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Relationships between some genetic parameters and test environments in open-pollinated families of *Pinus elliottii* in South Africa

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Summary. Growth traits, stem form and branch characteristics in three series of well-replicated trials, comprising open-pollinated families of *Pinus elliottii* Engelmann, were analysed to investigate whether the absolute value of the component of variance for family effect and its relative value (which is equivalent to one-quarter of heritability on individual values) were related, with trial averages of the traits studied taken as productivity indices of the sites tested. The first series, called the foreign selection series, consisted of four trials comprising open-pollinated families from single clones from a Florida seed orchard and from selected trees in Queensland, Australia. Two trials were established in the eastern Transvaal, at Tweefontein and Frankfort State Forests (SF), and two in Zululand, at Dukuduku and KwaMbonambi SF. The second series, called the Zululand selection series, consisted of open-pollinated families from single trees selected in Zululand that were compared in three trials: in the eastern Transvaal at Wilgeboom SF, in Zululand at Dukuduku SF and in the southern Cape at Lottering SF. The third series, called the South African selection series, consisted of open-pollinated families from single trees selected in the different forest areas of South Africa and compared in four trials: two trials in the eastern Transvaal at Tweefontein and Mariti SF and two in the Natal province at Dukuduku and Weza SF. Some positive and linear relationships between absolute sizes of the variance component for family and trial average for all traits studied, except stem form, were discernible for the foreign selections and for the Zululand selections. The South African selections presented a more erratic pattern of variation. However, when the origin of the genetic material was disregarded, the positive trends were undeniable. Curvilinear relationships between relative values and site averages were discernible, when the origin of the genetic material was disregarded. Further research is needed in order to confirm the suggested effect of site on genetic expressivity of open-pollinated families of slash pine grown in South Africa.

Key words: Open-pollinated progeny tests – Genetic variation – Genotype-by-environment interactions – Expressivity – Heritability

Introduction

Pinus elliottii Engelmann was first introduced in South Africa in 1916. Between 1918 and 1939, no less than 2.8 tons of seed were imported, most probably from southeastern Georgia (USA) (Poynton 1977). These introductions form the origin of the existing slash pine plantations, which covered about 144,000 ha in 1982, with a major concentration on the slopes and foothills of the Drakensberg escarpments of the eastern Transvaal and another second concentration in Zululand. Of all the pines planted in South Africa, slash pine is second only in importance to *Pinus patula* (Anon 1982). Pine breeding started in South Africa in 1958 with selection of plus trees in the existing plantations. At present, 964 plus trees of slash pine have been selected for lumber or pulp production and, of these, 474 have been or are being tested in progeny trials for the purpose of culling existing seed orchards and of selecting F_1 generation trees.

In this paper, I discuss the genetic variation detected in three series of open-pollinated family trials, repeated on a number of sites, to determine how the genetic parameters estimated in open-pollinated progeny trials are influenced by the genetic material itself and by the test sites where this material is growing.

Material and methods

Three series of trials were established to compare three series of selected parent trees (Fig. 1 and Table 1):

(1) The Zululand selection series, which comprised three trials of 133 open-pollinated families of trees selected in Zululand (Natal Province), repeated at three sites: at Wilgeboom, Dukuduku and Lottering State Forests (SF). A number of polycross families and a seed collection from normal production stands were also included in the trials.

(2) The foreign selection series was composed of the progeny of 50 open-pollinated parent trees selected in three plantations of Queensland (Australia), in each of 2 well-drained and poorly-drained sites, and collected in 1972–1975. The series also comprised progeny of 35 open-pollinated clones from a seed orchard of the University of Florida Co-operative Tree Breeding Programme, the seed having been collected in 1971–1973. In two Zululand trials (Dukuduku and KwaMbonambi SF), two controls were included, a *Pinus oocarpa* seed orchard seedlot and a *Pinus caribaea* var. *hondurensis* seed orchard seedlot. In the other two eastern Transvaal trials (Tweefontein and Frankfort SF), two seed orchard seedlots, a two-parent cross and a commercial collection were included as controls.

(3) The South African selection series. This series comprised the progeny of 17 open-pollinated parent trees selected in the Transvaal, of 9 from the Weza (Natal) area and of 32 trees from Zululand. Specific crosses, seed orchard seedlots and commercial collections were also used as genetic controls. All these were tested in four trials situated at Tweefontein, Mariti, Dukuduku and Weza SF.

The sites of all the trials of these series were chosen to represent the sites where *P. elliottii* is grown or could be grown, the latter case for Lottering.

The following traits were measured in these trials at 5 and 8 years: total height, with a graduated staff to the nearest 100 mm (symbolized HT); diameter at breast height to the nearest 5 mm (DBH); stem form according to a subjective scale with eight classes (STEM): class 1 = worst, class 8 = best.

Individual tree volume (VOL) was calculated using the following volume equation (N.C. Loveday, personal communication): Log VOL = −4.63703 + 1.93061 log (DBH) + 1.15669 log (HT).

Branch characteristics were quantified by measuring the diameter in millimeters, at a distance of 30 mm from the stem of the largest branch of the first and second whorl, which remain after pruning when trees reached a height of 3–4 m. The angle of the same branches to the nearest 5° was also measured. These pairs of measurements were averaged for each trait. The ratio of branch diameter to stem diameter was then calculated. The branch characteristics were only assessed at age 5 years for some trials of the first two series.

For the second series of trials, the problems of normality and homoscedasticity of the traits measured have been studied and reported elsewhere (Falkenhagen 1986). The variables analysed here were all fairly normally distributed and did not require any transformation.

For the calculation of heritabilities and variance components, a model using individual tree values was used. Single (individual) tree heritabilities have been calculated without correction for site or block effects.

In case of randomized complete block design, the following model was used:

$$Y_{ijk} = \mu + \tau_i + \beta_j + (\tau\beta)_{ij} + \varepsilon_{ijk}$$

Y_{ijk} : individual value of the k^{th} tree of the i^{th} family in the j^{th} block;

μ : general mean;

τ_i : effect of the i^{th} family;

β_j : effect of the j^{th} block;

$(\tau\beta)_{ij}$: effect of the interaction between the i^{th} family and the j^{th} block;

ε_{ijk} : sampling error.

In case of lattice design, the following model was used:

$$Y_{ijkl} = \mu + \tau_{ij} + \varrho_k + \beta_{i(k)} + (\tau_{ij}\beta_{i(k)}) + \varepsilon_{ijkl}$$

Y_{ijkl} : individual value of the l^{th} tree in the j^{th} family in the i^{t} block in the k^{th} replication;

μ : general mean;

τ_{ij} : effect of the j^{th} family in the i^{th} block;

ϱ_k : effect of the k^{th} replication;

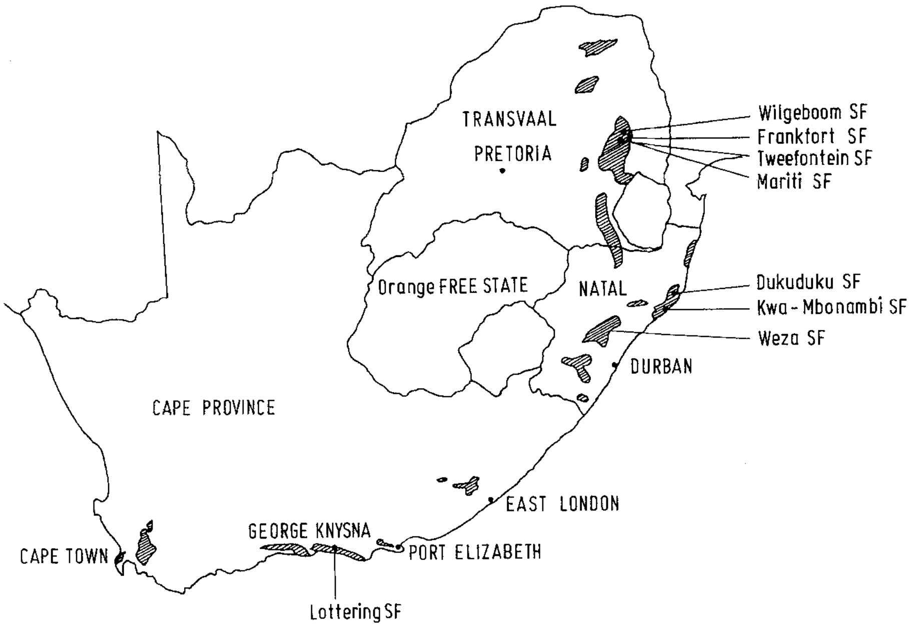

Fig. 1. Geographical localizatio of the trials studied. SF = Stat Forest

Table 1. Details on the slash pine trials analysed

Name	Location	Latitude (degrees min)	Longitude (degrees min)	Altitude (m)	Annual rainfall (mm)	Soil	Date planted	Total no. of families tested (excluding controls)	Design	Plot size	No. of replications	Remarks
Zululand selection series												
Wilgeboom I Wilgeboom II Wilgeboom III	Wilgeboom State Forest (E. Tvl.)	24 58 S	30 57 E	910	1,348	Deep uniform sandy clay	01/75	133	7 × 7 lattice 7 × 7 lattice 6 × 6 lattice	10 trees row plots	4 4 4	Planted on a clear-felling of old *P. patula* stand, slash burned. Partially balanced lattices with row plots parallel to contours of gentle slopes, each containing part of 133 progenies and controls
Dukuduku I Dukuduku II Dukuduku III	Dukuduku State Forest (Zululand)	28 21 S	32 15 E	60	950	Deep uniform coastal sands	09/75	133	Randomized complete block design	10 trees row plots	6 6 5	72 families including controls 56 families including controls 20 families including controls Planted in an old grazing field (firebreak)
Lottering	Lottering State Forest (S. Cape)	33 57 S	23 47 E	250	975	Heterogenous deep loam	04/75	121	11 × 11 lattice	5 trees row plots	6	Partially balanced lattice with one replication whose blocks have been planted in two separate sections. Three soil subtypes have been mapped within the trial. Most progenies are those of the Wilgeboom and Dukuduku trials
Foreign selection series												
Tweefontein	Tweefontein State Forest (E. Tvl.)	25 04 S	30 45 E	1,065	1,170	Heterogeneous shallow silty loam to silty clay loam	01/78	68	8 × 9 lattice	5 trees row plots	6	Planted on clear-felling of *P. taeda* stands, slash burned in two replications. Rectangular lattice, three subtypes of soil mapped with shallow rooting the rule. Heterogeneous soils
Frankfort	Frankfort State Forest (E. Tvl.)	25 03 S	30 50 E	950	1,247	Uniform sandy clay	02/78	68	8 × 9 lattice	6 trees row plots	3	Rectangular lattice. Planted on clear-felling of *P. patula* stands. Uniform soil throughout, although on a slope to the east
Dukuduku	Dukuduku State Forest (Zululand)	28 20 S	32 15 E	60	874	Deep uniform coastal sands	06/78	70	8 × 9 lattice	5 trees row plots	6	Rectangular lattice. Planted on clear-felling of *P. elliottii*; very uniform soil, level
KwaMbonambi	KwaMbonambi State Forest (Zululand)	28 40 S	32 09 E	60	1,553	Deep uniform coastal sand	07/78	70	8 × 9 lattice	5 trees row plants	3	Same as at Dukuduku but higher rainfall, more fertile area
South African selection series												
Tweefontein	Tweefontein State Forest (E. Tvl.)	25 03 S	30 47 E	1,152	1,100	–	02/80	45	7 × 7 lattice	6 trees row plots	5	Previous stand clear-felled *P. patula*
Mariti	Mariti State Forest (E. Tvl.)	24 54 S	30 54 E	1,004	1,556	–	02/80	52	7 × 8 lattice	6 trees row plots	6	Previous stand clear-felled *P. elliottii*
Dukuduku	Dukuduku State Forest (Zululand)	28 21 S	32 19 E	175	1,300	–	08/80	48	Randomized complete block design	6 trees row plots	6	Open grassland
Weza	Weza State Forest (Natal)	35 30 S	41 20 E	1,155	1,143	–	03/80	45	7 × 7 lattice	6 trees row plots	5	Open grassland

$\beta_{i(k)}$: effect of the i^{h} block within the k^{th} replication;
$\tau_{ij}\beta_{i(k)}$: effect of the interaction of the j^{th} family with the i^{th} block within the k^{th} replication;
ε_{ijkl} : residual error.

In both models, all effects were assumed to be random and distributed normally with the appropriate variance (random effect model or model II).

Variance components were estimated using the MIVQUEO method of the procedure VARCOMP of the SAS 1985 version of package of programmes (SAS 1985). There was no missing plot, and except for a few missing trees, the designs could all be considered as balanced.

The different components of variance, once estimated, were expressed as percentages of total variance. In other words, the different components of variances of the different effects were added to give the total variance, and each component was expressed as a percentage of the total variance. To obtain the heritability in a narrow sense, on individual tree basis, it is only necessary to multiply the percentage for family effect by four, if we accept that these families are composed only of half-sib progenies. The heritabilities so calculated are upper bounds of the true values (Namkoong 1966). The advantage of such an approach is that the relative effect of the different factors in the analysis of variance can be easily compared.

The trials of the foreign selections and of the Zululand selections were also used to calculate the genetic and phenotypic correlations between the traits studied. The relationships between site characteristics and these correlations are reported in Falkenhagen (1989). In order to calculate the standard deviation of the genetic correlations, the sampling error of the component of variance in absolute value and of the heritability of each trait were calculated for these two series of trials as follows.

The sampling variance of the family component of variance was estimated by using the following formula (Anderson and Bancroft 1952, p. 321):

$$S^2_{s^2_{\mathrm{Fam}}} = (\Sigma_i\ V_i^2/f_i + 2)\,2/c^2$$

c is the coefficient of the variance component;
V_i is the mean square used to calculate the component and f_i is the number of degrees of freedom corresponding to V_i.
S^2_{Fam} = estimator of the component of variance for family effect.
c was estimated using the value obtained in the expectation of the mean squares generated by the procedure GLM of the SAS package of programmes (SAS 1985).

For the Lottering trial, the procedure GLM was unable to estimate the expectations of the mean squares, because of the enormous amount of data involved, and sampling error has not been calculated.

The standard error of the heritability was obtained by using the following formula:

$$S_{h^2} = 4(S^2_{s^2_{\mathrm{Fam}}})^{1/2}/S^2_{\mathrm{TOTAL}}$$

S^2_{TOTAL} = sum of all the components of variance entering into the calculation of the heritability and h^2 is the heritability on a single tree basis (Becker 1967).

The standard error of the relative value is a quarter of that of the heritability.

In order to investigate whether there is any relationship between absolute and relative values of the family component of variance and testing sites, these values were plotted against the trial averages of the traits taken as an index of productivity of the sites at age of measurements.

Because the absolute and relative values of the family component of variance are not distributed normally, no attempt was made to use regression techniques to quantify the relationships with site fertility. Variance component estimators that are linear functions of mean squares have unknown distributions, although sampling variances can be derived (Searle 1971).

In order to determine whether soil heterogeneity within testing site might have masked any family variation, an extensive soil survey of the trials of the Zululand selection series was done. The Lottering, Wilgeboom and Dukuduku trials were intensively surveyed for soil heterogeneity. Observations were made using a soil auger on a grid system with observation density of one observation every 25 m.

In view of the intricate pattern of soil variation at Lottering, it was decided to study the influence of the three types of soil on the growth of the families. The detailed analysis was done using the 5-year data. The plots of the field design were classified according to soil type, and one-way analyses of variance were done with soil as unique factor: in the first analyses, any family was included; in the second analyses, only the families which appeared simultaneously in the three soils were included; and in the third case, only soil units I and II were compared by using only the families occuring in soil unit I and II.

Results

All the traits studied at age 5 years at all the trials, except those in the Zululand selections at the Lottering trial, showed at least significant differences among the families tested, and most traits showed large replication by family interactions. Site-by-family interactions were never significant and were negligible compared to site effect (Falkenhagen 1987). At age 8 years, all traits in the Zululand selections showed at least significant differences.

Although there is no statistically significant change in ranking of the genotypes over different sites, the relative differences between the genotypes may change. Both in relative and absolute values, the components of variance for family changed with sites for all traits.

Table 2 shows the absolute values and the relative values, in percentage of total variance, of the components of variance for family effect for height (HT), diameter at breast height (DBH), average volume per tree (VOL) and stem form at age 5 and 8 years, as well as the trial averages of these traits for the Zululand selection series. Tables 3 and 4 show the equivalent values for the foreign and South African series respectively. Tables 2 and 3 also show the standard deviation of the absolute and relative values of the component of variance for family effects.

Figures 2–5 show the global relationships between the absolute value of the components of variance for family effect and the average trial values for HT, DBH, VOL and stem form at age 5 years for the three selection series. It can be seen that the more fertile the site, the larger the component of variance for family, except in the case of stem form. For the South African selection series, the relationships are hardly discernible if taken in isolation. Because of the way analyses of variance are calculated, the absolute value of a component of variance is independent from the other components when the data are balanced. From a biological point of view, one hy-

Table 2. Absolute values and relative values of the components of variance for family effect in percentage of total variability and trial averages for different traits at Lottering, Wilgeboom and Dukuduku SF, on an individual tree basis. Zululand selections at 5 and 8 years of age. The standard deviation of the values is also indicated

Trait	Lottering*		Wilgeboom I		Wilgeboom II		Wilgeboom III	
	5 years	8 years	5 years	8 years	5 years	8 years	5 years	8 years
Absolute values of the components of variance for family effect and standard deviation								
HT	0.00185	0.5308	0.08504±0.027	0.16173±0.048	0.089456±0.023	0.10718±0.044	0.05761±0.02	0.09375±0.038
DBH	0.00000	0.13366	0.10235±0.073	0.33929±0.15	0.37065±0.098	0.62834±0.19	0.21515±0.073	0.42758±0.20
VOL	0.00000	0.00001064	0.0000875±0.0000038	0.0000912±0.00003	0.00002294±0.00001	0.0001481±0.00005	0.00000987±0.0000034	0.0000905±0.00004
STEM	0.00580	0.01650	0.28424±0.0099	0.044506±0.015	0.0506120±0.014	0.04159±0.016	0.020393±0.008	0.005824±0.018
Trial averages and their standard deviation								
HT (m)	5.0±0.2	8.6±1.2	7.6±0.3	12.0±1.2	7.9±0.3	12.0±1.2	7.4±0.3	11.4±1.1
DBH (mm)	88±3	148±24	128±5	180±24	132±7	183±22	125±6	172±22
VOL (m^3)	0.010±0.004	0.053±0.021	0.034±0.012	0.112±0.03	0.038±0.005	0.114±0.03	0.032±0.004	0.100±0.03
STEM	3.8±0.2	5.9±0.8	4.9±0.2	5.5±0.8	4.2±0.3	5.5±0.8	4.3±0.2	5.5±0.7
Relative values (%) of the components of variance for family effect and standard deviation								
HT	0.4	3.6	9.8±3.0	11.0±3.2	10.9±2.8	7.2±3.0	7.4±2.5	7.3±3.0
DBH	0.0	2.1	2.8±2.0	6.3±2.8	11.1±3.0	12.2±3.8	6.3±2.0	8.5±4.0
VOL	0.0	2.4	6.0±2.5	7.4±2.8	13.4±3.5	12.1±3.8	7.2±2.5	9.2±4.0
STEM	1.5	2.2	3.8±1.2	7.2±2.5	7.9±2.2	6.6±2.5	4.5±1.8	11.0±3.2

Trait	Dukuduku I		Dukuduku II		Dukuduku III	
	5 years	8 years	5 years	8 years	5 years	8 years
HT	0.047626±0.011	0.07483±0.018	0.05816±0.014	0.09286±0.022	0.03173±0.015	0.06799±0.30
DBH	0.18188±0.044	0.31212±0.066	0.19516±0.047	0.25465±0.063	0.18174±0.074	0.30991±0.13
VOL	0.0000422±0.000001	0.0000256±0.00001	0.00000380±0.00000080	0.00000199±0.00000048	0.0000175±0.000009	0.0000149±0.000010
STEM	0.018163±0.0088	0.0000±0.00035	0.011481±0.0065	0.001741±0.0010	0.030048±0.022	0.01416±0.0072
Trial averages and their standard deviation						
HT (m)	6.1±0.3	9.2±0.8	6.0±0.3	9.2±0.8	5.6±0.2	8.5±0.8
DBH (mm)	106±5	133±14	103±3	132±15	90±5	124±15
VOL (m^3)	0.018±0.006	0.045±0.01	0.018±0.006	0.045±0.01	0.012±0.004	0.036±0.01
STEM	6.1±0.2	6.0±0.2	6.3±0.2	6.1±0.3	6.3±0.2	6.4±0.5
Relative values (%) of the components of variance for family effect and standard deviation						
HT	11.6±2.8	10.9±2.8	12.3±3.0	14.5±3.5	8.4±4.0	11.4±5.0
DBH	10.9±2.5	15.1±3.0	9.6±2.2	11.4±2.8	12.0±4.8	13.8±5.5
VOL	13.1±4.2	16.8±3.5	10.2±2.5	12.2±3.0	9.9±4.2	11.8±5.0
STEM	2.6±1.2	0.0±0.5	1.8±1.0	1.8±1.0	3.5±2.5	5.9±3.0

* Standard deviation not estimated

Table 3. Absolute values and relative values of the components of variance for family effect in percentage of total variability and trial averages for different traits at Tweefontein, Frankfort, Dukuduku and KwaMbonambi SF on an individual tree basis. Foreign selections at age 5 years. The standard deviation of the values is also indicated

Tweefontein SF					Frankfort SF						
Components of variance for	HT (m)	DBH (mm)	VOL (m^3)	STEM	HT (m)	DBH (mm)	VOL (m^3)	STEM	Average branch diameter (mm)	Average branch angle (degrees)	Branch diameter to stem diameter ratio
Absolute value and standard deviation	0.0666 ± 0.018	0.2962 ± 0.083	0.00001328 ± 0.0000032	0.06303 ± 0.016	0.0733 ± 0.024	0.222 ± 0.064	0.00000685 ± 0.000001	0.0719 ± 0.024	1.3317 ± 0.80	13.8037 ± 3.82	0.02708 ± 0.00011
Relative value (%) and standard diviation	7.1 ± 1.9	6.9 ± 1.9	7.9 ± 2.1	11.0 ± 2.8	9.4 ± 3.0	9.1 ± 2.5	12.3 ± 4.0	8.7 ± 2.8	3.6 ± 2.2	11.7 ± 3.2	6.8 ± 2.8
Trial average and standard deviation	6.9 ± 0.3	127 ± 7	0.0309 ± 0.0128	4.7 ± 0.3	6.3 ± 0.4	110 ± 6	0.0206 ± 0.007	5.1 ± 0.4	24.5 ± 1.9	67.7 ± 4.5	0.25 ± 0.002

Dukuduku SF							KwaMbonambi SF						
HT (m)	DBH (mm)	VOL (m^3)	STEM	Average branch diameter (mm)	Average branch angle (degrees)	Branch diameter to stem diameter ratio	HT (m)	DBH (mm)	VOL (m^3)	STEM	Average branch diameter (mm)	Average branch angle (degrees)	Branch diameter to stem diameter ratio
0.0144 ± 0.010	0.0702 ± 0.044	0.00000034 ± 0.00000021	0.0308 ± 0.014	0.7585 ± 0.28	3.5434 ± 1.41	0.00968 ± 0.0063	0.0154 ± 0.0093	0.1346 ± 0.053	0.00000047 ± 0.00000015	0.05592 ± 0.0245	0.6449 ± 0.42	4.7831 ± 3.44	0.01328 ± 0.00843
1.4 ± 1.0	1.6 ± 1.0	1.5 ± 1.0	3.5 ± 2.5	3.4 ± 2.2	3.0 ± 2.2	1.8 ± 2.2	4.3 ± 2.5	7.3 ± 3.3	7.5 ± 3.1	7.5 ± 3.6	4.3 ± 3.3	3.5 ± 3.0	3.3 ± 2.8
4.1 ± 0.3	67 ± 6	0.0058 ± 0.0012	6.3 ± 0.3	16.0 ± 1.4	68.0 ± 3.0	0.26 ± 0.002	4.1 ± 0.2	67 ± 5	0.0051 ± 0.0009	6.1 ± 0.4	17.9 ± 1.4	64.1 ± 4.1	0.28 ± 0.002

Table 4. Absolute values and relative values of the components of variance for family effect in percentage of total variability and trial averages for different traits at Tweefontein, Mariti, Dukuduku and Weza SF. South African selections at age 5 years

	Trials											
	Tweefontein SF			Mariti SF			Dukuduku SF			Weza SF		
Traits	Trial average	Absolute value	Relative value (%)	Trial average	Absolute value	Relative value (%)	Trial average	Absolute value	Relative value (%)	Trial average	Absolute value	Relative value (%)
HT (m)	5.7	0.0788	11.8	7.3	0.0725	6.0	5.8	0.1355	15.5	5.4	0.04815	9.1
DBH (mm)	106.0	0.3179	12.1	124.0	0.3598	9.2	103.0	0.4312	14.0	116.0	0.1507	6.8
VOL (m^3)	0.018	0.00000643	12.2	0.031	0.0000142	9.6	0.017	0.00000920	14.5	0.019	0.00000341	7.9
STEM	4.0	0.1472	6.2	4.4	0.1827	7.5	5.6	0.005330	0.7	4.5	0.08785	6.8

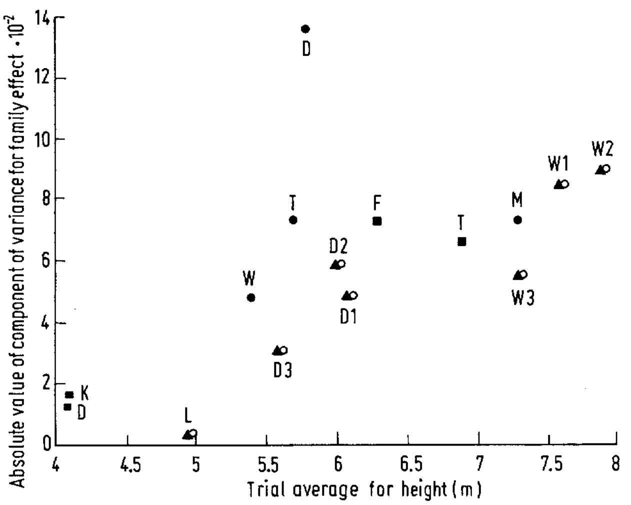

Fig. 2. Relationship between the components of variance for family effect in absolute value and the trial averages for height measured at age 5 years. ■ = foreign selection series, D = Dukuduku trial, F = Frankfort trial, K = Kwa-Mbonambi trial and T = Tweefontein trial. ▲ = Zululand selection series: D_1, D_2, D_3 stand for Dukuduku subtrials, L for Lottering trial, W_1, W_2, W_3, for Wilgeboom subtrials. ● = South African selection series: D = Dukuduku trial, M = Mariti trial, T = Tweefontein trial and W = Wilgeboom trial

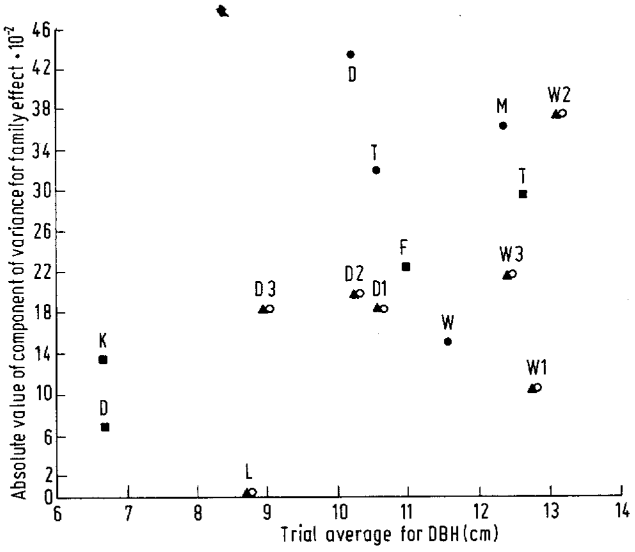

Fig. 3. Relationship between the components of variance for family effect in absolute value and the trial averages for DBH measured at age 5 years. Symbols as for Fig. 2

pothesis is that the genetic "expressivity" varies with site. According to Rieger et al. (1976), the term "expressivity" relates to the phenotypic expression (kind or degree) of a genotype that may be slight, intermediate or severe and depends on both genotype and external environment.

The soil survey of the Wilgeboom and Dukuduku trials showed their soil to be very uniform. At Lottering the observations were grouped into three soil map units. Soil unit I was the best-drained, loamy soil in the area and classified according to the South African soil classification system as Longlands soil form, Waldene series. (Macvicar et al. 1977). Soil unit II was transitional to the marshy soil unit III. It could be classified as a Kroonstad soil form, Bluebank series. It is a poorly drained loam to clay-loam soil. Soil unit III was defined as the wettest, with loam on clay ("vlei" area).

The variation between the families was much reduced or non-existent at age 5 years, although a little larger at age 8 years, at the Lottering trial.

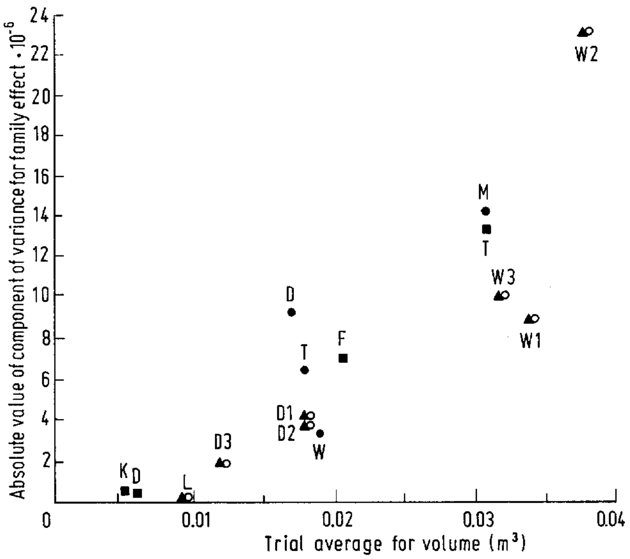

Fig. 4. Relationship between the components of variance for family effect in absolute value and the trial averages for average volume per tree at age 5 years. Symbols as for Fig. 2

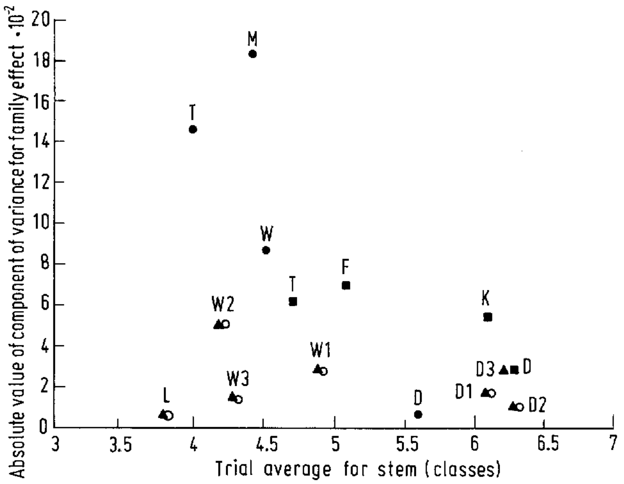

Fig. 5. Relationship between the components of variance for family effect in absolute value and the trial averages for stem form at age 5 years. Symbols as for Fig. 2

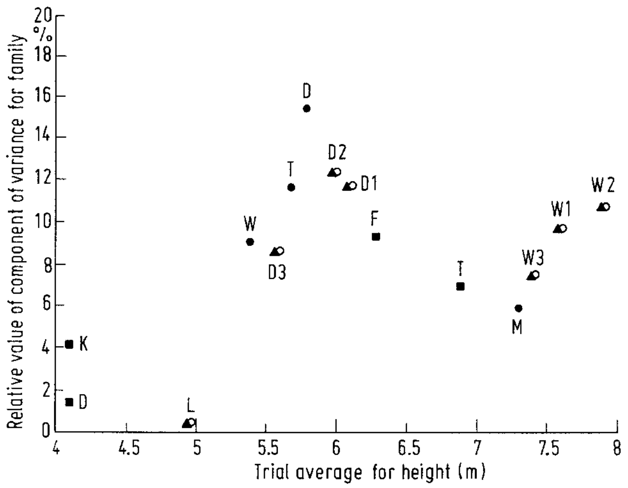

Fig. 6. Relationship between the components of variance for family effect in relative value (percent) and the trial averages for height at age 5 years. Symbols as for Fig. 2

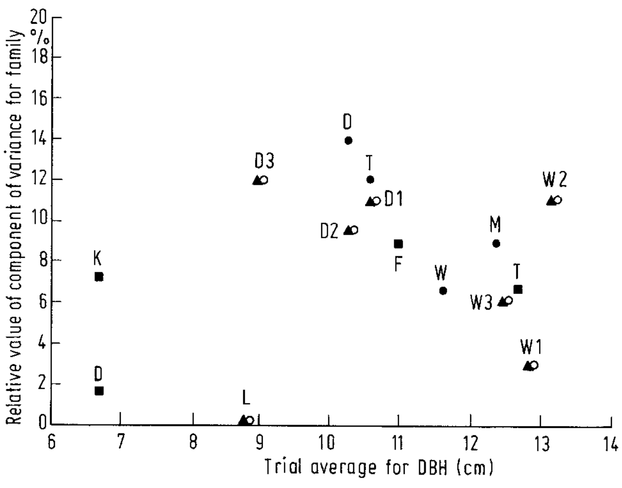

Fig. 7. Relationship between the components of variance for family effect in relative value (percent) and the trial averages for DBH at age 5 years. Symbols as for Fig. 2

Table 5. Soil heterogeneity at Lottering SF. Results of comparison test based on Tukey's test. Confidence intervals giving the simultaneous lower confidence limit and the simultaneous upper confidence limit of the difference between means

Comparisons	HT (m)	DBH (mm)	VOL (m^3)	STEM	Average branch angle	Average branch diameter
Case 1: Comparison of soils 1, 2, 3 when any family is included, appearing or not in soil types						
Soil 3-2	NS	$3.3 \leqslant 2.9 \leqslant 5.5$	NS	NS	NS	NS
3-1	$0.18 \leqslant 0.29 \leqslant 0.40$	$4.9 \leqslant 7.2 \leqslant 9.6$	$0.0017 \leqslant 0.0024 \leqslant 0.0031$	NS	NS	NS
2-1	$0.17 \leqslant 0.26 \leqslant 0.35$	$2.4 \leqslant 4.3 \leqslant 6.2$	$0.0012 \leqslant 0.0017 \leqslant 0.0023$	NS	NS	NS
Case 2: Comparison of soils 1, 2 and 3 when only the families which appear simultaneously in the three soils are included						
Soil 3-2	NS	$1.6 \leqslant 6.2 \leqslant 10.8$	NS	NS	NS	NS
3-1	$0.033 \leqslant 0.26 \leqslant 0.48$	$2.2 \leqslant 6.5 \leqslant 10.8$	$0.00082 \leqslant 0.0021 \leqslant 0.034$	NS	NS	NS
2-1	NS	NS	NS	NS	NS	NS
Case 3. Comparison of soil 1 and 2 when using families occurring only in soil 1 and 2						
Soil 2-1	$0.19 \leqslant 0.30 \leqslant 0.41$	$2.8 \leqslant 5.1 \leqslant 7.4$	$0.0012 \leqslant 0.0019 \leqslant 0.0026$	NS	NS	NS

There were few differences between the three types of analysis in the degree of significance of the traits studied; the differences at age 5 years in height, DBH, volume per tree due to soil types being very highly significant, stem form, branch angle and branch diameter being overall nonsignificant. In the second analysis, the standard error of the means was larger for all variables, thus, the precision of the estimate was lower because of smaller sample size, but the accuracy might have been larger, i.e. the true value of the soil parameters might have been better obtained. Table 5 gives the confidence limits of the differences between the means of the three types of soil for the different traits studied. Thus, the three types of soils seem to exert some small influence on the absolute growth of the families, and could lower somewhat the precision of the design. However, when an ANOVA is done by crossing soil and family, with soil effect fixed and the other effects random, the differences between the three soils are not significant, probably because of the lower power of the test due to smaller number of families, but also because of the very small effect of the different soils on the growth of the families. Thus there was no firm evidence that soil heterogeneity within the trial influenced in a significant way the growth of the families at the Lottering trial.

In most cases, the standard deviations are much smaller than the estimated value of the absolute and relative values of family component of variance. Tables 2 and 3 show as examples these standard deviations. For instance, taking the foreign selection series families, the standard error of the relative values were, for height, at Dukuduku SF: ±1.0% (relative value: 1.4%), Frankfort

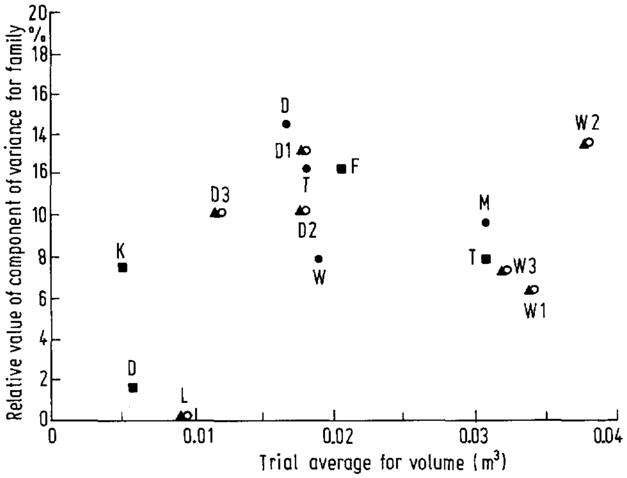

Fig. 8. Relationship between the components of variance for family effect in relative value (percent) and the trial averages for average volume per tree at age 5 years. Symbols as for Fig. 2

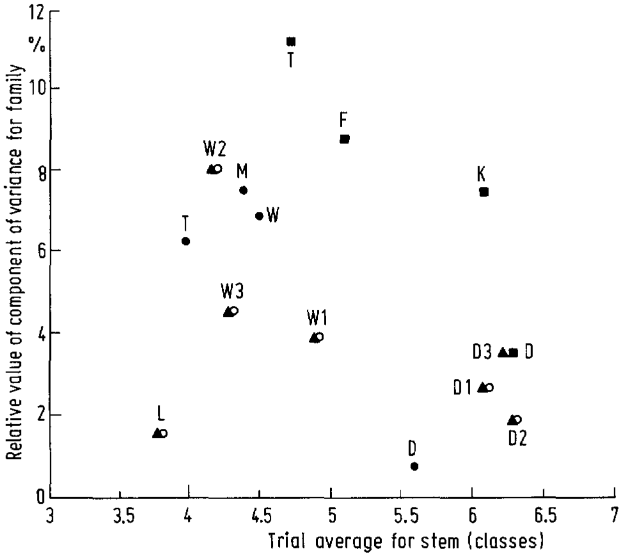

Fig. 9. Relationship between the components of variance for family effect in relative value (percent) and the trial averages for stemform at age 5 years. Symbols as for Fig. 2

SF: ±3.0% (9.4%), Kwambonambi SF: ±2.5% (4.3%) and Tweefontein SF: ±2.0% (7.1%). Thus, sampling error can be eliminated as a major cause of the variation detected.

In relative value (one-quarter of heritability), the global relationships between family component and site averages are curvilinear. For height (Fig. 6), there seems to be a peak at middle average trial values for height, then a decline and another increase. For DBH (Fig. 7) only one maximum seems to occur. The same applies for average tree volume (Fig. 8). For stem form (Fig. 9), no relationship seems to exist.

Note that there were some definite positive linear (nearly proportional) relationships between the relative value of the component of variance for family and its absolute value for all traits except volume per tree. These relationships could be explained by a tendency for the experimental error and interaction components to decrease in absolute value with increased value of the family component (except for average tree volume).

Plotting of the 8-year data for the Zululand selections showed the same trends as observed at 5 years. Only the absolute value of the components had increased while the relative value did not change much. Plotting of the branch characteristics did not show any relationship because of the small number of observations available.

Discussion

Three types of genotype-by-environment interaction (GEI) have been detected in the South African pine progeny trials: GEI within a trial, GEI over sites and "cryptic" GEI (Falkenhagen 1985 and unpublished data).

1 Genotype-by-environment interaction within a trial

Block (replication) by provenance or family interactions have been constantly detected in South African trials. The component of variance for interaction is often as large or much larger than the family component of variance. Four options to consider with that type of interaction have been discussed elsewhere (Falkenhagen 1985). Probably the best option is to study the blocks and families in order to estimate which blocks or families are responsible for the GEI interaction. More research is needed on the effect of the design on genotypic expressivity and genotypic competition between families, before one can decide whether it is necessary to use another design, e.g. such as single tree plot design.

2 Genotype-by-environment interaction over sites

In *P. elliottii*, this type of GEI does not seem to be very important in South Africa.

3 Cryptic genotype-by-environment interaction

Some linear relationship exists between the absolute value of the component of variance for family effect and site productivity in slash pine grown in South Africa.

One explanation could be the so-called "scale effect" which could be eliminated by some transformation of the data as explained by Falconer (1983). However as Falconer (1983, p. 269) himself concedes, a transformation is a statistical device that must be used with caution. Removing the relationship between mean and variance does not imply that no real genetic mechanisms are not at play to determine such relationship.

The hypothesis of site effect on genetic expressivity remains the most likely cause of the observed pattern of variation in absolute and relative value of the variance component for family effect. This is because at Lottering, where the expressivity was very small or zero, the detected soil differences in growth were very small and, if anything, could only mask very small differences between family means.

The interpretation of the variation observed in the relative value of the family component is difficult. However, the variation of the heritability of the traits studied with sites was real because of the small standard deviation of the relative values. The relative value of the family component on one site could be five times the value on another site, for instance. Thus, site influenced the rate of genetic gain in a way which raises the question as how to identify the sites which Foster an economically acceptable rate of genetic progress.

Plotting of similar data presented by Matheson and Raymond (1984) showed that, for *Pinus radiata* in Australia, none of the relationships detected here existed, except that there was a very strong positive linear relationship between the heritability of height and its family component of variance in absolute value.

Conclusions

In spite of the restricted number of sites tested, one can say that, in *P. elliottii*, cryptic genotype-by-environment existed, which implied that some sites would not enable acceptable genetic gains within an acceptable period of time. The Zululand and foreign selection series of trials showed that the expressivity of the same families as quantified by the absolute size of the component of variance for family was related to site fertility, with an increase in expressivity for growth traits as the site becomes more fertile. Such relationship was less evident for the South African selection series taken separately.

In relative value, that component was less distinctly related to site fertility and more research was needed to relate heritabilities to test sites. These relationships should be studied by using trials with the same genetic material replicated on a large number of different sites. What did seem true was that test site somehow modified the heritability of the traits studied, irrespective of design and its precision. That phenomenon complicates genetic gain prediction and index selection use. It is urgent to establish the law of the influence of site on the genetic expressivity of the principal traits bred for in-tree breeding.

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