Genotype-Environment Interaction in a Population of *Pinus elliottii* ENGELM. var. *elliottii*

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Summary

Five methods were used to investigate the importance of genotype-environment interaction in a progeny trial of *Pinus elliottii* ENGELM. established on 3 sites in Zimbabwe. Although statistically significant for many traits at 5, 8 and 15 years, genotype-environment interaction was judged by a number of criteria to be of little practical importance. Heritabilities were lowest at the site at which environmental conditions were nearest to optimum for the species; individual-tree phenotypic selection was more efficient at the 2 off-site plantings where heritabilities were higher. The lack of important genotype-environment interaction in this population of *P. elliottii* has implications for testing and deployment strategies.

Key words: genotype-environment interaction, *Pinus elliottii.*

FDC: 165.3; 165.5; 174.7 *Pinus elliottii.*

1. Introduction

The concept of genotype-environment interaction (*gei*) has been defined as the varying relative performance of genotypes with environment (BURDON, 1977). Judgements about the importance of *gei* in a breeding programme have profound consequences for testing and deployment strategies, and perhaps for the structure of breeding populations. Consequently, there is substantial literature on *gei* in pine species: for example, for *P. caribaea* MORELET (GIBSON, 1982; NIKLES, 1972; WOOLASTON *et al.,* 1990), *Pinus elliottii* ENGELM. (GODDARD and SMITH, 1969), *P. patula* SCHIEDE and DEPPE (BARNES *et al.,* 1992), *P. radiata* D. DON. (BURDON, 1977; JOHNSON and BURDON, 1990; MATHESON and RAYMOND, 1984; PEDERICK, 1990), and *P. taeda* L. (OWINO, 1977).

The issue of *gei* in tree breeding programmes and methodologies for its analysis have been reviewed by, amongst others, BURDON (1977), GIBSON (1982), MATHESON and COTTERILL (1990), MATHESON and RAYMOND (1984), RAYMOND and LINDGREN (1990), and SHELBOURNE (1972). Many of these papers draw from an extensive literature on the analysis of *gei* in agricultural crops (*eg,* CLARKE *et al.,* 1992; COX and SHELTON, 1992; FINLAY and WILKINSON, 1963; FREEMAN and PERKINS, 1971; ROBERTSON, 1959; SOUZA and SUNDERMAN, 1992), much of which has been directed to establishing whether interaction is present. However, as ROBERTSON (1959) commented, "these statistical statements do not specify whether any of this statistically significant interaction has any biological importance or whether the design was such that biologically important interactions would have been detected". MATHESON and RAYMOND's (1984) review distinguished between those analyses for which the primary objective was identification, and those which sought explanation of the interaction; only the former is of interest here.

Genetic tests of *P. elliottii* in Zimbabwe have been established across a range of environments, principally in the Eastern Highlands where commercial plantations are sited. However, some tests were established off-site, following proposals (*eg*

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Table 1. – Details of *Pinus elliottii* progeny tests.

Identification	Test		
	23a	23b	23c
Location	Tarka	Stapleford	Grasslands
Latitude	19° 59'S	18° 44'S	18° 10'S
Longitude	32° 56'E	32° 49'E	31° 30'E
Altitude (m)	967	1760	1646
Mean annual rainfall (mm)	2279	1836	884.7
Mean annual temperature	16.6°C	14.1°C	17.1°C
Soil type	Dolerite/quartzite-derived varying from reddish brown fine grained sandy loams to red brown clays.	Quartzite/dolerite-derived brown red clays.	Granite-derived greyish brown sandy loams.
Parental origin	Bulk commercial ex Georgia, Lousiana and South Carolina, USA, via South Africa.		
Mating design	Factorial 24♀ x 9♂	Factorial 23♀ x 9♂	Factorial 25♀ x 4♂
Environmental design	Randomized complete block	Randomized complete block	Randomized complete block
Plot size	10-tree line	10-tree line	10-tree line
Number of replications	6	6	6
Spacing	2.44 x 2.44 m	2.44 x 2.44 m	2.44 x 2.44 m

ALLARD, 1966; ANDERSEN *et al.,* 1974) that genotypic expression is amplified under conditions of environmental stress. This paper uses data from one progeny test series to investigate the practical significance of *gei* in the Zimbabwean breeding population of *P. elliottii.*

2. Genetic Material, Test Design and Assessment

The progeny tests from which data originate are part of a series established in January and February, 1976, by the Zimbabwe Forestry Commission. The 216 full-sib families represented in the tests derive from an incomplete factorial mating design involving 33 parents, which had been selected as superior phenotypes in unimproved plantations in Zimbabwe and South Africa. The tests are identified locally as 23a, 23b and 23c; relevant details are summarized in *table 1.* Tests 23a and 23b were established on typical low and high altitude sites, respectively, in Zimbabwe's Eastern Highlands; test 23c was planted on a less productive site in central Zimbabwe, too poor for the establishment of commercial plantations of *P. elliottii,* and one at which environmental stress would be expected. Analyses were restricted to the subset of 39 families common to all test environments, illustrated in *table 2.*

Table 2. – Parental representation in families common to the 3 *Pinus elliottii* progeny tests.

Females	Males				Total
	23	49	177	9	
58		x	x	x	3
76		x	x		2
126			x		1
128		x	x	x	3
174	x				1
175	x	x	x		3
200	x	x		x	3
43	x				1
57	x			x	2
125	x		x	x	3
132	x	x			2
172	x				1
173	x	x	x	x	4
176	x		x		2
86				x	1
88	x	x		x	3
89	x		x		2
203				x	1
224		x			1
Total	12	9	9	9	39

The tests were assessed for important production and quality traits at ages 5, 8 and 15 years, according to the procedures detailed by PSWARAYI *et al.* (1996).

3. Analytical Methodology

Five approaches were used to examine the extent and importance of *gei.* They represent only a sample of the variety of methodologies reported in the literature, and were selected because of their relevance to the particular objectives of this study. The methods applied are summarized in *table 3* and their application is explained below.

3.1. Variance components

Variance components were estimated by the Residual Maximum Likelihood (REML) methodology, as detailed by PSWARAYI *et al.* (in press). The linear model used for analysis across sites was:

$$Y_{ijklm} = \mu + F_i + M_j + FM_{ij} + S_l + R_k:S_l + FS_{il} + MS_{jl} + FMS_{ijl} + FMSRijkl + e_{ijklm} \quad (1)$$

where Y_{ijklm} = individual tree observation;
μ = population mean;
F_i = random effect of the i^{th} female;
M_j = fixed effect of the j^{th} male;
FM_{ij} = random effect of the ij^{th} family;
S_l = fixed effect of the l^{th} site;
$R_k:S_l$ = fixed effect of the k^{th} replicate within the l^{th} site;
FS_{il} = random effect of the i^{th} female x l^{th} site interaction;
MS_{jl} = random effect of the j^{th} male x l^{th} site interaction;
FMS_{ijl} = random effect of the ij^{th} family x l^{th} site interaction;
$FMSR_{ijlk}$ = random effect of the ij^{th} family x fixed effect of the k^{th} replicate within the l^{th} site interaction;
e_{ijklm} = residual error.

Assumptions of the model are that the levels of each random factor are uncorrelated, and normally distributed with a

Table 3. – Statistical methodologies used to investigate genotype-environment interaction.

Method	Key references	Advantages	Disadvantages
Estimation of variance components	Harville (1977) Patterson and Thompson (1971, 1975) Searle (1971, 1987)	Strength is dependent on the design but it is a general test of variation and it is robust in many respects.	Assumptions are not always met by data; when they do not hold the power of the test is reduced. Heterogeneity of variance may falsely signal significant interactions and, if interactions are found to be present, the test does not indicate whether they are of practical importance.
Ranks	Matheson and Raymond (1984)	Allows families to be compared and those that contribute most to the interaction, on the basis of rank changes, to be identified.	Sensitive only to rank changes, therefore the implications of a significant result should be considered carefully.
Spearman's rank correlation	Siegel and Castellan (1988) Snedecor and Cochran (1989)	Tests for a trend, ie, if there is a broad agreement between ranks. It has confidence limits and does not assume normal distribution.	As for ranks.
Genetic correlation	Burdon (1977) Falconer (1981) Robertson (1959)	The correlation is independent of whether environments represent a fixed or a random effect and is a quantitative measure of the importance of interaction.	Arbitrary definition of the values below which the correlation should fall before it is considered of practical importance; subject to usual difficulties of estimating genetic correlations (Robertson 1959).
Efficiency of selecting at one environment for planting on another	Burdon (1977) Matheson and Raymond (1984) Woolaston *et al* (1990)	Indication of the losses to be expected from gei. Easy to compute and the information obtained can be used for regionalisation.	Relies on accurate estimation of genetic parameters; arbitrary definition of values of practical importance.

common variance. Standard errors were calculated according to BECKER (1975). The proportion of total variance represented by each source of variation indicates their relative importance.

3.2. Ranks

Least square means of each family were ranked for each trait at each site, and the corresponding cross-site mean calculated as the arithmetic mean of single-site means. Absolute rank deviations from average across-site rankings were calculated as in MATHESON and RAYMOND (1984); the magnitude of rank changes across sites for each family suggest, on an arbitrary basis, those that are interactive – the greatest rank deviations identify the most interactive families. The following steps are involved in the process;

i. single- and cross-site means for the families are calculated for each trait and ranked;
ii. the rank deviations for each family are calculated by subtracting the ranking of each family at each site from the corresponding average cross-site ranking;
iii. absolute deviations were calculated as the sum of the absolute values of the ranks deviations at each site.

3.3. SPEARMAN's rank correlation

The hypothesis that there is no correlation between the ranks of any 2 pairs of ranks of family means for all combinations of the 3 sites was tested for significance at the 5% level. The assumptions required are minimal: both variables must be measured on at least an ordinal scale, so that the objects or individuals under study may be ranked in 2 ordered series (SIEGEL and CASTELLAN, 1988). A high correlation indicates that families perform similarly at both sites.

3.4. Genetic correlations

Genetic correlations between full-sib family performance at pairs of sites were estimated following the methodology presented by BURDON (1977). These "Type B" correlations were estimated as in equation (2):-

$$r_{G_{xy}} = \frac{r\,\bar{N}_{f_{xy}}}{(\sqrt{h^2_{fx}})\,(\sqrt{h^2_{fy}})} \qquad (2)$$

where r_{Gxy} = genetic correlation of family means of the traits x and y;

r_{Nfxy} = correlation of family means between trait x and trait y;

h^2_{fx}, h^2_{fy} = heritability of family means for traits x and y, respectively.

Family heritabilities were derived according to equation (3), following FALCONER (1981), from individual tree heritabilities estimated from maternal variances by PSWARAYI *et al.* (1996). Equation (3) is given by:

$$h^2_f = \frac{h^2\,(1+(n-1)\,r)}{(1+(n-1)\,t)} \qquad (3)$$

where h^2_f = heritability of family means for the relevant trait;

h^2 = the individual-tree heritability for the relevant trait;

n = number of individuals in each family (here, 60 at 5 years, and 30 at 8 and 15 years, due to the 50% thinning at age 8 years);

r = coefficient of relationship (assumed 0.50 for full sibs);

t = correlation of phenotypic values of members of the families.

Heritabilities estimated on an individual tree basis are listed in *table 4,* and phenotypic correlations in PSWARAYI *et al.* (1996). As the genetic correlation is based on full-sib family means, it could be biased by the particular sample of families represented (WHITE and HODGE, 1988). Here, the relatively large number of parents represented (23 maternal parents, *Table 1*) should mitigate against such a bias. It will also overestimate r_A, the correlation due only to additive genetic effects, but was used here as the best proxy for that value.

3.5. Efficiency of phenotypic selection

The efficiency of phenotypic selection at site x for planting at site y, relative to both selecting and planting at site y, was estimated following BURDON (1977). The estimates of efficiencies indicate the relative loss in gain from selection at one site for planting on another. Efficiencies of selection were calculated as in equation (4):-

$$E = \frac{r_{Gxy} h_x}{h_y} \qquad (4)$$

where E = the efficiency of phenotypic selection on a trait at site x for planting at environment y relative to both selecting at and planting at y, with the same intensity of selection at the 2 sites (ie $i_x = i_y$);

r_{Gxy} = the genetic correlation of full-sib family means, and;

h_x and h_y = are the square roots of the individual heritabilities for the traits under study at environments x and y, respectively.

The approximation of r_{Axy} by r_{Gxy} is a source of imprecision, but represents the best available estimate in the circumstances.

4. Results

Variance components resulting from the combined analysis of variance are presented in *table 4;* full details are available in PSWARAYI *et al.* (1996). All sources of variation were statistically significant (F-tests on REML approximate mean squares, $P < 0.05$) for all traits at all ages. The components of variance for the residual and for site together account for at least 70% of the variation for all traits at all ages. The female and male components are generally the next most important sources of variation. The magnitudes of family x site interactions are variable at all ages but generally smaller than those for all other sources of variation.

The mean values of family rank deviations for each trait are presented in *table 5,* as an indication of typical values. for these parameters. The values of SPEARMAN's rank correlation coefficient are also presented in *table 5*; these were significant ($P < 0.05$) in all cases.

Genetic correlations between family means for all traits at each pair of sites at the 3 ages are presented in *table 5.* Genetic correlations between family means across the 3 sites were consistently high for growth traits; correlations were generally lower and more variable for stem straightness than for growth traits. In the case of wood density, correlations were effectively (*ie* greater than) or actually unity. Estimates greater than unity could be modified, for example by the "bending" suggested by HAYES and HILL (1981) and applied to *P. elliottii* estimates by HODGE and WHITE (1992). Here, the simpler approximation of assuming they equalled unity was adopted.

Efficiencies of selection for each trait for all combinations of testing and planting sites are presented in *table 6.* In the case

Table 4. – Variance components and their standard errors estimated across the 3 progeny tests, and individual-tree narrow sense heritabilities (± standard errors) estimated from female components of variance.

Trait	Source									
	Site	Rep in Site	Female	Male	Fem x Male	Fem x Site	Male x Site	Fam x Site	Residual	h^2 ± s.e.
HT5	1.07±1.09	0.05±0.02	0.08±0.04	0.11±0.10	0.02±0.01	0.03±0.01	0.02±0.01	0.03±0.01	0.65±0.01	0.34 ±0.10
HT8	3.83±3.89	0.16±0.06	0.11±0.09	0.31±0.29	0.11±0.05	0.13±0.05	0.09±0.06	0.03±0.02	1.65±0.04	0.27 ±0.09
HT15	13.12±13.28	0.19±0.08	0.24±0.15	0.45±0.53	0.12±0.08	0.12±0.08	0.47±0.29	0.17±0.07	3.64±0.10	0.16 ± 0.08
DBH5	5.45±5.52	0.17±0.06	0.37±0.17	0.46±0.44	0.09±0.05	0.11±0.05	0.16±0.10	0.11±0.04	3.04±0.05	0.38±0.10
DBH8	6.57±6.73	0.19±0.09	0.42±0.28	1.45±1.40	0.31±0.16	0.29±0.14	0.56±0.33	0.13±0.09	6.83±0.18	0.30 ±0.09
DBH15	6.86±7.59	0.17±0.10	1.51±0.80	4.35±4.38	0.66±0.34	0.52±0.27	2.55±1.55	0.24±0.22	16.48±0.44	0.29 ± 0.10
VOL5	93.83±96.67	3.32±1.28	9.29±4.13	12.60±12.86	1.84±1.08	2.79±1.23	7.82±4.82	2.39±0.86	66.14±1.18	0.42 ± 0.11
VOL8	1163.3±1197	21.02±9.86	81.53±45.80	253.65±249.1	52.81±23.95	25.13±14.00	120.38±72.26	12.57±11.83	979.91±25.60	0.35 ± 0.10
VOL15	16826±17787	333.79±165.2	1853.5±903.9	4129.2±4446	684.04±345.9	587.75±283.6	3383.9±2025	185.07±219.0	18163.0±485.3	0.31 ± 0.10
STR5	0.06±0.06	0.02±0.01	0.01±0.01	0.04±0.03	0.01±0.01	0.02±0.01	0.01±0.01	0.01±0.01	0.49±0.01	0.12 ± 0.05
STR8	0.56±0.57	0.03±0.01	0.001±0.01	0.03±0.03	0.01±0.004	0.04±0.01	0.02±0.01	0.001±0.01	0.50±0.01	0.07 ± 0.06
STR15	0.0001±0.03	0.08±0.03	0.01±0.01	0.01±0.03	0.01±0.01	0.01±0.01	0.04±0.03	0.02±0.01	0.56±0.02	0.04 ± 0.04
DENS15	1117.7±1131	–	193.07±54.16	249.40±129.7	30.43±13.94	8.21±8.33	7.97±8.54	26.06±16.83	1913.6±35.37	0.36 ± 0.09

HTi: height at 5, 8 or 15 years (m); DBHi: diameter at 5, 8 or 15 years (cm); VOLi: volume at 5, 8 or 15 years (dm^3); STRi: stem straightness at 5, 8 or 15 years; (category 1 to 7 with 7 = straight) DENS15: density at 15 years ($kg\ m^{-3}$).

of growth traits at all ages, it is inefficient to select on site 23a for planting at the other sites, and almost invariably more efficient to select at site 23c for planting at site 23a. At 8 years, it would also be more efficient to select at site 23b for planting on site 23a. In the case of wood density, it is most efficient to select at site 23c for planting at the other sites and least efficient to select at site 23a for planting on sites 23b or 23c; selecting on site 23b for planting on site 23a is also more efficient than selection at site 23a. Consistent with the rank and correlation results reported above, there were few cases where selection for stem straightness would be more efficiently accomplished at a site other than that at which planting is to take place.

Table 5. – The mean sum of family absolute rank deviations, SPEARMAN's rank correlation coefficients and genetic correlations between family means for growth traits, stem straightness and wood density across the 3 sites at ages 5, 8 and 15 years.

Trait	Mean of family rank deviations	Rank correlation			Genetic correlation	
		Sites	23b	23c	23b	23c
HT5	9.5	**23a**	0.86	0.80	0.86	0.78
		23b		0.80		0.80
DBH5	9.3	**23a**	0.91	0.78	0.89	0.80
		23b		0.78		0.78
VOL5	8.9	**23a**	0.89	0.85	0.90	0.88
		23b		0.83		0.86
STR5	13.2	**23a**	0.81	0.55	0.80	0.58
		23b		0.59		0.64
HT8	10.8	**23a**	0.91	0.75	0.91	0.74
		23b		0.77		0.78
DBH8	8.5	**23a**	0.94	0.81	0.94	0.84
		23b		0.75		0.78
VOL8	8.5	**23a**	0.94	0.83	0.95	0.88
		23b		0.80		0.84
STR8	15.2	**23a**	0.55	0.43	0.60	0.42
		23b		0.65		0.61
HT15	11.5	**23a**	0.73	0.85	0.77	0.86
		23b		0.70		0.76
DBH15	8.2	**23a**	0.89	0.95	0.87	1.00
		23b		0.87		0.92
VOL15	8.3	**23a**	0.88	0.94	0.87	0.98
		23b		0.83		0.88
DENS15	6.1	**23a**	0.97	0.97	1.00	1.00
		23b		0.98		1.00
STR15	19.1	**23a**	0.23	0.54	0.21	0.64
		23b		0.39		0.48

Table 6. – Efficiencies of individual tree phenotypic selection for production and quality traits for all combinations of screening and planting sites at 5, 8 and 15 years.

		Selection site		
Trait	**Planting Site**	**23a**	**23b**	**23c**
HT5	23a		0.89	0.88
	23b	0.83		0.87
	23c	0.69	0.74	
DBH5	23a		1.04	1.00
	23b	0.76		0.84
	23c	0.64	0.73	
VOL5	23a		0.98	1.00
	23b	0.82		0.89
	23c	0.77	0.83	
STR5	23a		0.97	0.65
	23b	0.66		0.60
	23c	0.52	0.69	
HT8	23a		1.11	0.95
	23b	0.75		0.82
	23c	0.58	0.74	
DBH8	23a		1.07	1.05
	23b	0.83		0.86
	23c	0.68	0.71	
VOL8	23a		1.06	1.03
	23b	0.85		0.88
	23c	0.75	0.81	
STR8	23a		0.74	0.45
	23b	0.49		0.53
	23c	0.39	0.70	
HT15	23a		0.89	1.12
	23b	0.67		0.86
	23c	0.66	0.67	
DBH15	23a		0.94	1.16
	23b	0.81		0.99
	23c	0.86	0.85	
VOL15	23a		0.92	1.28
	23b	0.82		1.01
	23c	0.80	0.76	
DENS15	23a		1.16	1.25
	23b	0.86		1.07
	23c	0.80	0.93	
STR15	23a		0.23	0.74
	23b	0.19		0.50
	23c	0.55	0.46	

5. Discussion

A variety of responses has been proposed to address the challenge of *gei.* The first approach, illustrated by FINLAY and WILKINSON (1963) and MATHESON and RAYMOND (1984), is the identification of good general performers and their use across a wide range of sites; however, others (*eg* BURDON, 1992) have questioned the evidence for the existence of truly broadly-adapted genotypes. A second approach is to regionalize breeding populations, an option considered by KANOWSKI and NIKLES (1989) for *P. caribaea* in Queensland, Australia. However, as JOHNSON and BURDON (1990) and CARSON (1988) noted for the case of *P. radiata* in New Zealand, regionalization is costly and the additional expense may not be recouped by increased gains. A major difficulty in seeking to take advantage of *gei* is the difficulty of classifying sites as suitable for particular genotypes. MATHESON and COTTERILL (1990) and BORRALHO (1991) have both suggested that, in the case of most afforestation sites, small scale environmental variation limits our capacity to match genotypes to sites.

Although results of the analysis of variance here suggest that *gei* is statistically significant for all traits at all ages in these tests, the results of the other 4 analyses suggest that the interaction is generally of little practical importance. Some of the statistical significance is probably due to the presence of relatively few highly interactive families, as reported by MATHESON and RAYMOND (1984) for *P. radiata* in Australian tests; they suggested that such families may be particularly sensitive to specific site factors. Conversely, there are other families that appear stable across sites. Both relatively interactive and relatively stable families could be identified, arbitrarily, from the detailed table of family rank deviations, which is not presented here. Of the traits assessed, wood density appears to be least subject to *gei,* despite the statistical significance of the relevant terms in *table 4.* Elsewhere with industrial pines, little *gei* has been found for wood density in *P. elliottii* in the south-east USA (HAMILTON and HARRIS, 1965) or for *P. caribaea* (BARNES *et al.,* 1977) or *P. patula* (BARNES *et al.,* 1992) in Zimbabwe.

The apparently greater sensitivity of stem straightness to environmental differences may be real, or may be a consequence of the use of a standardised absolute assessment scale, and the relative difficulty of attempting to apply it across all sites. There has been considerable debate about the merits of standard versus site-specific scales for the assessment of stem straightness (see COTTERILL *et al.,* 1987; SHELBOURNE and NAMKOONG, 1966; HANS, 1972; MILLER, 1975; BARNES and GIBSON, 1986; KANOWSKI *et al.,* 1986; RAYMOND and COTTERILL, 1990). One of the major arguments advanced in favour of a single scoring system was that it would facilitate comparisons across sites. While this may be true in one sense (*i.e.* the average quality of sites is easily apparent), the restricted scale thus used on some sites (*e.g.* where trees are all relatively crooked or relatively straight), and the difficulty of maintaining standardization across sites, may limit the utility of these data in genetic analyses. Results reported by JOHNSON and BURDON (1990) and WOOLASTON *et al.* (1990), both of which were based on assessments of multi-site tests with site-specific, albeit consistently applied, straightness scales, suggests that site-specific scales are quite appropriate for the purposes of cross-site genetic analyses. Results of this study may well demonstrate the limitations of using a standard scale.

The values of genetic correlations between traits across sites are generally higher than those of SPEARMAN's rank correlations and are probably a more useful estimator of the practical significance of *gei.* As most genetic correlations exceed ROBERTSON's (1959) suggested (and arbitrary) threshold of 0.8, they also suggest that *gei* apears to be of little practical significance.

The efficiencies of selection are of greatest relevance to decisions on selection strategy. As detailed by BURDON (1977) and evident from equation (4), the efficiency of selection is determined by the magnitude of the correlation between traits across sites and of the heritability of the trait at the selection site. If heritability at one site is much greater than that at another, and there is a high genetic correlation, it will be more efficient to select in the environment at which heritability is greater. Here, the most efficient selection would be achieved by using different tests for selection of different traits; although the environment of test 23a represents the optimum conditions for commercial production, selection for performance there is generally more efficiently conducted at site 23c or 23b. It is of interest to note that, in the original search for plus trees, outstanding phenotypes were much easier to identify in plantations in the high altitude environment of test 23b than they were in the low altitude environment of test 23a where there was much greater tree to tree uniformity in the stands (BARNES, 1973; MULLIN *et al.,* 1978); there were no plantations in the environment of test 23c.

Given the absence of any *gei* of practical consequence, the greatest efficiency of phenotypic individual tree selection could be achieved through the establishment of progeny tests in the environment of test 23b. Results reported here are consistent with that observation, and with the suggestion (ALLARD, 1966; ANDERSON *et al.,* 1974) that genotypic expression is amplified under conditions of environmental stress. However, selection at site 23b could complicate breeding strategy because of the lack of pollen production under the lower summer temperatures experienced at the higher altitudes in that test environment (BARNES and MULLIN, 1974).

6. Conclusions

In terms of assessment of the importance of *gei,* the contrast between the results of the analysis of variance, which found *gei* to be significant for all traits, and those of the other 4 methodologies, which suggested this interaction to be of little practical importance, demonstrates the advantage of using more than one approach for the analyses of *gei.* The analysis of variance is a sensitive test if assumptions are not violated, but it fails to show whether *gei* is of practical importance. In this case, the statistically significant results may have been caused by lack of homogeneity in the family variance resulting from a few highly interactive families, or confounding of the family and family x site interaction effects resulting from the limited number of sites being used in the analysis (JOHNSON and BURDON, 1990).

The results of all 4 methods used to investigate the importance of the statistically significant *gei* were consistent in suggesting *gei* not to be of practical importance in the Zimbabwean *P. elliottii* breeding programme. In terms of the information generated by the different methods, the value of identifying interactive and stable families through ranking will depend on the breeding strategy adopted. BURDON's (1977) type-B genetic correlation seems more useful than SPEARMAN's rank correlation coefficient, particularly as the former also constitutes a step towards estimating the efficiencies of selection across sites. The efficiencies of selection provide information of practical value to breeders, through the identification of the site(s) at which selection might best be conducted.

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