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Age Trends in Variances and Heritabilities for Diameter and Height in Maritime Pine (*Pinus pinaster* AIT.) in Western Australia

By D. KUSNANDAR[1]), N. W. GALWEY[1]), G. L. HERTZLER[1]) and T. B. BUTCHER[2])

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Abstract

The inheritance of variables related to growth was studied in a progeny trial of maritime pine (*Pinus pinaster* AIT.) in Wanneroo, Western Australia. The trial consists of the progeny of three parent trees used as females and five used as males, crossed in 14 of the 15 possible combinations (full-sib families), plus a routine commercial control family. There were 108 trees/cross, planted at a spacing of 3 m x 3 m.

Certain families had consistently large diameters and were consistently tall, indicating that early selection between families may be effective. Genetic and environmental variance components of the diameters and heights were estimated using the restricted maximum likelihood (REML) method. Both phenotypic and additive-genetic variances increased as trees became older, rapidly up to age 6 years, then more gradually up to 25 years. However, the heritabilities were fairly constant, in the range 0.14 to 0.16 for diameter and 0.11 to 0.14 for height. This is in contrast to other studies of pines in which heritability increased with age, and was greater for height than for diameter.

In a principal component analysis of the diameters the first component represented an average of the successive measurements and accounted for 93% of the variation. The second component contrasted early and late measurements and accounted for only 6% of the variation, but was more heritable ($h^2 = 0.35$) than the first component ($h^2 = 0.14$). A similar pattern was found for the heights. It is concluded that selection between families at an early age for diameter or height will be effective. It is also suggested that the second principal components reflect the genetic distance between trees, and could be used to ensure retention of genetic diversity in a tree breeding program.

Key words: Genetic variance, phenotypic variance, heritability, principal component analysis, progeny trial.

FDC: 165.3; 165.44; 181.65; 232.13; 561; 174.7 *Pinus pinaster;* (941).

Introduction

Forest trees are typified by long rotations and long breeding cycles, and selection at early ages is therefore a common practice in the improvement of these species. The assumption is made that early performance is indicative of later performance (LAMBETH et al., 1983). However, genetic and phenotypic parameters of trees reflect growth of the tree under the varying control of the genotype, the environment, and the genotype x environment interaction during its development. Hence they are expected to change over time (VÁSQUEZ and DVORAK, 1996). Determination of trends in variances and heritabilities with age may therefore be of value in the estimation of an optimal age for early selection. Stem volume production is an important goal in silviculture and tree breeding programs, and is largely determined by height and diameter. Of the two components, height is commonly used as a selection criterion for volume growth, since it is less sensitive to competition (KREMER, 1992).

The first objective of the research presented here was to determine the trends in genetic and phenotypic parameters for height and diameter during stand development in maritime pine (*Pinus pinaster* AIT.), and hence to seek trends in the heritability of these variables. A second objective was to explore whether the deviations from the major trends over time could provide further information of value to the tree breeder.

Materials and Methods

Materials

Data were obtained from a progeny trial of maritime pine in Gnangara Plantation, Wanneroo, Western Australia (latitude 115° 50'E, longitude 31° 38'S, altitude 60 m above sea level). The site is about 50 km north of Perth. The trial consists of the progeny of three parent trees used as females and five used as males, crossed in 14 of the 15 possible combinations (full-sib families), plus a routine commercial control family, and comprises 108 trees of each family (*Table 1*). The trees were planted in 1971, at a 3 m x 3 m spacing. The experiment was arranged in three replications, each consisting of six blocks of

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[1]) School of Agriculture, The University of Western Australia, Nedlands 6907, Western Australia.

[2]) Department of Conservation and Land Management, Research Centre, Como 6152, Western Australia.

90 trees. The blocks were separated by buffers consisting of two rows of trees. The trees in the buffers were a mixture of several full-sib families. Six fertiliser treatments were assigned to the blocks in each replication. These consisted of the combination of three different levels of superphospate and two levels of ammonium sulphate. Further details of the fertiliser treatments are given by HOPKINS and BUTCHER (1994). Each block was divided into six plots, each containing one tree of each of the 15 families, but no specific treatments factor was assigned to the plots.

Table 1. — Pedigree Information.

Female parents	Male parents				
	E029	E033	E041	E154	E182
E019	S057	S056	S055	S099	S100
E040	S064	S063	S017	S202	S125
E046	S161	S168	---	S205	S215

4076: Routine commercial control

Measurements

Diameter at breast height (DBH) and height (HT) were the characters of interest. DBH was measured at ages 9, 12, 16 and 25 years, and HT at ages 4, 6, 9 and 25 years. The traits analysed in this study are referred to as DBH9, HT4 etc., the numbers indicating the ages.

Statistical analysis of the experimental design

The design of this experiment, with regard to its genetic components, is similar to the North Carolina Design 2 (MATHER and JINKS, 1971), except that the cross E046 x E041 is replaced by the routine family. To simplify the analysis, especially in variance component estimation, the routine family was treated as this cross, but the corresponding observations were replaced by missing values.

Analysis of variance was performed on each variable measured. Effects of fertilisers were considered as fixed, and those of the male and female parents were considered as random. The model used in the analysis was as follows:

$$y_{ijklm}=\mu+t_j+m_l+f_m+(mf)_{lm}+(mt)_{lj}+(ft)_{mj}+(mft)_{lmj}+r_i+(rb)_{ij}+(rbp)_{ijk}+\varepsilon_{ijklm} \quad \text{.....} \quad (1)$$

where y_{ijklm} = the phenotypic observation (diameter or height) of the individual tree from the cross of *m*th female and *l*th male in the *k*th plot in the *j*th block in the *i*th replication

μ = the general mean

t_j = the effect of the *j*th level of fertiliser

m_l = the effect of the *l*th male

f_m = the effect of the *m*th female

$(mf)_{lm}$, $(mt)_{lj}$, $(ft)_{mj}$, and $(mft)_{lmj}$ = the interaction effects between the *l*th male, the *m*th female and the *j*th level of fertiliser

r_i = the effect of the *i*th replication

$(rb)_{ij}$ = the effect of the *j*th block in the *i*th replication

$(rbp)_{ijk}$ = the residual effect of the *k*th plot in the *j*th block in the *i*th replication

ε_{ijklm} = the residual effect of the individual tree from the cross of *m*th female and *l*th male in the *k*th plot in the *j*th block in the *i*th replication.

The assumptions used in the analysis were that the random effects m_l, f_m, $(mf)_{lm}$, $(mt)_{lj}$, $(ft)_{mj}$, $(mft)_{lmj}$ and ε_{ijklm} are normally distributed with means zero and variances σ^2_m, σ^2_f, σ^2_{mf}, σ^2_{mt}, σ^2_{ft}, σ^2_{mft} and σ^2_ε, respectively.

Estimation of genetic parameters

Variance components are commonly estimated by analysis of variance (HENDERSON, 1953), equating the mean squares in the ANOVA table to their expected values and solving the resulting simultaneous equations. In this investigation, however, we estimated variance components using the restricted maximum likelihood (REML) method (PATTERSON and THOMPSON, 1971; HARVILLE, 1977). In this method, variance components are estimated by maximising a marginal (or restricted) likelihood function, that is, a likelihood function obtained after the model has been transformed to eliminate the fixed effects. This method produces unambiguous estimates of variance components from unbalanced data. KUSNANDAR (1993) has confirmed by simulation studies that these are less biased than the estimates produced by ANOVA.

The estimates of variance components were then used to estimate the heritability values for each character. Variance components associated with male parent effects (σ^2_m) and female parent effects (σ^2_f) are both estimates of the phenotypic covariances of half-sib families, and are both assumed to be a quarter of V_A, where V_A is the additive genetic variance (FALCONER, 1981). The estimates of these variance components were therefore pooled to obtain an estimate of additive genetic variance by weighting them with the corresponding degrees of freedom (KREMER and LASCOUX, 1988), as follows:

$$V_A = 4\left\{\frac{(M-1)\sigma^2_m + (F-1)\sigma^2_f}{M+F-2}\right\} \qquad (2)$$

where *M* and *F* are the numbers of male and female parents, respectively.

The estimate of phenotypic variance (V_p) was calculated as the sum of variance components, that is:

$$V_p=\sigma^2_m+\sigma^2_f+\sigma^2_{mf}+\sigma^2_{mt}+\sigma^2_{ft}+\sigma^2_{mft}+\sigma^2_\varepsilon \quad \text{.....} \quad (3)$$

An estimate of narrow-sense heritability (h^2) was then obtained as

$$h^2 = \frac{V_A}{V_p} \qquad (4)$$

Standard errors for the estimates of heritability were calculated from the SEs of the variance components using the formula derived from a TAYLOR expansion (HOHLS, 1996), namely:

$$\operatorname{var}[f(x,y)] \approx \left(\frac{\partial f}{\partial x}\right)^2 \operatorname{var}(x) + \left(\frac{\partial f}{\partial y}\right)^2 \operatorname{var}(y) + 2\left(\frac{\partial f}{\partial x}\right)\left(\frac{\partial f}{\partial y}\right)\operatorname{cov}(x,y) \qquad (5)$$

where $\frac{\partial f}{\partial x}$ and $\frac{\partial f}{\partial y}$ are partial derivatives of the function *f(x, y)* with respect to *x* and *y*, respectively. These standard errors were calculated by the Genstat procedure VFUNCTION (Genstat 5 Committee, 1995), which calculates functions of variance components from a REML analysis and obtains the standard errors of these functions on the basis of the above TAYLOR expansion.

In order to explore the relationships between the successive measurements of diameter, a principal component analysis was performed on them. This analysis re-expresses the information

Table 2. — Analyses of variance for tree diameters.

Source of variation	d.f	Mean squares			
		DBH9	DBH12	DBH16	DBH25
Rep. Stratum	2	826.77	431.33	212.60	296.82
Rep.Block Stratum					
Fertiliser	5	413.65 ***	177.34 *	85.60 ns	72.83 ns
Residual	10	33.27	35.39	39.11	55.32
Rep.Block.Plot Stratum	90	7.72	9.59	11.51	18.60
Rep.Block.Plot.Tree Stratum					
Male	4	119.82 ***	153.86 ***	185.25 ***	301.56 ***
Female	2	50.87 ***	86.90 ***	117.02 ***	244.67 ***
Male.Female	7	4.50 ns	3.75 ns	6.28 ns	29.81 ns
Male.Fertiliser	20	14.02 ***	18.44 ***	21.75 **	25.31 *
Female.Fertiliser	10	7.24 ns	9.98 ns	12.94 ns	21.23 ns
Male.Female.Fertiliser	35	8.12 *	11.68 *	13.53 ns	20.92 ns
Residual		5.56	7.82	10.31	15.39
		df = 1326	df = 1258	df = 1257	df = 1119

ns: not significant; *) significant at 5% level; **) significant at 1% level; ***) significant at 0.1% level

Table 3. — Analyses of variance for tree heights[1]).

Source of Variation	d.f	Mean squares			
		HT4	HT6	HT9	HT25
Rep. Stratum	2	35.358	292.179	330.216	35.742
Rep.Block Stratum					
Fertiliser	5	10.682 *	93.351 ***	176.317 ***	38.044 ns
Residual	10	2.032	5.332	13.122	30.092
Rep.Block.Plot Stratum	90	0.410	1.041	1.442	3.601
Rep.Block.Plot.Tree Stratum					
Male	4	4.491 ***	8.411 ***	9.558 ***	28.188 ***
Female	2	1.878 ***	8.789 ***	13.919 ***	9.957 **
Male.Female	7	0.568 *	0.827 ns	0.729 ns	1.979 ns
Male.Fertiliser	20	0.573 ***	1.021 *	1.711 **	1.837 ns
Female.Fertiliser	10	0.421 *	0.815 ns	1.143 ns	2.056 ns
Male.Female.Fertiliser	5	0.289 ns	0.862 *	1.037 ns	2.234 ns
Residual		0.206	0.584	0.789	1.743
		df = 1326	df = 1326	df = 1326	df = 1119

[1]) For conventions see *table 2.*

contained in the four measurements of diameter as four principal components, mutually orthogonal linear combinations of the original variables (DIGBY and KEMPTON, 1987). Variance components and heritabilities were then estimated for each principal component. A similar analysis was performed on the successive measurements of height.

Results and Discussion

Growth in diameter and height

The analyses of variance for tree diameter and height on different occasions (*Tables 2* and *3*) show that the main effect of fertiliser remained significant only until age 12, when the last application of fertilisers was given. However, the male parent x fertiliser interaction effect on diameter remained significant for longer, though the female parent x fertiliser interaction effect did not. It is perhaps surprising that there were no significant residual effects of the fertiliser treatments at later dates. The effects of fertilisers in this experiment have been discussed elsewhere (HOPKINS and BUTCHER, 1994) and will not be considered further here.

The increase in diameter and height follows a similar pattern in the 15 families, but there are consistent differences in the rate of increase between families (*Figures 1* and *2*). For both variables, all the families derived from crosses had consistently higher values than the commercial control family. The curves for diameter varied more among families than those for height, and the families formed two groups with regard to this variable. The group with greater diameters consists of families S062, S057, S202 and S099, which are derived from the crosses between two male parents (E029 and E154) and two female parents (E040 and E019). Families S064 and S202 had consistently larger diameters and heights than the others. These consistent patterns indicate that selection between families at an early age will be effective.

The main effects of male and female parents were highly significant for both traits on every occasion. The interaction effect between male and female parents, on the other hand, was significant only for HT4. E029 appeared to be best male parent, though at age 25 it was not significantly different from E154, and E040 appeared to be the best female parent.

Estimates of variance components and heritabilities

The magnitude of the variance component associated with male parent effects (σ^2_m) was generally greater than that associated with female parent effects (σ^2_f), except for HT9, where the magnitude was almost equal (*Table 4*). The number of parents in this study is small, and the variables measured are not independent: these differences may therefore represent sampling error. The variance component associated with male parent effects for diameter ranged from 4.36% to 5.20% of the total variance, while for height this component ranged from 2.74% to 4.65% of the total variance.

Since the F values for the male x female interaction are usually less than 1, the estimates of the variance component σ^2_{mf} are mostly negative, and the true value can be taken to be zero. This indicates that the genetic effects on the variables studied are largely additive.

Phenotypic and additive genetic variances increased with age for both diameter and height (*Figure 3* and *4*), the rate of increase being nearly constant after the trees were 6 years old.

Heritabilities, on the other hand, were fairly constant over time, in the range 0.14 to 0.16 for diameter and 0.11 to 0.14 for height. Standard errors for heritabilities were large, almost certainly because of small sample sizes of parent trees. This constancy of heritability for diameter was similar to the finding of COSTA and DUREL (1996), though the heritabilities that they

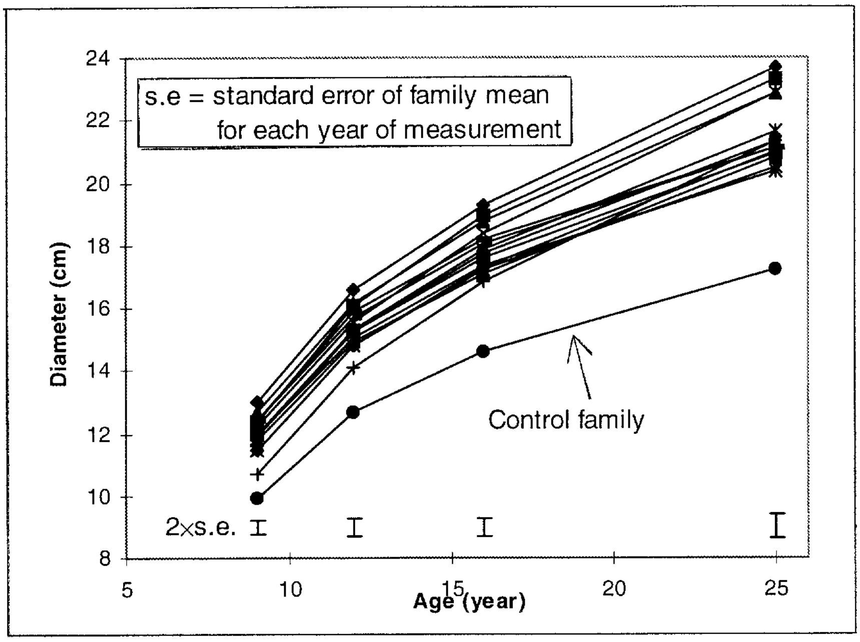

Figure 1. – Diameters of progeny families at different ages.

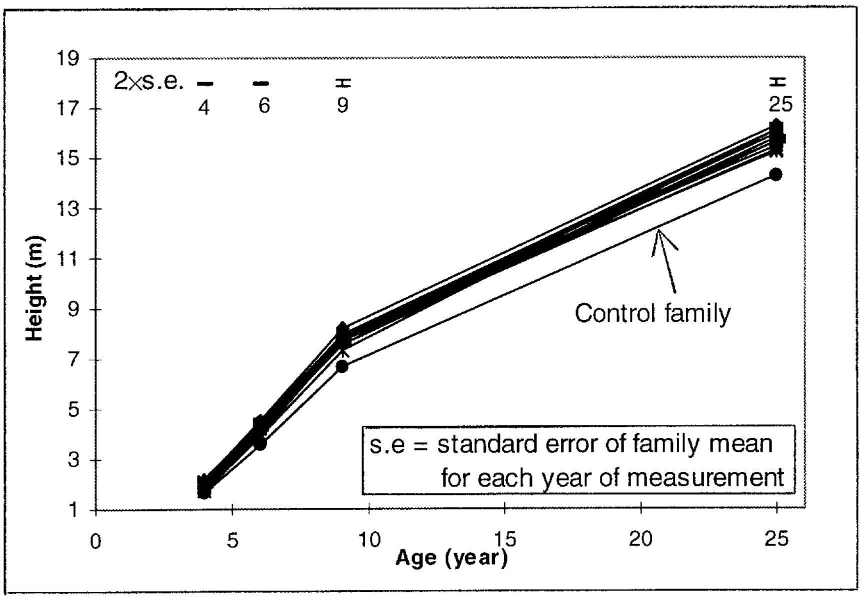

Figure 2. – Heights of progeny families at different ages.

observed were considerably higher (0.35 to 0.40). On the other hand, COTTERILL et al. (1987) reported even lower heritabilities for diameter of maritime pine at the age of 8.5 years (0.03 to 0.05). These discrepancies may be due to the use of different populations and environments.

Table 4. — Estimates of variance components for tree diameters and heights.

Estimates	DBH9	DBH12	DBH16	DBH25	HT4	HT6	HT9	HT25
σ^2_m	0.324	0.414	0.490	0.803	0.0108	0.0221	0.0237	0.0825
σ^2_f	0.089	0.147	0.187	0.371	0.0026	0.0156	0.0241	0.0139
σ^2_{mf}	-0.033	-0.068	-0.058	0.092	0.0025	-0.0002	-0.0025	-0.0016
$\sigma^2_{m,fert}$	0.112	0.131	0.174	0.106	0.0043	0.0034	0.0145	-0.0028
$\sigma^2_{f,fert}$	-0.028	-0.034	-0.002	0.003	0.0008	-0.0018	0.0003	0.0039
$\sigma^2_{mf,fert}$	0.140	0.174	0.108	0.016	0.0048	0.0145	0.0121	-0.0040
σ^2_ε	5.565	7.824	10.310	15.420	0.2063	0.5842	0.7887	1.7450

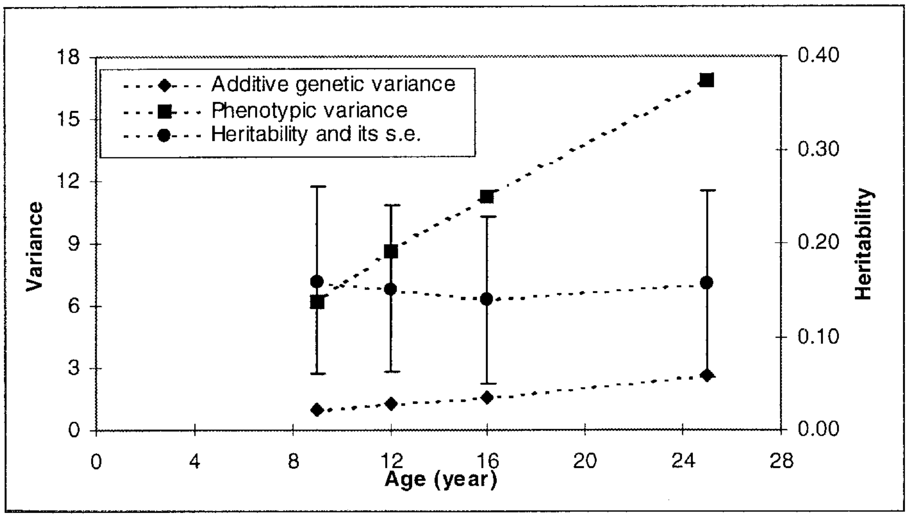

Figure 3. – Trend for additive genetic variance, phenotypic variance and heritability for tree diameter.

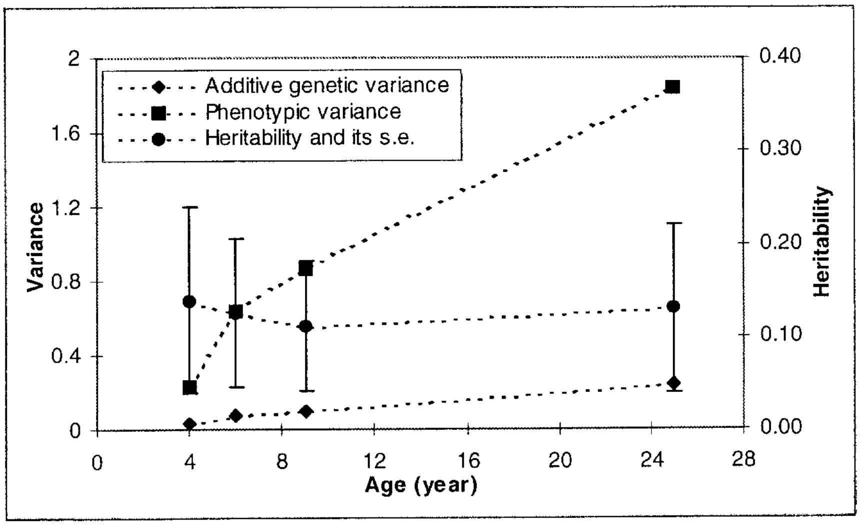

Figure 4. – Trend for additive genetic variance, phenotypic variance and heritability for tree height.

The constancy of the heritability of height in this study is in contrast to some other studies in maritime pine, in which the heritability of this variable was found to increase with age. DANJON (1994) found that heritability for height increased after age 5 years and remained fairly constant after age 10 years,

Table 5. — Principal component analysis of diameter and height.

Diameter	Principal component 1st	Principal component 2nd	Height	Principal component 1st	Principal component 2nd
Latent vectors (loadings):			Latent vectors (loadings):		
DBH9	0.489	0.645	HT4	0.508	-0.312
DBH12	0.513	0.234	HT6	0.550	-0.269
DBH16	0.513	-0.186	HT9	0.532	-0.099
DBH25	0.484	-0.703	HT25	0.396	0.906
% variation	93.1	6.1	% variation	75.3	15.9
h^2	0.14±0.10	0.35±0.18	h^2	0.11±0.08	0.22±0.12

and Costa and Durel (1996) found that heritability increased up to age 20 years. In another study, heritability of height at different ages in loblolly pine (*Pinus taeda* L.) in Georgia was estimated on the basis of predicted values from a growth curve, and was found to reach a maximum between ages 14 and 16 years (Balocchi et al., 1993). In the present case there may have been a peak between the ages of 9 and 25 years when no observations were taken. However, the trend in heritability of height is not consistent between different studies. Vásquez and Dvorak (1996) investigated the trend of heritability for height in tropical pine species during the first 8 years of growth. They found that in *Pinus tecunumanii* and *Pinus chiapensis* the heritability of height decreased with age, but that in *Pinus caribea* it increased.

The first two principal components derived from the successive measurements of diameter explained over 99% of the variation present (*Table 5*). The very large proportion of the variation accounted for by the first principal component confirmed that there was a strong relationship between successive diameter measurements. This component weighted the four diameter measurements almost equally and is therefore approximately an average of the diameter measurement. Its heritability is therefore about the average of the heritabilities of the four diameter measurements. The second principal component contrasted early and late measurements, and though it explained only a small proportion of the variation, it was more heritable than the first component. A similar pattern was found in principal component analysis for height measurements.

Conclusions

The growth curves of the families, and the principal component analyses, indicate that selection between families at an early age will be effective for both diameter and height. Diameter has been considered to be more sensitive to environmental conditions than height (Kremer, 1992). In contrast, in this study diameter was found to be more heritable than height. Moreover, diameter is easier to measure. It would be of value to know in what circumstances diameter will have relatively high heritability, in order to make greater use of this variable in tree breeding programs.

These results of the principal component analysis suggest that the second principal components for both diameter and height reflect detailed variations in the pattern of growth which do not affect the trees' adaptation or fitness, and in which genetic variation therefore persists. Such variation could be used as an indicator of the closeness of the genetic relationship between trees, in order to maintain genetic diversity in a breeding program.

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