Family-Site Interactions in Radiata Pine Families in New South Wales, Australia

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Summary

The magnitude and practical importance of family x site interactions for growth and form traits in radiata pine (*Pinus radiata* D. DON) breeding in New South Wales were analysed using several different techniques. Data were from 73 half-sib families in progeny tests. Considerable interactions for all traits were indicated by combined analyses of variance and by rank changes between sites.

The ratio of interaction to family variance component showed the interactions to be of little practical importance, except for stem straightness. Calculated losses in potential genetic gain in a breeding population were found to be of concern for all traits under individual selection but only for stem straightness under family selection. Deletion of the eight most interactive families reduced these losses considerably, indicating that this would be an effective strategy in selection for stability in performance across sites. In practice, families should preferably be selected for average performance across the range of trial sites, with some interactive but overall superior families retained.

Genetic correlations between the same trait at different sites were moderate to high (0.62 to 1.00), and generally lowest for stem straightness. The greatest genetic gains were generally expected from selecting and planting families on the same site, but relative efficiencies of selecting and planting on different sites were mostly high. These and the other analyses of the practical importance of the interactions do not give substantial support to a strategy of regionalising breeding operations in New South Wales, particularly where diameter is the main selection trait.

Key words: Family x site interactions, genetic correlations, genetic gains, *Pinus radiata*.

Introduction

Interactions between genotypes and sites may reduce genetic gains achievable in breeding programmes for trees if, for example, selections adapted to a narrow range of site conditions are used over a wider range. A fundamental question facing breeders of radiata pine interested in improving growth and form is whether breeding operations should be regionalised (separate breeding populations or seed orchards each employing only "locally" adapted selections) or generally-adapted, using selections adapted to a wide range of sites.

To answer this question it is necessary to quantify the degree of interaction between the tested families available for selection and the sites where they grow, and to determine whether the interactions are large enough to have practical significance in terms of their effect on potential gains.

Families of radiata pine are currently being selected, primarily for growth and form, for use in advanced-generation breeding populations in New South Wales. The majority of available families occur in three progeny tests in the International Gene Pool series. These trial sites have widely varying geology, soil fertility and rainfall, and cover most of the range of site conditions represented in New South Wales plantations.

Although factors of predictable natural environmental variation (SHELBOURNE, 1972), such as soil depth, drainage and fertility, have not been quantified for the individual Gene Pool Trial sites, the gross environmental differences between sites might be expected to lead to large family x site interactions, for growth at least. It is important in the New South Wales breeding programme to quantify these interactions and determine their practical significance so that the available genetic resources can be used most efficiently.

The development of a number of separate breeding or production populations, to serve regions defined in terms of environmental factors such as geology or climate, would be more costly and logistically more difficult than forming a single, generally-adapted population. Regionalised populations could only be advocated if there were firm evidence that family x site interactions among the candidate families were so large that potential gains would be reduced to a degree regarded as practically serious if alternative breeding population structures were adopted.

A number of different methods have been used by tree breeders to ascertain the magnitude and pattern of genotype x environment interaction, and to give predictions of the effect of interactions on genetic gain, for example, SHELBOURNE (1972), MATHESON and RAYMOND (1984), JOHNSON and BURDON (1990), MATHESON and COTTERILL (1990), and PEDERICK (1990).

In the present study, several established methods of analysis were applied to data for three growth and form traits in 73 half-sib families of diverse origin in the three Gene Pool trials, to determine the presence and magnitude of interactions. These methods included analysis of variance, an examination of rank changes, and an approximation devised by SHELBOURNE (1972), called a "rule of thumb" by MATHESON and RAYMOND (1984). Changes in potential gain due to interactions were also determined, using a method developed by MATHESON and RAYMOND (1984) and from genetic correlations for each trait between trial sites (BURDON, 1977).

The purpose of this paper is to address the question of regionalisation of radiata pine breeding in New South Wales, through a study of family x site interactions and assessment of their practical importance, in a group of families in the International Gene Pool Trials.

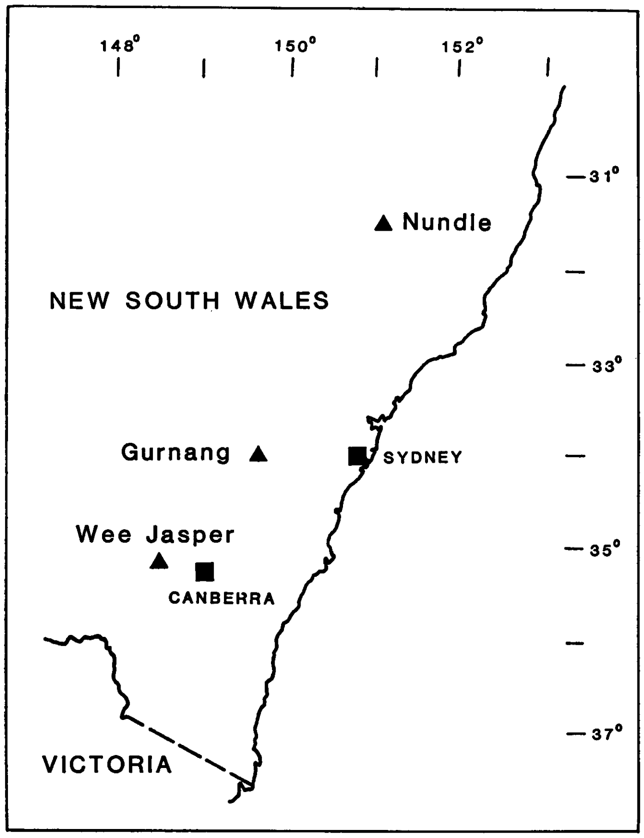

Figure 1. — Locations of the International Gene Pool Trials in New South Wales.

Materials and Methods

Trial sites and assessments

Data for this study were collected from three International Gene Pool trials in New South Wales, which were established in 1973 in Wee Jasper State Forest, Gurnang State Forest and Nundle State Forest (*Fig. 1*). The total number of families (seedlots) and the number of replications of these varies from trial to trial, as a result of variable numbers of seedlings of each family being available at the time of establishment. The layout at each site is a randomised complete block design, with 10-tree row plots. The history of establishment and detailed descriptions of the composition of these three trials are given by JOHNSON (1989).

Trial site details are given in *table 1*. The trials cover a range of soil fertility as determined by foliar levels of the major elements phosphorus (P, in ppm) and nitrogen (N, as a percentage). Foliar sampling was not carried out on the actual trial sites; nutrient levels were assumed to be generally similar to those obtained from trees on nearby sites with similar geology and establishment history. The range of foliar P in the trials was estimated in this way to be 950 ppm (Gurnang), through 1450 ppm (Wee Jasper) to 1720 ppm (Nundle). Similarly, the range of foliar N in the trials was estimated to be 1.4% (Gurnang), through 1.5% (Wee Jasper) to 1.7% (Nundle).

The extreme values of foliar P across radiata pine planting sites in New South Wales are about 800 ppm and 2100 ppm, a range of 1300 ppm, of which the range in the Gene Pool Trials covers 59%. The extremes for foliar N are about 1.0% and 1.9%, of which the range in the Trials covers 33%. Only small areas of plantation have P levels below 900 ppm or above 1800 ppm, or N levels below about 1.2% or above 1.8%. Thus, the Trial sites are representative of a much greater area of planting sites than these comparisons indicate.

An assessment of all the trials was carried out in winter 1985, at an age of 12 years from planting. Because of the high degree of imbalance in design within and between trials (with replications beyond number 4 in all trials containing few families), only replications 1 to 4 of each trial were assessed.

The overbark diameter at 1.3 metres above ground (dbhob) was measured on all trees except those severely suppressed (obvious runts) and those heavily damaged by wind or snow. A score for stem straightness and a score for branch quality were also assigned to each of these trees. These scores were both on a scale of 1 to 6, based on a method recommended by RAYMOND and COTTERILL (1990), by which a score of 1 is assigned to about the poorest five percent of trees and a score of 6 to about the best five percent of trees at each individual trial site. The aim was to approximate a normal distribution of scores for each form trait. The stem straightness score integrated sweep, lean and kinks, while that for branch quality integrated branch diameter and angle, and branching habit (nodality), with a multi-nodal habit being most desirable.

Analyses

A subset of 73 open-pollinated and polycrossed families was selected for several different types of analyses to determine the magnitude and practical importance of family x site interactions (*Table 3*). These were families represented by at least four trees in each of the first three or four replications in each trial (i.e. a minimum of 12 trees per family per trial). Details of the origins of the families are given by JOHNSON (1989).

Table 1 gives trial site descriptions, overall means for diameter, and percentage survival calculated for the 73-family data set at each site. Both within-site and across-site data sets for diameter, stem straightness and branch quality were analysed using analysis of variance. These were carried out using plot mean values, since the number of replications in which many families occurred varied within and between sites, and plots contained varying numbers of surviving trees (between four and ten). The SAS^{R} General Linear Models (GLM) Procedure (Anon., 1987) was used in both cases.

For the within-site analyses, the following random model was fitted:

$$Y_{ij} = \mu + R_i + F_j + \varepsilon_{ij},$$

where Y_{ij} is the effect of the ijth plot, R_i is the effect of the ith replication, F_j is the effect of the jth family, and ε_{ij} is the residual, including interaction between families and replications. Family heritabilities at each site were calculated using a formula ~~of~~ WRIGHT (1976):

$$h^2_f = \sigma^2_f \,/\, (\sigma^2_e/R + \sigma^2_f) \qquad (1)$$

where σ^2_f is the variance component due to families and σ^2_e is due to interaction between families and replicates (residual), and R is the number of replicates per trial.

The combined across-site data set was analysed for the three traits, by fitting the following random model:

$$Y_{ijk} = \mu + S_i + R_{ij} + F_k + SF_{ik} + \varepsilon_{ijk},$$

where Y_{ijk} is the observation of the $_{ijk}$th plot, μ is the overall mean, S_i is the ith site effect, R_{ij} is the jth replicate effect within the ith site, F_k is the kth family effect, SF_{ik} is the interaction between the ith site and the kth family, and ε_{ijk} is the residual.

Variance components for family (σ^2_f) and family x site interactions (σ^2_{fs}) for the three traits were calculated from the analysis of variance, by equating observed to expected mean squares (*Table 2*). Family heritabilities across sites (*Table 5*) were calculated using a formula of WRIGHT (1976):

$$h^2_f = \sigma^2_f / (\sigma^2_e/RS + \sigma^2_{fs}/S + \sigma^2_f) \qquad (2)$$

where R is the number of replicates per trial, and S is the number of trial sites (*Table 2*).

Least-squares means for diameter, stem straightness and branch quality were obtained for each family in each trial.

The ranking of the mean of each family for each trait was calculated at each site, and also the rankings for each trait over all sites. An overall estimate of the degree of rank change for each family was obtained by the method of MATHESON and RAYMOND (1984), whereby the absolute deviation of the ranking at each site from the overall ranking (over all sites) was calculated, and these were added across the three sites. This total was divided by three, to give a mean rank deviation (*Table 3*). The families contributing most to the interaction on the basis of rank changes (those with the greatest mean rank deviations) were identified.

To test whether the interaction was the result of a few families reacting more than others to large-scale geographic factors across the trial sites, the eight most interactive families for each of the three traits were deleted and the data reanalysed. The effect of this on the magnitude and statistical significance of interactions was observed. The number of families deleted was arbitrarily chosen, being about 10% of the number in the full data set.

SHELBOURNE (1972) suggested, as an approximation, that the effects of family x site interaction are "likely to be serious on gains from selection and testing" when the interaction component reaches 50% or more of the family component of variance. The ratio of σ^2_{fs}/σ^2_f was calculated for the combined data set for each trait, and also for the data sets from which interactive families were deleted.

MATHESON and RAYMOND (1984) developed formulae to estimate losses in potential genetic gain in a random-mating breeding or seed orchard population, due to selecting individual trees or families for use in a population for one site, on the basis of an overall analysis of variance covering several sites, compared with selecting for a population to serve that site on the basis of an analysis of data from the same site only. Any loss of potential gain would be due to family x site interactions. The loss of gain from mass selection, C_I (expressed as a percentage) is given by Equation 3, where V_f is the family variance component, V_i is the interaction variance component, and V_e is the residual variance component.

Loss of potential gain from family selection, C_F, is given by Equation 4, where S is the number of sites analysed, and B is the number of replicates (or blocks) per site. In this case the analysis was based on plot means. Family and error variances are assumed to be constant over all sites, and the same standardised selection differential (i) would be applied on all sites.

C_I and C_F factors were calculated for the whole 73-family combined data set, for each of diameter, stem straightness and branch quality. The most interactive families for each trait were also deleted, to investigate the effect on the magnitude of C_I and C_F, following a method of MATHESON and RAYMOND (1984).

Implications of family x site interactions in these trials were examined from calculations of genetic correlations for each of the traits between sites, and from calculations of the relative efficiency of selection of families for each trait at one site for potential use at another site. Genetic correlations for a trait such as diameter, measured on a similar group of families at two different sites, are "Type B" correlations (BURDON, 1977).

Genetic correlations for the same trait at two sites (x and y) were estimated by the equation of BURDON (1977) — Equation 5, where h^2_f is the heritability of family means calculated by the method of WRIGHT (1976) — *table 7*. The phenotypic correlations between traits at the three pairs of sites (*Table 7*) were computed using the SAS^R CORR Procedure (Anon.. 1987).

Predicted genetic gains at each site, per unit of selection intensity (i), from selecting phenotypically at other

$$C_I = [1 - (V_f + V_e)^{0.5} / (V_f + V_i + V_e)^{0.5}] \times 100 \qquad (3)$$

$$C_F = [1 - (V_f + V_e/BS)^{0.5} / (V_f + V_i/S + V_e/BS)^{0.5}] \times 100 \qquad (4)$$

$$r_{Gxy} = \frac{\text{phenotypic correlation of family means at sites x, y}}{\sqrt{[(h^2_f \text{ site x})\,(h^2_f \text{ site y})]}} \qquad (5)$$

sites, were calculated for each trait (*Table 8*). The formula for correlated response at site y from selection at site x (BURDON, 1977) was used:

$$G_{y.x} = h_x h_y \cdot r_{Gxy} \cdot 2\sigma^2_{Py} \qquad (6)$$

where h_x is the square root of h^2_f at selection site x, h_y is the square root of h^2_f at planting site y, and $2\sigma^2_{py}$ is twice the variance of family means (since selection of families in this case is on the basis of half-sib progeny tests).

The efficiency of phenotypic selection of families on each trait at site x for planting at site y, relative to both selecting and planting at site y (assuming the same intensity of selection at both sites) was also calculated, from BURDON's (1977) formula:

$$G_{x/y} / G_{y/y} = r_{Gxy} \cdot h_x/h_y \qquad (7)$$

where $G_{y.x}$ is the genetic gain from selecting at site x for planting at site y; $G_{y.y}$ is the gain from selecting at site y for planting at site y; r_{Gxy} is the genetic correlation between sites x and y for a trait; h_x is the square root of the family heritability at site x, and h_y is the square root of the family heritability at site y (*Table 8*).

Results and Discussion

Site data

Diameter varied over the trial sites, with a mean of 19.6 cm at Wee Jasper, 17.1 cm at Nundle and 16.4 cm at Gurnang (*Table 1*). There were significant differences between replicate means at all trial sites.

Wee Jasper Gene Pool Trial was expected to be a more favourable growth environment for radiata pine than the other two trial sites, since it alone was fertilised at establishment and, while it is on metabasic parent material like the Nundle site, this parent material is weathered to a greater depth than that at Nundle (P. J. RYAN, Forestry Commission of N.S.W., pers. comm.). The site at Gurnang is less fertile than the others, with lower soil phosphorus and nitrogen, and a lower annual rainfall. The slower growth rate at Nundle compared with Wee Jasper may have partly been due to infection by *Dothistroma septospora* (DOROG.) MORELET and severe weed growth, especially blackberries, on the site.

Table 1. — Site descriptions for the International Gene Pool Trials in New South Wales, and some phenotypic and genetic parameters of the 73 families studied.

	Trial Site		
	Wee Jasper	Gurnang	Nundle
Latitude S. (deg., min.)	35.10	33.57	31.28
Elevation (m)	890	1 140	1 160
Rainfall (mm)	1 300	900	1 500
Soil parent material	Metabasics/ granodiorite	Siltstone/ fine sandstones	Tertiary basalt
Mean diameter at 12 years overall (cm)	19.55	16.36	17.14
Mean diameter: Rep. 1	18.93	16.78	17.24
Rep. 2	19.76	16.15	17.86
Rep. 3	19.66	16.41	16.84
Rep. 4	19.86	15.94	16.55
% Survival in families studied	81.2	88.2	81.2
Genetic variance of diameter	9.52	4.75	10.26
Family heritability of:			
Diameter	0.70	0.59	0.74
Stem straightness	0.69	0.59	0.56
Branch quality	0.70	0.76	0.75

Survival of the 73 families studied was high at 12 years in all the trials, ranging from 81% at both Wee Jasper and Nundle, to 88% at Gurnang.

Analysis of variance within-sites

The analyses of variance for individual trial sites revealed highly significant differences among families ($p<0.01$) at all sites, for all traits. Values of family heritability were moderate to high at all sites, 0.59 to 0.74 for diameter, 0.56 to 0.69 for stem straightness, and 0.70 to 0.76 for branch quality (*Table 1*).

Rank reversals

In many families, rank changes for different traits between sites were large. For example, family 80091 ranked in the worst nine for diameter at Wee Jasper but in the top nine at Gurnang. Rank changes of such magnitude were more common for straightness than for diameter or branch quality, and implied the presence of considerable family x site interactions, particularly for straightness. Data showing the rankings of the 73 families in each Gene Pool Trial are given by JOHNSON (1989).

The mean rank deviations for all traits (*Table 3*) revealed a wide range in the apparent stability of rank in families. Eight families of the 73 analysed had mean deviations for diameter exceeding 16.0, and eight had mean deviations for straightness exceeding 18.0. These seem to be the most interactive families for this trait.

Combined analyses of variance

Mean-squares from the combined analysis of variance of the whole 73-family data set (*Table 2*) are presented in *Table 4*, for diameter, stem straightness and branch quality. All terms in the analyses of variance were highly significant ($p<0.01$), including the family x site interaction term.

Table 2. — Expectations of mean squares for estimating genetic parameters from the combined GLM analysis of 73 families in the International Gene Pool Trials in New South Wales.
There are 73 half-sib families, 4 replications per site and 3 sites. The variance component σ^2_f is due to families, σ^2_{fs} is due to family x site interaction, σ^2_r is due to replications within sites, σ^2_s s due to sites, σ^2_e is due to interactions between families and replications within sites (plot error).

Source of variation	d.f.	Type III Expectations of mean squares
Family	72	$\sigma^2_e + 3.59\,\sigma^2_{fs} + 10.78\,\sigma^2_f$
Site	2	$\sigma^2_e + 62.29\,\sigma^2_r + 3.41\,\sigma^2_{fs} + 249.17\,\sigma^2_s$
Family x Site	144	$\sigma^2_e + 3.61\,\sigma^2_{fs}$
Rep(Site)	9	$\sigma^2_e + 64.22\,\sigma^2_r$
Error	569	σ^2_e

Table 3. — **Mean Rank Deviations for Diameter, Stem straightness and Branch quality, for each of 73 families in the International Gene Pool Trials in New South Wales.**

Seedlot No.	Family	Mean rank deviations for:		
		Diameter	Stem str.	Br. qual.
4	Cambria HB	6.00	8.00	0.33
5	Cambria HC	2.67	18.67	3.00
11	Cambria HI	8.00	5.33	1.67
12	Cambria HJ	8.33	21.33	14.00
13	Cambria HK	14.33	6.67	5.00
14	Ano Nuevo HO	18.67	9.67	4.33
16	Ano Nuevo HR	10.67	6.67	17.00
17	Ano Nuevo HS	7.33	4.00	2.33
18	Ano Nuevo HU	9.00	5.67	7.67
19	Ano Nuevo HV	2.33	1.67	4.00
20	Ano Nuevo HW	7.33	13.33	12.33
85	12001	15.33	14.00	11.00
86	12038	16.33	16.67	15.67
87	12040	13.33	18.33	17.00
88	12112	5.67	16.00	8.67
89	12130	5.33	13.67	13.33
90	12187	11.67	15.00	6.00
91	12197	12.00	20.67	7.67
92	12236	18.33	17.67	10.00
93	12247	13.00	8.33	8.33
97	12351	17.67	12.67	11.67
99	12374	12.00	4.67	5.33
109	10954	4.67	5.33	13.33
118	RAD 9	8.67	4.67	5.67
119	RAD 10	8.33	8.00	5.67
124	70052	1.33	1.00	4.67
125	30048	15.00	15.00	18.33
126	30055	7.33	9.00	14.33
127	30002	3.67	9.67	2.33
128	30043	12.67	6.67	8.33
129	30026	5.67	16.33	6.00
131	30006	14.67	7.33	4.00
133	30022	4.00	10.33	10.67
134	30011	11.67	7.67	11.67
135	30016	14.33	10.00	3.33
138	30036	3.00	17.67	6.33
183	40012	15.00	15.67	2.00
184	40013	10.67	9.00	10.33
185	40014	14.00	11.00	6.67
205	Cam. 5 (ACT)	14.67	16.33	5.33
211	50002	11.00	20.00	22.67
213	50004	8.33	3.00	2.67
214	50007	13.33	20.33	7.33
215	50017	5.67	9.33	8.00
216	50019	7.00	2.67	8.33
218	50266	1.33	8.67	4.67
219	50268	1.33	11.67	9.67
226	50015	2.33	6.00	6.00
251	80007	9.00	13.00	6.33
254	80019	6.67	11.67	12.67
255	80037	3.00	20.00	14.67
257	80055	6.00	8.00	7.67
262	80081	16.00	12.33	13.33
268	80093	15.00	20.67	9.67
273	80110	7.67	18.00	7.67
274	80111	21.33	12.33	10.33
275	80101	6.33	11.33	4.00
278	80119	10.33	9.00	7.67
279	80120	15.00	10.67	19.67
280	80191	2.67	8.67	8.00
281	80091	22.67	9.00	2.67
286	80088	2.33	12.67	8.67
287	80089	16.33	15.33	17.33
288	80090	16.33	4.33	4.00
291	80099	13.67	14.67	8.00
293	Cam. 1 (NZ)	6.33	7.33	16.67
294	Cam. 2 (NZ)	3.00	10.00	11.00
295	Cam. 3 (NZ)	6.33	12.67	8.33
296	Cam. 4 (NZ)	7.00	12.33	12.67
297	Cam. 5 (NZ)	5.00	3.67	2.00
308	RSA 7	14.33	17.67	14.67
315	RSA 38	3.33	15.33	12.33
318	RSA 42	12.67	9.67	9.00

Table 4. — **Mean squares for diameter, stem straightness and branch quality from the GLM analysis of the combined 73-family data set.**

Source	d.f.	Mean Square Diameter	prob. > f	Mean Square Stem str.	prob. > f	Mean Square Branch qual.	prob. > f
Family	72	22.28	0.0001	0.77	0.0001	1.16	0.0001
Site	2	730.73	0.0001	1.76	0.0001	6.44	0.0001
Family x site	144	4.77	0.002	0.25	0.0002	0.20	0.003
Rep (site)	9	12.89	0.0001	1.04	0.0001	0.98	0.0001
Error	569	3.34		0.16		0.14	

The deletion of the 8 (10%) most interactive families for each trait on the basis of mean rank deviations reduced the family x site interaction mean square for that trait. When eight interactive families for diameter and stem straightness respectively were deleted, the interaction mean-squares for these traits were reduced only slightly. In the case of diameter, however, the probability level p increased from 0.002 to 0.058; for straightness, p increased from 0.0002 to 0.052; and for branch quality, p increased from 0.003 to 0.285. While deletion of eight families reduced the interactions for diameter and straightness to a statistically non-significant level (at $\alpha =$ 0.05), it cannot be concluded that these interactions are definitely of no practical importance, although this importance is marginal. For branch quality, the interaction was reduced below a practically important level.

Values of family heritability for all traits were raised slightly when the eight most interactive families were deleted, by 0.04 for diameter, 0.08 for stem straightness, and 0.05 for branch quality (*Table 5*).

Shelbourne's Approximation

Ratios of interaction to family variance component (σ^2_{fs}/σ^2_f) for the complete combined data set were 0.244 for diameter, 0.521 for stem straightness and 0.180 for branch quality (*Table 5*). The differences between ratios suggest that in this set of families, stem straightness was the most sensitive trait to changes in site. These results differ from those of MATHESON and RAYMOND (1984), who found this ratio to be greatest for diameter and least for straightness in their study of 30 open-pollinated families. Only the ratio for stem straightness in this

Table 5. — **Variance components across sites for three assessed traits, for families (σ^2_f), interaction between families and sites (σ^2_{fs}), the ratio of σ^2_{fs}/σ^2_f, and family heritability estimates, for all 73 families and for data sets with apparently interactive families deleted.**

Trait (family set)	Parameter			
	σ^2_f	σ^2_{fs}	σ^2_{fs}/σ^2_f	h^2_f
Diameter (73 families)	1.625	0.396	0.244	0.79
Diameter (minus 8 fam. interactive for diameter)	1.849	0.221	0.120	0.83
Stem straightness (73 families)	0.048	0.025	0.521	0.68
Stem straightness (minus 8 families interactive for straightness)	0.059	0.011	0.186	0.76
Branch quality (73 families)	0.089	0.016	0.180	0.83
Branch quality (minus 8 families interactive for Branch quality)	0.103	0.003	0.029	0.88

Table 6. — **Estimated losses in potential genetic gain due to family x site interactions, for mass selection (C_I) and family selection (C_F), from sets of families of differing size.**

A. C_I values (%)

Data set	Trait		
	Diameter	Stem str.	Branch qual.
All (73) families	3.76	5.57	3.22
Minus 8 families interactive* for Diameter	2.05	5.30	3.06
Minus 8 families interactive for Stem str.	3.97	2.41	2.27
Minus 8 families interactive for Branch qual.	2.78	5.02	0.62

B. C_F values (%)

Data set	Trait		
	Diameter	Stem str.	Branch qual.
All (73) families	3.20	5.99	2.74
Minus 8 families interactive* for Diameter	1.67	5.76	2.25
Minus 8 families interactive for Stem str.	3.43	2.40	1.68
Minus 8 families interactive for Br. qual.	2.33	5.43	0.44

*) most interactive families based on mean rank deviation

study was above SHELBOURNE's (1972) proposed "serious" level of 0.5 (and then only slightly), suggesting that the interactions in these trials would not be of practical importance in the selection of families for the traits other than straightness.

Deletion of the eight most "interactive" families for straightness from the data set, on the basis of rank changes, reduced the ratio of σ^2_{fs}/σ^2_f for that trait to 0.186 (below the critical level). This resulted from a large reduction of the value of σ^2_{fs}, by 56%. There was also an accompanying smaller rise in the value of σ^2_f, of 23%, and an increase in family heritability of 0.08 (*Table 5*).

Loss of potential genetic gain from selection, due to interactions

Losses of potential genetic gain from individual tree selection (C_I) and family selection (C_F), calculated for the various combined data sets using equations 3 and 4, are shown in *table 6*. Values of C_I were slightly greater than those of C_F, except for stem straightness. The C_I and C_F values were generally lower than those of MATHESON and RAYMOND (1984) for the same traits, except straightness. This study included more families over fewer sites than MATHESON and RAYMOND used, although the range of site types was probably as wide.

The C_I values for the complete 73-family data set were 3.76%, 5.57% and 3.22%, for diameter, straightness and branch quality, respectively. These were above the value of 2% to 3% considered by MATHESON and RAYMOND (1984) to "provide grounds for concern" over interactions. Deletion of the eight families with the largest rank changes reduced the C_I values to 2.05%, 2.41% and 0.62% (*Table 6*). The values for diameter and straightness could still be considered to be of marginal concern.

C_F values for diameter and branch quality from the whole data set were 3.20% and 2.74%, below the level of concern of 5% suggested by MATHESON and RAYMOND (1984). The value for stem straightness (5.99%) was slightly above this level. Deleting eight families with the largest rank change for straightness reduced C_F to 2.40% (*Table 6*), well below the level of concern.

These results indicate that selection for generally-adapted populations, based on overall superiority for diameter or branch quality, could be carried out among these families without incurring practically significant losses in gain. If straightness were the main selection trait (which is unlikely in practice), serious reduction in potential gain could be avoided by deletion of a few (under 10%) highly interactive families.

A better approach to family selection, in the case of a trait showing a practically important level of interaction, would be to retain apparently interactive families showing superior mean performance across all sites. There is a danger that deletion of all families deemed to be highly interactive from a breeding programme catering for a range of sites could cause a reduction in overall genetic gain. In the present case, the interactive families 12038, 12236, 12351 and 80111 would probably be retained (if selection were for diameter), as would families 12197 and

Table 7. — **Estimates of genetic correlations (above diagonal) and family mean (phenotypic) correlations (below diagonal) for three traits across sites in the International Gene Pool Trials in New South Wales.**

	Trial site		
	Wee Jasper	Gurnang	Nundle
Diameter			
Wee Jasper	-	0.699	0.797
Gurnang	0.451	-	1.004
Nundle	0.572	0.664	-
Stem straightness			
Wee Jasper	-	0.622	0.646
Gurnang	0.396	-	0.777
Nundle	0.402	0.446	-
Branch quality			
Wee Jasper	-	0.949	0.810
Gurnang	0.690	-	0.776
Nundle	0.586	0.583	-

Table 8. — Predicted genetic gains per unit of selection intensity, with efficiency of selection of families expressed as a percentage (in brackets), for the traits diameter, stem straightness and branch quality, assuming selection at site x for planting at site y; efficiency of selection at site y for planting at site y assumed to be 100%.

Selection site (x)	Planting site (y)		
	Wee Jasper	Gurnang	Nundle
Diameter			
Wee Jasper	4.76 (100)	1.80 (76)	3.99 (78)
Gurnang	3.06 (64)	2.38 (100)	4.63 (90)
Nundle	3.89 (82)	2.66 (112)	5.13 (100)
Stem straightness			
Wee Jasper	0.187 (100)	0.072 (67)	0.101 (72)
Gurnang	0.107 (57)	0.106 (100)	0.112 (80)
Nundle	0.109 (58)	0.081 (76)	0.140 (100)
Branch quality			
Wee Jasper	0.212 (100)	0.187 (91)	0.175 (79)
Gurnang	0.209 (99)	0.205 (100)	0.174 (78)
Nundle	0.177 (84)	0.158 (77)	0.222 (100)

80093 (if selection were for straightness alone), as these had high family mean values across the sites.

Genetic correlations

Genetic correlations between trial sites based on family mean diameter, stem straightness and branch quality, calculated from equation 5, are shown in *Table 7*. The correlations for all traits were fairly high, ranging from 0.70 to 1.00 for diameter; 0.62 to 0.78 for straightness; and 0.78 to 0.95 for branch quality. These values indicate that differences in ranking between any two trial sites, in terms of growth or form of families, were not great, despite differences in soil parent material and rainfall. All three sites would thus be considered to belong in the same breeding zone if any of the traits were the main criterion for selection.

There is no widely accepted figure below which these types of genetic correlations are considered to be "low". Burdon (1977) notes, in an example for stem straightness, correlations of 0.57 and 0.35 between one site and each of two others as suggesting that the first site would be considered a separate breeding zone if straightness were the main criterion of selection. Johnson and Burdon (1990) reported correlations of 0.16 to 0.55 (mean 0.38) for stem volume between sites with pumice and clay soils in New Zealand, concluding that these values were evidence of marked family x site interaction and low enough to consider designating the clays as a separate breeding region, if selecting on volume.

Predicted genetic gains per unit of selection intensity (i), for selecting and planting families at different combinations of test sites (from Equation 6), are shown in *Table 8*. In the case of selection and planting at the same site, x = y and r_{Gxy} is assumed to be 1. Percentage efficiencies of selection of families on the different traits at one trial site for planting at a different site (from Equation 7) are also presented in *Table 8*.

Genetic gains were not predicted to be consistently greater from selecting at any one trial site, for any of the three traits. The greatest genetic gains would mostly occur from selection of families on a site similar to the proposed planting site. Calculated losses in genetic progress from the transfer of "outside" selections to most sites, in the case of diameter and branch quality, were generally low; efficiencies were mostly above 76%, and the lowest was 64% (*Table 8*). Due to lower genetic correlations for stem straightness, some quite large reductions in genetic gains were predicted from transferring selections for this trait between sites, with some efficiencies as low as 57% (Gurnang to Wee Jasper).

In practice, diameter is likely to be more important than form traits in selection of families for radiata pine breeding programmes, in New South Wales and elsewhere. Both the genetic correlations between trial sites for this trait, and the relative efficiencies of selecting at given sites for planting at other sites (mostly exceeding 75%), were sufficiently large that selecting families on diameter and breeding for adaptation across the range of sites as represented by these trials would be a viable strategy.

When considering the alternative option of regionalised breeding, aiming to utilise family x site interactions by selecting for specific adaptation, it is important to realise that it is not possible to exactly duplicate a selection site when planting later. Such duplication would be necessary to achieve 100% efficiency as calculated from genetic correlations between trial sites (Matheson and Cotterill, 1990); thus, the relative efficiencies in transferring selections across sites in the present trials may well be underestimated. If so, the option of regionalised breeding is even less attractive.

Conclusions

1. In these three trials, stem straightness was the trait for which family x site interactions were most likely to be of practical importance, and branch quality the least likely.

2. The results of the different analysis methods overall give little support to a strategy of regionalising breeding or production populations in New South Wales, developed from families selected for growth and form in these trials. Family rank changes and analyses of variance indicated considerable interactions in all traits, especially stem straightness. However, tests of the practical importance of these interactions, including Shelbourne's approximation and calculations of C_I and C_F factors, suggested that the interactions were of no importance, or only marginally so, for diameter and branch quality, but of more concern for straightness. Deletion of about 10% of the most interactive families on the basis of rank change would apparently reduce potential losses in genetic gain due to interactions to practically unimportant levels for all traits. In the process of deleting interactive families, one should not discard apparently unstable families with a superior mean performance over the range of test sites.

3. Although the genetic correlation analyses implied that the greatest gains would almost always result from selecting and replanting at the same site, calculated losses in genetic progress for the major selection trait (diameter)

from selecting and planting at different sites were generally small enough to suggest that selecting for a single, generally-adapted breeding or production population would be a better strategy than regionalising breeding operations on the basis of the major environmental characteristics of these trial sites.

4. No one trial site was superior for discriminating among families. All sites had fairly high family heritabilities for the three traits, and gave high rates of survival.

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Thanks are due to Dr. Peter Ades, Ms. Carolyn Raymond and Dr. Colin Matheson, who kindly reviewed earlier drafts of the article and suggested improvements; also to Dr. C. J. A. Shelbourne for providing seed for the trials, and to CSIRO Division of Forestry, who provided planting stock for the Wee Jasper trial.

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Anon., SAS Institute Inc. SAS/STAT^{TM} Guide for Personal Computers. Version 6 Edition. SAS Institute Inc., Cary, NC. 1028 pp. (1987). — Burdon, R. D.: Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. Silv. Genet. 26: 168—175 (1977). — Johnson, G. R. and Burdon, R. D.: Family-site interaction in *Pinus radiata:* implications for progeny testing strategy and regionalised breeding in New Zealand. Silv. Genet. 39: 55—62 (1990). — Johnson, I. G.: Performance of radiata pine families in the Shelbourne Gene Pool Trials in New South Wales. Forestry Comm. of N.S.W. Res. Paper 7. 31 pp. plus appendices. (1989). — Matheson, A. C. and Cotterill, P. P.: Utility of genotype x environment interactions. For. Ecol. Manage. 30: 159—174 (1990). — Matheson, A. C. and Raymond, C. A.: The impact of genotype x environment interactions on Australian *Pinus radiata* breeding programs. Aust. For. Res. 14: 11—25 (1984). — Pederick, L. A.: Family x site interactions in *Pinus radiata* in Victoria, Australia, and implications for breeding strategy. Silv. Genet. 39: 134—140 (1990). — Raymond, C. A. and Cotterill, P. P.: Methods of assessing crown form of *Pinus radiata*. Silv. Genet. 39: 67—71 (1990). — Shelbourne, C. J. A.: Genotype-environment interaction: its study and its implications in forest tree improvement. Proc. IUFRO Genetics-SABRAO Joint Symposia, Tokyo (1972). — Wright, J. W.: Introduction to Forest Genetics. Academic Press Inc., New York. 463 pp. (1976).

Buchbesprechungen

Die Verjüngungsentwicklung der Buche (Fagus silvatica L.). Bericht einer langfristigen Beobachtung im Solling. Schriften aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt, Band 97. Von A. Dohrenbusch. 1990. J. D. Sauerländer's Verlag, Frankfurt/Main. 70 Seiten mit 14 Abbildungen und 11 Tabellen. Kartoniert DM 19,—.

Als Fortsetzung und Ergänzung der 1985 von Dohrenbusch veröffentlichten Arbeit zu dem 1976 von Prof. Röhrig angelegten Versuch ist die vorliegende Schrift erschienen. Ziel des Versuchs war einerseits, die Wirkung verschiedener Bodenbearbeitungsformen, u. z. Scheibenegge (TTS 25), schwerer Scheibenpflug (Rome) und Grubberzinken (montiert am Frontpolterschild), zu untersuchen und andererseits die Entwicklung der Naturverjüngung zu verfolgen. Ergebnisse der ersten zehn Beobachtungsjahre werden dargestellt, wobei bodenkundliche Parameter, Samenmenge und -qualität, Überschirmungsgrad, Bodenvegetation, Pflanzendichte und weitere Einflüsse wie Überwinterung der Bucheckern und morphologische Pflanzenmerkmale in Betracht gezogen werden. Auch nach elf Jahren kann noch ein deutlich positiver Effekt der Bodenbearbeitung gezeigt werden, wobei zwischen den angewendeten Verfahren keine wesentlichen Unterschiede festzustellen sind.

Ergebnisse über Kombinationen der Bodenbearbeitung mit Kalkungsmaßnahmen wären aufschlußreich gewesen, sie sind bei der Versuchsanstellung jedoch unterblieben. Ein weiterer Nachteil ist, daß der Versuch nicht parallel auf anderen Standorten angelegt worden ist. So muß sich mit dem Hinweis begnügt werden, daß der gewählte Standort für viele andere repräsentativ ist. Dennoch liegt in der vorliegenden Arbeit ein besonderer Wert, der in der kontinuierlichen Beobachtung der Naturverjüngung liegt, die vom Samenfall über die ersten kritischen Jahre hinaus bis zum Alter elf reicht, wobei maßgebliche Faktoren, ob anthropogen beeinflußbar oder nicht, erfaßt und in Beziehung gesetzt werden. G. von Wühlisch (Großhansdorf)

Nachhaltswirtschaft. Der Schlüssel für Naturerhaltung und menschliches Überleben. Band 2 der “Schriften zur Organik”. Von R. Hennig. 1991. Verlag Braun und Behrmann, Quickborn. ISBN 3-927947-02-4. 112 Seiten. DM 16,—.

Mit dem Verbrauch nicht erneuerbarer Naturdünger läßt sich für einige von ihnen deren Erschöpfung in absehbarer Zukunft berechnen. Immer mehr ist die Menschheit daher auf regenerierende Pflanzen und Tiere angewiesen und schenkt der Selbsterhaltung dieser organischen Produkte zunehmend größere Aufmerksamkeit. Wenn auch die Nachhaltigkeit im Jagdwesen mehr oder weniger unterbewußt schon seit Jahrtausenden befolgt wurde, so ist sie doch zu einem bewußten Wirtschaftssystem erst in der planmäßigen Forstwirtschaft entwickelt worden. Grundgedanke der Nachhaltigkeit ist es, nur so viel nachwachsenden Rohstoffes zu ernten, wie nachwächst.

Neben einer ausführlichen Beschreibung des forstlichen Nachhaltsprinzips, wird dieses auch für alle erneuerbaren Naturgüter und für das ganze “Ökosystem Erde” definiert und erläutert sowie dessen Bedeutung anhand einiger gegenwärtig in der öffentlichen Diskussion befindlicher Beispiele (u. a. Tropenwald, Treibhauseffekt) dargestellt.

Der Autor zeigt, daß die Erhaltung unseres Lebensraumes nur dann auf Dauer möglich ist, wenn wir den Menschen und seine Kultur als funktionellen Bestandteil des Ökosystems Erde betrachten. Schutz und Nutzung dürfen keine Gegensätze sein — weder in der Naturschutz- noch in der Tropenwalddiskussion. Im Verlauf des Buches erfährt der Leser, daß im Umgang mit den natürlichen Gütern unserer Erde eine das Gesamtsystem berücksichtigende Nachhaltswirtschaft praktiziert werden muß.

Sowohl in seinen allgemein geistigen Leitlinien als auch in vielen Einzelheiten enthält dieses Buch zahlreiche zukunftsweisende Gedanken. Jedem, der sich für grundlegende Zukunftsfragen interessiert, bietet es eine Fülle von Anregungen.

M. Liesebach (Großhansdorf)

Farbatlas der Basidiomyceten. Color Atlas of Basidiomycetes. 9. Lieferung. Von M. Moser und W. Jülich unter Mitarbeit von C. Furrer-Ziogas. 1991. Gustav Fischer Verlag, Stuttgart, New York. ISBN 3-437-30652-9. XIII und 32 Seiten mit 140 farbigen Abbildungen. DM 98,—.

Die 9. Lieferung des Farbatlas der Basidiomyceten enthäl Gattungsdiagnosen für weitere 8 Gattungen und Farbtafeln mit 101 Pilzarten und Varietäten. Darunter ist eine weitere Abbildung der forstpathologisch bedeutenden Art *Heterobasidion annosum* sowie Tafeln für mehrere Holzfäulepilze aus der Ordnung *Aphyllophorales*. Somit sind inzwischen etwa 1000 Pilzarten abgebildet. Die Fotografien sind überwiegend gut, besonders die am natürlichen Standort aufgenommenen. Durch das umfangreiche, bei jeder Lieferung aktualisierte Gattungs- und Artenregister kann man den Farbatlas als sehr nützliche Hilfe bei der Pilzbestimmung verwenden.

B. R. Stephan (Großhansdorf)

Epidemics of Plant Diseases. Mathematical Analysis and Modeling. Ecological Studies, Volume 13. 2nd, completely revised edition. By J. Kranz (edited). 1990. Springer-Ver-