Influences of testing sites on the genetic correlations in open-pollinated family trials of *Pinus elliottii* in South Africa

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Summary. Two series of open-pollinated family trials of *Pinus elliottii,* the so-called foreign selection series and the Zululand selection series were repeated, respectively, on four and three sites situated in sub-tropical and cooler-temperate climates of the summer rainfall and constant rainfall areas of South Africa. These series were studied in order to determine how testing sites influence the genetic correlations between traits commonly measured in progeny trials. No trend was detected between site index and genetic correlation, but site drastically changed the size and sign of the genetic correlations between growth traits and stem form. Even the genetic correlation between height and diameter at breast height was strongly affected by site.

Key words: Open-pollinated family tests – *Pinus elliottii* – Genetic correlations – Testing sites

Introduction

The present paper is a sequel to the article by Falkenhagen (1989), where an attempt was made to relate the absolute value of the component of variance for family effect and its relative value with respect to total variation (1/4 of heritability) to some characteristics of the testing sites. This was done by using three series of open-pollinated family trials of *Pinus elliottii* Engelmann growing in South Africa.

The fact that genetic correlations depend on testing environment is often neglected in tree breeding programmes. Clark (1987) has theoretically shown that genetic correlations do depend on the environment and that genotype-by-environment interactions affect genetic correlations. Genetic correlations are used in indirect genetic gain predictions and in index selection calculations (Falconer 1983).

This paper tries to answer the important question as to how large the changes are, due to testing sites, in the correlation between the breeding (also called additive) values of traits commonly measured in open-pollinated family trials of an important forest tree species: slash pine. The influence of testing sites on the corresponding phenotypic correlations and of age on both types of correlations will also be addressed.

Materials and methods

The trials of open-pollinated families of slash pine used in the present paper and the measurements done in these trials have been described in Falkenhagen (1989).

Two series of trials (the so-called Zululand selection series and foreign selection series) were used to calculate the phenotypic and genetic correlations between silvicultural traits measured at the age of 5 and 8 years by using the Harvey procedure (SAS 1986). In two trials of the Zululand selection series, the Wilgeboom and Dukuduku trials, the families were planted into three different subtrials.

A randomized complete block design was assumed throughout the calculations. The plot means were used in the calculations done by the Harvey procedure; consequently, the standard deviation of the genetic correlation was estimated by using the approximate formula given by Falconer (1983, p. 285). In order to use that formula, the sampling variance of the family component of variance was estimated by using the following formula (Anderson and Bancroft 1952, p. 321):

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

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 by using the value obtained in the expectation of the mean squares generated by the procedure GLM of the SAS package of programmes (SAS 1985a).

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. In that case the standard deviation of the genetic correlation was not estimated.

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

$$S_{h^2} = 4 \, (S^2_{S^2_{F_{am}}})^{1/2} / S^2_{TOTAL}$$

S^2_{TOTAL} = sum of all the components of variance entering into the calculation of the heritability (= total phenotypic variance); h^2 is the heritability on a single tree basis calculated as explained in Falkenhagen (1989).

Three-dimension graphs were obtained which plotted the genetic correlation between two traits against the trial averages of these traits for each trial, using the SAS graph procedure (SAS 1985 b). The graphs were visually examined for the detection of possible trends and biological interpretation.

The standard deviation of a genetic correlation is approximate and no test of significance and, thus, no test of difference is possible because the distribution of the genetic correlation is unknown (Scheinberg 1966). Nevertheless, two genetic correlation coefficients will be considered as probably different when their difference is larger than twice their average standard deviation.

For the phenotypic correlations, the exact test of equality of two correlation coefficients was used (Dagnelie 1970).

Results and discussion

Tables 1–10 present the phenotypic correlations with their significance above the diagonal, and the genetic

Table 1. Phenotypic correlations with significance (above diagonal) and genetic correlations with their standard deviation (below diagonal), between the traits measured at Tweefontein at age 5 years 10 months. Foreign selection series. Number of families: 72

	HT	DBH	VOL	STEM
HT	1.00	0.89***	0.89***	0.14 NS
DBH	0.90±0.04	1.00	0.95***	0.06 NS
VOL	0.97±0.01	0.98±0.01	1.00	0.10 NS
STEM	0.31±0.17	0.32±0.17	0.35±0.16	1.00

NS – Not significant
* – Significant at the 5% level
** – Significant at the 1% level
*** – Significant at the 0.1% level

correlations with their standard deviation below the diagonal, for each trial at the age of 5 and 8 years (the latter when available).

The phenotypic and genetic correlations between height (HT) and diameter at breast height (DBH) with average tree volume (VOL) will not be discussed in detail, because volume is a combination of HT and DBH and, thus, VOL is automatically highly correlated with the first two variables.

Foreign selection series

1 Phenotypic correlations

Tables 1–4 show that HT and DBH are very highly significantly correlated ($r = 0.70–0.91$). However, HT and DBH are not significantly correlated with stem form (STEM) ($r = -0.005–0.14$), except at the Frankfort State Forest (SF) site, where HT and DBH are significantly correlated with STEM ($r = 0.29$ and 0.30).

At Frankfort SF, HT, DBH and STEM are generally not significantly correlated with average branch diameter and average branch angle, but highly significantly correlated with branch-to-stem diameter ratio (-0.31 to -0.37). All branch characteristics are very highly significantly correlated between themselves.

In contrast with the preceeding sites, at Dukuduku and KwaMbonambi SF, HT and DBH are very highly significantly correlated with average branch diameter ($r = 0.44–0.77$). The correlations of HT and DBH with average branch angle are nonsignificant, but negative and very highly significant with branch-to-stem diameter ratio. Only STEM is not significantly correlated with branch-to-stem diameter ratio. At Dukuduku and KwaMbonambi SF, the branch characteristics are not significantly correlated between themselves.

2 Genetic correlations

The genetic correlations between HT and DBH are uniformly very high with very low standard deviation on all

Table 2. Phenotypic correlations with significance (above diagonal) and genetic correlations with their standard deviation (below diagonal), between the traits measured at Frankfurt at age 5 years 5 months. Foreign selection series. Number of families: 72

	HT	DBH	VOL	STEM	Average branch diameter	Average branch angle	Branch-to-stem diameter ratio
HT	1.00	0.70***	0.86***	0.30*	0.06 NS	0.17 NS	−0.33**
DBH	0.86±0.05	1.00	0.92***	0.29*	0.25*	0.22 NS	−0.31**
VOL	0.94±0.03	0.98±0.01	1.00	0.29*	0.13 NS	0.26*	−0.37**
STEM	0.24±0.21	0.29±0.19	0.29±0.21	1.00	0.14 NS	0.19 NS	−0.32**
Average branch diameter	−0.04±0.31	0.09±0.29	0.02±0.32	−0.55±0.22	1.00	−0.53***	0.80***
Average branch angle	0.32±0.19	0.45±0.16	0.39±0.18	0.32±0.19	−0.32±0.26	1.00	0.67***
Branch-to-stem diameter ratio	−0.66±0.14	−0.64±0.14	−0.68±0.14	−0.71±0.13	0.69±0.19	−0.58±0.16	1.00

Table 3. Phenotypic correlations with significance (above diagonal) and genetic correlations with their standard deviation (below diagonal), between the traits measured at Dukuduku at age 5 years. Foreign selection series. Number of families: 72

	HT	DBH	VOL	STEM	Average branch diameter	Average branch angle	Branch-to-stem diameter ratio
HT	1.00	0.91***	0.87***	0.06 NS	0.65***	0.18 NS	−0.40***
DBH	0.90±0.09	1.00	0.95***	−0.005 NS	0.77***	0.13 NS	−0.33**
VOL	0.97±0.03	1.00±0.00	1.00	0.02 NS	0.70***	0.12 NS	−0.30*
STEM	0.09±0.39	−0.18±0.37	−0.34±0.34	1.00	−0.16 NS	0.01 NS	−0.23 NS
Average branch diameter	0.49±0.27	0.64±0.20	0.61±0.22	−0.28±0.27	1.00	−0.06 NS	0.13 NS
Average branch angle	−0.28±0.34	−0.20±0.34	−0.07±0.36	−0.16±0.29	−0.18±0.26	1.00	−0.21 NS
Branch-to-stem diameter ratio	0.04±0.67	0.14±0.64	0.03±0.67	−0.29±0.50	0.85±0.14	−0.10±0.51	1.00

Table 4. Phenotypic correlations with significance (above diagonal) and genetic correlations with their standard deviation (below diagonal), between the traits measured at KwaMbonambi at age 5 years. Foreign selection series. Number of families: 72

	HT	DBH	VOL	STEM	Average branch diameter	Average branch angle	Branch-to-stem diameter ratio
HT	1.00	0.88***	0.90***	0.07 NS	0.44***	0.14 NS	−0.54***
DBH	0.98±0.01	1.00	0.96***	−0.05 NS	0.58***	0.16 NS	−0.50***
VOL	0.98±0.01	0.96±0.02	1.00	−0.09 NS	0.48***	0.23 NS	−0.54***
STEM	−0.67±0.20	−0.56±0.20	−0.70±0.14	1.00	−0.06 NS	−0.22 NS	−0.08 NS
Average branch diameter	0.75±0.19	0.84±0.10	0.71±0.16	−0.67±0.21	1.00	−0.16 NS	0.32*
Average branch angle	0.41±0.36	0.34±0.31	0.44±0.26	−0.61±0.23	0.35±0.40	1.00	−0.24 NS
Branch-to-stem diameter ratio	−0.77±0.15	−0.57±0.23	−0.60±0.21	−0.11±0.37	0.005±0.45	−0.08±0.45	1.00

four sites ($r = 0.86-0.98$) (Tables 1–4). The genetic correlations between STEM and HT and DBH are similar at Tweefontein and Frankfort SF (0.24–0.31) with large standard deviation (0.16–0.21), but these genetic correlations become negative and particularly high at KwaMbonambi (−0.56 to −0.67), indicating that at least at KwaMbonambi, the testing site significantly affects the genetic correlations between HT, DBH and STEM, which are negative as compared to positive at Frankfort SF. The Frankfort site has a cooler-temperate climate in contrast with KwaMbonambi SF, which has a subtropical climate.

This would imply that at Frankfort SF, selecting for high volume production would result in better stem form, while perhaps at Dukuduku and certainly at KwaMbonambi, selecting for high volume production would result in poorer stem form.

For branch characteristics, the Frankfort site displays a different image from that of the Dukuduku and KwaMbonambi sites: HT, DBH and STEM are not genetically correlated with average branch diameter (except for STEM), hardly with average branch angle and negatively and strongly with branch-to-stem diameter ratio, when one takes into account the standard deviation of the genetic correlations.

Note that STEM is negatively correlated with all branch characteristics except at Frankfort for branch angle, a feature unfavourable because average branch angle would tend to decrease with better stem form.

Average branch diameter and average branch angle are negatively correlated except at KwaMbonambi, where their correlation becomes negligible because of large sampling error.

At KwaMbonambi, in contrast with the other trials, the genetic correlations between branch characteristics become low or negligible.

Zululand selection series

1 Phenotypic and genetic correlations at age 5 years

Tables 5–7 present these correlations.

Table 5. Phenotypic correlations with significance (above diagonal) and genetic correlations (below diagonal), between the traits measured at Lottering at age 5 years 2 months. Zululand selections. Number of families: 121. The standard deviation of the genetic correlations could not be estimated

	HT	DBH	VOL	STEM	Average branch diameter	Average branch angle	Branch-to-stem diameter ratio
HT	1.00	0.75***	0.86***	-0.07 NS	-0.03 NS	0.003 NS	-0.004 NS
DBH	0.00	1.00	0.92***	-0.01 NS	0.05 NS	0.006 NS	0.05 NS
VOL	0.00	0.00	1.00	-0.01 NS	0.02 NS	-0.002 NS	0.02 NS
STEM	-0.92	0.00	0.00	1.00	-0.02 NS	0.04 NS	-0.39***
Average branch diameter	-0.68	0.00	0.00	0.28	1.00	-0.09 NS	0.91***
Average branch angle	0.00	0.00	0.00	0.00	0.00	1.00	-0.10 NS
Branch-to-stem diameter ratio	-0.45	0.00	0.00	-0.10	0.92	0.00	1.00

Table 6. Phenotypic correlations with significance (above diagonal) and genetic correlations with their standard deviation (below diagonal), between the traits measured at Wilgeboom at age 5 years 8 months. Zululand selections. The three successive numbers refer to the three separate subtrials. Number of families: 49, 49, and 36 respectively

	HT	DBH	VOL	STEM
HT	1.00	0.59***/0.78***/0.71***	0.82***/0.89***/0.85***	-0.11 NS/0.01 NS/0.01 NS
DBH	0.78/ 0.81/ 0.72 ±0.01/±0.06/±0.11	1.00	0.92***/0.96***/0.95***	0.01 NS/0.05 NS/0.03 NS
VOL	0.93/ 0.91/ 0.86 ±0.03/±0.03/±0.06	0.92/ 0.98/ 0.97 ±0.06/±0.01/±0.01	1.00	0.04 NS/0.04 NS/0.05 NS
STEM	-0.50/-0.07/-0.16 ±0.17/±0.19/±0.25	-0.40/-0.06/-0.03 ±0.29/±0.20/±0.25	-0.41/-0.07/-0.06 ±0.22/±0.19/±0.26	1.00

Table 7. Phenotypic correlations with significance (above diagonal) and genetic correlations with their standard deviation (below diagonal), between the traits measured at Dukuduku at age 5 years 2 months. Zululand selections. The three successive numbers refer to the three separate subtrials. Number of families: 70, 55 and 20, respectively

	HT	DBH	VOL
HT	1.0	0.72***/0.74***/0.70***	0.86***/0.87***/0.84***
DBH	0.70/ 0.62/ 0.52 ±0.09/±0.10/±0.22	1.00	0.96***/0.95***/0.96***
VOL	0.86/ 0.84/ 0.75 ±0.05/±0.05/±0.14	0.96/ 0.94/ 0.95 ±0.02/±0.02/±0.03	1.00
STEM	0.73/ 0.56/ 0.40 ±0.11/±0.18/±0.34	0.97/ 0.97/ 1.00 ±0.01/±0.02/±0.00	0.96/ 0.89/ 0.91 ±0.02/±0.05/±0.07
Average branch diameter	0.10/-0.07/-0.03 ±0.21/±0.19/±0.32	0.50/ 0.35/ 0.57 ±0.16/±0.17/±0.20	0.40/ 0.21/ 0.42 ±0.21/±0.18/±0.25
Average branch angle	0.66/ 0.38/ 0.56 ±0.11/±0.16/±0.24	0.51/ 0.14/-0.13 ±0.14/±0.18/±0.31	0.58/ 0.24/ 0.10 ±0.15/±0.17/±0.32
Branch-to-stem diameter ratio	-0.46/-0.50/-0.22 ±0.17/±0.14/±0.31	-0.004/-0.24/ 0.13 ±0.22 /±0.18/±0.29	-0.15/-0.37/ 0.01 ±0.25/±0.16/±0.30

1.1 Phenotypic correlations

At Lottering, HT and DBH (and VOL) are very highly significantly correlated $(r=0.75)$, as is STEM with branch-to-stem diameter ratio $(r=-0.39)$ and average branch diameter with branch-to-stem diameter ratio $(r=0.91)$. The latter correlation is unfavourable (Table 5).

At Wilgeboom, the three subtrials show the same picture as at Lottering for HT, DBH and STEM (Table 6). At Dukuduku, the phenotypic correlations are the same as at Lottering except that HT and DBH are uniformly very highly correlated with STEM, over the three subtrials. In addition, STEM is not correlated with branch-to-stem diameter ratio and average branch angle is negatively correlated with branch-to-stem diameter ratio, in contrast with the Lottering site (Table 7).

1.2 Genetic correlations

At Lottering, the genetic correlation between HT and DBH is zero because the heritability of DBH is zero. Because the component of variance for family effect for DBH is zero, the heritability is zero for DBH and VOL. Thus, the genetic correlation was not estimated by the Harvey programme for the correlations involving DBH or VOL (because a fraction with a zero denominator is not defined). However the correlation between a random variable and a constant is, in theory, zero; consequently, the genetic correlations involving DBH or VOL were all considered as zero, although small components of co-variance were estimated between DBH or VOL and other traits. HT and STEM are negatively correlated (-0.92). HT is also negatively correlated with average branch diameter and branch-to-stem diameter ratio, a favourable feature (Table 5).

At Wilgeboom, by contrast, HT and DBH are very highly correlated, and negatively with STEM in one sub-trial, but not in the other subtrials (Table 6). At Duku-duku (Table 7), HT and DBH are highly correlated, but HT and DBH are now positively correlated with STEM in all three subtrials.

In contrast with the Lottering trial, the Dukuduku trial shows poor or no genetic correlations between HT and average branch diameter, but good correlations between DBH and average branch diameter. The correlations of HT and DBH with average branch angle is generally positive (a favourable feature), but fluctuates in size and even sign $(-0.13$ for one subtrial). The correlations with branch-to-stem diameter ratio are generally negative but fluctuate in size and sign (Table 7).

In two of the subtrials, the correlations indicate that the larger the branch diameter, the smaller the branch angle (Table 7).

One can accept that, at age 5 years, the genetic correlations vary significantly between the three trials: at Lottering, the correlation between HT and DBH is zero or not defined, at Wilgeboom it is from 0.72 to 0.81 and it is slightly lower at Dukuduku. The genetic correlations between HT and DBH and STEM are negative (or zero) at Lottering and Wilgeboom, but positive at Duku-duku. In other words, unfavourable correlations exist at Lottering and Wilgeboom, but very favourable ones exist at Dukuduku, and the differences are probably signifi-cant (the differences are larger than twice the standard deviation of the genetic correlations).

2 Phenotypic and genetic correlations at age 8 years

2.1 Phenotypic correlations

At Lottering, HT and DBH are poorly correlated (0.39); HT is also poorly correlated with STEM. The reason for

Table 7. (continued)

STEM	Average branch diameter	Average branch angle	Branch-to-stem diameter ratio
0.70***/0.66***/0.62***	0.37** /0.21 NS/0.25 NS	0.04NS/ 0.08 NS/ 0.14 NS	0.02 NS/−0.17 NS/−0.07 NS
0.80***/0.87***/0.92***	0.62***/0.47***/0.52*	−0.06 NS/−0.04 NS/−0.12 NS	0.25* /−0.01 NS/ 0.06 NS
0.79***/0.80***/0.88***	0.56***/0.39**/0.45*	−0.01 NS/ 0.02 NS/−0.03 NS	0.19 NS/−0.05 NS/ 0.02 NS
1.00	0.53***/0.44**/0.56**	0.01 NS/ 0.003 NS/−0.21 NS	−0.08 NS/ 0.18 NS/ 0.07 NS
0.48/ 0.34/ 0.66	1.00	−0.46***/−0.50***/−0.56**	0.68***/ 0.73***/ 0.85***
±0.24/±0.26/±0.22	0.16/−0.43/−0.56	1.00	−0.43***/−0.50***/−0.54*
±0.14/±0.27/±0.40	±0.24/±0.16/±0.23		
−0.05/−0.23/ 0.24	0.86/ 0.83/ 0.88	−0.21/−0.60/−0.54	1.00
±0.32/±0.27/±0.37	±0.07/±0.07/±0.07	±0.23/±0.13/±0.23	

that phenomenon is not clear, as thinning was done after the measurements were taken (Table 8). At Wilgeboom, the correlation between HT and DBH is somewhat higher, but the correlations betwen HT and DBH with STEM are not significant (Table 9).

At Dukuduku, the picture is the same (Table 10).

The disappearance of the phenotypic correlations between growth traits and stem form at Wilgeboom and Dukuduku is probably due to the fact that the trees which were measured were those left after thinning.

2.2 Genetic correlations

At age 8 years, at Lottering, the genetic correlations are now very high, HT being highly and positively correlated with STEM (0.93) (Table 8).

At Wilgeboom, HT and DBH are moderately correlated (0.40, 0.50 and 0.80); however, HT and DBH are
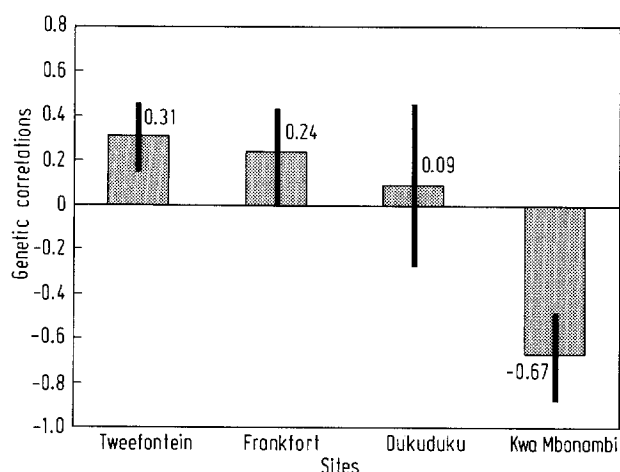
poorly or not correlated with STEM (Table 9). At Dukuduku, the picture is the same, HT and DBH being better correlated. In one subtrial, however, a negative correlation appears between DBH and STEM (Table 10).

One can accept that at Dukuduku the genetic correlation between DBH and STEM is different from that at Lottering (the difference between +0.10 and −0.51 is larger than twice the standard error of 0.23). The same is true for the genetic correlation between HT and STEM, which tends to be negligible at Dukuduku.
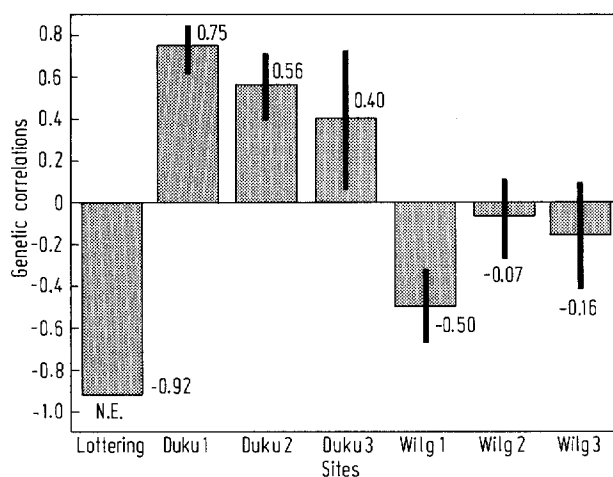
3 Influences of test sites

In order to study the influence of site on the genetic correlations, three-dimensional colour graphs, plotting the genetic correlations against the trial average of the traits involved in the correlations, were examined visually in order to detect any trend. A total of 20 three-dimension graphs were studied.

No relationship could be found between the three variables studied, undoubtedly because of the small number of sites on which the foreign selection and the Zululand selection families were repeated (four and three sites, respectively). However, because I have used a conservative measure of distance between two genetic correlations (twice their standard deviation), there is no doubt that site somehow drastically affects the genetic correlation between two traits. Although no confidence interval could be calculated for the differences between the genetic correlations, I can say that site can change the
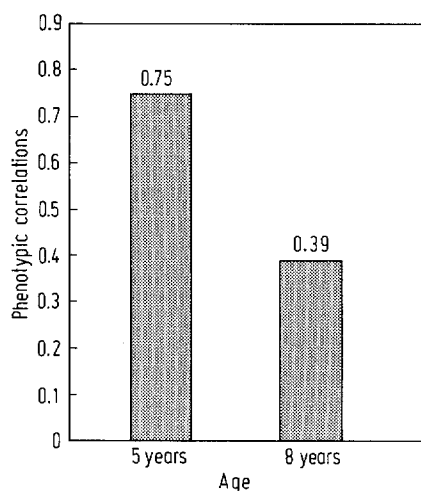
Table 8. Phenotypic correlations with significance (above diagonal) and genetic correlations (below diagonal), between the traits measured at Lottering at age 8 years 2 months. Zululand selections. Number of families: 121. The standard deviation of the genetic correlations could not be estimated

	HT	DBH	VOL	STEM
HT	1.00	0.39***	0.58***	0.25**
DBH	0.82	1.00	0.92***	0.29**
VOL	1.38	0.95	1.00	0.34***
STEM	0.93	0.10	0.32	1.00

Table 9. Phenotypic correlations with significance (above diagonal) and genetic correlations with their standard deviation (below diagonal), between the traits measured at Wilgeboom at age 8 years 8 months. Zululand selections. The three successive numbers refer to the three separate subtrials. Number of families: 49, 49 and 36, respectively

	HT	DBH	VOL	STEM
HT	1.00	0.53***/0.58***/0.52***	0.77***/0.78***/0.73***	−0.08 NS/−0.01 NS/−0.08 NS
DBH	0.40/ 0.80/ 0.50 ±0.21/±0.09/±0.23	1.00	0.93***/0.95***/0.96***	−0.03 NS/−0.11 NS/−0.16 NS
VOL	0.72/ 0.87/ 0.72 ±0.11/±0.06/±0.14	0.92/ 0.99 / 0.96 ±0.04/±0.004/±0.03	1.00	−0.04 NS/−0.06 NS/−0.17 NS
STEM	0.10/−0.26/−0.22 ±0.22/±0.26/±0.24	0.10/−0.24 /−0.06 ±0.27/±0.23 /±0.26	0.16/−0.27/−0.16 ±0.24/±0.23/±0.25	1.00

Table 10. Phenotypic correlations with significance (above diagonal) and genetic correlations with their standard deviation (below diagonal), between the traits measured at Dukuduku at 7 years 5 months. Zululand selections. The three successive numbers refer to the three separate subtrials. Number of families: 70, 55 and 20, respectively

	HT	DBH	VOL	STEM
HT	1.00	0.65***/0.62***/0.67***	0.80***/0.82***/0.84***	0.12 NS/0.00 NS /−0.13 NS
DBH	0.80/ 0.63/ 0.57 ±0.06/±0.10/±0.20	1.00	0.96***/0.94***/0.96***	0.12 NS/0.01 NS /−0.24 NS
VOL	0.90/ 0.84/ 0.78 ±0.03/±0.05/±0.12	0.98/ 0.95/ 0.96 ±0.01/±0.02/±0.02	1.00	0.13 NS/0.004 NS/−0.24 NS
STEM	0.00/ 0.02/−0.23 − /±0.26/±0.31	0.00/−0.22/−0.51 − /±0.25/±0.23	0.00/−0.15/−0.45 − /±0.26/±0.26	1.00

Fig. 1. Bar chart of the genetic correlations between height and stem form at four sites for the foreign selections. The *vertical lines* are proportional to twice the standard deviation of the genetic correlation. Age: 5 years
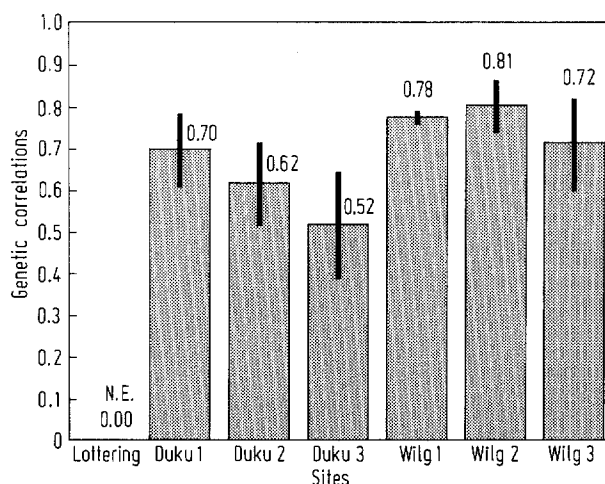
Fig. 3. Bar chart of the genetic correlations between height and diameter at breast height at three sites for the Zululand selections. The *vertical lines* are proportional to twice the standard deviation of the genetic correlation. Age: 5 years

Fig. 2. Bar chart of the genetic correlations between height and stem form at three sites for the Zululand selections. The *vertical lines* are proportional to twice the standard deviation of the genetic correlation. Age: 5 years

Fig. 4. Bar chart of the phenotypic correlations between height and diameter at breast height at two ages at one site for the Zululand selections. Test of equality: highly significant. Lottering site

sign and the size of the genetic correlation between HT and STEM (Figs. 1 and 2). Even the genetic correlation between HT and DBH can be affected by site (Fig. 3).

The genetic correlations between growth traits and branch characteristics are affected by large standard deviation, and my data do not show clearly how site affects these parameters.

4 Influence of age

For the Zululand selections series of trials we have measurements made at 5 years and 8 years.

Age significantly affects the phenotypic correlation between HT and DBH at Lottering (from $r = 0.75$ to $r = 0.39$) (Fig. 4).

At Lottering, there seems to be an age effect with drastic change of the genetic correlation from zero to high correlation (HT with DBH) or complete sign inversion from -0.92 to $+0.93$ (HT with STEM). At Duku-duku, large changes in the genetic correlations betwen growth traits and stem form appear from age 5 to age 8 years, but these large changes seem to be due to the effect of thinning, as only the remaining trees have been measured (Fig. 4). However, at Wilgeboom, the same genetic correlations do not change over age.

5 Changes in phenotypic correlations

The phenotypic correlations between two traits can be drastically affected by site. This is the case for the corre-
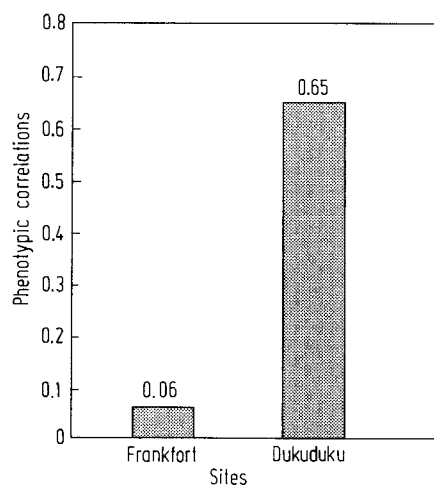
Fig. 5. Bar chart of the phenotypic correlations between height and average branch diameter at two sites for the foreign selections. Test of equality: very highly significant. Age: 5 years
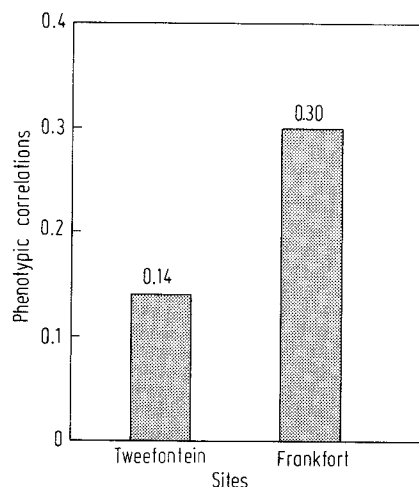
Fig. 6. Bar chart of the phenotypic correlations between height and stemform at two sites for the foreign selections. Test of equality: not significant. Age: 5 years

lation between height and average branch diameter (Fig. 5). For the correlation between height and stem form, the change is large but not significant (Fig. 6). Differences between subtrials are not significant (example: Dukuduku HT and average branch diameter at 5 years).

Conclusions

It seems, thus, that site may affect the phenotypic and genetic correlations in *Pinus elliottii* in such a way that the correlated responses to one trait selection may change from site to site, and that index calculations and selections which are based on point estimation of genetic and phenotypic correlations may also change drastically from site to site.

It is urgent to determine the laws which govern the genetic expressivity of forest tree genomes in relation to testing sites, in order to define breeding zones where a given genetic material will evolve in a pre-determined direction. The danger exists of applying uni- or multiple-trait selection methods which might yield trees with unacceptable characteristics on one site while yielding acceptable trees on another site. To ecologically and genet-

ically identify these breeding zones, the same open-pollinated families should be tested on a large number of sites sampling the diversity of ecological conditions where *Pinus elliottii* is planted.

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