GENOTYPE × ENVIRONMENT INTERACTION AND OPTIMAL NUMBER OF PROGENY TEST SITES FOR IMPROVING *PINUS RADIATA* IN NEW ZEALAND*

S.D. CARSON

Forest Research Institute, Private Bag 3020,
Rotorua, New Zealand

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ABSTRACT

A progeny test of 25 parents mated in a series of five, five-parent, disconnected diallels was established on 11 sites chosen to represent all major site types for growing *Pinus radiata* D. Don in New Zealand. Statistical analysis of an assessment at age 9 years suggested that for diameter, the most important trait in the New Zealand tree improvement programme, genotype × environment interaction was important. However, genetic gains predicted for diameter for several regionalisation options, using multi-site index selection, suggested that regionalisation of seed orchards would increase the average genetic gain in diameter over all sites only slightly.

Further, many fewer than the full 11 sites were required for selection in order to capture essentially all of the predicted genetic gain for a national programme. Selection using the best site resulted in 90% of the maximum possible predicted gain, but the poorest site only 23%. Sites which were "very good" for selection had rapid growth, high phenotypic variance, and high repeatability of general combining ability (GCA) effects. Sites which were "very poor" for selection had slow growth, low variance, and low repeatability.

Keywords: genotype × environment interaction; progeny testing; selection index; predicted genetic gains; specific combining ability; heritability; breeding strategy; *Dothistroma pini*; *Cyclaneusma minus*; *Pinus radiata*.

INTRODUCTION

Choice of the number of breeding and/or seed production regions within a tree improvement programme should depend on the trade-off between relative costs and benefits of regionalising. Breeding regions have often been initially defined on the basis of differing soil, climatic, or topographical conditions, with the assumption that different sets of tree genotypes will perform best in these varying environments. Differential performance of genetic entities grown under differing environments is an expression of "genotype × environment interaction" (GE). If GE is quantified in designed trials, by comparing the performance of common seedlots in differing regions, informed decisions can be made about the appropriate number of breeding regions.

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If GE is very pronounced, then for the same expenditure of resources a regionalised tree improvement programme would result in greater realised gains than would a non-regionalised programme. In situations of extremely high GE, it may be appropriate to operate separate breeding populations in different regions. Less extreme GE may be handled by producing different commercial seed orchard "breeds" for different regions, with each regional breed comprising a different set of genotypes selected from a single, national, breeding population. If GE is not large, a non-regionalised programme could yield greater gains for the same expenditure of resources, because of the increased selection intensities possible in a larger breeding population of select parents, and reduced progeny testing and implementation costs relative to those required for regionalised programmes.

Costs of applied breeding programmes should always be evaluated against the potential gain from breeding. In discussing GE, Matheson & Raymond (1984) proposed that the loss of potential genetic gain be used as a criterion to assess the level of practical importance of interactions. They went on to say, "Every breeder must have a level of loss of potential gain which is regarded as serious." Burdon (1977) suggested "evaluating the expected genetic gains from the various possible options" for regionalising a breeding programme. These considerations guided this evaluation of GE.

It has been suggested that selection for growth rate and adaptation to particular regions in New Zealand is warranted (Shelbourne *et al.* 1987). This investigation set out to evaluate the importance of GE in improving *Pinus radiata* in New Zealand as reflected in a well-designed trial planted on 11 sites. The objective was to determine if GE is large enough to warrant a regionalised breeding and/or seed production programme with primary emphasis on the latter. GE was estimated for six important selection criteria on trees assessed at 11 sites which represented the important site types for growing *P. radiata* in New Zealand. Predicted genetic gains from several different selection strategies were calculated and compared for diameter growth, the most important selection criterion in the New Zealand *P. radiata* improvement programme.

The number of progeny tests required to represent a region can also be decided on the basis of the trade-off between relative costs and benefits of planting more tests. The optimum number of progeny tests required to attain a high genetic gain while minimising costs is an important consideration for any breeding programme. The high cost of progeny testing will usually place an upper limit on the number of test sites, while a lower limit will depend on the precision of breeding value estimates obtained at each site, risk of losing a test site, and the extent to which the site can be considered to represent the region. Equally important is to identify the particular test environments which give best resolution of genetic differences and, therefore, the most effective screening of progenies (Burdon 1977).

A second objective of this investigation was to examine the effect of varying the number and nature of progeny tests used for selection on genetic gain, in order to determine an optimum strategy for future progeny testing.

EXPERIMENTAL METHODS

Trials and Assessment

A series of trials was planted at 11 locations in 1975 for the purpose of evaluating GE. Test seedlings were from 25 parents ("850" series) which were selected for improved growth and

form in the 1950s from land-race stands in New Zealand. Parents were crossed in a series of five disconnected, modified, half-diallels (Griffing 1956). Seed was sown in Rotorua and Rangiora nurseries in January 1974 as five separate experiments for diallels one to five, and with four nursery replications of each diallel. Seedlings from the different nursery replicates were mixed during lifting, before allocation to field replications. Sites ranged from the northern part of the North Island to the southern part of the South Island (Fig. 1), represented a wide range of rainfall and temperature conditions (Table 1), and were selected to represent all major site "types" (Shelbourne *et al.* 1987).

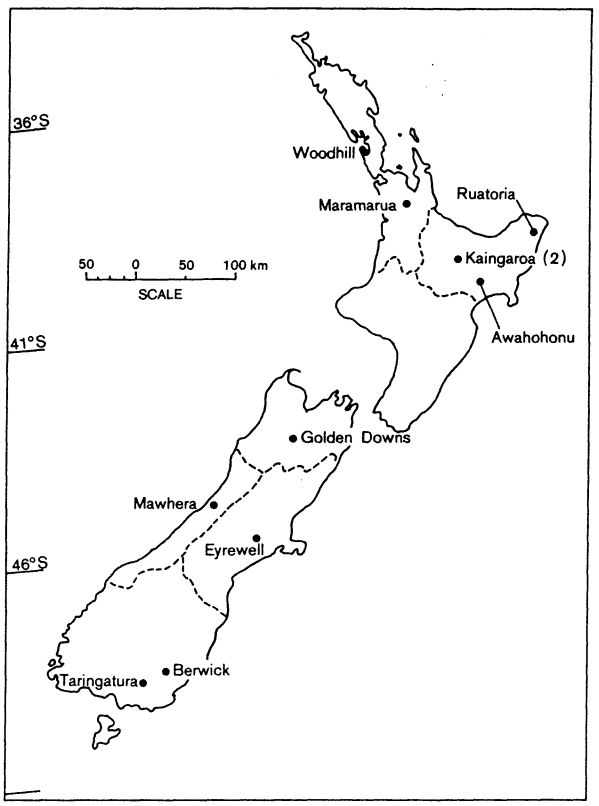

FIG. 1–Eleven sites included in the genotype × environment interaction study

Rotorua nursery supplied plant material for sites at Maramarua, Kaingaroa (Cpt 327 and 905), Awahohonu, Golden Downs, and Mawhera. Rangiora nursery supplied Woodhill, Ruatoria, Eyrewell, Berwick, and Taringatura. Six block replicates (reps) (each 0.7 ha) were planted at each site in 1975 at 5 × 5 m spacing, with each block replicate divided into five sub-blocks. Within each block replicate, each of the five diallels was randomly assigned to one of the sub-blocks. Five trees from each full-sib cross per diallel were randomised as single-tree plots within that diallel's sub-block. There were, therefore, 30 trees per full-sib cross and 120 trees per parent represented at each trial site.

Six traits were assessed at each site 9 years from planting, including:

- **diameter** in centimetres at 1.4 m height on the uphill side of the tree (dbh),

TABLE 1–Site latitude, rainfall, temperature, and diameter mean, repeatability, phenotypic variance, genetic (above diagonal) and phenotypic correlations of breeding values

	1 Woodhill	2 Maramarua	3 Ruatoria	4 Kaingaroa Cpt 327	5 Kaingaroa Cpt 905	6 Awahohonu	7 Golden Downs	8 Mawhera	9 Eyrewell	10 Berwick	11 Taringatura	All sites
Latitude	35°00′	37°15′	37°54′	38°30′	38°30′	39°10′	41°43′	42°27′	43°25′	45°58′	45°59′	
Mean annual rainfall (mm)*	1328	1263	1877	1483	1483	1756†	1307	1892‡	849	734	839§	
Mean annual temp. (°C)†	14.6	13.6	14.4	10.7	10.7	11.9†	10.5	11.3‡	11.0	10.3	10.1§	
Mean	21.3	16.9	20.6	25.7	23.6	23.6	15.4	19.3	12.4	9.8	16.7	18.7
Repeatability of half-sib family effects	0.79	0.31	0.46	0.82	0.64	0.81	0.43	0.50	0.25	0.01	0.56	0.75
Phenotypic variance of half-sib family effects	158	42	67	109	77	122	35	65	30	34	47	34
Site: 1	—	0.55	0.79	0.67	0.71	0.69	1.00	0.74	1.02	2.41	0.33	
2	0.27	—	–0.16	0.39	0.29	0.31	0.45	0.80	0.10	–3.46	0.48	
3	0.47	–0.06	—	0.93	1.04	0.97	1.14	0.82	1.42	5.89	0.88	
4	0.54	0.20	0.57	—	0.83	0.91	1.14	0.82	0.71	4.69	0.93	
5	0.51	0.13	0.56	0.60	—	0.93	0.94	1.22	0.96	3.68	0.52	
6	0.55	0.15	0.59	0.74	0.67	—	1.17	0.70	1.08	5.04	0.93	
7	0.58	0.16	0.51	0.68	0.50	0.70	—	0.59	1.39	5.69	1.09	
8	0.47	0.31	0.40	0.53	0.69	0.45	0.28	—	0.93	–0.22	0.33	
9	0.45	0.03	0.48	0.32	0.38	0.48	0.46	0.33	—	6.48	1.04	
10	0.24	–0.22	0.46	0.48	0.34	0.52	0.43	–0.02	0.37	—	6.28	
11	0.22	0.20	0.44	0.62	0.31	0.62	0.53	0.17	0.39	0.53	—	
Mean phenotypic correlation with all sites	0.43	0.12	0.44	0.53	0.47	0.55	0.48	0.36	0.37	0.31	0.40	
Relative importance of SCA	17%	19%	36%	12%	17%	6%	34%	28%	67%	98%	28%	

* From New Zealand Meteorological Service (1983).
† From Esk Station.
‡ From Totara Flat Station.
§ From Winton Station.

- **straightness** using a 1–9 subjective score where 1 = crooked, 9 = very straight,
- **branch habit** using a 1–9 subjective score where 1 = extremely uninodal, 9 = extremely multinodal,
- **malformation** using a 1–9 subjective score where
  9 = no malformation,
  8 = 1 ramicorn,
  7 = 2 ramicorns or 1 ramicorn intermediate in diameter between normal ramicorn and a fork,
  6 = 3 or more ramicorns or 1 severe plus one average ramicorn,
  5 = basket whorl with stem not deflected,
  4 = basket whorl with stem deflection up to half diameter,
  3 = basket whorl with stem deflection greater than diameter,
  2 = fork,
  1 = more than one fork,
- **Dothistroma needle blight** using a 1–9 scale reflecting the percentage of crown length infected where 1 = 10% infected, and 10 = 100% infected (two sites only),
- **needle retention** using a 1–6 scale reflecting the number of years' needles remaining on a branch at mid-crown (or above the level of Dothistroma infection) where 1 = about half of first-year needles retained, 6 = all first-, second-, and third-year needles retained (10 sites only).

Infection by *Dothistroma pini* Hulbary reduces growth in proportion to disease severity (van der Pas 1981). Needle retention is related to infection by *Cyclaneusma minus* (Butin) DiCosmo, Peredo & Minter (Gadgil 1984), and its effect on growth has also been demonstrated (van der Pas, Slater-Hayes, Gadgil & Bulman 1984).

Evaluation of Genotype × Environment Interaction

Arithmetic full-sib family (cross) means were calculated for each sub-block for each trait at each site. Separate analyses of variance were made for each diallel at each site using program DIALL (Schaffer & Usanis 1969) and following the linear model:

$$Y_{ijk} = \mu + b_k + g_i + g_j + s_{ij} + e_{ijk}$$

where Y_{ijk} is the mean score of the progeny of the i^{th} female and j^{th} male in the k^{th} block replicate; μ is the mean score for the diallel; b_k is the effect of the k^{th} replicate; g_i is the general combining ability (GCA) effect of the i^{th} female; g_j is the GCA effect of the j^{th} male: s_{ij} is the specific combining ability (SCA) of the cross between the i^{th} female and j^{th} male; and e_{ijk} represents an error effect (Wilcox 1982). Griffing's Method 4 (Model I), which assumes GCA and SCA effects are fixed, was followed for the estimation and testing of GCA and SCA effects (Griffing 1956) in each diallel. Parental breeding values at each site, defined as $BV_i = 2g_i + \mu$, were estimated as outlined by Snyder (1975).

Narrow-sense heritability (h^2), repeatability of half-sib family effects (h^2_{hs}), and phenotypic variance of individuals (σ^2_P) and of half-sib family effects ($\sigma^2_{P_{hs}}$) were estimated for each trait at each site as follows:

$$h^2 = \frac{4\sigma^2_{GCA}}{\sigma^2_P} = \frac{4\sigma^2_{GCA}}{\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_p + \sigma^2_w}, \text{ and}$$

$$h^2_{hs} = \frac{\sigma^2_{GCA}}{\sigma^2_{P_{hs}}} = \frac{\sigma^2_{GCA}}{\sigma^2_{GCA} + \sigma^2_{SCA} / 3 + \sigma^2_p / 18 + \sigma^2_w / 18H}$$

where σ^2_{GCA} = general combining ability variance,
σ^2_P = phenotypic variance of individuals,
$\sigma^2_{P_{hs}}$ = phenotypic variance of half-sib family effects,
σ^2_{SCA} = specific combining ability variance,
σ^2_p = variance due to interaction between full-sib families and block replicates,
σ^2_w = within sub-class variance, and
H = harmonic mean of number of trees within each subclass (which ranged from 2.4 to 4.2).

For the purpose of estimating GCA and SCA variance components, Griffing's Method 4 (Model II) was followed (Griffing 1956; Wilcox 1982). This entails no change to the method of calculating mean squares in the analysis of variance of each diallel, though their expected values are different to allow for the assumption that GCA and SCA effects are now random. Since the structures of the five diallels were compatible, sums of squares from the individual diallels were pooled to give an overall analysis, and estimates of GCA and SCA variance components based on all 50 full-sib crosses and all 25 parents.

An analysis of variance for each trait over all sites was carried out using PROC GLM in SAS (SAS Institute Inc. 1985) with the following model:

$$Y_{ijklm} = \mu + S_i + b(S)_{ij} + D_k + SD_{ik} + Db(S)_{ijk} + C(D)_{kl} + SC(D)_{ikl} + Cb(SD)_{ijkl} + e_{ijklm}$$

where Y_{ijklm} is the score of the m^{th} tree from the l^{th} full-sib family cross in the k^{th} diallel in the j^{th} block at the i^{th} site; μ is the mean score over all diallels and sites; S_i is the effect of the i^{th} site; $b(S)_{ij}$ is the effect of the j^{th} block at the i^{th} site; D_k is the effect of the k^{th} diallel; SD_{ik} is the effect of the k^{th} diallel at the i^{th} site; $Db(S)_{ijk}$ is the effect of the k^{th} diallel in the j^{th} block at the i^{th} site; $C(D)_{kl}$ is the effect of the l^{th} cross within the k^{th} diallel; $SC(D)_{ikl}$ is the effect of the l^{th} cross within the k^{th} diallel at the i^{th} site; $Cb(SD)_{ijkl}$ is the effect of the l^{th} cross within the k^{th} diallel in the j^{th} block at the i^{th} site; and e_{ijklm} represents an error effect. Variance components were calculated by equating estimated mean squares to their expectations as outlined by M.D.Wilcox (unpubl. data). Sums of squares for the first eight terms of the model were calculated using sub-block means. The sum of squares for the error term was calculated in separate analyses by treating all sub-blocks as separate treatments. The model provided direct tests and estimates of the variance of crosses within diallels ($\sigma^2_{C(D)}$) and the interaction variance of crosses × sites within diallels ($\sigma^2_{SC(D)}$). The ratio of the interaction variance of crosses × sites within diallels to the variance of crosses within diallels was calculated for each trait, as suggested by Shelbourne (1972).

For the purpose of estimating GCA and SCA variance components over all sites, each diallel was analysed over all locations using programme DIALL and following the linear model:

$$Y_{ijkm} = \mu + g_i + g_j + s_{ij} + S_m + b(S)_{km} + gS_{im} + gS_{jm} + sS_{ijm} + e_{ijkm}$$

where μ, g_i, g_j, and s_{ij} are defined as before; Y_{ijkl} is the mean score of the i^{th} female and the j^{th} male in the k^{th} block at the m^{th} site; S_m is the effect of the m^{th} site; $b(S)_{km}$ is the effect of

the k^{th} block at the m^{th} site; gS_{im} and gS_{jm} are interaction effects involving GCA and sites; and sS_{ijm} is the interaction effect between the SCA of the ij^{th} cross and the m^{th} site (Wilcox unpubl. data). Griffing's Method 4 (Model II) was again followed (Griffing 1956). Sums of squares from the individual diallels were again pooled to give an overall analysis and estimates of GCA, SCA, GCA × site interaction, and SCA × site interaction variance components based on all 50 full-sib families and all 25 parents over all sites. The ratio of GCA × site interaction variance to GCA variance was calculated (Shelbourne 1972).

Narrow sense heritability (h^2), repeatability of half-sib family effects (h^2_{hs}), and phenotypic variance of individuals (σ^2_P) and of half-sib family effects ($\sigma^2_{P_{hs}}$) were estimated for each trait over all sites as follows:

$$h^2 = \frac{4\sigma^2_{GCA}}{\sigma^2_P} = \frac{4\sigma^2_{GCA}}{\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{GCAxS} + \sigma^2_{SCAxS} + \sigma^2_p + \sigma^2_w}, \text{ and}$$

$$h^2_{hs} = \frac{\sigma^2_{GCA}}{\sigma^2_{P_{hs}}} = \frac{\sigma^2_{GCA}}{\sigma^2_{GCA} + \sigma^2_{SCA}/3 + \sigma^2_{GCAxS}/n + \sigma^2_{SCAxS}/3n + \sigma^2_p/18n + \sigma^2_w/18nH}$$

where σ^2_{GCA} = general combining ability variance estimated from all sites,
σ^2_P = phenotypic variance of individuals,
$\sigma^2_{P_{hs}}$ = phenotypic variance of half-sib family effects estimated from all sites,
σ^2_{SCA} = specific combining ability variance estimated from all sites,
σ^2_{GCAxS} = general combining ability by site interaction variance,
n = number of sites,
σ^2_{SCAxS} = specific combining ability by site interaction variance,
σ^2_p = variance due to interaction between full-sib families and block replicates estimated from all sites,
σ^2_w = within sub-class variance estimated from all sites, and
H = harmonic mean of number of trees within each sub-class over all sites.

Estimates of the relative importance of specific combining ability (R) (Baker 1978) were calculated both for each trait over all sites and for each trait at each site as

$$R = \sigma^2_{SCA} / (2\sigma^2_{GCA} + \sigma^2_{SCA}) \times 100\%.$$

Genetic correlations of diameters at different sites were approximated as follows (Burdon 1977):

$$r_G = \frac{r_P}{h_A \times h_B}$$

where r_G = genetic correlations of parental GCAs or GCA correlations for diameter from site A with site B (an approximation to additive genetic correlations),
r_P = correlation of parent breeding values from site A with site B,
h_A = square-root of repeatability of half-sib family effects for site A,
h_B = square-root of repeatability of half-sib family effects for site B.

This method can lead to genetic correlations greater than one, especially with exceptionally low repeatability estimates.

Predicted Gains from Different Selection Strategies

Predicted genetic gains from selection for increased dbh were calculated for several regionalisation options using genetic selection indices (Hazel 1943) adapting the method of Burdon (1979) whereby the expression of a trait at each site is handled as a separate index trait. The index was of the form

$$I = b_1 S_1 + b_2 S_2 + \ldots + b_{11} S_{11}$$

where S_1 to S_{11} are parent breeding values for dbh at sites 1 to 11, respectively, and b_1 to b_{11} are the corresponding index coefficients.

Programme RESI (Cotterill & Jackson 1981), which is based on equations presented by James (1968), was used to calculate all indices and predicted gains. A single selection intensity was chosen to approximate the operational selection of best parents in the New Zealand *P. radiata* improvement programme for use in control-pollinated clonal seed orchards, that is, a choice of 20 parents out of a breeding population of about 350.

In order to simulate the performance of a single, national, improved seed product, predicted gains in dbh at each site were compared for selection of one set of parents for New Zealand, using four alternative sets of economic weights. Economic weights for each site were either (1) one, (2) the reciprocal of the mean diameter of all trees at that site (in order to achieve the same percentage gain on all sites), (3) the proportional area of *P. radiata* plantations represented by the site as defined using data presented by Stewart & Burrows (1986) and I. R. Hunter (pers. comm.), or (4) reciprocal of the mean diameter of trees at the site multiplied by the proportional area of plantations represented by the site.

The effect of selecting different sets of seed orchard parents to produce improved seed for different forest regions was then modelled. Nine different regionalisation strategies were devised, using hypotheses of regional structure based on inspection of correlations of parental GCAs among sites for dbh, rank changes in breeding values over sites, and local knowledge about how *P. radiata* trees grow on New Zealand sites. For all of the nine regionalisation strategies, each of the 11 sites in the trial was allocated to hypothetical regions. For each of the nine strategies selection indices were used to calculate predicted gains for each hypothetical region. Information from all 11 sites was used in each index with economic weights of zero assigned to sites not in the designated region. This approach simulates selection using all information available, whether it be from within a region or from outside the region.

Best Sites for Selection

For either a national or a regionalised seed production programme, it is necessary to determine both the appropriate number and the location of progeny trials needed to achieve maximum genetic gains. To simulate the selection of one set of parents for countrywide use, predicted gains from every possible combination of selection sites were calculated using selection indices with Binet restrictions (Binet 1965; Cotterill & Jackson 1981). The Binet restriction placed on a site forces the coefficient in the index for that site (the b value) to be zero, allowing the predicted gain on that site to be calculated without using information from that site for selection (as would result from a national seed production programme that relies on progeny test data from a limited number of sites).

Selection indices were calculated using RESI with the Binet restriction to obtain average predicted gains over all sites from all possible combinations of one site, two sites, three sites, etc., up to 10 sites. The stand error of prediction was calculated for the average predicted gain over all sites from the index using data from 11 sites (White & Hodge 1989). For each possible number of progeny test sites (from 1 to 11), the mean overall gain and standard deviation for all possible site combinations were calculated and plotted. The number of times each site occurred in the four "best" combinations of sites and the four "worst" combinations of sites were counted for sets of one, two, three, four, and five sites used for selection. "Best" and "worst" were determined by having the highest and lowest overall gains, respectively.

RESULTS

Evaluation of Genotype × Environment Interaction

Results from analyses of variance suggested that GE interaction might be important for only two of the six traits assessed, dbh and needle retention. Although there were significant crosses × site interactions for all traits except Dothistroma infection (Table 2), the F statistics were not much greater than one (all but one were less than 2.0). These F statistics were tested with high degrees of freedom in the denominator (2404 for the analyses with data from 11 sites), with the result that even very small F statistics were significant in a statistical sense. For example, an F of 1.23 was highly significant for malformation. Further, there were

TABLE 2–Genetic parameters for six traits of *Pinus radiata* assessed on all sites at age 9

	Dbh	Straight-ness	Branch habit	Malfor-mation	Needle retention	Dothis-troma
	(cm)	(1–9)	(1–9)	(1–9)	(1–6)	(1–10)
Number of sites:	11	11	11	11	10*	2†
Crosses (diallels)						
$\sigma^2_{C(D)}$	48.91	0.153	0.264	0.032	0.031	0.156
F‡	7.27**	8.53**	12.32**	2.39**	5.84**	2.72**
Sites × Crosses (diallels)						
$\sigma^2_{SC(D)}$	37.91	0.044	0.081	0.046	0.034	0.023
F§	1.79**	1.25**	1.46**	1.23**	2.12**	1.14^{NS}
$\sigma^2_{SC(D)} / \sigma^2_{C(D)}$	0.78	0.29	0.31	1.45	1.09	0.15
Sites × GCA (diallels)						
$\sigma^2_{GCAxS} / \sigma^2_{GCA}$	0.70	0.26	0.24	0.79	0.86	0.57
Relative importance of SCA¶	22%	8%	3%	0%	4%	18%
Narrow-sense heritability and repeatability of half-sib family effects						
h^2	0.10	0.11	0.21	0.03	0.13	0.14
h^2_{hs}	0.75	0.88	0.93	0.76	0.85	0.58

** Statistically significant at $p \leq 0.01$.
* Berwick not included.
† Kaingaroa Cpt 905 and Mawhera.
‡ 45/450 d.f. for 11 sites.
§ 450/2404 d.f. for 11 sites.
¶ $\sigma^2_{SCA} / (2\sigma^2_{GCA} + \sigma^2_{SCA}) \times 100\%$.

heterogeneous variances among sites, which could well have been the source of the significant interaction, rather than rank changes. The ratio of the interaction variance of crosses × sites to the variance among crosses was less than 0.5 for straightness and branch habit, suggesting less important GE (Shelbourne 1972). GCA variance was much more important than SCA variance for all traits (Table 2). The ratio of GCA × site interaction variance to GCA variance was less than the ratio of the interaction variance of crosses × sites to the variance of crosses for every trait except Dothistroma infection, which was only slightly more than 0.5. Dothistroma infection was similar for the two sites on which it was measured, with an average of 30% and 34% of the needles infected and a similar range of cross means (Carson 1989). Cross means for malformation differed significantly on only two sites, and heritability of this trait over all sites was particularly low (0.03). Taken together, these results suggest that GE is not important in *P. radiata* in New Zealand for Dothistroma infection, straightness, branch habit, or malformation.

For dbh and needle retention, the F statistics for the crosses × site interaction and the ratio of the interaction variance to the variance among crosses were largest for the six traits (Table 2). Both dbh and needle retention are used as selection criteria for *P. radiata* in New Zealand, but dbh is always given greater emphasis than other traits, while needle retention is of indirect importance through an influence on later diameter growth. Extensive analysis of the practical importance of GE was, therefore, carried out for dbh.

The 11 sites of this trial produced a wide range of different growth rates for *P. radiata* families (Table 1). Mean dbh ranged from 9.8 cm at Berwick to 25.7 cm at Kaingaroa Forest, Cpt 327. The repeatability of half-sib family effects was highly correlated with mean dbh ($r=0.91$, $p \leq 0.001$). Phenotypic variance for dbh also ranged widely, from 30 to 158, and was largest on the sites with better growth. Diallels were not significantly different on any site. Over all 11 sites, the estimate of the repeatability of half-sib family effects for dbh was 0.75, which is high enough to indicate that selection of parents using breeding values calculated from this trial would be successful in achieving moderate to high average gains in dbh for the country as a whole. Selection using individual-site information for nationwide gains, however, would achieve varying success, since the estimated repeatability of half-sib family effects varied from a very low 0.01 to 0.82 for individual sites (Table 1).

No clear regional pattern of site combinations was apparent from inspection of the pair-wise correlations of breeding values (Table 1). There was no indication that nursery effects carried over in the between-site correlations. Phenotypic correlations between sites ranged from –0.22 to 0.82. The mean of the correlations of any one site with other sites was higher for some sites than others, ranging from 0.12 to 0.55 (Table 1), with each site exhibiting a fairly wide range of correlations with the other sites.

Inspection of rank changes of parent breeding values for dbh (details not shown) also failed to reveal a clear pattern favouring a regionalised strategy. There were large changes in ranks of some parents from site to site. For example, parent 120 ranked first at one site and twentieth at another, parent 55 ranked first or second at six sites yet ranked eighteenth at two sites, and parent 110 ranked first at two sites, yet last at another. Despite these large rank changes, however, no clear-cut site-to-site pattern emerged. There was no evident tendency for groups of parents to change rank together, but rather each parent tended to vary differently from site to site.

Predicted Gains from Different Selection Strategies

Predicted gain in dbh was affected very little by varying economic weights for different sites in the genetic selection index. Averaged gain over all sites for the four different sets of economic weights ranged from 2.10 cm (or 11.2%) to 2.15 cm (or 11.5%). Differences in predicted gain for the four different sets of economic weights on a single site were never more than 0.6 cm, and were almost always in the range 0.0–0.2 cm. Of the four types of economic weighting compared, the reciprocal of the site mean diameter was used for the remainder of the analyses.

Predicted overall gain in dbh did vary among the nine hypothesised regionalisation schemes (Table 3). The differences were, however, not very great even for the extreme case of comparing selection of one set of parents for the whole country (2.1 cm or 11.2% gain) with selection of 11 differing sets of parents for 11 regions (2.7 cm or 14.4% gain) (columns 1 & 2, Table 3). Differences in predicted gains from national *versus* regionalisation strategies involving only two or three regions were even smaller. The maximum predicted gain from selection strategies using either two or three regions was 2.4 cm or 12.8%. Both of these schemes involved at least one region represented by only one site, raising the question of whether within-region variation among sites was adequately represented and, therefore, whether predicted gains could be realised. The maximum gain from strategies using regions with two or more sites was 2.2 cm or 11.8%, which is only marginally greater than gains for a national strategy.

Best Sites for Selection

Both the number of progeny-test sites used for selection and the choice of specific sites influenced predicted genetic gains (Fig. 2). Far fewer than the full 11 sites were required for selection to capture essentially all of the predicted genetic gain. Some sets of two, three, or four sites yielded predicted gains very close (above 95%) to the maximum predicted gain obtained when using all 11 sites for selection. Even use of a random choice of five sites would result in a predicted gain of more than 80% of the maximum. The standard error of the prediction for gain using all 11 sites for selection was 32% of the predicted gain.

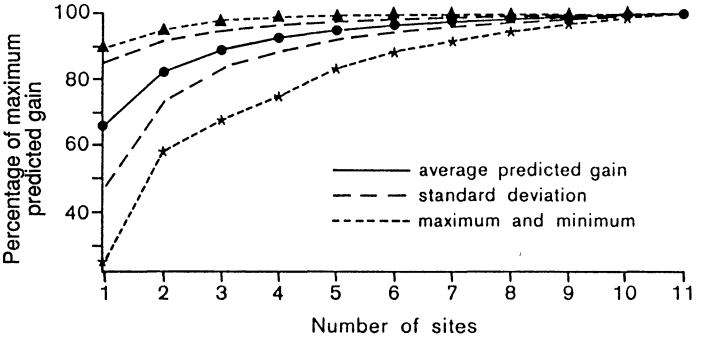

FIG. 2–Average predicted gain over 11 sites when different sites and different numbers of sites are used for selection of parents for improvement of diameter

TABLE 3–Gain in dbh (cm) predicted for nine different regionalisation schemes. Indices were constructed to represent selection of 20 out of 350 *Pinus radiata* parents for control-pollinated orchards.

Regionalisation scheme	1		2		3		4		5		6		7		8		9	
	Region	Gain	Region	Gain	Region	Gain	Region	Gain	Region	Gain	Region	Gain	Region	Gain	Region	Gain	Region	Gain
Woodhill	1	4.1	1	3.4	2	3.3	2	3.6	2	3.6	3	3.5	3	3.6	3	3.6	3	3.6
Maramarua	2	1.5	1	0.6	1	1.5	1	0.7	1	0.7	1	1.5	1	1.5	1	1.5	1	1.5
Ruatoria	3	2.4	1	2.1	2	2.2	2	2.2	1	2.0	3	2.2	3	2.2	3	2.2	2	2.0
Kaingaroa, Cpt 327	4	3.7	1	3.3	2	3.3	2	3.4	2	3.4	3	3.4	3	3.4	3	3.4	3	3.4
Kaingaroa, Cpt 905	5	2.9	1	2.3	2	2.3	2	2.5	2	2.5	3	2.5	3	2.6	3	2.5	3	2.5
Awahohonu	6	3.8	1	3.7	2	3.7	2	3.7	2	3.7	3	3.7	3	3.7	3	3.7	3	3.7
Golden Downs	7	2.0	1	1.8	2	1.8	2	1.7	2	1.7	3	1.8	3	1.7	3	1.7	3	1.7
Mawhera	8	2.9	1	2.0	2	2.0	1	2.1	1	2.1	3	1.9	3	2.0	2	2.1	2	2.0
Eyrewell	9	1.6	1	1.0	2	1.0	1	0.8	1	0.9	3	1.1	3	1.1	2	0.7	2	0.7
Berwick	10	2.6	1	1.6	2	1.6	1	2.1	1	2.0	2	2.6	2	2.4	2	2.2	2	2.1
Taringatura	11	2.2	1	1.5	2	1.6	1	1.3	1	1.4	3	1.6	2	1.4	2	1.4	2	1.5
No. regions in regionalisation scheme	11		1		2		2		2		3		3		3		3	
Av. gain over all sites		2.7		2.1		2.4		2.2		2.2		2.4		2.3		2.3		2.3

Some sites were consistently good for selection, while others were consistently poor. When Cpt 327 at Kaingaroa Forest was used alone for selection, predicted gains were 90% of the maximum possible predicted gain. Conversely, when Maramarua was used as the only selection site, gains were only 23% of the maximum possible. For selection indices using information from one to five sites, individual sites could be classified either as frequently being in sets of sites which had the highest predicted gains, or frequently being in sets of sites with the lowest predicted gains (Table 4). The sites which would be "very good" for selection (Woodhill, both sites within Kaingaroa Forest, and Awahohonu) had high phenotypic variances and high repeatabilities of family means, and the sites which would be "very poor" (Maramarua, Eyrewell, Berwick, and Taringatura) had low variances and low repeatabilities. Average correlations with other sites tended to be higher for the "very good" sites than for the "very poor" sites (Table 1).

TABLE 4–Number of times a site occurred in the best and worst sets of sites using 1 to 5 sites for selection

Site	4 best sets (highest predicted gain)	4 worst sets (lowest predicted gain)	Worth as selection site
Woodhill	12	0	Very good
Maramarua	0	13	Very poor
Ruatoria	1	5	Poor
Kaingaroa, Cpt 327	16	0	Very good
Kaingaroa, Cpt 905	9	0	Very good
Awahohonu	14	0	Very good
Golden Downs	2	1	Moderate
Mawhera	1	6	Poor
Eyrewell	3	13	Very poor
Berwick	1	14	Very poor
Taringatura	1	9	Very poor

DISCUSSION AND CONCLUSIONS

Importance of Genotype × Environment Interaction

The estimate of repeatability of half-sib family effects at the Berwick site was exceptionally low (0.01). A trial of 104 polycrossed families from the same selection series ("850" series) (C.J.A.Shelbourne unpubl. data) was planted adjacent to the Berwick site and had an estimate of family mean repeatability of 0.62. The Berwick site had many missing and damaged trees as a result of severe weather conditions and was partially thinned in error, so it was generally of very poor quality as a progeny trial. The estimate of the SCA variance was very high as compared with that of GCA variance (Table 1), probably a result of poor trial conditions rather than a real difference in importance of SCA at this site. The same applies to some extent to the Eyrewell site (estimated repeatability of half-sib family effects 0.25), which also had a polycross trial planted adjacent (estimated repeatability of family means 0.74). Phenotypic correlations of breeding values for these two sites with the other sites, however, were in a range similar to the other sites (Table 1) and to those calculated in other studies (Johnson & Burdon 1990; Shelbourne unpubl. data; Shelbourne & Low 1980), and so subsequent analyses and interpretations are thought to be valid.

The size of the GE interaction in *P. radiata* in New Zealand appears to be too small to warrant regionalised breeding populations. A tree improvement programme with regionalised breeding populations would by necessity have smaller breeding populations in each region, lower selection intensities, and, therefore, lower genetic gains than a national programme of the same size. However, even a regionalised selection programme (with a national breeding population) for seed production would be more expensive to operate than a non-regionalised programme for several reasons. Seed orchard land requirements would be somewhat greater, and operating costs proportionally higher. Additional records and extension efforts would be required to ensure that the appropriate regional breeds were planted in the specified regions.

Further, substantial additional costs arise from the progeny-testing phase. In the analysis presented here, progeny test size and selection intensities were assumed to be the same for each region in a regionalised programme as for a non-regionalised programme. In practice, regionalisation of seed production with fixed costs for progeny testing would reduce selection intensities and/or precision applied within each region, which in turn reduces the magnitude of predicted gain. In order to achieve a similar selection intensity to that for a non-regionalised programme, an overall bigger and more expensive progeny-testing or reselection programme would be required, since each potential seed orchard parent must be represented in a number of progeny tests in every region. The additional costs of progeny testing would need to be offset by substantial increases in genetic gain.

Given the data presented here, regionalisation of commercial seed production for the New Zealand *P. radiata* programme for the purpose of obtaining increased diameter growth would not be economically sound. A fully regionalised seed production programme, that is, one in which separate selections of seed orchard parents would be made for each of the 11 sites in the trial, did increase predictions of genetic gain across New Zealand from 11.2% to 14.4% of the mean dbh at age 9. Although this represents a fairly substantial increase in gain, it is probably not realisable, since genetic gains calculated from regions represented by one site cannot be considered to broadly apply to a whole region. The assumption that the site exactly represents the region (that is, that the phenotypic and genetic correlations with other sites within the region are one) is very unlikely to be met, especially in heterogeneous regions such as, for example, the phosphate-retentive soils in the Northland region. Even on sites as similar as are those on the volcanic pumice soils in the central North Island region (represented here by the two sites in Kaingaroa Forest and Awahohonu), phenotypic and genetic correlations are less than unity.

The gain estimate for "regions" represented by more than one site is probably a more realistic one. The small increase in predicted gain (0.1 cm, or 0.6% of mean dbh at age 9) probably does not outweigh the cost of regionalisation, and resources spent in other areas are likely to yield greater returns for the expenditure. The small increase in predicted genetic gain with regionalisation of this type suggests that for the sites represented the amount of "within region" GE is comparable with the overall New Zealand-wide GE for *P. radiata*.

Other studies of GE for diameter growth in *P. radiata* have reached a similar conclusion. Shelbourne & Low (1980) found that expected gains for three sites were only slightly less than those from selecting families specifically for each site. Another New Zealand study compared two sites from the phosphate-retentive clay soils in the Northland region (which includes the Maramarua site, the site this study suggested was the most different from the

others) with two sites on volcanic pumice soils in the central North Island region (Johnson & Burdon 1990). Although strong genetic correlations were observed between sites within each of the two regions and relatively weak correlations between sites in different regions, predicted genetic gains from regionalisation were still not sufficient for the authors to advocate regionalised seed production. Average gains over all four sites in the study were greater, however, when sites from both regions were used for selection. Although the data from the trial reported here suggest that the Maramarua site would be very poor for selection with its low repeatability and low phenotypic variance, this site had less than ideal progeny test conditions because of severe weed competition. It is possible that better quality progeny tests in the Northland clay region could raise the overall genetic gains in that region. However, this is likely to have only a small impact on raising the average genetic gain over all New Zealand, because the Northland clay region is relatively small and was the only region represented in this trial which appeared to behave in any way anomalously with respect to family rankings.

Results from studies of *P. radiata* in Australia suggested that GE may be of greater importance in Australia than in New Zealand (ratios of GE variance to family variance were higher) (Matheson & Raymond 1984), but did not include an analysis of predicted gains. Even so, the authors did not advocate a regionalised breeding programme and suggested instead that the most interactive parents be discarded. Discarding the most interactive parents, however, does not appear to be an ideal approach, because identification of the interactive parents requires a larger progeny-test programme for very little, if any, additional gain. In addition, the best parents overall can be the most interactive, as was apparent in the performance of parents reported here.

The index approach quantified the effects of GE in terms which were easily evaluated. Comparisons of predicted gains in diameter from regionalised *versus* non-regionalised seed production strategies allowed evaluation of the practical importance of GE. Even with some of the estimated genetic correlations in excess of unity, the majority of the indices did not have counter-intuitive negative weights. Using untransformed site variances allowed comparison of the magnitude of expected gains per site for different regionalisation strategies. Comparison of predicted genetic gains puts the effect of GE into realistic terms, rather than just abstract statistics.

Results for several other traits assessed in this trial also failed to support regionalisation due to GE. Statistics for Dothistroma infection, stem straightness, branch habit, and stem malformation indicated that there was substantially less GE in these traits than for stem diameter, suggesting that a regionalised programme would not result in much increased gain in these traits. GE has not been reported for needle retention before, but growth rate has been found to show more GE than tree-form traits in several New Zealand studies (Johnson & Burdon 1990; Shelbourne unpubl. data; Wilcox unpubl. data), but about the same low level of GE in another study (Shelbourne & Low 1980). GE for Dothistroma resistance was also small in another study involving different parents planted on different sites (Carson 1989).

Needle retention did appear from variance-component estimates to have as great a GE relative to GCA effects as dbh. Pathogenicity tests have shown that needle loss is associated with infection by *Cyclaneusma minus* (Gadgil 1984). Needle retention, however, appears to involve a complex set of variables rather than simply being closely related to the size of the fungus population and the suitability of climatic conditions for spore production and

dissemination (as with Dothistroma needle blight). On four pine species in the Pacific Northwest (not including *P. radiata*) *C. minus* has been identified as an endophytic fungus, that is, one which is commonly isolated from green needles (Carroll & Carroll 1978). Infection first occurs in *P. radiata* in New Zealand when needles are about 6 months old (Gadgil 1984). Needle-cast may occur when needles are about a year old or not until they are 20–21 months old. It is possible that when symptoms appear soon after infection, it is because the tree is under stress of some sort, rather than simply because the fungus has been able to infect a susceptible genotype. This stress might be related to different factors on different sites.

The New Zealand breeding programme should not at this point be regionalised for needle retention. Predicted genetic gains were not calculated for this trait, but would probably present a similar story to dbh. In addition, it may be that needle loss is related to different stresses on trees in different regions (for example, drought, wind, poor soil, cold climate). Resistance to each of these stresses can probably be identified with further research, but each is probably under different genetic control, that is, independently inherited. If this is the case, regional selection becomes more difficult and expensive because data from one region cannot be used to select trees in another region. Much more should be known about the biology of needle retention before a regionalised selection programme is considered for this trait.

Other Reasons for a Regionalised Programme

Results from this investigation suggest that regionalisation as a response to GE which is found in New Zealand would not be warranted. However, there may be other reasons for pursuing regionalised breeding and/or selection programmes. For example, the relatively higher cost of regionalisation could become warranted by higher gains if different sets of selection criteria are appropriate in different regions. One such example arises with internode length, which is expressed differently on some New Zealand sites. Average internode length varies as much with site as with genotype, and variance among families depends strongly on site (Carson & Inglis 1988). It might be desirable to include internode length as a selection criterion on the pumice plateau where there are larger differences among families. However, in Southland all trees tend to have long internodes and in Northland all trees tend to have short internodes, and so genetic gains in internode length would be much smaller. It might, therefore, be desirable to distinguish between long internode and short internode breeds for use on the pumice plateau, while concentrating on use of a single growth and form breed in Southland and Northland. Another example concerns the relative weighting of growth and tree-form traits in regions where tree form tends to be generally good, such as in the coastal sands (represented by the Woodhill site), compared with regions where tree form is highly variable and varies beyond the threshold of desirability.

Regionalisation of selection criteria might be warranted by higher gains if there are regional demands for different end products. If wood from a given region is used primarily in a pulp mill, selection criteria could be designed around requirements for that mill. In contrast, wood intended primarily for clearwood export markets might suggest a different set of selection criteria.

Regionalisation of selection criteria might also give significantly higher gains than a non-regionalised programme if there are specific problems on some sites. For example, Dothistroma needle blight is severe in roughly 10% of New Zealand's *P. radiata* forest (van der Pas, Bulman & Horgan 1984). In these areas major emphasis on selection for Dothistroma resistance in both seed production and breeding populations is desirable to maximise yield (Carson *et al.* 1991). In the other forests there is little impact from the disease, presumably because climatic conditions which have been identified as suboptimal for survival and reproduction of the causal agent (the fungus *Dothistroma pini*) (Gadgil 1977) prevail in these areas. Because gains in growth (the most important selection criterion) in the absence of the disease are reduced when resistance is included as an additional selection criterion (Carson 1989), it is desirable to place little emphasis on resistance to Dothistroma needle blight as a selection criterion both in seed production and breeding populations for sites where the disease has little or no impact.

Choice of Selection Sites

Comparisons of predicted gains for selection across the entire country, calculated from different numbers of sites and different sets of sites in genetic selection indices, suggest that for *P. radiata* in New Zealand sites can be classified as either "good" or "poor" selection sites. A few well-chosen selection sites could yield as much gain as many poorly chosen sites. Good selection sites were characterised by rapid growth, high repeatability of GCA effects, high phenotypic variance, and on average the highest correlations with other sites, while poor selection sites had low repeatability, small phenotypic variance, and the lowest correlations with other sites. Although this now appears to be intuitively obvious, before this analysis was done the poor sites often tended to be identified as those which indicated a need for regional seed production programmes, and they were therefore seen to be important progeny test sites.

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