Genetic Control of Growth of Eucalyptus globulus in Portugal

I. Genetic and Phenotypic Parameters

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Summary

Heritabilities and genetic and phenotypic correlations of height and sectional area growth were investigated in three open-pollinated progeny trials of *Eucalyptus globulus* in central Portugal. These trials were established between 1966 and 1980 and measured on several occasions. The 82 families represented in these trials came from phenotypically superior female parents selected in Portugal, Australia and from good stands in the USA.

Results across trials were consistent and suggest strong genetic control of height growth (individual heritabilities between 0.18 and 0.34) and moderate genetic control of sectional area (heritabilities between 0.13 and 0.17). The two growth traits were always highly correlated with each other. Genetic correlations between early and late measurements of height and sectional area decrease as pairs of measurements became further apart in time. However, the correlations were always positive and high, particularly after two years (when genetic correlations were greater than 0.76).

Trends in genetic parameters did not seem to be related to growth rate of trees, even when considering short-term increments. Trends in estimates of heritabilities and correlations were similar for both increments and absolute measurements.

Key words: Heritability, juvenile-mature correlations, *Eucalyptus globulus*.

Introduction

Various environmental factors (such as nutrients, water, light) and competition between trees (stocking density) affect the growth of individual trees and hence stands over time. These factors have been used by physiologists and modellers to study growth and dynamics of stands of different ages. For the geneticists, these factors are important because they greatly influence expression of genetic potential over time. Geneticists need to know how early in the tree's life are data a good predictor of ultimate performance? At what age is there maximum resolution between genotypes? The objective of this series of papers is to study these questions for the case of growth of *Eucalyptus globulus* Labill. in central Portugal.

Variances and Heritabilities

It is clear from the forestry literature that the magnitude of additive genetic and phenotypic variances of growth traits generally change over time (*e. g.* Namkoong and Conkle, 1976; Franklin, 1979; Foster, 1986; Cotterill and Dean, 1988; Dean *et al.*, 1991) It is also clear that the ratios of these two components (*i.e.*, heritabilities) also change over time. Not surprisingly these changes in components have been different for different species and environments.

In the case of conifers, Foster (1986) reported a substantial increase in the additive genetic variance of height of *Pinus taeda* from one to 15 years, with a slight decline at age seven. Similar results are presented by Nienstaedt and Riemenschneider (1985) for *Picea glauca*. However, most published results show a general decline in relative levels of additive variance, and hence heritabilities, of height growth of *Pinus* spp. over time (Namkoong et al., 1972; Namkoong and Conkle, 1976; Franklin, 1979; Ying and Morgenstern, 1979; Birot and Christophe, 1983; Gill, 1987; Cotterill and Dean, 1988; Dean *et al.*, 1991). Cotterill and Dean (1988) reported different trends in heritability for height and diameter growth of *P. radiata* over time. Heritabilities of height decreased and those for diameter increased from around four to 16 years. In some cases (like the data presented by Namkoong and Conkle, 1976; Birot and Christophe, 1983; Foster, 1986; Cotterill and Dean, 1988; Dean *et al.*, 1991) the changes reported in additive variance over time are associated to varying degrees with different thinning regimes (*i. e.*, stocking density) and are not genetic effects *per se* (Matheson and Raymond, 1984).

In the case of hardwoods, Rink (1984) reported a rapid decline in heritability of height of *Juglans nigra* from ages one to four years, followed by a gradual increase in additive variance and heritability to 10 years. Comparable results were reported for *Liquidambar styraciflua* and *Platanus occidentalis* by Schultz (1983).

Results from *Eucalyptus* are scarce and based on relatively young trees. Kedharnath (1983) reported constant heritability of around $h^2 = 0.2$ for height of *E. grandis* to three years, increasing to $h^2 = 0.34$ at 4.5 years when trees had reached 6.5 m tall. Kedharnath and Vakashasya (1977) reported decreasing heritabilities of height of *E. tereticornis* from $h^2 = 0.42$ at one year to 0.25 at four years. Unfortunately no estimates of variance components were presented. The only published estimates of heritability of *E. globulus* appear to be Volker *et al.* (1990) who present results for growth measurements for one trial measured at six years in Tasmania, Australia. This trial was later reanalysed by Dean *et al.* (1990) with wood traits included.

Juvenile-Mature Correlations

Trends in juvenile-mature correlations over time, and the way they change according to environmental effects, has been the subject of some debate (Jiang, 1987). Early studies in *Pinus* spp. tended to conclude that juvenile-mature correlations were higher when both measurements were taken either before or after what the authors considered to be the onset of competition (Wakely, 1971; Namkoong *et al.*, 1972; Namkoong and Conkle, 1976; Franklin, 1979). To reinforce this concept Franklin (1979) attempted to divide the plantation rotation in genotype-competition phases. However, more recent studies of pines and other species suggest that juvenile-mature correlations change steadily with time and do not tend to show any strong evidence of "phases" of growth (Squillace and Gansel, 1974; McKeand *et al.*, 1979; Lambeth, 1980; Borges *et al.*, 1980; Clausen, 1982; Lambeth *et al.*, 1983b; van

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HAVERBEKE, 1983; RINK, 1984; NEBGEN and LOWE, 1985; NIENSTAEDT and RIEMENSCHNEIDER, 1985; FOSTER, 1986; GILL, 1987; COTTERILL and DEAN, 1988; DEAN et al., 1991).

Of the above studies, MCKEAND *et al.* (1979), CLAUSEN (1982), VAN HAVERBEKE (1983), FOSTER (1986), GILL (1987), COTTERILL and DEAN (1988) and DEAN et al. (1991) were able to estimate separately additive genetic correlations that reflect the extent to which genes influence both juvenile and mature traits. Several authors have wrongly assumed that genetic correlations would be approximately equal to phenotypic correlations.

In the case of *Eucalyptus* the only published report of phenotypic juvenile-mature correlations is that of GRUNDWALD and KARSHON (1984) for *E. camaldulensis*. There appear to be no published reports of genetic correlations for any species of *Eucalyptus*.

Absolute versus Increment Measurements

Most studies of trends in variance components and juvenile-mature correlations over time have been based on absolute values of growth traits and do not consider increment traits. LAMBETH *et al.* (1983b) analysed increments of height and volume between juvenile and subsequent growth to maturity in *P. taeda*, KREMER and LASCOUX (1988) analysed annual increments for height of *P. pinaster* and COTTERILL and DEAN (1988) and DEAN *et al.* (1991) analysed increments converted to an annual basis for height and sectional area of *P. radiata*. The major advantage of using increments is that it removes from the analysis the cumulative nature of growth traits, and can, therefore, provide a better indication of patterns of growth and genetic control over time. However, in the case of the present study, there was generally little difference between genetic parameters for absolute versus increment traits.

Present Study

This paper presents additive genetic and phenotypic variance components and juvenile-mature correlations over time for height and sectional area of *E. globulus*. The results are based on several measurements taken between one and 18 years of age in three open-pollinated progeny trials in central Portugal. Part II of this series (BORRALHO *et al.*, 1992) presents corresponding efficiencies of early selection based on these genetic and phenotypic parameter estimates. This series of papers appears to be the first detailed study of genetic control of growth for any species of *Eucalyptus*.

Materials and Methods

Location

All progeny trials were established by Celulose Beira Industrial (CELBI), S. A.. Two of the progeny trials study (identified locally as trials 2 and 3) are located at CELBI's Quinta do Furadouro property, central-coastal Portugal, about 10 km west of Obidos (lat. 39°15'N; long. 9°25'W; alt. 50 m). Soil is a podzolic of moderate to low fertility. Climate is Mediterranean with an average annual rainfall of 600 mm. Mean monthly temperatures for January and July are 14 °C and 23° C respectively. Previous vegetation consisted of shrubs and occasional pines.

The third progeny trial (known locally as trial 4) is located at CELBI's Calha do Grou property, central-west Portugal, about 20 km west of Santarém (lat. 39°15'N; long. 8°30'W; alt. 70m). Soil is an eutric-cambisol from sedimentary stone, of moderate fertility. Precipitation is similar to that on Quinta do Furadouro and the previous vegetation consisted of shrubs.

Silviculture

Trial 2 was disced and ploughed before trees were planted in November 1966 at a spacing of 3 m x 3 m. At planting, 100g of Foskamonia 7:21:7 fertilizer (*i. e.*, 7% N, 21% P_2O_5, 7% K_2O) was applied to each plant. Trial 3 was disced, ripped to a depth of 60 cm, and ploughed in 4 m spaced contours before trees were planted in May 1981. Spacing along each contour was 2 m. At planting, 150 g of the Foskamonia 7:7:7 fertilizer was applied to each plant. Trial 4 was disced, ripped to a depth of 60 cm, and ploughed before trees were planted in April 1980 at 3 m x 3 m spacing. At planting, 150 g of Foskamonia 7:21:7 fertilizer was applied to each plant.

Genetic Material

The 20 families in trial 2 were grown from open-pollinated seed collected in 1965 from first-generation parents selected in three genetically unimproved stands of *E. globulus* over 20-years-old, and growing in central Portugal at Quinta do Caima, Escaroupim and Quiaios.

The families assembled in trial 3 came from open-pollinated *E. globulus* seed collected in California, U.S.A., and Australia. There were 20 Californian families collected in 1979 by Drs. F. T. LEDIG and S. L. KRUGMAN (US Department of Agriculture) from trees at Folsom, Sacramento County and the University of California, Berkeley. There were 23 Australian families collected by Mr. R. K. ORME (Forestry Commission of Tasmania), from native stands at Cape Otway (Victoria), Henty River and Macquary Harbour (Tasmania), and Flinders and King Islands.

The open-pollinated seed from trial 4 was collected in 1979 from 27 clones in CELBI's Bogalheira and Quiaios clonal seed orchards. The clones represented in these orchards are first-generation parents selected between 1964 and 1970 in the same stands of *E. globulus* from which parents represented in trial 2 were selected. Only eight of these parents present in trial 4 were also included in trial 2.

Field Design

Trial 2 was established as six randomized complete blocks of 49-tree plots of 7 x 7 trees. However, only the inner 5 x 5 trees of each plot were included in the analyses of data. Trial 3 involves only two blocks with each family represented between five and 55 times in each block by 4-tree row plots. The total number of trees planted per family varied from 20 to 440. Trial 4 was established as five randomized complete blocks with each seedlot represented at least once, but sometimes up to three times, in each block by a 4-tree plot of 2 x 2 trees.

Measurements

Diameter at breast-height (1.3 m) over-bark was assessed by two measurements at right angles with a standard caliper. The diameter measurements (denoted DIA) were converted to sectional areas of stems ($SA = \pi (DIA/2)^2$). Height was assessed with a telescopic rod when trees were less than three years of age, and subsequently with a Suunto clinometer. The final height measurement reported for trial 4 was made using a tape measure after trees were felled. Between 86% and 90% of trees survived to final measurement of all trials.

All surviving trees in trial 2 were measured for height in July 1968 at *ca.* 1 year (HT1), July 1969 at *ca.* 2 years

(HT2) and December 1970 at 4 years (HT4), and for sectional area at 4 years (SA4), 8 (SA8) and 18 years (SA18). All trees from trial 3 were measured for sectional area in May 1984 at 3 years (SA3) and in January 1988, at *ca.* 6 years (SA6). A random sample of 10 to 12 trees per family were measured for height in August 1989 at ca. 8 years (HT8). Trees in trial 4 were measured for sectional area at 4 (SA4), *ca.* 6 (SA6) and 8 (SA8) years. In trial 4, height was measured by clinometer in blocks 1 and 4 at *ca.* 6 years (HT6) and by tape measure in blocks 1, 2 and 3 at 9 years when all trees in these blocks were felled.

Increments of height and sectional area were calculated for the intervals between each measurement and converted to an annual basis, assuming equal annual increments between measurements.

Data Analyses

Analyses were carried out using a mixed model least-squares program, LSMLMW, written by HARVEY (1987). The data from each progeny trial were analysed separately using the following random model - (1)

$$Y_{ijk} = \mu + f_i + b_j + (fb)_{ij} + e_{ijk} \qquad (1)$$

where Y_{ijk} representes an individual tree observation, μ the overall trial mean, f_i the effect of the ith open-pollinated family, b_j the effect of the jth randomized block, fb_{ij} the family - block interaction and e_{ijk} the within-plot error. Expected values of mean-squares for this model are shown in *table 1*. Variance components for family (σ^2_f), family-block interaction (σ^2_{fb}), and within-plot error (σ^2_w) were estimated from the analyses of variance by equating appropriate mean-squares to their expectation for random effects. Total phenotypic variance (σ^2_p) was calculated as - (2)

$$\sigma^2_P = \sigma^2_f + \sigma^2_{fb} + \sigma^2_w \qquad (2)$$

Standard errors of variance components were calculated according to BECKER (1985). Narrow-sense heritabilities (h^2) were calculated on an individual tree basis as - (3)

$$h^2 = \frac{3.3 \times \sigma^2_f}{\sigma^2_P} \qquad (3)$$

Standard errors of heritabilities were estimated according to SWIGER *et al.* (1964). The coefficient 3.3 used in Equation 3 is based on the assumption that 10% of the open-pollinated progeny in each trial are selfed. This coefficient can be read from tables in SQUILLACE (1974) under the assumption that there was 10% selfing and at least 30 unrelated pollen parents (*i. e.*, 30 non-local males; using SQUILLACE's terminology).

Although there are no direct estimates of outcrossing rates for *E. globulus*, analyses of allozyme data suggests that the mating system of a wide range of *Symphyomyrtus* (HODGSON, 1976; FRIPP, 1982; MORAN and BELL, 1983) and *Monocalyptus* (MORAN and BROWN, 1980) involves around 20% selfing and 80% outcrossing at pollination, with subsequent selection against selfed progeny (ELDRIDGE and GRIFFIN, 1983; POTTS *et al.*, 1987). In this paper we assume that the 20% selfing at pollination is reduced to around 10% selfed progeny by the time trees are planted and measured. Other authors (*e. g.* VOLKER *et al.*, 1990) have calculated heritabilities for *Eucalyptus* using slightly different assumptions of outcrossing and hence different coefficients in Equation 3. However, results are easily compared by adjusting for these different coefficients.

Table 1. — Expected mean squares for analysis of variance and covariance of individual progeny trials, where σ^2_f is the variance due to families, σ^2_{fb} family-block interaction and σ^2_w within-plot error. The k coefficients are constants estimated by the direct approach of HARVEY (1987) and were calculated as $k_1 = 20.195$, 22.156 and 4.375; $k_2 = 20.732$, 26.357 and 4.545; and $k_3 = 121.71$, 88.331 and 21.855 for trials 2, 3 and 4, respectively. In case of height traits in trial 4, the k values are lower than those given here because only a sample of trees were measured.

Source of Variation	Expected Mean Squares
Family	$\sigma^2_w + k_2\sigma^2_{fb} + k_3\sigma^2_f$
Fam x Blk	$\sigma^2_w + k_1\sigma^2_{fb}$
Within Plot	σ^2_w

Additive genetic correlations (r_A) were calculated following HAZEL *et al* (1943) and their standard errors according to TALLIS (1959). Phenotypic correlations (r_p) were based on individual tree analyses.

Results and Discussion

Trends in Growth

Table 2 presents overall means for absolute measurements and corresponding increments of sectional area and height in trials 2, 3 and 4. Height growth in trial 2 was initially slow (HT1-2 = 1.3m) but increased markedly after year two to average 3.6 m/year between two and four years (HT2-4).

It was not possible to estimate height increments for the other two trials. In the case of trial 3, height was measured twice but generally using different sets of trees at each measurement. The trees in trial 4 showed faster sectional area growth to around 4 years (*i. e.*, SA0-4 = 25 cm²/year) than in trial 3 (SA0-3 = 17 cm²/year) and, in particular, trial 2 (SA0-4 = 13 cm²/year). This faster initial growth in trial 4 is probably due to better soil preparation in the field and seedling conditioning in the nursery. The soil type and climate are reasonably similar across all three sites. Sectional area growth between three or four and six years was reasonably similar in trial 3 (SA3-6 = 24 cm²/year) and 4 (SA4-6 = 27 cm²/year). Trial 2 showed rapid growth of 32 cm²/year between 4 and 8 years.

Additive Genetic Variances and Heritabilities

Estimates of variance components, their significance and relative (percent) magnitudes are presented in *Tables 3* and *4*, for height and sectional area, respectively. Although standard errors of variances are not presented in *Tables 3* and *4*, it was apparent from analyses that for all traits across all sites, coefficients of variation were around 5% for the within-plot variance components, 15% to 37% for interactions, and 33% to 78% for family components.

Table 2. — Overall means (x ± standard deviations) for absolute and incremental height and sectional area in trials 2, 3, and 4.

Absolute Traits	x ± s.d.	Increment Traits	x ± s.d.
Trial 2			
HT1 (m)	0.8 ± 0.4		
HT2 (m)	2.7 ± 1.1	HT1-2 (m/yr)	1.3 ± 0.6
HT4 (m)	7.9 ± 2.4	HT2-4 (m/yr)	3.6 ± 1.2
SA4 (cm^2)	49 ± 35	SA0-4 (cm^2/yr)	13 ± 9
SA8 (cm^2)	176 ± 92	SA4-8 (cm^2/yr)	32 ± 16
SA18 (cm^2)	345 ± 208	SA8-18 (cm^2/yr)	17 ± 13
Trial 3			
HT8 (m)	19.2 ± 3.0		
SA3 (cm^2)	49 ± 29	SA0-3 (cm^2/yr)	17 ± 10
SA6 (cm^2)	132 ± 85	SA3-6 (cm^2/yr)	24 ± 17
Trial 4			
HT6 (m)	15.5 ± 1.9		
HT9 (m)	21.3 ± 4.0		
SA4 (cm^2)	98 ± 34	SA0-4 (cm^2/yr)	25 ± 8
SA6 (cm^2)	150 ± 54	SA4-6 (cm^2/yr)	27 ± 12
SA8 (cm^2)	195 ± 74	SA6-8 (cm^2/yr)	23 ± 11

(1) Height

Changes in the relative proportions of σ^2_f, σ^2_{fb}, and σ^2_w over time were similar for increments and absolute measurements of height. Although never more than 12% of the total variance, the family variance component (σ^2_f) for height trait were always highly significant. Family-block interaction variances (σ^2_{fb}) were negligible and non-significant in trials 3 and 4. By contrast, the interaction component in trial 2 (which had large, 49-tree plots) was between 25% and 43% of total variance and always significant. The differences between trials in relative magnitude of family-block interactions reflects the differences in trial design and plot size, as pointed out by LAMBETH *et al.* (1983b). In all trials the within-plot variance was the major source of variation averaging 54% of total phenotypic variance in trial 2, 91% in trial 3 and 88% in trial 4.

Table 3. — Estimates of family (σ^2_f), family-block interaction (σ^2_{fb}), within-plot error (σ^2_w), additive genetic (σ^2_A) and phenotypic (σ^2_P) variance components, significance levels, variance components as percentage of total variance (in parenthesis), and heritabilities (h^2 ± standard errors) for absolute measurements and incremental of height traits in trials 2, 3, and 4.

Trait	σ^2_f	σ^2_{fb}	σ^2_w	h^2 ± s.e.	σ^2_A	σ^2_P
Trial 2						
HT1	0.01 ** (7)	0.05 ** (42)	0.06 (51)	0.23±.08	0.03	0.11
HT2	0.06 ** (5)	0.44 ** (43)	0.54 (52)	0.18±.07	0.18	1.04
HT4	0.40 ** (8)	1.51 ** (32)	2.85 (60)	0.29±.09	1.31	4.75
HT1-2	0.03 ** (5)	0.22 ** (37)	0.35 (58)	0.17±.06	0.10	0.60
HT2-4	0.08 ** (8)	0.26 ** (25)	0.69 (67)	0.27±.09	0.28	1.03
Trial3						
HT8	1.42 ** (12)	0.00 ns (0)	14.71 (91)	0.29±.19	4.72	16.12
Trial 4						
HT6	0.45 ** (12)	0.00 ns (0)	4.90 (87)	0.34±.20	1.24	3.72
HT9	0.55 ** (10)	0.11 ns (2)	4.90 (88)	0.33±.19	1.81	5.56

**) $P<0.01$ *) $P<0.05$ ns Not significant

Table 4. — Estimates of family (σ^2_f), family-block interaction (σ^2_{fb}), within-plot error (σ^2_w), additive genetic (σ^2_A) and phenotypic (σ^2_P) variance components, significance levels, variance components as percentage of total variance (in parenthesis), and heritabilities (h^2 ± standard errors) for absolute measurements and incremental of sectional area traits in trials 2, 3, and 4.

Trait	σ^2_f	σ^2_{fb}	σ^2_w	h^2±s.e.	σ^2_A	σ^2_P
Trial2						
SA4	54 ** (5)	286 ** (27)	739 (68)	0.17±.06	180	1080
SA8	383 ** (6)	613 ** (8)	7157 (88)	0.16±.06	1278	8154
SA18	1677 ** (4)	990 ns (2)	40342 (94)	0.13±.05	5588	43009
SA0-4	3 ** (5)	18 ** (27)	46 (68)	0.17±.06	11	67
SA4-8	9 ** (3)	12 ** (5)	237 (92)	0.12±.05	30	258
SA8-18	5 ** (3)	3 ** (2)	154 (95)	0.11±.04	18	162
Trial3						
SA3	38 ** (4)	33 ** (4)	783 (92)	0.15±.04	127	852
SA6	324 ** (4)	190 ** (3)	6713 (93)	0.15±.04	1081	7226
SA0-3	4 ** (4)	4 ** (4)	87 (92)	0.15±.04	14	95
SA3-6	14 ** (5)	5 ** (2)	264 (93)	0.15±.04	46	283
Trial4						
SA4	64 ** (6)	0 ns (0)	1076 (94)	0.19±.10	212	1139
SA6	130 ** (4)	0 ns (0)	2912 (96)	0.14±.09	433	3042
SA8	267 ** (5)	0 ns (0)	5375 (95)	0.16±.10	891	5642
SA0-4	4 ** (6)	0 ns (0)	67 (94)	0.19±.11	13	71
SA4-6	7 ** (4)	0 ns (0)	141 (96)	0.15±.09	22	148
SA6-8	7 * (5)	0 ns (0)	124 (95)	0.18±.10	24	131

**) $P<0.01$ *) $P<0.05$ ns Not significant

Estimates of additive genetic (σ^2_A) and phenotypic variances (σ^2_P) and individual heritabilities (h^2) are also presented in *table 3*. The standard errors of heritabilities were lower in trial 2 compared with trials 3 and 4 due to the fact that more progeny were measured per family in trial 2. In trial 2 the individual heritability of height increments increased from $h^2_{HT1-2} = 0.17$ to $h^2_{HT2-4} = 0.27$. There was a substantial increase in both σ^2_A and σ^2_P between the 1 to 2 and 2 to 4 year periods (*Table 3*) which corresponded to the increased rate of growth from 1.3 m/year to 3.6 m/year over these two periods (*Table 2*). It is apparent from *table 3* that σ^2_A increased more than σ^2_P between 1 to 2 and 2 to 4 years, leading to the increase in heritability. These trends in increment traits are reflected in the increase in heritability of absolute measurements from two ($h^2 = 0.18$ for HT2) to four years $h^2 = 0.29$ for HT4).

In trial 4 the individual heritabilities of HT6 and HT9 were consistent at $h^2 = 0.34$ and 0.33. There was an increase in both σ^2_A and σ^2_P from six to nine years (*Table 3*) reflecting the increased size of trees from 15.5 m to 21.3 m (*Table 2*). Although the two traits HT6 and HT9 are not directly comparable because they are based on different data sets, is clear that σ^2_A increased by the same propor-

tion as σ^2_P, and heritabilities, therefore, remained constant.

It is interesting to note that σ^2_P for HT8 in trial 3 is around three times larger than σ^2_P for HT9 in trial 4. This is despite the fact that mean height at nine years in trial 4 is actually greater than the mean height at eight years in trial 3 (21.3 versus 19.2, *Table 2*). One explanation for this much greater phenotypic variation in trial 3 is the fact that the families in this trial are from different origins (Australia and California) and may be more variable. By contrast the families in trial 4 are from clonal seed orchards in Portugal and would be expected to be more uniform. This is discussed in more detail later in this paper. Despite these differences in genetic origin of progeny between trials 3 and 4 the heritabilities of absolute height at eight or nine years in the two trials were essentially the same at $h^2 = 0.29$ and 0.33.

In conclusion, from results of these trials it appears that the heritability of height growth for *E. globulus* in central Portugal is moderate to high (between $h^2 = 0.17$ and 0.34). Since many stands are felled at around 10 years the heritabilities reported here span the productive life of commercial plantations. Heritability estimates were similar for both absolute and incremental data, and did not appear to be greatly affected by the magnitude of phenotypic variation in different trials. VOLKER *et al.* (1990) estimated $h^2 = 0.16$ for height at nine years of *E. globulus* in Tasmania. Note this estimate attributed to VOLKER and colleagues has been adjusted to meet the same assumptions of an average 10% selfing as used herein.

(2) Sectional Area

Within-plot error was the most important source of variation for sectional area accounting for up to 96% of total phenotypic variance. Family-block interactions were absent from trial 4, but significant in trials 2 and 3 with the exception of the trait based on measurement at 18 years. The component of variance due to families were similar in all trials, between 3% and 6% of total variation and consistently statistical significant (*Table 4*).

In trial 2 the individual heritability of sectional area increment decreased over time from $h^2_{SA0-4} = 0.17$ to $h^2_{SA4-8} = 0.12$, and $h^2_{SA8-18} = 0.11$, although differences between pairs of estimates were always less than one standard error. This trend of decreasing heritability is due to a much larger increase in σ^2_P compared with σ^2_A over time. The increase in σ^2_P after four years corresponds to more than doubling in actual growth increments between the 0 to 4 and 4 to 8 year periods (*Table 2*). Sectional area growth in the subsequent period from 8 to 18 years almost halved (*Table 2*) and both σ^2_A and σ^2_P decreased (*Table 4*), but the ratios of σ^2_A/σ^2_P (and, therefore, heritability) remained approximately constant.

As found for height, it is apparent that the changes in heritability from period to period are not directly related to the size of growth increments and associated phenotypic variances. In trial 2, for example, there was a clear decrease in heritability between 0 to 4 and 4 to 8 years despite the actual growth increments more than doubling from 13 cm²/year for SA0-4 to 32 cm²/year for SA4-8 (*Table 2*). However, for the 4 to 8 and 8 to 18 year periods the halving of sectional area increment was not followed by any significant change in heritability.

It is interesting that in trial 4 the decrease and increase in heritability of sectional area increments corresponds to exact opposite trends in sectional area growth rates (*Table 2*) and, hence, levels of σ^2_P (*Table 4*). However, the actual size of changes in sectional area increments from one period to another in trial 4 were not as great as they were in trial 2. In trial 3 the heritability of sectional area remained the same ($h^2 = 0.15$) between 0 to 3 and 3 to 6 years, reflecting an equivalent increase in both σ^2_A and σ^2_P. This constant heritability is despite a substantial increase in the actual rate of growth between the two periods.

Heritabilities of absolute sectional area measurements reflected changes in heritabilities of increments. For instance, in trial 2, SA4 had the same heritability as SA0-4 ($h^2 = 0.17$). However, the lower heritability of the subsequent 4 to 8 years sectional area increments ($h^2_{SA4-8} = 0.12$) lead to a reduction in heritability of absolute SA8 to $h^2_{SA8} = 0.16$. There was further decrease in heritability of the corresponding increment.

In conclusion, the heritability of absolute and increment sectional area traits seem to be moderate (between $h^2 = 0.11$ and 0.19) and lower, but more stable, than those for height. There was no apparent association between trends in heritability and actual sectional area growth rates. In some cases (trials 2 and 4), increases in growth rate lead to increase in σ^2_P of increment traits but no change in heritability.

The finding of higher heritabilities for height compared with diameter of *E. globulus* in this study is not supported by VOLKER *et al.* (1990). However, their study was based on one small progeny trial which had been thinned to a wide spacing (6 m x 6 m). It is known that thinning can substantially increase heritabilities of diameter (MATHESON and RAYMOND, 1984).

Population Differences in Variance

In trial 3 separate analyses of variance were carried out on Californian versus Australian families. Although results are not presented in *tables 3* and *4* it was apparent that the Californian families gave slightly more additive (σ^2_A) and less phenotypic (σ^2_P) variance than Australian families. For instance, in the case of SA6, $\sigma^2_A = 833$ cm² and 963 cm², $\sigma^2_P = 7480$ cm² and 6592 cm² for analyses of Australian and Californian families, respectively. The lower σ^2_P for Californian families was due to lower growth with means of SA6 = 125 cm² for progeny of Californian parents versus 134 cm² for progeny of Australian parents.

Unfortunatly, it is difficult to include Portuguese families in these populations comparisons because they were represented in trials 2 and 4, but not in trial 3. However, sectional area also happened to be measured at six years in trial 4. Although the overall trial mean for SA6 was higher in trial 4 compared with trial 3 (*Table 2*), the phenotypic variance of the Portuguese families in trial 4 was lower (*Table 4*). This may not be surprising since trial 4 is in a more homogeneous site and the Portuguese families in trial 4 are of seed orchard origin and, therefore, represent a more narrow genetic base.

Correlations Between Juvenile Traits and SA8/SA18

Additive genetic and phenotypic correlations between juvenile growth traits measured to eight years and the mature traits SA8 or SA18 measured in trials 2 and 4 are presented in *table 5*. The best information on juvenile-mature correlations is from trial 2 which was measured for height and sectional area at reasonably frequent intervals over 18 years.

Table 5. — Additive genetic ($r_A \pm$ standard errors) and phenotypic (r_P) correlations among absolute height traits in trial 2.

Juvenile Traits	SA8		SA18	
	$r_A \pm$ s.e	r_P	$r_A \pm$ s.e	r_P
Trial 2 Height				
HT1	0.40±.24	0.45	0.46±.23	0.36
HT2	0.81±.14	0.59	0.76±.16	0.48
HT4	0.96±.04	0.82	0.91±.07	0.70
Trial 2 Sect.Area				
SA4	0.99±.02	0.86	0.95±.05	0.71
SA8	1.00	1.00	0.95±.03	0.93
Trial 4 Sect.Area				
SA4	0.99±.03	0.90		
SA6	0.99±.09	0.96		

(1) Juvenile Height

All height traits in trial 2 were positively correlated with SA 8 and SA18, but it is apparent that correlations increased as pairs of measurements become less temporally separated. For instance, the additive genetic correlation between HT1 and SA18 (r_A = 0.46 ± 0.23, *Table 5*) was lower in magnitude and with a higher standard error than corresponding correlations between HT2-SA18 (r_A = 0.76 ± 0.16) and HT4-SA18 (r_A = 0.91 ± 0.07). The genetic correlations between juvenile height traits and SA8 were generally somewhat higher in magnitude than corresponding correlations involving SA18 (whith the exception of the correlations between HT1-SA8 and SA18, *Table 5*). Although results are not presented, the correlations involving juvenile height increments were, in general, reasonably similar to corresponding correlations involving juvenile absolute height traits.

Perhaps the most interesting feature of the trends for height traits in trial 2 is the substantial increase in juvenile-mature correlations involving HT2 (measured when the average size of trees was *ca.* 3 m, *Table 2*) compared with corresponding correlations involving HT1 (when trees averaged *ca.* 1 m). It is apparent that HT2 is a much better predictor than HT1 of subsequent sectional area at 8 or 18 years. This increase in correlation may be due primarily to better resolution between genotypes at around two years in their genetic potential for subsequent growth. It is possible that HT1 and HT2 are two very different traits. HT1 may measure ability to grow in the nursery and withstand transplanting stress. HT2 reflects ability to grow after planting in field. In the case of *Pinus* spp., Lambeth (1980) commented that trees should be more than around 3 m tall before juvenile-mature correlations become significant for growth traits.

The juvenile-mature correlations involving absolute height traits increased further between two and four years in trial 2. However, during this period the mean height of trees increased very substantially from *ca.* 3 m (for HT2) to *ca.* 8 m (for HT4). These higher correlations between HT4-SA18 compared with HT2-SA18 must be due at least partly to the fact that the height measurement of 8 m trees represents a substantial contribution to the final size of trees at 8 to 18 years. Lambeth *et al.* (1983b) and McKinley and Lowe (1986) point out that because growth traits are cumulative, the magnitude of juvenile-mature correlations reflect not only genetic and phenotypic effects, but also the amount of early growth in the mature stage.

Another interesting feature of *table 5* is the fact that genetic correlations were generally higher than the corresponding phenotypic correlations. Similar findings were reported by Lambeth *et al.* (1983b) for *P. taeda,* and Cotterill and Dean (1988) and Dean *et al.* (1991) for *P. radiata.*

(2) Juvenile Sectional Area

The additive genetic correlations between SA4 and SA8 or SA18 in Trial 2 were consistently strongly positive ($r_A \geqslant 0.95$) with very low standard errors (*Table 5*). Corresponding correlations involving juvenile sectional area traits were also very strong in trial 4. The phenotypic correlations were again lower than corresponding additive genetic correlations.

Correlation Among Juvenile Traits

(1) Height

Table 6 presents correlations between absolute juvenile height traits in trial 2. The trend is again apparent for correlations to increase as pairs of measurements become closer in time. Results are not presented for increments traits but the general trends were similar.

(2) Sectional Area

The sectional area traits measured at 3, 4 or 6 years in trial 3 and 4 were very strongly positively correlated, with r_A and $r_P \geqslant 0.86$. It is interesting that *E. globulus* in Portugal changes foliage type from juvenile glaucous leaves to adult leaves at between two and four years, but this does not appear to have any major influence on correlations among traits at differents ages.

Conclusions

Height was shown to be under strong additive genetic control with heritabilities being larger for later measurements, whereas sectional area was under moderate genetic control. It seems more efficient, therefore, to base selection on height rather than on sectional area to improve growth in *E. globulus* in central Portugal. The genetic and phenotypic variances for growth traits appeared to be somewhat different across the various populations of *E. globulus* studied *(i. e.* Portuguese, Australian, and Californian families).

Changes in heritability of sectional area and height appeared to have little relationship with trends in the

Table 6. — Additive genetic ($r_A \pm$ standard errors) and phenotypic (r_P) correlations among absolute height traits in trial 2.

Trait	HT1	HT2	HT4
HT1		0.83±.09[A]	0.56±.19
HT2	0.82[B]		0.90±.07
HT4	0.62	0.88	

A) Additive genetic correlations above diagonal.
B) Phenotypic correlations bellow diagonal.

actual growth rates of trees. This was particularly evident for sectional area where, despite substantial changes in the magnitude of growth and phenotypic variance over time and from trial to trial, estimates of heritability remained relatively stable. Another interesting feature was that no marked differences were found between the estimates of heritability from absolute and incremental measurements. All absolute and incremental height and sectional area traits measured between two and six years were strongly genetically correlated with SA8 and SA18.

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