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Inheritance of autumn frost hardiness in *Pinus sylvestris* L. seedlings

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Summary. Inheritance of frost hardiness was analysed making use of a 12 × 12 incomplete factorial mating design. Owing to space limitations only 59 families could be tested in four experiments. To link the four experiments, some families were common to two or more experiments. The seedlings were grown in climate chambers under conditions inducing autumn hardening. The plants were exposed to a freezing temperature of −10 °C for three hours at night lengths of 11 − 13 h. A statistical model was developed for analyses of variance of our data. The genetic variation and the variation due to the cultivation regimes during autumn hardening were of the same magnitude. The additive effects were the most important ones for induction of frost damage. No interaction following long-distance crossing was noted. Mixed model equations were used for ranking of the parents. The results obtained support a polygenic inheritance of frost hardiness. The large within-population variation offers good opportunities for hardiness breeding.

Key words: *Pinus sylvestris* – Freezing test – Climate chamber – Incomplete factorial – Mixed model equation – Inheritance – Variance components

Introduction

Frost hardiness is of decisive importance for successful reforestation in many areas of the northern temperate zone. Breeding for frost hardiness is therefore one of the main objectives of the breeding programmes designed for these areas. The relative importance of frost hardiness throughout the year varies depending upon the climatic conditions prevailing in the breeding zones and the species used (Glerum 1973; Cannell and Sheppard 1982; Dormling 1982). The further north the reforestation site is located in Fennoscandia, the greater the importance of early hardening. The main environmental factor that controls autumn hardiness is the declining photoperiod (for references see Jonsson et al. ,1981) although temperature also plays a major role (Cannell and Sheppard 1982).

Although only a few investigations have been carried out to determine the inheritance patterns of the photoperiodic response, all indicate genetic control largely by genes with additive effects. This was observed in three within-population full diallels of *Picea abies* for winter bud formation in the second growing season (Tho 1977) and for bud-set in three growth periods in climate chambers in half diallels between trees of widely different origin (Eriksson et al. 1978). In hybrids between the interior and the coastal variety of *Pseudotsuga menziesii,* Rehfeldt (1977) observed weak additive genetic effects for bud-set and frost hardiness in 4-year-old plants.

Mikola (1982) reported an intermediate inheritance of bud-set in *Pinus sylvestris* based on long-distance plus trees crosses in Finland.

The present article is the first to present genetic parameters on frost hardiness in seedlings of *Pinus sylvestris* based on within-origin and long-distance crosses. A factorial mating design was used. The seedlings were grown in climate chambers and freeze tested at different photoperiods according to the method of Jonsson et al. (1981). The degree of frost damage was determined visually on the seedlings after exposing them to favourable growth conditions.

Material and methods

Material

Six plus trees from each of four different origins in Sweden were used as parents (Fig. 1). The matings were made in three different seed orchards (Fig. 1) according to a 12 x 12 factorial design of the type suggested by Hinkelman and Stern (1960) (Fig. 3). Owing to limited space in the phytotron, some of the hybrid families had to be discarded whereas all within-origin families were included. Altogether 59 full-sib families were involved in the experiments.

Methods

Cultivation technique. After germination, the seedlings were transplanted to mineral wool, which provided a good control over the water and nutrient supply. A complete nutrient solution (Ingestad 1979) of low concentration (100 mg N/l) was given once or twice a day, the proportions of N : K : P being 100 : 65 : 13. The air humidity was kept at 75% relative humidity. The light intensity at seedling level was 30,000 lux (Osram HQI-R-250 W, NDL lamps).

Treatments. Owing to space limitations in the phytotron the families had to be tested successivley in four experiments. To link the four experiments, some families were always common to two or more experiments (Fig. 3). Slightly varying photo- and thermoperiodic regimes had to be used in the four experiments (Fig. 2) due to practical arrangements.

The cultivation regimes were subdivided into five periods (Fig. 2).

Period 1. Germination. At the end of this period the plants were transplanted to pots.
Period 2. Conditions favourable for growth were given to the seedlings until they started to form secondary needles. After that the nights were gradually lengthened.
Period 3. Induction of growth cessation and hardening. Nights were gradually lengthened by 1 h a week.
Period 4. Frost hardiness was determined following freezing tests, which were performed when a slowing down of the elongation of the needles occurred, a character that is well correlated with frost hardiness (Jonsson et al. 1981). The seedlings were transferred to trucks so that only the upper parts of the plants were exposed to frost while the roots were protected. A gradual cooling to − 10 °C for 6 to 7 h and after another 3 h, a gradual thawing to + 10 °C for 6 to 7 h, was applied. After that they received the same light and temperature conditions as before freezing. Since the freezing chamber could house 100 plants only, the seedlings of each family had to be subdivided into three groups on each occasion of freezing (i.e. 11, 12 or 13 h night). These groups were freeze-tested separately for three successive nights. In the statistical analysis, these are called sub-occasions of freezing.
Period 5. Conditions stimulating growth were given to the seedlings one week after the freezing test. After another six weeks the extent of frost damage was recorded.

Frost-hardiness characters studied. The frost injury was classified in six classes (0−5) depending upon the degree of damage (Jonsson et al. 1981), 5 = the most severe injury. The statistical analyses were based on mean frost damage scores calculated for each family.

Statistical method. In the statistical models used, we included both genetic effects and effects caused by night length, sub-occasions of freezing, and experiment. The freezing tests, comprising about 100 plants each, were considered as main plots. The models are therefore rather extensive, and to facilitate the computations the analysis was made in four steps, Model 1−4. In Model 1 we analysed genotype × environment and environment × environment interactions; the three other models were used for a detailed analysis of the genetic effects.

To obtain samples that approximately followed normal distributions we used the class values of the injury, 0, 1, ..., 5, and calculated the mean value $\bar{x}_{ijmnq}$ for every existing combination of group of family (i), family within group (j), night-length (m), sub-occasion (n) and experiment (q). The analysis of variance also requires that the variances of the corresponding random variables $\bar{X}_{ijmnq}$ are the same. Those of $\bar{X}_{ijmnq}$, which have expectations near the extreme values 0 or 5, will have a smaller variance than the others. This resembles the situation where relative frequencies are analysed. A common technique in such cases is to use the arcsin-root-transformation (Anscombe 1948). We therefore set

$$y_{ijmnq} = \arcsin\,(\bar{x}_{ijmnq}/5)^{1/2}\,.$$

Only 568 combinations of the $11 \times 6 \times 3 \times 3 \times 4 = 2{,}376$ possible combinations of ijmnq occurred thus reducing the number of degrees of freedom for most of the interaction effects.

The first model, Model 1, was

$$y_{ijmnq} = \mu + \gamma_i + g_{j(i)} + \eta_m + \phi_n + t_q + (\gamma\times\eta)_{im} + (\gamma\times\phi)_{in} + (\gamma\times t)_{iq} + (\eta\times\phi)_{mn} + (\eta\times t)_{mq} + (\phi\times t)_{nq} + p_{mnq} + e_{ijmnq}\,,$$

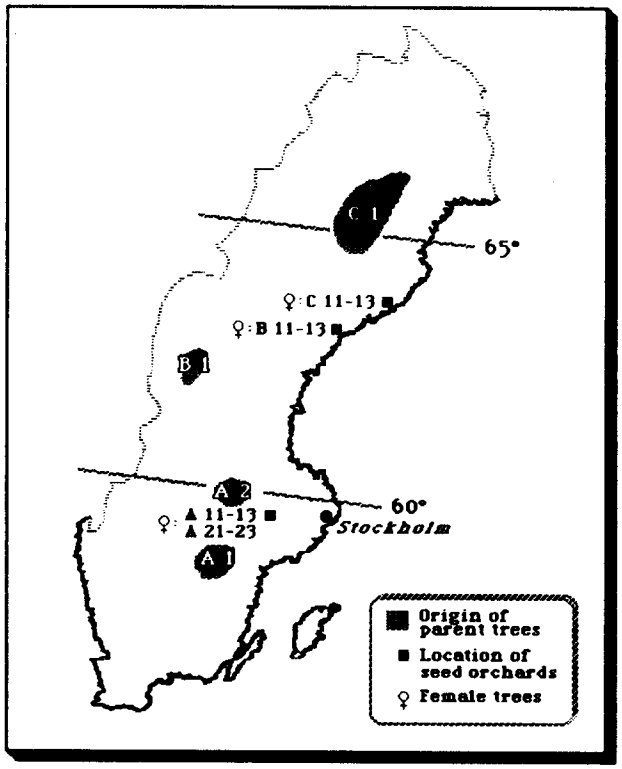

Fig. 1. Map of Sweden showing the origin of the parent trees and the location of the seed orchards in which the matings were performed

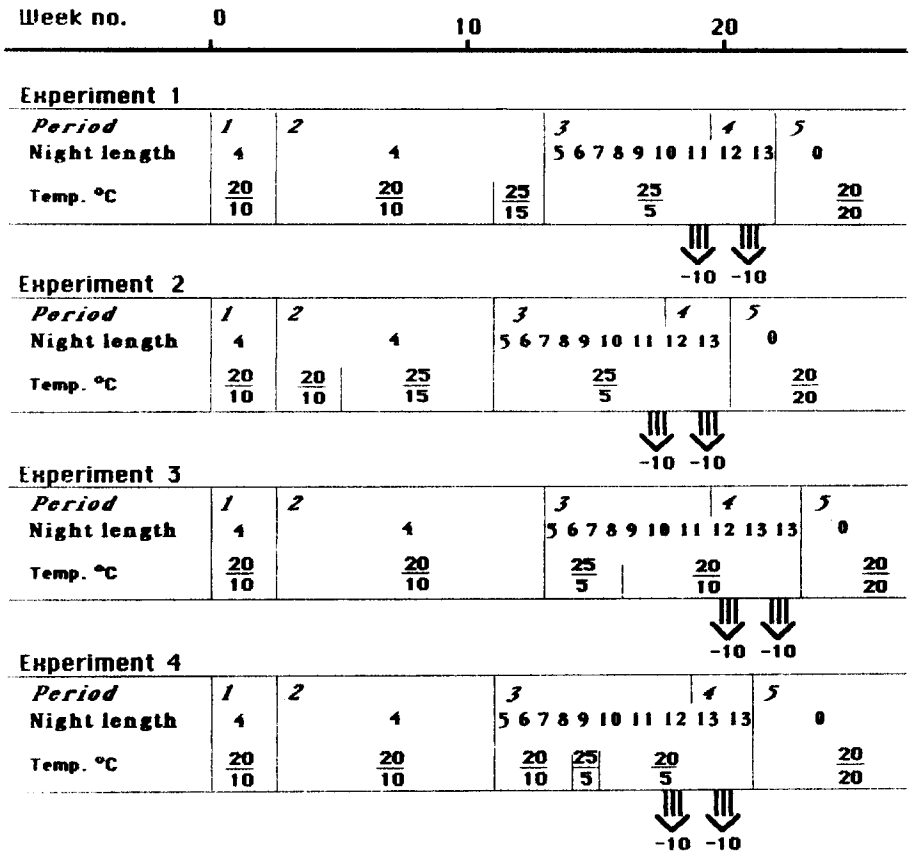

Fig. 2. Cultivation regimes in the climate chambers during experiments 1–4

where

μ = overall mean,
γ_i = effect of family group i, i = 1, ..., 11 (d.f. = 10),
$g_{j(i)}$ = effect of family j within group i, j = 1, ..., 6 (d.f. = 48),
η_m = effect of night length (11, 12, 13 h), m = 1, 2, 3 (d.f. = 2),
ϕ_n = effect of sub-occasion, n = 1, 2, 3 (d.f. = 2),
$t_q \sim N(0, \sigma_t^2)$ = effect of experiment, q = 1, 2, 3, 4 (d.f. = 3).

The interaction effects in the model were

$(\gamma \times \eta)_{im}$ = family group × night length (d.f. = 11),
$(\gamma \times \phi)_{in}$ = family group × sub-occasion (d.f. = 20),
$(\gamma \times t)_{iq} \sim N(0, \sigma^2_{\gamma \times t})$ = family group × experiment (d.f. = 5),
$(\eta \times \phi)_{mn}$ = night length × sub-occasion (d.f. = 4),
$(\eta \times t)_{mq} \sim N(0, \sigma^2_{\eta \times t})$ = night length × experiment (d.f. = 2),
$(\phi \times t)_{nq} \sim N(0, \sigma^2_{\phi \times t})$ = sub-occasion × experiment (d.f. = 6),

and the random errors were

$p_{mnq} \sim N(0, \sigma_p^2)$ = main-plot effects (freezings) (d.f. = 4),
$e_{ijmnq} \sim N(0, \sigma_e^2)$ = residuals (d.f. = 450).

Model 2 was

$$y_{ijklmnq} = \mu + M_i + F_j + (M \times F)_{ij} + m(M)_{k(i)} + f(F)_{l(j)} + m \times f(M \times F)_{kl(ij)} + \eta_m + \phi_n + t_q + p_{mnq} + e_{ijklmnq},$$

where $y_{ijklmnq}$ was as in Model 1, but more subscripts were used here. In other respects,

μ = overall mean
M_i = average effect of males from origin i, i = 1, 2, 3, 4,
F_j = average effect of females from origin j, j = 1, 2, 3, 4,
$(M \times F)_{ij}$ = interaction between M_i and F_j,
$m(M)_{k(i)} \sim N(0, \sigma_m^2)$ = additive effect of male k within origin i, k = 1, 2, 3,
$f(F)_{l(j)} \sim N(0, \sigma_f^2)$ = additive effect of female l within origin j, l = 1, 2, 3,
$m \times f(M \times F)_{kl(ij)} \sim N(0, \sigma^2_{m \times f})$ = specific effect of male k and female l within origins i and j,
$p_{mnq} \sim N(0, \sigma_p^2)$ = main-plot effect (as earlier, but here with d.f. = 16),
$e_{ijklmnq} \sim N(0, \sigma_e^2)$ = residual,
η_m, ϕ_n, and t_q have the same meaning as in Model 1.

In the next model, Model 3, we replaced the factorial effects of origin with a diallel representation, i.e.

$$M_i + F_j + (M \times F)_{ij} = G_i + G_j + M'_i + S_{ij}.$$

G_i = average general combining ability of parents from origin i,
M'_i = average maternal/paternal effect of parents from origin i,
S_{ij} = average specific combining ability of crossing of parents from origins i and j.

Models 2 and 3 coincided in other respects. The effects M'_i in Model 3 was interpreted as the lack of fit for the additive origin effects when the diallel model was used. To find the denominator for the F-ratios we studied the coefficients in the expressions for the expectations of the mean sum of squares.

The last step of the analysis was to rank the females, the males, the night lengths and the experiments. We neglected the interaction effects in Model 2 and used a model that is purely additive. The model, named Model 4, was

$$y_{ijklmnq} = \mu + M_i + F_j + m(M)_{k(i)} + f(F)_{l(j)} + \eta_m + \phi_n + t_q + p_{mnq} + e_{ijklmnq}.$$

Contrasts between fixed effects and/or random effects were estimated and predicted by help of the so-called Mixed Model Equations (MME). The method is described in Searle (1971) and requires known values of σ^2_m, σ^2_f, σ^2_t, σ^2_p and σ^2_e. We used "the fitting constants method" to estimate these variance components, i.e. the estimates were based on the expected values of the mean sum of squares. The Bonferroni method was used for the multiple comparisons in order to control the experimental error rate.

The SAS-procedures MEANS, GLM, VARCOMP, and MATRIX were used for the numerical calculations. For Model 1 we used the option ABSORB of PROC GLM for the genetic effects; for Model 4, the FIXED option of PROC VARCOMP in connection with the estimation of the variance components.

Results and discussion

Remarks on the experimental design

There were significant differences between the four experiments (Tables 1 and 2). This was mainly due to a higher level of frost damage assessed in experiment 4. One reason might be that the day temperature during hardening (period 3 in Fig. 2) was 5 °C lower in this experiment.

The frost damage varied significantly between the three successive nights of freezing tests (sub-occasions of freezing in Tables 1 and 2). Usually the damage decreased in order first – second – third night. Also, the residual variation between the sub-occasions of freezing was significant (main plots in Tables 1–3).

The "variance components" of experiments, sub-occasions of freezing and main plots were comparatively low.

Statistics

The analysis of interactions between genotype and environment was restricted to groups of families (A1×A1, A1×A2, etc., Model 1, Table 1). All sums of

Table 1. Analysis of variance for Model 1

Source of variation		df	SS	F (main-plot)	F (residual)	"Variance component" ×100	"Variance component" in %
γ:	Groups of families	10	20.14	unadjusted SS		2.70	27.1
g:	Families within groups	48	7.063	unadjusted SS		1.29	13.0
η:	Night lengths	2	10.96	79.15***		3.95	39.7
ϕ:	Sub-occasions of freezing	2	1.861	13.43*		0.439	4.4
t:	Experiments	3	2.504	12.05*		0.887	8.9
$\gamma\times\eta$:	Groups of families × night lengths	11	0.931	1.22	4.71***	0.377	3.8
$\gamma\times\phi$:	Groups of families × sub-occasions of freezing	20	0.525	0.38	1.46	0.134	1.3
$\gamma\times$t:	Groups of families × experiments	5	0.204	0.59	2.27*	0.073	0.7
$\eta\times\phi$:	Night lengths × sub-occasions of freezing	4	0.129	0.46		−0.033	–
$\eta\times$t:	Night lengths × experiments	2	0.114	0.83		0.024	0.2
$\phi\times$t:	Sub-occasions of freezing × experiments	6	0.410	0.99		0.080	0.8
p:	Main plots	4	0.277		3.86**	0.224	–
e:	Residuals	450	8.083			1.80	–

* Significant at $P \leqq 0.05$; ** $P \leqq 0.01$; *** $P \leqq 0.001$

Table 2. Analysis of variance for Model 2

Source of variation		df	SS	F	Denominator	"Variance component" ×100	"Variance component" in %
M:	Males, between origins	3	4.956	11.55**	m(M)	1.04	9.7
F:	Females, between origins	3	15.69	17.77***	f(F)	2.90	27.1
M×F:	Males × females, between origins	4	0.912	2.23	m×f(M×F)	−0.324	–
m(M):	Males, within origins	8	1.145	1.40	m×f(M×F)	0.110	1.0
f(F):	Females, within origins	8	2.354	2.88*	m×f(M×F)	0.356	3.3
m×f(M×F):	Males × females, within origins	32	3.265	5.02***	e	0.897	8.4
η:	Night lengths	2	10.98	55.32***	p	3.99	37.3
ϕ:	Sub-occasions of freezing	2	1.870	9.42**	p	0.446	4.2
t:	Experiments	3	2.168	7.28**	p	0.947	8.9
p:	Main plots	16	1.588	4.88***	e	0.339	–
e:	Residual	486	9.888			2.03	–

* Significant at $P \leqq 0.05$; ** $P \leqq 0.01$; *** $P \leqq 0.001$

Table 3. Analysis of variance for Model 2. Only trees from origins A1 and A2 are included

Source of variation		df	SS	F	Denominator	"Variance component" ×100	"Variance component" in %
M:	Males, between origins	1	0.063	1.53	m (M)	−0.919	–
F:	Females, between origins	1	0.816	2.13	f (F)	1.56	19.3
M×F:	Males × females, between origins	–					
m (M):	Males, within origins	4	0.166	2.04	m×f (M×F)	0.282	3.5
f (F):	Females, within origins	4	1.534	18.85***	m×f (M×F)	0.991	12.2
m×f (M×F):	Males × females, within origins	7	0.142	1.28	e	−0.086	–
η:	Night lengths	2	1.792	31.97***	p	2.63	32.5
ϕ:	Sub-occasions of freezing	2	0.199	3.55	p	0.118	1.5
t:	Experiments	3	2.089	24.85***	p	2.52	31.1
p:	Main plots	16	0.448	1.77*	e	0.157	–
e:	Residual	156	2.474			1.59	–

* Significant at $P \leqq 0.05$; *** $P \leqq 0.001$

Table 4. Analysis of variance for Model 3

Source of variation		df	SS	F	Denominator	"Variance component" ×100
G:	GCA, between origins	3	17.86	unadjusted SS		1.50
M′:	Maternal/paternal effects (between origins)	3	3.112	7.36**	[1]	2.03
S:	SCA, between origins	4	0.792	1.94	m×f (M×F)	0.217

[1] In proportions, the denominator is based on $\frac{1}{3}$ (m (M) + f (F)) + $\frac{2}{3}$ m×f (M×F)
** Significant at $P \leqq 0.01$

squares except those for γ and g were adjusted for the other effects.

Since some of the groups of families occurred at the same freezing test (main plot) we calculated two F-ratios for the interaction effects involving γ. In these F-ratios the main plot and the residual mean sums of squares, respectively, were used as the denominator. The F-ratios for the additive environmental effects ought to be calculated with the appropriate interactions as denominators. To simplify the calculations the main-plot sum was used as the denominator, which only slightly biases the F-ratios. To illustrate the practical importance of the effects we considered each effect as random and estimated the "variance components" (cf. the last column of Table 1).

The interactions are of minor practical importance (Table 1). The $\gamma \times \eta$ effect shows a significant result in one of the F-tests, but the relative importance is only 3.8 per cent. We therefore neglected all the interactions in further analyses. In Model 2 the sums of squares for the interactions between two non-genetic factors were pooled with the sum of squares for the main plots. The sums of squares for the interaction between factors, from which one is genetic, were pooled with the residual sum of squares.

The results from the analysis according to Model 2 are presented in Table 2. The estimates of the "variance components" were based on the assumption that all effects were random. The F-ratios were based on the adjusted sum of squares whereas the estimates of the variance components were based on the unadjusted sum of squares. This causes the seeming contradiction for M×F with such a high F-ratio as 2.23 and a negative component (−0.324).

The reason for using Model 3 was to test whether a diallel model was valid for the means of origin×origin crosses (A1×A1, A1×A2, ..., C1×C1). Table 4 shows the results for the three first effects in Model 3. The results for the rest of the effects are identical with the ones for Model 2. Table 4 shows that the diallel approach was not justified for our results.

The design does not permit a simultaneous ranking of all parents, but separate rankings of the females as well as the males are possible. In spite of the fact that the m×f (M×F) effects were significant with a relatively large variance component in Model 2, we neglected the specific effects and used Model 4 for a ranking of the parents. In order to use the Mixed Model Equations (MME) we estimated the variance components (Table 5). These values were considered as known in the MME.

Figure 4 illustrates the estimated average injury in the original scale. For the parents and the experiments, we have indicated the non-significant differences by

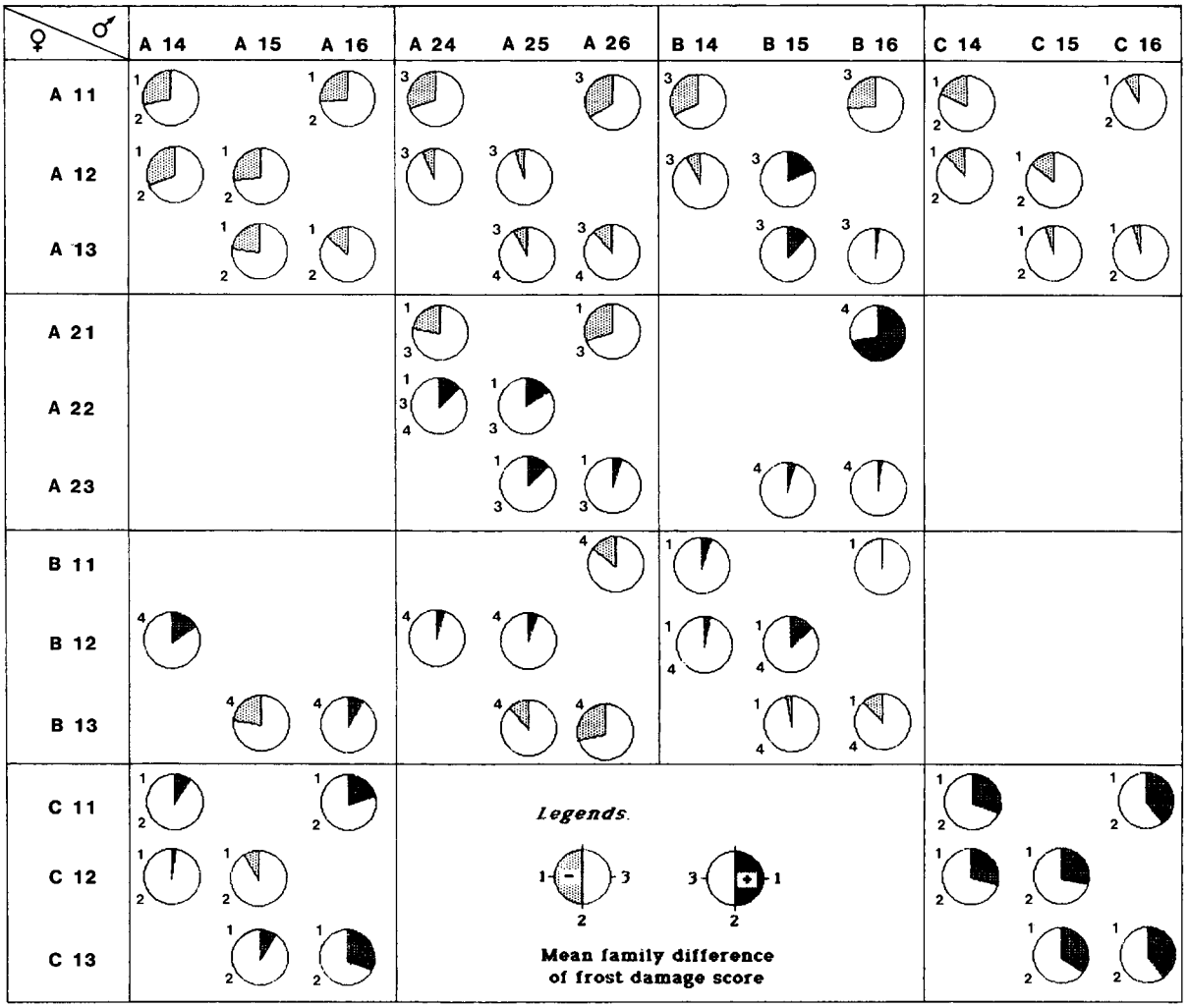

Fig. 3. Mating design of the progeny trial. The mean family difference of frost damage score expressed in standard deviation units is shown for each family tested. The reference numbers of the parent trees and of the experiments in which the families were included are given

Table 5. Estimated values of variance components in Model 4

Variance component $\times 100$	σ_m^2	σ_f^2	σ_t^2	σ_p^2	σ_e^2
Estimate	0.319	0.597	0.784	0.311	2.69

lines. It should be noted that parents originating from the same origin are compared with better precision than parents from different origins. The precision of the pairwise comparisons is also influenced by the number of times the two parents occurred in the same freezing (main plots). These conditions cause inconsistence in ranking. One example is the significantly higher injuries of the offsprings of B13 as compared to those of B12. Such inconsistencies are marked by dots in Fig. 4.

Genetics and implications for breeding

In Fig. 3 we have tried to illustrate the performance of the families included in our study. Since each family was included in 1–3 experiments and since the experiments included different night lengths for freezing tests, we used the following technique to get an estimate of the family performance. For each freezing occasion the family difference from the experimental mean, expressed with the standard deviation of this particular experiment as a unit, was calculated. For each family a mean over all experiments and freezing occasions was calculated. The lower the value of a family in Fig. 3 the lower the hardiness of this family.

The families A1×A1 were consistently of poor hardiness as expected from their southerly origin. Conversely, the C1×C1 families were consistently hardy, as expected. One family A21×B16 deviated

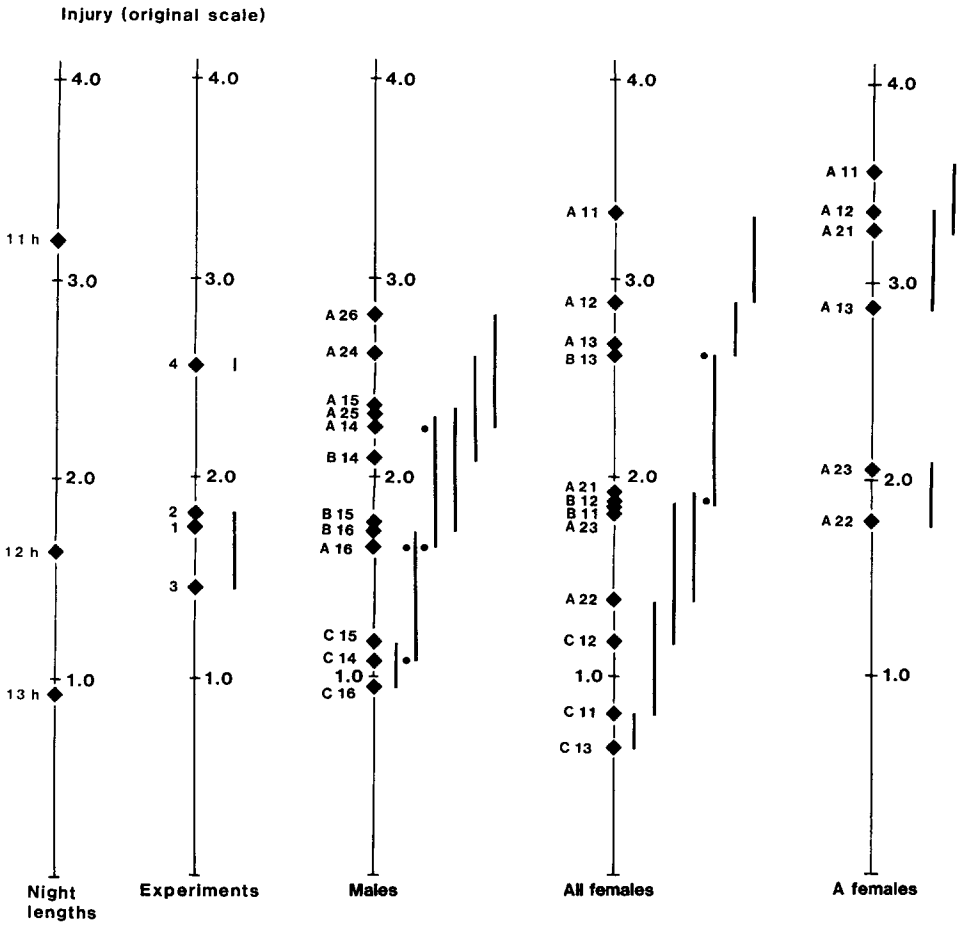

Fig. 4. Estimated average frost damage assuming only additive variance effects (Model 4). Non-significant differences are indicated by solid lines. Exceptions to the straight-forward ranking are shown by dots. The first four rankings are based on all parents whereas the rightmost ranking is based on A parents only

conspicuously from what could be expected from the parental GCAs, suggesting the occurrence of a positive specific combining ability. A reservation must be given since this family was only tested in experiment 4.

As discussed in other papers by our group (Ekberg et al. 1982; Eriksson and Ilstedt 1986) the prerequisites for an estimate of general and specific combining ability from experiments with long-distance hybrids are not prevailing. The results must therefore be treated with care. Such estimates as we present, however, are of value for related types of matings.

As expected, the night lenght at freeze testing influenced the degree of injury in a pronounced way (Table 2, Fig. 4).

As in many other studies on the genetics of characters of high adaptive value in northern conifers, additive effects were of greater importance than specific effects (Nilsson and Andersson 1969; Rehfeldt 1977; Tho 1977; Eriksson et al. 1978). From Table 2 it may be seen that the relative importance of the additive effects – M, F, m (M), and f (F) – were almost five times larger than the ones for specific combining effects – M×F and m×f (M×F). Most of the additive effects originated from the origin components (M and F in Table 2).

To get estimates of the ratio between additive and specific components for more realistic breeding populations, two additional ANOVAs were run. In the first, the families with A parents were included (Table 3) while in the second, families with A and B parents were included. This separation was done since the clones in our study could be regarded as belonging to three breeding zones A, B and C, respectively. In the southern breeding zone (A in Fig. 1) there are usually no problems with frost hardiness of *Pinus sylvestris*.

When the clones could be regarded as members of the same breeding population, the additive effects were the only ones of importance for frost hardiness (Table 3). When individuals from the southern breeding zones (A and B) were included, the additive variance component was almost twice as large as the specific one. From the results of the three ANOVAs

according to Model 2, it is obvious that the data from the family A21×B16 is the main source of the observed specific components in our study.

No interaction on the origin level was noted (the bottom line in Table 4 and the third line of Table 2). Thus, our result agrees with the intermediate inheritance of bud-set in *Pinus sylvestris* reported by Mikola (1982). Our data support a polygenic inheritance of frost hardiness.

The significant change in ranking of the origins between female and male groups is noteworthy (M′ in Table 4, see also Fig. 4). The trees of the northernmost origin (C) ranked consistently as the most hardy ones. This might reflect that the prerequisites for attaining hardiness in the northernmost material are several times higher than in the other origins. The fairly high frost hardiness of the female tree A21 when based on the whole material can largely be attributed to the unexpected high frost hardiness of family A21×B16 (cf. the two rankings of female trees in Fig. 4). There was a considerable overlap in ranking between trees originating from the two southernmost breeding zones (Fig. 4) in spite of the large difference in requirement on hardiness in the two zones. This is a consequence of the large within-population variation in frost hardiness. As discussed previously (Eriksson 1982), long-living tree species need an assurance against unpredictable regeneration conditions in the future. This is accomplished by carrying a broad genetic within-population variation of adaptive characters (Levins 1963; Stern and Roche 1974).

The noted large within-population variation agrees with earlier observations on growth rhythm and frost hardiness among open-pollinated single tree progenies of temperate conifers (Wright 1963; Dietrichson 1969, 1971; Rehfeldt 1974, 1983; Eriksson et al. 1976, 1978; Campbell 1979; Pollard and Ying 1979a, b; Eriksson 1982; Mikola 1982; Skrøppa 1982; Buchert 1983; Ståhl 1984; Ekberg et al. 1985; Jonsson et al. 1985).

The implications of our results on breeding for autumn hardiness in *Pinus sylvestris* are as follows:

A. The large within-population variation offers good opportunities for breeding.

B. Freezing tests can be applied to identify the desirable autumn hardiness of a parent.

C. The commercial seed of a selected sample of hardy parents might be produced after random mating among the parents independently of their origin, since there was no interaction following long-distance crossing.

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