

Genetic parameter estimates for growth traits in *Eucalyptus grandis*: some implications for breeding and commercial seed production

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ABSTRACT

Data from five first-generation open-pollinated progeny tests of *Eucalyptus grandis* growing in Uruguay were used to estimate genetic parameters for survival and growth traits at 8, 32, and 56 months. Family heritability for survival ranged from 0 to 0.86. Single site heritabilities for height varied from 0.10 to 0.38; for diameter at breast height (DBH) they varied from 0.08 to 0.43 and for volume from 0.08 to 0.38. Genetic correlations for a given trait at different ages were moderate to high for height (between 0.58 to 0.92) and for DBH (0.69 to 0.91) and they were high for individual tree volume (0.80 to 0.91). Genetic correlations between survival and volume per tree were low to moderate (0.09 to 0.57) but always positive. Genetic correlations between growth traits at a given age were high, ranging from 0.88 to 0.99 at 32 months and between 0.85 to 0.99 at 56 months. Type B genetic correlations for volume were very low to moderate (-0.01 to 0.68) at 32 months and low to moderate (0.21 to 0.72) at 56 months, indicating high genotype x environment interactions. Implications of these genetic parameters for breeding (breeding units, progeny test designs, selection criteria and selection ages) and for commercial seed production (deployment, upgrading and directed harvest of seed orchards) are discussed.

KEYWORDS: heritability, genetic correlation, Type B genetic correlation, *Eucalyptus grandis*, Uruguay

INTRODUCTION

Because of its fast growth, good form and wood suitable for different uses (pulpwood, poles and sawn timber) *Eucalyptus grandis* is the most widely planted species in Uruguay, with about 130 thousand hectares (Division Forestal 1999). Most of the seed used for old plantations in the country with this species derived from the first introduction, in 1963, from South Africa (Brussa 1994). Although this source, known as Bañado Medina, is still used for its relatively well performance, new large scale plantations are established with other seed sources, mainly from seed orchards of South Africa and USA, often without any local evaluation.

The necessity to provide nurseries and growers with a regular supply of locally improved seed lead INIA's Forestry Program (National Institute of Agricultural Research) to start in 1992 with a Tree Improvement Program for *Eucalyptus grandis*. Due to the limited availability of resources, mainly of personnel, the feasibility of this plan depends largely on its simplicity and low cost. The breeding strategy has, therefore, the following key features: (a) a multipurpose population managed to serve successively as progeny test, breeding population and production population; (b) a series of progeny tests that support the multipurpose population with genetic information; (c) open-pollinated management of the breeding and production populations; (d) short generation interval; (e) important infusion of new material each generation.

Currently, INIA's plan for *E. grandis* has two overlapping generations with a 5-year interval. The first-generation, through the transformation of the multipurpose population on a seedling seed orchard, is producing commercial seed from 1998. However, first-generation progeny tests will continue generating genetic information along with the second-

generation progeny tests. As the short term breeding objective is to maximize productivity per unit area, genetic parameters for survival and growth rate are estimated and used to take decisions in many stages of both the first and the second generations. The overall goal of this paper is to present locally estimated genetic parameters (heritabilities, age-age genetic correlations, between trait genetic correlations and type B genetic correlations) for survival and growth traits from the first generation of *E. grandis* and to discuss some implications of them for the breeding and seed production strategies.

MATERIALS AND METHODS

Progeny tests

In 1993 INIA installed its first-generation base population of *E. grandis*, composed by a multipurpose population and a series of progeny tests in different sites. The first-generation genetic base has 180 open-pollinated families from two mayor sources: provenances from most of the natural range and mass selected trees on local commercial plantations. The sites and trial designs details of the five progeny tests assessed and utilized to estimate genetic parameters are summarized in Table 1.

Traits assessed

Total height was measured and survival calculated at 8, 32 and 56 months after planting. Diameter at breast height (DBH) was measured at 32 and 56 months and individual tree volume (overbark) calculated for those two ages. The multipurpose population (test OL-30) was measured only until 32 months because at that age it was selectively rouged.

Table 1. Details of the sites, experimental design and composition of the progeny tests and multipurpose population.

Test code	Forestry zone	Latitude	Longitude	Soil type	Experimental design	Trees per plot	Seed sources	Number of families
O-21	7	31° 39' S	56° 02' W	Deep Sandy	RCB with 6 replications	10	Australian provenances	80
O-23	8	32° 10' S	55° 32' W	Medium depth Loamy/Sandy	RCB with 6 replications	10	Australian provenances	58
L-27	7	31° 10' S	55° 50' W	Deep Sandy	RCB with 10 replications	5	Local selections	111
L-29	8	32° 10' S	55° 32' W	Medium depth Loamy/Sandy	RCB with 10 replications	5	Local selections	85
OL-30	7	31° 40' S	56° 00' W	Deep Sandy	RCB with 30 replications	1	Aust. prov. + Local select.	180

Data analysis

Variance component estimates were calculated using Proc Varcomp (method REML) of SAS (1989). Family heritability for survival and standard errors were estimated as:

$$h_f^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{\sigma_e^2}{r}} \quad \text{and} \quad \text{s.d.}(h_f^2) = \frac{\sqrt{\text{Var}(\sigma_f^2)}}{\sqrt{\left(\sigma_f^2 + \frac{\sigma_e^2}{r}\right)^2}}$$

where σ_f^2 and σ_e^2 are variance components due to families and error; r is the number of replications and $\text{Var}(\sigma_f^2)$ is the variance of the variance component for families.

Assuming a coefficient of relationship of 0.4 to adjust for deviations from a half-sib relationship, single-site individual heritabilities and standard errors for growth traits were estimated as:

$$h_i^2 = \frac{2.5(\sigma_f^2)}{\sigma_f^2 + \sigma_{br}^2 + \sigma_e^2} \quad \text{and} \quad \text{s.e.}(h_i^2) = \frac{\sqrt{6.25 * \text{Var}(\sigma_f^2)}}{\sqrt{(\sigma_f^2 + \sigma_{br}^2 + \sigma_e^2)^2}}$$

where σ_f^2 ; σ_{br}^2 and σ_e^2 are variance components due to families, block by family interaction and error, respectively and $\text{Var}(\sigma_f^2)$ is the variance of the variance component for families.

Genetic correlations between ages for a given trait, between traits and between a trait on different sites (Type B) and corresponding standard errors were estimated as:

$$r_g = \frac{\text{COV}_f(xy)}{\sqrt{\text{Var}_f(x)} * \sqrt{\text{Var}_f(y)}} \quad \text{and} \quad \text{s.e.}(r_g) = \frac{1 - r_g^2}{\sqrt{2}} * \frac{\sqrt{\sigma(h_x^2) * \sigma(h_y^2)}}{\sqrt{h_x^2 * h_y^2}}$$

where $\text{COV}_f(xy)$ is the covariance among family means of traits x and y ; $\text{Var}_f(x)$ and $\text{Var}_f(y)$ are the variance of family means of both traits; h_x^2 and h_y^2 are heritabilities for x and y ; $\sigma(h_x^2)$ and $\sigma(h_y^2)$ are standard errors of the heritability of x and y .

RESULTS AND DISCUSSIONS

Heritability estimates

Family heritability and standard errors for survival at different ages are presented in **Table 2**. Family heritability estimates for survival ranged from 0 to 0.86. Due to the very high survival at early ages family variation was negligible and family heritability very low, ranging from 0 to 0.35 at 8 months and from 0.25 to 0.59 at 32 months. At 56 months mortality was slightly higher and family heritability increased, ranging from 0.39 to 0.86.

Table 2. Test mean survival, family heritability and standard errors for survival at 8, 32 and 56 months (S8, S32 and S56).

Trait	Test	O-21	O-23	L-27	L-29
S (8)	Mean (%)	97.9	98.4	90.3	95.1
	$h_f^2 \pm \text{s.e.}$	0.00 \pm 0.00	0.26 \pm 0.20	0.00 \pm 0.00	0.35 \pm 0.16
S (32)	Mean (%)	87.7	95.9	87.5	93.8
	$h_f^2 \pm \text{s.e.}$	0.37 \pm 0.17	0.59 \pm 0.19	0.25 \pm 0.14	0.33 \pm 0.16
S (56)	Mean (%)	85.9	88.7	86.3	91.5
	$h_f^2 \pm \text{s.e.}$	0.78 \pm 0.16	0.86 \pm 0.19	0.40 \pm 0.14	0.39 \pm 0.16

Single-site narrow-sense heritability estimates for growth traits (height, DBH and tree volume) at different ages are presented in **Table 3**. Heritability estimates were similar for different traits, ranging between 0.10 and 0.38 for height; between 0.08 and 0.43 for DBH and between 0.08 and 0.38 for tree volume. Standard errors were relatively low in all cases, ranging between 0.02 and 0.09. These heritability estimates were calculated for a single site and therefore they may be biased upwards by the presence of genotype x environment interaction (Hodge and White 1992).

In general, there is no clear effect of soil type, seed source or test design on heritability estimates with the exception of the higher

heritability values and lower standard errors obtained on progeny test OL-30, which has a single-tree-plot design and larger number of families. The effect of age on heritability seems to be erratic, increasing in some tests but not in others or first increasing and then decreasing, contrasting with other reports for growth traits on *E. grandis* where heritability increases with age (Borges and Brune 1983; Reddy 1985; Van Wyk 1990). Previously published heritability estimates for growth traits on open-pollinated *E. grandis* range between 0.08 and 0.75 (Assis and Brune 1983; Bierwagen et al. 1996; Borges and Brune 1983; Reddy 1985; Van Wyk 1983; Verryn et al. 1997). The estimates presented here tends to lie towards the lower end of that range, being a possible reason for that the low coefficient of relationship (0.4) used to adjust heritabilities for deviations from a half-sib relationship. Heritability estimates in progeny test OL-30 for tree volume on each source separately were higher for Australian progenies (0.38 \pm 0.07) than for locally selected progenies (0.21 \pm 0.05), suggesting that a coefficient of 0.4 could be adequate when progenies came from natural stands but it might be too conservative for commercial plantations selections.

Table 3. Heritability and standard errors for height at 8, 32 and 56 months (H8, H32 and H56); DBH at 32 and 56 months (D32 and D56) and tree volume at 32 and 56 months (V32 and V56).

Trait Test	O-21	O-23	L-27	L-29	OL-30
H8	0.10 \pm 0.04	0.25 \pm 0.07	0.10 \pm 0.03	0.17 \pm 0.08	0.27 \pm 0.04
H32	0.13 \pm 0.04	0.38 \pm 0.09	0.17 \pm 0.04	0.13 \pm 0.07	0.29 \pm 0.04
H56	0.22 \pm 0.05	0.28 \pm 0.07	0.13 \pm 0.03	0.12 \pm 0.05	-
D32	0.10 \pm 0.04	0.33 \pm 0.08	0.16 \pm 0.03	0.08 \pm 0.06	0.43 \pm 0.05
D56	0.29 \pm 0.06	0.29 \pm 0.06	0.12 \pm 0.02	0.08 \pm 0.03	-
V32	0.08 \pm 0.03	0.25 \pm 0.07	0.17 \pm 0.03	0.10 \pm 0.06	0.38 \pm 0.05
V56	0.24 \pm 0.05	0.26 \pm 0.06	0.13 \pm 0.03	0.10 \pm 0.04	-

Genetic correlations

Age-age genetic correlation estimates for height, DBH and tree volume are shown in **Table 4**. Height at 8 months was in general moderately correlated with the same trait at 32 or 56 months (r_g range between 0.58 to 0.91). Between 32 and 56 months (third and fifth years) genetic correlations for height, DBH and tree volume were generally high, ranging between 0.69 to 0.92. These values are within the range of previously reported estimates of genetic correlations for growth traits on *E. grandis* which range between 0.50 and 0.98 (Borges and Brune 1983; Malan 1988; Lambeth et al. 1994; Van Wyk 1990).

Genetic correlation estimates between survival, height and DBH with tree volume at a given age are presented in **Table 5**. Genetic correlations between survival and tree volume were all positive but low to moderate (0.09 to 0.57). Chambers et al. (1995) reported similar results for *E. globulus* at age 4 years, with genetic correlations between survival and diameter ranging from 0.08 to 0.81. Genetic correlations between height and DBH with individual tree volume were high, ranging between 0.85 and 0.99, being slightly higher for DBH.

Type B genetic correlations (i.e. calculated for the same trait expressed in two different sites) are presented in **Table 6**. Genetic correlations between sites for tree volume (V) were very low to moderate (-0.01 to 0.68) at 32 months and low to moderate (0.21 to 0.72) at 56 months, indicating the presence of high genotype x environment interaction. However, if pair of sites involving progeny test L-29 are excluded, correlations are moderate (ranging from 0.52 to 0.72), suggesting that genotype x environment interaction could be less important than it appears at first view. Although forestry zones 7 and 8 are climatically similar, some level of genotype x environment interaction may be expected due to differences in soil type, site history and cultural practices.

Table 4. Genetic correlations between ages (8, 32 and 56 months) for height (H), DBH (D) and tree volume (V) and corresponding standard errors.

Test Trait (ages)	O-21	O-23	L-27	L-29	OL-30
H (8-32)	0.63±0.15	0.72±0.09	0.68±0.10	0.91±0.06	0.72±0.05
H (8-56)	0.58±0.14	0.58±0.12	0.62±0.11	0.76±0.13	-
H (32-56)	0.92±0.03	0.88±0.04	0.78±0.06	0.84±0.10	-
D (32-56)	0.87±0.05	0.91±0.03	0.89±0.03	0.69±0.20	-
V (32-56)	0.91±0.03	0.90±0.03	0.88±0.03	0.80±0.12	-

Table 5. Genetic correlations between survival (S), height (H) and DBH (D) with tree volume (V) at ages 32 and 56 months and corresponding standard errors.

Test Traits (age)	O-21	O-23	L-27	L-29	OL-30
S - V (32)	0.57±0.20	0.44±0.17	0.25±0.21	0.14±0.37	-
S - V (56)	0.54±0.10	0.57±0.11	0.26±0.19	0.09±0.28	-
H - V (32)	0.88±0.05	0.92±0.03	0.88±0.03	0.92±0.06	0.89±0.02
H - V (56)	0.92±0.02	0.92±0.03	0.90±0.03	0.85±0.08	-
D - V (32)	0.96±0.02	0.98±0.01	0.99±0.003	0.97±0.03	0.99±0.002
D - V (56)	0.98±0.01	0.98±0.01	0.99±0.003	0.97±0.02	-

Table 6. Site-site genetic correlation estimates for tree volume at 32 and 56 months and corresponding standard errors.

Tests Trait (age)	O-21/O-23	O-21/OL-30	O-23/OL-30	L-27/L-29	L-27/OL-30	L-29/OL-30
V(32)	0.52±0.17	0.56±0.11	0.62±0.08	-0.01±0.23	0.68±0.06	0.22±0.19
V(56)	0.72±0.07	-	-	0.21±0.21	-	-

IMPLICATIONS FOR SELECTION

The breeding objective of a tree improvement plan should be under at least moderate genetic control and must have considerable economic value (Zobel and Talbert 1984). Productivity, which is dependent on both the volume per tree and survival, is one of the main factors affecting profitability for any final product. Within INIA's tests, family heritability for survival was low at early ages, when average survival was high. As stated by Chambers and Borralho (1996), the importance of including survival as a selection trait increases as mortality increase. When survival exceeds 90 % it seems that family information for survival is of little relevance in order to improve productivity per unit area. Growth traits, however, are at least under moderate genetic control (h^2 from 0.08 to 0.43), suggesting that selection for productivity in the *E. grandis* breeding plan of INIA is likely to be successful. The higher heritabilities and lower standard errors found for all traits in test OL-30 indicates that the single-tree-plot design provides a better environmental control and a higher precision on genetic parameter estimates. Besides, this design allows to accommodate a larger number of progenies in a single test, simplifying the prediction of breeding values and the ranking of parents.

Shortening the generation interval in forest tree breeding is essential to maximize genetic gains per unit time (Borralho et al. 1992). The presence of high juvenile-mature correlations is one of the most important factors to achieve an efficient early selection (Falconer and Mackay 1996). Genetic correlations between growth traits at ages 32 and 56 months were high (r_g between 0.67 and 0.92), suggesting that selection for growth characters at the third year of evaluation is feasible on INIA's plan. Even first-year growth has moderate correlation with fifth-year (r_g between 0.58 and 0.76) and that could be theoretically the selection age. However, in that case genetic gain would be lower than with third-year selection and, as *E. grandis* begin to flower at the

third or fourth year, there is no practical advantage from the breeding point of view to reduce the testing phase of the plan. In other words, trees could be selected for the second generation (forward selections) as early as the first-year but they will not flower massively and therefore no seed will be obtained until the fourth year. In fact, INIA's multipurpose population functioned as breeding population on its fourth year and the second generation was effectively installed in 1998, five years after the first generation.

Genetic correlation estimates between traits give an indication of the opportunity for indirect selection and give also an indication of the impact of selecting for a trait over other traits. In the analyzed tests, survival was rather poorly but positively correlated with individual tree volume. This positive relationship proves that selecting families with superior growth will also improve survival. Genetic correlations between growth traits (height, diameter and volume) are very high for a given age indicating that indirect selection for volume is possible. Tests measurement is costly and time consuming, particularly the measurement of height after the third or fifth year. Tree volume and DBH have similar levels of genetic control and are highly correlated, suggesting that DBH after the third year could be used as selection criteria, being a clear opportunity to reduce costs and time without sacrifice volume gain. Although not estimated here, there are evidences that growth traits in *E. grandis* are positively correlated with other important traits as cold hardiness (Van Wyk 1976; Meskimen et al. 1987; Franklin and Meskimen 1983; Rockwood 1991; Balmelli 1997) and stem straightness (Van Wyk 1990; Lambeth et al. 1994), implying that selection for those traits could be simultaneously accomplished. From another point of view, even more important for a low cost breeding plan, selection for fast growth could indirectly improve cold tolerance and stem form.

The knowledge of the magnitude and type of genotype x environment interaction is crucial for any breeding program to delineate breeding units (Burdon 1977). Type B genetic correlations calculated for volume in two different sites (forestry zones 7 and 8) were low to moderate, suggesting that the level of genotype x environment interaction is important enough to be taken into account on INIA's plan. The extreme decision will be the establishment of two separate breeding units, that is, one complete breeding program for each forestry zone. Although the relation benefit/cost might be positive, it is operationally impossible for the current availability of resources. A less ambitious alternative would be the concentration of resources in only one zone to maximize genetic gains in it. However, the low correlations and high standard errors found when involving test L-29 and the tendency for Type B correlations to increase with age suggests that further analysis is required to better understand genotype x environment interaction before any decision on breeding unit delineation is to be taken. In the meantime, a cautious alternative for INIA's breeding program is to continue working for both forestry zones, either by selecting genotypes suited for both zones or by selecting genotypes suitable for each specific zone.

IMPLICATIONS FOR BREEDING AND COMMERCIAL SEED PRODUCTION

Besides the advantages of the completely randomized single-tree-plot design for testing and ranking large number of parents, this design is adequate for breeding and for seed production, particularly for breeding plans that rely entirely on open pollination. After the first selection has been applied and the multipurpose population is rouged, mating between selected trees are allowed to induce genetic recombination. Outcrossing will be favored by single tree plots and the offspring from these matings (forwards selections), will contribute with great genetic variability to the second generation. Once a broad genetic base is assured for the next generation, a more intensive second selection

will give the multipurpose population the function of production population. Outcrossing in a seed orchard is also desirable to avoid inbreeding depression which reduces the amount of seeds and their germination capacity, decreases nursery and field survival and reduces field growth (Eldridge et al. 1994).

The estimated first-generation genetic parameters are used to guide the multipurpose population management. High age-age genetic correlations for growth traits suggest that deployment on the multipurpose population could be effectively done in two steps: a first rogue with low intensity at the third year and a second rogue, more intense, at the fifth year. In the first step the poorest families are completely eliminated together with the poorest trees of the remaining families. This rogue reduces the stand density and thus promotes abundant flowering, allowing to obtain forward selections at the fourth year. After a new rank of families at the fifth year, the second rogue will leave the best families and trees to produce commercial seed on successive years. Provided an important number of families remains after the second rogue, the production population could even be upgraded later if other characters, like wood traits or pest and disease tolerance, become important.

Part of the genotype x environment interaction, inferred from the Type B genetic correlations, could be exploited through directed harvest on the production population. Although all the retained families contribute pollen, only the very best families for each zone will serve as mother trees, being harvested separately to conform two different seedlots. In this way, trees from generally adapted families will serve as both, father and mother trees, and trees from families adapted for a specific zone will only serve as mother trees.

CONCLUSIONS

The single-tree-plot design is especially suited to the "multipurpose population" strategy. For the progeny test function, it provides good environmental control and high precision on genetic parameter estimates. For the breeding and seed production functions, it favors outcrossing which permits its open-pollinated management. Overall, single-tree-plot allows different functions for a single field location, reducing the costs and time of breeding.

From the selection point of view, family heritabilities for survival and genetic correlations between survival and volume per tree were in general relatively low, indicating that in order to maximize productivity per unit area, family information for survival will be of little help. Instead, individual heritabilities for growth traits were moderate and genetic correlations between growth traits were high, suggesting a higher efficiency of selecting for DBH or volume per tree. Early selection for growth traits is also possible, permitting a rapid turnover of generations to maximize genetic gain per unit time.

The INIA's breeding plan for *E. grandis* is simple and of low cost, however, a similar plan for this species has proved to be very successful in Florida (USA) where realized gains of 100 % for stem volume at 2.5 years were obtained after four generations of selection (Franklin 1988). Realized gains from the first-generation of INIA's plan will be quantified through yield trials that were installed in 1999 on different sites.

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