Impact of Family-by-trial Interaction on the Utility of Progeny Testing Methods for Scots Pine

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Summary

The magnitude of family-by-trial interaction in the progeny testing of Scots pine (*Pinus sylvestris* L.) was studied by estimating genetic and rank correlations between 40 pairs of progeny trials. The data originated from 20 conventional long-term forestry trials and 15 test orchards, all assessed for total tree height at the age of 10 years. The study material consisted of half-sib progenies of the first generation Scots pine plus trees. Family-by-trial interaction was found to be at least moderate but its pattern was largely unpredictable. None of the studied environmental or design variables (the difference in trial mean height, survival and planting density) explained a significant portion of the variation in across-site correlations. Family by field test design interaction was also absent, i.e. the across-site correlations were rather similar in the groups of test orchards and forestry trials. Site type strongly affected mean height and survival, as well as the heritabilities. The highest estimates of family heritability were derived from test orchards on agricultural land. On forest soil, the test orchards and forestry trials performed comparably, but clearly poorer than the test orchards on agricultural land. The results suggest that the efficient discrimination of genetic differences achieved through intensive field testing on homogeneous sites overrules the interaction bias due to the disparity between test orchard and forestry conditions, which appeared to be negligible.

Key words: Pinus sylvestris, genotype-environment interaction, genetic correlation, heritability, progeny testing, selection, experimental design.

FDC: 232.11; 165.3; 165.5; 165.4; 174.7 *Pinus sylvestris.*

Introduction

The genetic testing of Scots pine (*Pinus sylvestris* L.) in Finland is largely based on information from long-term trials that are managed analogously to operational reforestation sites. During the past 2 decades, however, the use of accelerated trial procedures has become more popular (MIKOLA, 1985; PAJAMÄKI and KARVINEN, 1995). The concept of test orchard, synonymous to 'farm-field trial', was suggested by TIGERSTEDT (1973) to describe a field testing method aimed at rapid and cost-effective screening of genetic entries. Test orchards are regularly established as high density stands (up to 10000 trees/ha), usually on uniform and fertile sites, such as abandoned agricultural land. Weed control and site preparation are commonly used to further reduce the microsite variability. In addition, the trials are occasionally fenced to prevent damage due to browsing animals (MIKOLA, 1985). The purpose of all these measures is 1) to reduce the experimental error, 2) to enhance the early manifestation of genetic differences, and 3) to accelerate the growth of trees and, consequently, to minimize the time period from planting to the onset of root and crown competition. Selection for test orchard performance is, in turn, expected to provide higher genetic gains per unit time than selection carried out in normal forestry trials. In Finland, test orchards are intended for selection for height at a target age of 10 to 15 years (MIKOLA, 1985).

The various hypotheses presented to date about the superiority of accelerated test methods have remained unverified. Furthermore, the obvious disparity between test orchard and operational planting conditions has given rise to concern among tree breeders. If correlation between selection and deployment environments is decreased, the additional selection gain expected from accelerate field trials could be seriously diminished (LINDGREN, 1984; HODGE and WHITE, 1992). In the worst of scenarios, the relative ranking of genotypes in test orchard conditions would be reversed on conventional plantations. The degree to which different testing procedures actually generate genotype-environment interaction (GEI) is poorly known because the subject has received surprisingly little attention in the forestry literature. Many of the interaction studies have focused on determining safe ranges for seed transfer or evaluating the need for delineated breeding zones (MATHESON and RAYMOND, 1984; CARSON, 1990; JOHNSON and BURDON, 1990; PEDERICK, 1990; JOHNSON, 1992). These studies have usually refered to situations where the genetic entries or test environments, or both, differ substantially (e.g. provenances, regions) and interactions are fairly repeatable. In progeny testing, on the other hand, the material being tested is relatively homogeneous, and intended to be deployed within a predefined target environment. In spite of this, family by microsite interaction can be as high as family by macrosite interaction (MATHESON and COTTERILL, 1990). In the latter case, high GEI may be exploited by breeding for specific environments. In the first case, this option is not available; instead, the main concern is the efficiency of indirect selection: How should tree breeders respond to data from test orchards and other unconventional test environments?

The impact of GEI is most conveniently measured in terms of genetic correlation and correlated response for selection. The idea of treating the expression of a trait assessed at 2 sites as 2 distinct traits, and estimating their correlation, was originally presented by FALCONER (1952). *Type-b* genetic correlation (r_B) was first introduced in forestry by BURDON (1977) who claimed that, in the genetic testing of forest trees, the stability of test sites is essentially more important than that of genotypes. Interpretation of r_B in terms of GEI is selfevident, since any degradation of the coefficient of correlation from unity arises from the inability of genotypes to perform equally at two sites. Genetic across-site correlations possess some favorable statistical properties as compared to ANOVA based estimates of GEI. For instance, genetic correlations are robust against heterogenous site variances, and can be effectively incorporated into selection indices (BURDON,1977; WHITE and HODGE, 1991) and formulae predicting the response to indirect selection (FALCONER, 1981). During the last few years, the use of r_B has become established in forest genetics literature as a measure of stability (MATHESON and RAYMOND, 1984; NIENSTAEDT and RIEMENSCHNEIDER, 1985; CARSON, 1990; JOHNSON and BURDON, 1990; JOHNSON, 1992; HODGE and WHITE, 1992; LAMBETH *et al.*, 1994).

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The principal objective of this paper was to estimate the importance of family-trial interaction in the Finnish Scots pine breeding programme. This was done by studying the magnitude and variation of across-site correlations between families in progeny trials representing different experimental designs and site types. Identification of the factors generating the interactions was also addressed.

Material and Methods

Material

The study material consisted of 10 test orchard trials and 20 long-term forestry trials of Scots pine. The trials were planted in central and southern Finland between 1977 and 1981, and measured for tree height at the age of 10 years. The 30 trials were distributed into 8 series, each consisting of 2 to 6 replicated trials, of which at least one trial was established as a test orchard. Four of the test orchard trials were located on abandoned agricultural land, whereas the rest of the trials were situated on forest sites of varying fertility. The initial spacing ranged from 2 m x 2 m in the forestry trials (2500 trees per hectare) to 0.75 m x 1.5 m or 1 m x 1 m in the test orchards (8888 and 10000 trees per hectare, respectively). All the trials consisted of 4 to 6 randomised complete blocks (*Table 1*).

Most of the entries represented windpollinated offspring of first generation plus trees. Family members were assumed to be true half-sibs. Other types of entry, such as a few full-sib families and standard seed lots (4 to 10 per trial), were excluded from the more detailed analyses. In most series, the family

Table 1. – Description of the Scots pine progeny trials. The first value in the 'Entries' column indicates the total number of entries originally planted, and the second value the number of entries left after the removal of standard seedlots. *Trials No. 573/1 and 573/2 have the same entries as the trials in the 572 series, and are referred to as trials 572/3 and 572/4 in this study.

Trial	Entries	Blocks	Trees/ plot	Trees/ entry	Area, ha	Planting density, trees / ha	Mean height,dm (age 10)	Mean survival, % (age 10)	Trial type	Site type
572/1	45/31	7	18	129	0.64	8888	45.8	98.9	Test orchard	Agricultural land
572/2	38/30	4	16	63	0.97	2500	26.1	60.2	Forestry trial	Agricultural land
*572/3	45/31	10	16	160	2.88	2500	21.6	68.3	Forestry trial	Dryish heath forest land
*572/4	44/31	10	16	158	2.80	2500	24.8	47.0	Forestry trial	Moist forest land
624/1	50/41	5	25	125	0.70	8888	32.0	91.1	Test orchard	Agricultural land
624/2	50/41	5	25	125	2.50	2500	32.7	79.7	Forestry trial	Agricultural land
624/3	50/41	5	25	122	2.45	2500	13.6	61.8	Forestry trial	Dryish heath forest land
698/1	33/23	4	25	86	0.32	8888	43.8	88.2	Test orchard	Agricultural land
698/2	31/22	4	25	97	1.20	2500	22.3	84.8	Forestry trial	Moist forest land
699/1	69/59	6	25	150	1.06	10000	18.3	27.3	Test orchard	Dryish heath forest land
699/3	68/59	6	25	149	4.06	2500	27.1	53.4	Forestry trial	Dryish heath forest land
739/2	88/88	6	25	150	1.49	8888	48.9	71.0	Test orchard	Agricultural land
739/5	46/42	6	25	150	2.76	2500	25.6	44.9	Forestry trial	Dryish heath forest land
740/1	63/53	6	25	149	1.06	8888	20.4	46.5	Test orchard	Dryish heath forest land
740/2	64/54	6	25	150	0.96	10000	19.8	39.1	Test orchard	Dryish heath forest land
740/3	33/28	6	25	150	1.98	2500	25.5	63.6	Forestry trial	Moist forest land
740/4	33/28	6	25	150	1.98	2500	28.9	61.6	Forestry trial	Dryish heath forest land
740/5	29/24	6	25	150	1.74	2500	21.1	57.1	Forestry trial	Dryish heath forest land
740/6	30/25	6	25	150	1.80	2500	23.2	46.6	Forestry trial	Dryish heath forest land
741/1	61/51	6	25	141	0.98	8888	19.1	54.2	Test orchard	Dryish heath forest land
741/2	60/51	6	25	149	0.90	10000	17.4	20.0	Test orchard	Dryish heath forest land
741/3	27/22	6	25	147	1.59	2500	22.5	51.1	Forestry trial	Moist forest land
741/4	26/21	6	25	139	1.45	2500	23.5	55.8	Forestry trial	Moist forest land
741/5	33/28	6	25	150	1.98	2500	25.7	59.9	Forestry trial	Dryish heath forest land
741/6	32/27	6	25	150	1.92	2500	20.9	34.7	Forestry trial	Dryish heath forest land
742/2	66/56	6	25	150	0.99	10000	18.8	46.9	Test orchard	Dryish heath forest land
742/3	32/27	6	25	150	1.92	2500	30.6	69.1	Forestry trial	Dryish heath forest land
742/4	30/25	6	25	135	1.62	2500	28.2	69.5	Forestry trial	Moist forest land
742/5	34/29	6	25	150	2.04	2500	26.3	61.3	Forestry trial	Dryish heath forest land
742/6	34/29	6	25	146	1.98	2500	21.5	40.6	Forestry trial	Dryish heath forest land

composition was identical across the trial replicates. Exceptions were series Nos. 740, 741 and 742, in which only the test orchard replicates consisted of all the families tested, whereas each of the remaining forestry trials contained only half of the families (*Table 1*). For this reason, the analyses of across-trial correlations in these series were defective.

Analysis

The total height of all the living and healthy trees in each trial was measured. Plot mean of the measured trees (y_{ij}) was the basic observation unit used in the analyses. In order to estimate the genetic parameters, total variance was partitioned into statistical variance components in each trial, as well as across all trials within each series using the MIXED procedure in SAS/STAT package (SAS Inc., 1992). The linear models used in the single-site (Eq. 1) and across-site (Eq. 2) analyses where

$$y_{ij} = \mu + f_i + b_j + e_{ij} \qquad [1]$$

$$y_{ijk} = \mu + f_i + b_{j(k)} + t_k + ft_{ik} + e_{ijk} \qquad [2]$$

f_i, $b_{j(k)}$, t_k and ft_{ik} are the effects of family, block, trial site and family by trial interaction, respectively, and e_{ijk} denotes the random plot error. The respective variance components were σ^2_f, σ^2_b, σ^2_t, σ^2_{ft}, and σ^2_e.

The family heritability was calculated for each site as (r denotes the harmonic mean number of blocks):

$$h^2_f = \sigma^2_f \; / \; (\sigma^2_f + \sigma^2_e \; r^{-1}) \qquad [3]$$

Coefficients of family and family mean variation (cv_f, cv_F) were obtained by dividing the square roots of the family variance component and the phenotypic variance of family means, respectively, by the trial mean height (X):

$$cv_f = 100 \; s_f \; / \; x \qquad [4]$$

$$cv_F = 100 \; [\; \sigma_f + (\; \sigma_e \; r^{-1/2} \;) \;] \; / \; x \qquad [5]$$

Genetic correlation was computed between all pairs of replicated trials by dividing the phenotypic correlation of family means in 2 trials ($r_{F(ii')}$) by the geometric mean of the respective single-site family heritabilities (Eq. 6) (BURDON, 1977). The phenotypic type-b family correlations, as well as SPEARMAN rank correlations (r_{rank}), were computed using the CORR procedure of SAS (SAS Inc., 1985). Based on the fact that only genetic covariance contributes to the correlation of phenotypic observations across sites, this method effectively by-passes the need to partition the total covariance into its components through a separate cross-product analysis of variance (BECKER, 1984), a feature that is not directly implemented in most statistical packages.

$$r_B = r_{F(ii')} \; / \; (\; h_{f(i)} \; h_{f(i')} \;) \qquad [6]$$

PEARSON's product-moment correlation analysis and one-way analysis of variance were used to test whether any relationship existed between r_B and r_{rank} and a few environmental and experimental design variables.

Assuming homogeneity of the variances between trial replications, an alternative set of estimates of type-b genetic correlation (r_{B2}) was computed for each trial series using a formula from YAMADA (1962):

$$r_{B2} = \sigma^2_f \; / \; (\; \sigma^2_f + \sigma^2_{ft} \;) \qquad [7]$$

where σ^2_f and σ^2_{ft} are obtained from the across-site analysis.

The selection gain per intensity of unit standard deviation was estimated for both direct (Eq. 8) and indirect (Eq. 9) family selection. The direct gain, relative to trial mean height (μ_i), was obtained as (FALCONER, 1981)

$$G_i = 2 \; h^2_{f(i)} \; cv_{(i)} \qquad [8]$$

When the material selected in trial *i* is deployed in conditions identical to those in trial *i'*, the expected correlated response, relative to the direct gain estimated at the deployment site, becomes (BURDON, 1977):

$$G_{i'/i} = r_B \; h_{f(i)} \; / \; h_{f(i')} \qquad [9]$$

Results

The across-site correlations varied considerably among all the trial series. With a couple of exceptions, all the correlations were positive. Some of the genetic correlations exceeded unity, indicating large standard errors associated with the estimates. The unweighted mean of the 39 type-b genetic correlations was 0.61 (s.d. = 0.39). The genetic correlations based on YAMADA's equation (*Eq. 7*) were of the same magnitude (mean = 0.58). The family-by-trial interaction component was over 80 % of the family component of variance, as averaged over the eight across-site analyses (*Table 2*). The rank correlations were significantly lower than the genetic correlations (mean = 0.30) and less than half of them were statistically significant at the 5 % risk level (*Table 3*).

The type-b correlations did not depend on differences between the trials in planting density (r with r_B = –0.09 n.s., r with r_{rank} = –0.21 n.s.), mean height (r with r_B = 0.02 n.s., r with r_{rank} = 0.16 n.s.) or survival percentage (r with r_B = –0.06 n.s., r with r_{rank} = 0.13 n.s.). Neither did the different types of paired trials (forestry trial x forestry trial *vs.* forestry trial x test orchard *vs.* test orchard x test orchard) show significantly different levels of correlation (1-way ANOVA obs. prob. = 0.97). The average genetic correlations for the pairs of forestry trials and pairs of test orchard and forestry trial, respectively, were similar (mean = 0.62 in the both cases). Exceptions were series No. 572 and 624, where a test orchard on agricultural land trial showed better genetic correlation with a replicate trial located on forest land than with another trial on agricultural land.

The estimates of family heritability were also variable between the sites, the maximum range (0.00 to 0.85) being found in series No. 698 (*Table 3*). The influence of site type on the heritability estimates was distinct. The highest family heritabilities were found among the four test orchard trials established on agricultural land (mean h^2_f = 0.83). In contrast, family heritability in the trials laid out on forest sites, including test orchards, was noticeably small (mean h^2_f = 0.50).

The agricultural land trials were distinguished by their excellent height growth which proved to be double that on forest sites. Respectively, the mean survival ranged from about

70% to 100% in agricultural land test orchards, and from 20% to 70% (*Table 1*) in the forest land trials. In the latter set of trials, the test orchards even showed poorer height growth and survival than the parallel forestry trials (*Table 1*). Overall, the test orchards established on forest soil were about as informative as the ordinary forestry trials.

The percentage expected gains for backward family selection, varying from 0 % to 12 %, did not show any clear trend. The highest absolute gains can, however, be expected from the agricultural land test orchards, as suggested by the family variance components (*Table 3*). The estimates of relative indirect gain also appeared to be variable and unpredictable.

Table 2. – Estimates of variance components from the across-site analyses (Eq. 2). Rel. FSI denotes the relative family-by-trial interaction, calculated as $\sigma^2_{ft}\ 100/\sigma^2_f$. The type-b genetic correlation (r_{B2}) was obtained from Eq. 7. Variance components significant at 5% level are underlined.

	REML Variance Components						
Series	Trial	Family	Block	Family x trial	Residual	Rel. FSI, %	r_{B2}
572	120.610	1.311	0.973	0.787	6.268	60.05	0.63
624	116.350	0.450	3.597	0.728	4.671	161.59	0.38
698	232.350	1.521	2.742	2.090	10.471	137.44	0.42
699	38.780	0.384	0.442	0.359	6.503	93.65	0.52
739	273.940	1.890	0.997	1.583	9.055	83.73	0.55
740	13.390	0.964	2.015	0.401	6.398	41.56	0.71
741	8.960	0.583	0.732	0.244	5.955	41.86	0.71
742	24.720	1.175	1.541	0.432	4.986	36.80	0.73
Mean						82.09	0.58

Table 3. – Left: Across-site genetic (upper triangular matrices) and rank correlations (lower triangular matrices) for height at age 10. The shadowed diagonal contains the average genetic correlations. In the calculation of means, estimates exceeding unity were truncated to 1. Middle: Direct selecetion gain, given as percentage of the trial mean height (Eq. 8) on diagonal. The off-diagonal elements are gains from indirect selection, relative to the direct selection gain obtained on site i' (Eq. 9). Right: Family component of variance (σ^2_f), single-site family heritability (h^2_f), coefficients of family (CV_f) and phenotypic family mean variation (CV_F). The underlined rank correlations and family variance components are significant at 5% risk level. The test ochards are distinguished by bold trial numbers.

	Type-b genetic and rank correlations						Direct and indirect selection gains									
	Site i'						Trial site i'									
Trial site i	/1	/2	/3	/4	/5	/6	/1	/2	/3	/4	/5	/6	σ^2_f	h^2_f	CV_f, %	CV_F,
572/1	0.71	0.59	0.69	0.85			7.73	0.65	0.72	0.91			3.80	0.79	4.26	4.86
572/2	0.45	0.55	0.45	0.61			0.54	9.33	0.43	0.60			2.12	0.66	5.58	7.04
572/3	0.39	0.20	0.64	0.78			0.66	0.48	10.45	0.80			1.70	0.73	6.05	7.15
572/4	0.54	0.40	0.51	0.75			0.79	0.62	0.76	7.58			1.17	0.69	4.37	5.47
624/1	0.58	0.39	0.76				8.05	0.60	1.02				1.92	0.86	4.33	4.66
624/2	0.25	0.19	-0.01				0.25	3.18	0.00				0.80	0.36	2.74	4.42
624/3	0.43	0.04	0.38				0.57	0.00	9.28				0.82	0.48	6.68	9.65
698/1	-	n/a					12.25	0.00					7.82	0.85	6.39	7.29
698/2	0.33	-					0.00	0.00					0.00	0.00	0.00	8.94
699/1	0.38	0.38					7.68	0.46					0.96	0.48	5.35	7.91
699/3	0.25	0.38					0.31	3.39					0.58	0.33	2.81	5.08
739/2	0.77	0.77					8.14	1.16					4.75	0.83	4.46	4.88
739/5	0.37	0.77					0.51	5.80					1.52	0.36	4.82	8.01
740/1	0.40	0.73	0.58	0.52	0.29	0.19	10.29	0.68	0.76	0.50	0.29	0.19	2.01	0.54	6.95	9.45
740/2	0.25	0.72	1.15	1.00	0.51	0.34	0.78	8.88	1.39	1.03	0.54	0.37	1.16	0.62	5.43	7.13
740/3	0.16	0.40	0.86	1.31	-	-	0.45	0.72	2.98	0.74	-	-	0.44	0.32	2.61	4.66
740/4	0.40	0.38	0.44	0.84	-	-	0.54	0.98	4.05	7.67	-	-	2.05	0.59	4.95	6.46
740/5	0.11	0.35	-	-	0.46	0.58	0.29	0.48	-	-	5.37	0.59	0.57	0.55	3.58	4.85
740/6	0.15	0.18	-	-	0.25	0.37	0.19	0.32	-	-	0.58	5.79	0.81	0.55	3.89	5.31
741/1	0.87	0.37	0.85	0.93	1.40	1.18	3.82	0.29	0.82	0.82	0.62	0.64	0.52	0.26	3.78	7.37
741/2	0.09	0.25	0.47	0.01	0.28	0.11	0.47	5.90	0.58	0.01	0.22	0.09	0.60	0.42	4.46	6.94
741/3	0.19	0.32	0.30	-0.33	-	-	0.89	0.38	3.11	-0.30	-	-	0.42	0.28	2.90	5.55
741/4	0.36	0.11	-0.08	0.20	-	-	1.06	0.01	-0.37	3.32	-	-	0.43	0.34	2.78	4.91
741/5	0.55	0.15	-	-	0.76	1.15	1.61	0.35	-	-	8.53	1.02	1.78	0.67	5.19	6.37
741/6	0.38	0.02	-	-	0.76	0.70	1.59	0.13	-	-	0.98	9.43	1.46	0.65	5.79	7.22
742/2		0.61	0.26	0.22	1.05	0.95		11.80	0.31	0.24	1.11	1.10	1.61	0.76	6.74	7.78
742/3		0.20	0.41	0.55	-	-		0.22	5.97	0.50	-	-	1.54	0.53	4.06	5.63
742/4		0.06	0.24	0.39	-	-		0.20	0.60	7.59	-	-	1.94	0.63	4.94	6.01
742/5		0.73	-	-	1.00	1.10		0.90	-	-	6.70	0.99	1.25	0.62	4.25	5.38
742/6		0.61	-	-	0.70	0.98		0.86	-	-	1.01	9.04	1.48	0.63	5.65	7.20

As with the genetic correlations, no trend was observed indicating the dependence of indirect gains on any of the factors.

Discussion and Conclusions

Importance and causes of family-by-trial interaction

The genetic correlations between trials, as found in this study, reflect at least moderate family-by-trial interaction. Moreover, the interaction was present in the form of substantial changes in family ranking. This finding agrees with some earlier studies that have demonstrated strong interactions between genetically close entries, like the plus tree progenies in this study, and experimental sites or even with blocks in a single field trial (e. g. JOHNSON and BURDON, 1990; MATHESON and COTTERILL, 1990; PEDERICK, 1990). Although nearly all the correlations were positive in sign, the behaviour of the families was clearly inconsistent enough to deserve notice. On the other hand, GEI appeared to be largely unpredictable and therefore difficult to avoid or exploit in breeding. The variation in correlations could not be attributed to any single external variable. Earlier studies have shown that genotypes can respond differently to biotic damage (HODGE and WHITE, 1986), stocking (CHANNELL, 1982) or site quality (e. g. HODGE and WHITE, 1992). In addition, statistically significant pseudo-interactions resulting, for instance, from heteroscedasticy of trait variances at different sites, are feasible (ROBERTSON, 1959; CAMPBELL and WILSON, 1973; BURDON, 1977; CAMPBELL *et al.*, 1986).

Significant family by fertiliser or soil fertility interactions have frequently been reported in other pine species (BURDON, 1971; JAHROMI *et al.*, 1976; JOHNSON and BURDON, 1990; MATHESON and COTTERILL, 1990). Therefore, it was supposed that the magnitude of height difference between 2 sites might correlate with the frequency of family rank changes. However, no evidence of such an association was found in this study. This contradicts with the recent finding of HODGE and WHITE (1992), who classified pairs of Slash pine (*Pinus elliottii* var. *elliottii*) progeny trials as either 'Same' or 'Different' using a site index (base age 25 years) difference of 2.6 m as the threshold, and found consistently smaller correlations for the pairs of 'Different' trials. The discrepancy in the correlations they found was not large at an age of 10 years (r_B = 0.71 and r_B = 0.63 for the 'Same' and 'Different' groups, respectively). Whether the described relationship would have been observed had the magnitude of the differences between paired trials been greater than in this study, remains open. Alternatively, the lack of site type effects could simply result from phenotypic plasticity, as Scots pine naturally performs well across a fairly wide edaphic gradient (KUUSELA, 1990).

Planting density was another factor that varied strikingly in the sample of trials studied here. The practical importance of spacing-driven interactions is generally estimated to be trivial (FRIES, 1984; MAGNUSSEN and YEATMAN, 1986; GULLBERG and VEGERFORS, 1987; WILLIAMS, 1988; ST. CLAIR and ADAMS, 1991). This is in harmony with the low, nonsignificant correlation found here between planting density and both r_B and r_{rank} values.

Distinguishing between biologically significant and repeatable GEI, and on the other hand, pseudo-interaction due to nuisance factors, is difficult. In the absence of major climatic differences and GEI due to spacing or fertility, the low across-site correlations observed in this study probably reflected the microsite variability and success of experimental design, rather than true biological interactions. In poorly designed or insufficiently replicated trials the precision of observed family performances is low, which naturally degrades the accuracy of family ranking, and consequently, the correlation between other trials. In this study, the pairs of trials with low single-site heritabilities tended to be poorly correlated, suggesting that a part of the interaction can be eliminated simply by enhancing the experimental precision of progeny trials.

It can be further speculated whether the trials studied were at different developmental phases at the time of measurement (10 years old) (see e. g. FRANKLIN, 1979). If the establishment of final family ranking depends on the size rather than on the age of trees, high correlations between trials can not be expected. Further studies are needed to determine the trends that type-b genetic and rank correlations may exhibit in relation to age, stage of stand development and experimental design. Such research would significantly increase our knowledge of the true nature of the interactions, as well as the best age or stage for selection in different conditions.

Efficacy of progeny test methods

The correlations between test orchards and forestry trials and between pairs of parallel forestry trials were of similar magnitude. This result strongly suggests that the test orchard method as such is not likely to be a notable source of GEI, and the risk of biased family ranking in test orchards is small. When both heritability and consistency of family performance with the other trials are considered simultaneously, the test orchards were clearly more effective than the forestry trials. Especially when laid out on fertile agricultural lands, the test orchard trials appeared to discriminate genetic differences considerably better than the normal forestry trials. This probably resulted from both homogeneous growing conditions and the relatively fast transition of the test orchard stands into the inter-tree competition phase, as suggested by MIKOLA (1985). This latter phenomenon was demonstrated in Douglas fir and loblolly pine by FRANKLIN (1978), who showed that the closure of stands was accompanied by an abrupt increase in additive genetic variance and heritability.

The contrasting performance of test orchards established on less fertile forest sites, i. e. poor height and survival even when compared to the forestry trials, could probably be attributed to inter-tree competition for nutrients. The effects of competition logically intensify earlier in dense test orchards stands than in forestry trials with lower densities.

As far as height growth is concerned, the testing of trees on homogeneous and fertile sites with narrow spacings probably involves no great risk. The validity of this conclusion as generalised to cover other important traits, such as branching quality, still remains to be studied. Use of the test orchard method on forest sites, on the other hand, does not seem reasonable, as there may be no additional gain to compensate for the higher management costs. However, statistically less efficient forestry trials are still necessary as they provide the sort of essential long-term data on time trends in genetic parameters, yield development on the stand level etc., that do not come within the scope of intensive field experiments.

When evaluating genetic values, the family-by-trial interaction is best managed by exploiting all available data and incorporating estimates of type-b correlations and heritabilities into the selection index (BURDON, 1979), BLP or BLUP equations (WHITE and HODGE, 1989). Observations from trials showing the lowest heritability, the smallest phenotypic variation and the poorest correlations with other sites are, accordingly, given the least index weights. Although this method theoretically leads to maximum genetic gain, it suffers from erroneous estimates of genetic parameters, especially

genetic correlations (HODGE and WHITE, 1992). The precision mainly depends on the number of families, which was probably too small for this purpose in most of the trials studied. More work is obviously needed, both with experimental designs and the statistical analysis of genetic field trials, to improve the precision of estimates of genetic parameters used as the basis of selection.

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