. Clonal differences in expected germination percentage were statistically significant, the estimates of broad-sense heritability ranging from 0.33 to 0.79 (*Table 5*). Broad-sense heritabilities were high at the northern test site especially. Clonal composition varied slightly between the years and sites, but had no apparent influence on the estimates of broad-sense heritability.

In repeated measures analysis of variance for the expected germination percentage all the effects were statistically significant (*Table 6*). The location of the test site had a decisive effect on the expected germination percentage. However, because it was treated as a fixed effect, no variance component could be estimated. The year × test site interaction accounted for the greatest part (75%) of the total variance in the random effects. The effect of clone and the interaction between clone and test site explained 6% and 5% of the total variation, respectively (*Table 6*). Two other environment × genotype effects were statistically significant, but they accounted for only 2.5% in all of the total variance (*Table 6*).

Table 4. – Correlation matrix between expected germination percentage of Scots pine seeds in the southern test site (STS), in the northern test site (NTS), and in the plus tree population in Inari during 1990 and 1991. Statistical significance level (p) of correlation coefficients and sample sizes (n) are also given. Data were arcsin $\sqrt{x}$ transformed prior to analysis.

	STS90	STS91	NTS90	NTS91	Inari 90
STS91	0.52				
p	0.0847				
n	12				
NTS90	**0.71**	0.28			
p	0.0096	0.3262			
n	12	14			
NTS91	0.12	-.22	**0.66**		
p	0.7090	0.4517	0.0070		
n	12	14	15		
Inari 90	0.70	-.32	0.50	0.44	
p	0.1890	0.4821	0.2050	0.2716	
n	5	7	8	8	
Inari 91	0.23	-.33	0.37	0.55	0.55
p	0.6663	0.4198	0.3228	0.1238	0.1608
n	6	8	9	9	8

Table 5. – Broad sense heritabilities (H) and their standard deviations (SD) for the expected germination percentage of Scots pine seeds in the northern (NTS) and southern (STS) test sites during 1990 and 1991. Data were arcsin $\sqrt{x}$ transformed prior to analysis. The within clone variation (MS_w) is also given.

		Expected germination percentage		
Site	Year	MS_W	H	SD
NTS	1990	0.002	0.79	0.06
	1991	0.004	0.73	0.08
STS	1990	0.005	0.34	0.12
	1991	0.003	0.33	0.11

Discussion

Environmental variation in seed maturity

Seed maturation in Scots pine is dependent on the temperature sum, which was evident also in our data (*Tables 2* and *6*). To achieve 50% maturity of the seeds, 890 degree days are needed according to HENTTONEN *et al.* (1986), and 845 degree days in the northern Finland according to SARVAS (1970). In our material, the limit for 50% seed maturity was about 800 degree days (*Figure 2*). The difference between our results and those of HENTTONEN *et al.* (1986) is in fact greater than presented, bacause the criteria for seed maturity in our data was stricter

Table 6. – Repeated measures ANOVA for expected germination percentage with 2 test sites (S) and 2 years (Y). C stands for clone as source of variance. Test site is considered as a fixed effect, while the other effects are random. Data were arcsin $\sqrt{x}$ transformed prior to analysis.

Source of variance	EMS	Expected df	df	MS	F-value	p	Obs. var. comp.	% var. comp.
Between subjects								
Site (S)	$\sigma^2_B + w\sigma^2_{SC} + wc/(s-1)\Sigma\pi^2$	s-1	1	7.605	214.92	0.0001		
Clone (C)	$\sigma^2_B + ws\sigma^2_C$	c-1	11	0.069	16.89	0.0001	0.007	6
S×C	$\sigma^2_B + w\sigma^2_{SC}$	(s-1)(c-1)	11	0.035	8.71	0.0001	0.007	5
Error$_B$	σ^2_B	sc(w-1)	85	0.004			0.004	3
Within subjects								
Year (Y)	$\sigma^2_W + ws\sigma^2_{YC} + wsc\sigma^2_Y$	y-1	1	0.167	12.63	<0.01	0.009	7
Y×S	$\sigma^2_W + w\sigma^2_{YSC} + wc\sigma^2_{YS}$	(y-1)(s-1)	1	0.848	69.65	0.0001	0.095	75
Y×C	$\sigma^2_W + ws\sigma^2_{YC}$	(y-1)(c-1)	11	0.013	6.27	0.0001	0.001	1
Y×(S×C)	$\sigma^2_W + w\sigma^2_{YSC}$	(y-1)(c-1)(s-1)	11	0.012	5.77	0.0001	0.002	1.5
Error$_W$	σ^2_W	sc(y-1)(w-1)	85	0.002			0.002	1.5

than theirs. It remains unsolved whether this discrepancy is caused by different methods for determining the seed maturity (visual observation of dissected seeds compared to X-ray radiographs).

There was much variation within populations in the seed maturity. The greatest variation between the trees was observed when the annual temperature sums ranged from 700 to 850 degree days, which are common in Finland between the latitudes 66 °N and 68 °N. Locally, shading may result in differences in microclimate causing within- and between-tree variation in seed maturity. Although within-crown shading affects seed maturation (NUMMINEN, 1974; BERGMANN, 1976), distance to the nearest shading tree did not explain the differences between the trees in the timber line population. It remains unsolved whether the method was relevant for measuring between-tree shading.

Environmental factors other than the temperature sum may also have influenced the observed variation in seed maturity. The occurrence of frost in the beginning and at the end of the growing season have been found to effect anatomical seed quality (*cf.* SIMAK, 1972). The length of the photoperiod (SAHLÉN and BERGSTEN, 1994), precipitation, and differences in mating pattern may also exert an effect. The within-tree variation, which may be significant (NUMMINEN, 1974; BERGMANN, 1976; STOEHR and FARMER, 1986), was not estimated.

Genetic variation of seed maturity

The degree of genetic determination in seed maturity was high at the northern test site especially (*Table 5*). Since the same genotypes were studied at both the northern and southern test sites, the differences between the heritability estimates must be due to differences in the environment. When the temperature sum is high, as at the southern test site in 1991, the variation in seed maturity decreases because almost all the seeds mature. During warm summers, the differences in embryo development may be caused by environmental and genetic factors other than those prevailing in cool conditions *e.g.* by variation in the level of inbreeding (EHRENBERG *et al.*, 1955; PLYM FORSHELL, 1974; HAGNER, 1982). The temperature sum at the northern test site was at a level where genetic differences were clearly manifested. BRAMLETT *et al. (1983)* reported that, in controlled crosses, the pollen parents also influence the germination behaviour of the seeds in some extent. In our study, the embryo development of open pollinated seed was regarded as a character of the seed parent.

When material from geographically distant areas and climatically different years were combined, the proportion of genetic variation in seed maturity declined because of a high year × test site interaction. This high interaction was caused by the fact that the ranking order of the years as regards the temperature sum was reversed between the latitudes (*Table 2*). Because the purpose of our research was to study genetic differences in seed maturity between trees in certain climatic conditions, separate analyses are more suitable than analyses with all data combined.

Our estimates of broad-sense heritability for the seed maturity at the northern test site were of the same order of magnitude as those for germination in some other conifers (VERHEGGEN and FARMER, 1983; STOEHR and FARMER, 1986; CHAISURISRI *et al.*, 1992). Our results were based purely on anatomical determinations and no germination tests were conducted. An anatomical approach to seed maturity was chosen because it gave us the opportunity to study seed maturity without the problems associated with the germination conditions or the physiological state of the seeds, which are known to affect germination in conifers (Nygren, 1987; Edwards and El-Kassaby, 1988; Chaisurisri *et al.,* 1992). However, the results obtained here are also rather applicable to actual germination, because expected and actual germination correlate reasonably well in Scots pine (Müller-Olsen and Simak, 1954; Ryynänen, 1980).

Does the observed high genetic determination in seed maturity mean that it is not an important fitness-related character? This seeming dilemma has several possible explanations. First, our method overestimates the broad-sense heritability, because part of the non-genetic differences between the trees may be transmitted to all their clonal descendants (Falconer, 1981; Griffin, 1982). Moreover the broad-sense heritability gives only an upper limit for the proportion of additive genetic variance on which natural selection operates. However, Bramlett *et al.* (1983) found that the proportion of additive genetic variance was clearly greater than the proportion of non-additive genetic and maternal variance in seed germination in *Pinus virginiana* Mill.. Secondly, the heritability is bound to the experimental environment where it is estimated (*e.g.* Falconer, 1981; Nyquist, 1991). In the northern populations, environmental variation may override the effect of genotype, thus buffering the effects of selection and allowing a wide range of genotypes to persist in the population. Thirdly, in northern populations of Scots pine, the rare warm years with abundant and good quality seed crops may be so important in the reproduction process that intermediate years may have only a limited effect on regeneration (Renvall, 1912; Ågren and Zackrisson, 1990). And finally, high genetic variation in a fitness-related character can be maintained by migration (Koski, 1970; Charlesworth, 1987) and by negative genetic correlation with other fitness-related characters (Charlesworth, 1987).

Implications for tree breeding

The high broad-sense heritability estimates for seed maturity in northern conditions presented in this study indicate that it is possible to increase seed maturity through selection as suggested by Ehrenberg *et al.* (1955) and Mork (1957). Broad-sense heritability gives a proper estimate of the genetic variation available when selecting clones for seed production purposes. However, narrow-sense heritability would be a more appropriate parameter for evaluating the possibility of natural selection and advanced generation breeding (Nyquist, 1991).

In our study, the genetic differences between genotypes were most clearly expressed in the northern test site where the problems caused by the poor seed maturity are greatest. The estimates of broad-sense heritability obtained in the north are applicable to those conditions where seed orchards should be established to avoid the harmful effects of background pollination. A low correlation between sites (*Table 4*) suggests that it may be difficult to select clones successfully in climate greatly differing from that of the target area. This causes practical problems in Finland, because the amount of clonally propagated material of plus trees is low in climatically cold areas. Further studies are needed to evaluate the possibilities of improving seed maturity through artificial selection.

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Provenance Variation of *Pinus muricata* Grown in Greece

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Summary

Provenance trials of muricata pine (*Pinus muricata* D. DON) were planted in 1980 and 1983 in 2 locations in Greece. The seed was from the 1978 International Collection. Six (in 1980) and 8 (in 1983) provenances were included in the experimental plantings. Assessments were made at the ages of 12 and 9 years from planting and the following results were obtained.

There are significant differences between provenances for total tree height, diameter at breast height, bark thickness, branch diameter and the percentages of forked trees. In both locations the Mendocino inland blue provenance (provenance 09/2) was the best (average height 9.09 m at the age of 12 years) followed by Sonoma coastal (provenance 08/1). The northern provenance from Humboldt Trinidad Head (provenance 10) was the slowest growing (average height at the age of 12 years 7.51 m) with the higher proportion of forked trees (20% of the total).

It is concluded that muricata pine may have some merit in the hardier sites of higher elevations in Greece (above the optimum sites of radiata pine) and that the best provenance of Mendocino inland (provenance 09/2) must be compared, in common experiments with *Pinus brutia* and *Pinus pinaster.*

Key words: Pinus muricata, provenance, population, variation, correlation, foxtailed trees.

FDC: 232.12; 165.5; 174.7 *Pinus muricata;* (495).

Introduction

Pinus muricata D. DON also called bishop or muricata pine is a native species of the west coast of N. America, extending from near the California-Oregon border to northern Baja California of Mexico including the islands of Sanda Gruz and Sanda Rosa (SCOTT, 1960; CRITCHFIELD and LITTLE, 1966; GRIFFING and CRITCHFIELD, 1976; Anonymous, 1978; ELDRIDGE, 1979a). It occurs between latitude 31 at San Vicente in Mexico to 41 N at Trinidad Head at Humboldt County, California. The distribution is very limited and discontinuous. Altitudinally it is found from sea level to about 500 m and usually within 5 km from the coast. It grows in a variety of soils from the best to worst and in cool cloudy areas in the north with annual rainfall 1000 mm. Moisture availability is decreasing from north to south and this change is followed by the associated species (*Pseudotsuga menziesii, Pinus radiata, Quercus agrifolia,* to mixed chaparral scrub in the south). It is considered as one of the most shade tolerant species of pines that can grow as understory in the north and as overstory in the south (ELDRIDGE, 1979a). It is also very resistant to seawinds and it is considered as an invaliable tree for early shelter in gardens exposed to strong winds (MITCHELL, 1972). Although muricata

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