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Age–age and trait–trait correlations for *Eucalyptus grandis* Hill ex Maiden and their implications for optimal selection age and design of clonal trials

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Abstract Previous results from seven locations of *Eucalyptus grandis* clonal trials in Colombia supported the *a priori* contention of sub-dividing them into three different environmental zones for testing and deployment. Within these zones, the determination of age–age genetic correlations for both height and mean annual increment (MAI) showed that strong age–age correlations are present for a rotation age of 6 years starting at 3 years age and, thereafter, suggesting this age as appropriate for selection. This biological selection age coincides with an "economical" age for selection based on discounted selection efficiency in perpetuity, considering a range of interest rates between 10% and 20%. High genetic correlations between wood density at 3 years and 6 years as well as the lack of genetic correlation between this trait and growth traits, also favors selection at age 3 and facilitates breeding strategies that consider the utilization of both traits for improvement. A simulation of optimal clonal test designs indicated that by using six locations and six blocks per location in a single-tree plot design, between 80% and 90% of the maximum selection efficiency could be obtained. This type of design allows testing of a large number of genotypes across a reasonable number of locations in a cost-effective manner.

Keywords *Eucalyptus grandis* · Clonal locations · Genetic correlations · Selection age

Introduction

Developing clonal forestry in *Eucalyptus* spp. to enhance both plantation productivity and product uniformity (Lambeth et al. 1989; Denison and Kietzka 1993; Bertolucci et al. 1995; Araujo et al. 1997) requires estimation of basic genetic parameters in order to determine the best strategies for clonal testing and breeding, and to predict genetic gains from deploying the best clones (White 1996). Genetic parameters such as heritabilities and genotype by environment interaction for growth traits and wood density from these trials were reported in a previous paper (Osorio et al. 2001), but age–age and trait–trait correlations are also needed for choosing trial locations, determining optimal selection age, and formulating breeding strategies.

Selection in trials is usually conducted before rotation age with the purpose of minimizing the generation interval and consequently increasing genetic gain per unit of time. Half rotation age is a common age for final assessment of families and individuals (Franklin 1979; Zobel and Talbert 1984) and several studies have been done to examine selection at a much earlier age (Lambeth 1980; Cotterill and Dean 1988), even in the nursery or in a controlled environment facility (Williams 1988; Surles et al. 1993).

Optimal selection ages are commonly based either on gains per unit of time (Lambeth et al. 1983; Falconer 1993) or on a method that incorporates the time value of money such as in present value analyses in economics (McKeand 1988; White and Hodge 1992; Balocchi et al. 1994). These latter methods calculate discounted selection efficiencies that penalize (or discount) the value of selection at later ages to various degrees based on an interest or discount rate. The incorporation of the risk associated with selection at juvenile ages has also been explored as a criterion for decision making of the optimum selection age (Newman and Williams 1991).

For *Eucalyptus* species managed on short rotations of 6 to 8 years, optimal selection age based on discounted selection efficiencies (DSE) could be based on an infinite number of generations. This concept, called discounted selection efficiency in perpetuity, would account for the repeated benefits of early selection in all subsequent rotations, assuming that gain is obtained at the end of each generation cycle. The expectation is that consideration of returns in perpetuity would lead to shorter

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rotations than consideration of a single cycle of return, assuming a concave increasing-value function (Samuelson 1976). The value function for our usage is approximated by the product of the age–age genetic correlation, the square root of the heritability at time one and the square root of the heritability at rotation age, and tends to be a concave increasing function as age at time one approaches rotation age. To our knowledge, this method has not been used in forest genetics.

Information on age–age correlations for short-rotation species, such as *Eucalyptus*, has been generated in the last decade with commercially planted species such as *Eucalyptus globulus* (Borralho et al. 1992a), *Eucalyptus grandis* (van Wyk 1990; Lambeth et al. 1994), *Eucalyptus nitens* (Greaves et al. 1997) and *Eucalyptus urophylla* (Wei and Borralho 1998), or eucalypt hybrids (Bouvet 1991; Bertolucci et al. 1995). However, most estimates are additive genetic correlations from open-pollinated or full-sib progeny. Few reports on genetic correlations from clonal trials of *Eucalyptus* are available (Ikemori 1990; Bouvet 1991; Lambeth et al. 1994) and those that are only cover the first few years of a rotation.

This research utilizes data from seven clonal trial locations of *E. grandis* containing 65 clones to: (1) estimate age–age correlations for height, mean annual increment (MAI) and wood density, between age 1 through age 5, with the target trait MAI at the rotation age (6 years), (2) estimate genetic correlations between traits at 3 and 6 years of age, (3) determine optimal test designs for clonal selection, and (4) examine the effect of discounted selection efficiency in perpetuity on selection age. The results of this study should provide useful insights for planning the breeding, testing and clonal deployment programs of *E. grandis*.

Materials and methods

Field location, design and traits measured

The seven locations were classified into three distinct groups representing a target environment (five locations representative of the main *E. grandis* planting area) and two marginal locations (Guachicona and Maravillas) with extreme ecological conditions where the species has been planted on a minor scale (Table 1). Compared to the target environment, “Guachicona” is a hot, dry, low-elevation environment, while “Maravillas” is a cold high-elevation environment. The distinctness of these environments for growth was verified by previous analyses with type B genetic correlations of 0.02, 0.01 and –0.49 for MAI at age 6 between the target and “Guachicona” environments, the target and “Maravillas” environments, and the “Guachicona” and “Maravillas” environments, respectively (Osorio et al. 2001). The type B genetic correlation within the target environment (five locations) was 0.65 for MAI at age 6.

The experimental design was a randomized complete block design with variable numbers of blocks per location and a 6-ramet row plot per clone within a block at 3 × 3 m between trees. From 29 to 65 unrelated clones were planted at each location with 27 clones common to all locations and almost all clones in at least three locations. Survival and total height (H) were measured annually at ages 1 through 6 and wood density at 3 and 6 years. Diameter at breast height (D) was assessed from ages 2 to 6. Basic wood density was sampled by randomly selecting three ramets in each 6-ramet row plot per block and extracting a 5-mm wood increment core at breast height diameter. Basic wood density was estimated by the water volume displacement method (ASTM 1969).

Individual tree volume and mean annual increment (MAI) were calculated at ages 2 through 6. Individual tree volume, outside bark, determinations were made according to the following volume equation developed for clones by the Planning Department of Smurfit Cartón de Colombia (Uribe 1990):

$$\text{Individual Tree Volume}(\text{m}^3) = 0.024 + 0.335\,\text{D}^2\text{H},$$

where D is diameter at breast height and H is total height, both expressed in meters.

Mean annual increment (MAI) was estimated by multiplying each tree’s volume by the corresponding plot survival and expressing the result on a volume per unit area per annum basis in $\text{m}^3\ \text{ha}^{-1}\ \text{yr}^{-1}$ (Osorio et al. 2001).

Prior to analyses, editing of the data was performed to remove questionable measurements and recording errors. In all, fewer than 2% of the observations were deleted from the data based not only on their statistical information (SAS 1993), but also on the physical and biological information supplied at the time of measurements. In order to remove scale effects and help to create homogeneous variance structures across locations, the square root of the block phenotypic variance was used to standardize all traits before analyses (Gianola 1986; Falconer 1993; White 1996). That is, for each growth trait and wood density, each tree’s measurement was divided by the phenotypic standard deviation of its corresponding block producing a transformed variable with a phenotypic variance of one.

Estimation of genetic parameters

Estimates of variance and covariance components for total height (m), MAI ($\text{m}^3\ \text{ha}^{-1}\ \text{yr}^{-1}$) and wood density ($\text{gcm}^{-3}$) were based on bivariate mixed-model equations (Mrode 1996) and obtained from the multivariate computer program MTDFREML (Boldman et al. 1993). MTDFREML uses restricted maximum likelihood (REML) to estimate variance components (Searle et al. 1992). In addition to variance and covariance components, MTDFREML provided estimates of genetic, environmental and phenotypic correlations (r_{xy}) for pairs of traits or ages.

Multivariate methods allow simultaneous estimation of variances and covariances between different traits in a closed system, yielding empirically unbiased estimates of type B genetic correlations for unbalanced data with heterogeneous variances (Lu et al. 1999). Moreover, multivariate methods are more efficient than univariate methods and MTDFREML maintains all variance component estimates within the parameter space, facilitating their interpretation and practical applications (Lu et al. 1999).

The type B genetic correlation (r_B) measuring genotype by environment interaction for the five locations composing the target environment was calculated with the estimates of variance components obtained from MTDFREML following Yamada (1962).

Table 1 Climatic conditions and field layout of clonal tests, of *E. grandis* planted in three different types of environments at Smurfit Cartón de Colombia

Environment	Tests (no.)	Altitude (m)	Mean annual rainfall (mm)	Mean annual temp. (°C)	Blocks (no.)	Clones (no.)
Guachicona	1	950	1,052	24.0	2	65
Maravillas	1	2,400	2,340	13.0	6	29
Target	5	1,560–1,970	1,156–2,820	17.0–18.9	6–8	29–65

Type B genetic correlations between environments were obtained directly from MTDFREML (Lu et al. 1999).

For the target environment, broad-sense individual heritabilities (H^2, Foster 1990) for each trait were obtained from combined analyses over five locations and were calculated by MTDFREML with the estimates of variance components as follows:

$$H^2 = \sigma_c^2 / \left(\sigma_c^2 + \sigma_{cs}^2 + \sigma_{bsc}^2 + \sigma_e^2\right). \tag{1}$$

Broad-sense individual heritabilities for the single-location analyses (Guachicona and Maravillas) were obtained from MTDFREML according to the following equations:

$$H^2 = \sigma_c^2 / \left(\sigma_c^2 + \sigma_{bsc}^2 + \sigma_e^2\right),$$

where σ^2_{c}, σ^2_{cs}, σ^2_{bsc}, σ^2_{e} are the variances of clonal effects, clone by location, block within location by clone, and residual effects, respectively.

Optimal test designs

Using parameter estimates from this study, a simulation study was conducted to determine optimal genetic test designs for clones in order to improve tree growth (MAI) as a breeding objective. The approach used for the optimal design objective, clonal selection, was a randomized complete block design (RCBD) with a plot configuration of single-tree plots (STP) and a variable number of locations (1 to 10) and blocks (1 to 12) per location. Single-tree plots (STP) have been shown to be more efficient than row plots (Loo-Dinkins and Tauer 1987) and they can be used effectively for both backward and forward selection, allowing not only efficient ranking of genotypes but also effective estimation of genetic parameters (White 1996). As the single-tree plot (STP) configuration is likely to be used for future clonal tests, the plot variance (σ^2_{bsc}) and the residual error (σ^2_{e}) from the row-plot clonal tests were pooled together in the simulation to represent the residual error (σ^2_{e}) of the single-tree plot.

The estimates of broad-sense heritability and type B genetic correlations obtained from the five clonal tests in the target environment were used as a basic set of genetic parameter estimates from which "standard parameter estimates" were developed for the simulation. The goal was to create a set of standard parameter estimates that are generally applicable and useful for selection purposes in the *E. grandis* program in Colombia (Cotterill and Dean 1990; White and Hodge 1992).

To smooth the estimates and obtain standard parameter estimates, various models were tried to fit individual tree heritability (H^2), the type B genetic correlation (r_B) and age–age correlations (r_{xy}) using linear regressions with the parameters (H^2, r_B, r_{xy}) as dependent variables and age as the independent regressor. These standard parameter estimates were then used in the simulation study to determine the optimal number of locations and blocks for clonal tests.

To evaluate the effectiveness of different numbers of locations and blocks per location, genetic gains were estimated for mean annual increment (MAI), at the time of harvesting (6 years), which is the trait of interest. Expected genetic gain from clonal selection for the target environment (five locations pooled) was estimated according to Falconer (1993):

$$Gy = i_y H_{\bar{c}y}^2 \sigma_{\bar{c}y},$$

where $H_{\bar{c}y}^2$ is broad-sense heritability based on clonal means at 6 years, i is intensity of selection at 6 years, and $\sigma_{\bar{c}y}$ is the square root of the phenotypic variance of clonal means at 6 years.

Broad-sense heritability of clonal means was calculated based on the clonal phenotypic standard deviation and expressed as:

$$H_{\bar{c}}^2 = \sigma_c^2 / \left(\sigma_c^2 + \sigma_{cs}^2/s + \sigma_e^2/bs\right),$$

where s is the number of locations, and b is the number of blocks per location.

The simulation to determine the efficiency of early selection involved calculating genetic gains at 3 and 4 years of age, since preliminary analyses had shown these to be the best ages for early selection. Thus, the relative genetic gain for MAI was calculated using the ratio of expected genetic gain from selection at 3 and 4 years age (G_x) and maximum direct genetic gain at the same ages ($G_{\max}$), for a variable number of locations, up to 10 locations, and a maximum number of 12 blocks for each selection age.

The maximum direct genetic response at 3 and 4 years was obtained assuming an infinite number of locations and blocks and is considered the maximum possible gain achievable at that age. Efficiency of early selection is thus expressed as:

$$E = G_x / G_{\max} = i_x H_{\bar{c}x}^2 \sigma_{\bar{c}x} / i_y H_{\bar{c}y\infty}^2 \sigma_{\bar{c}y\infty},$$

where $H_{\bar{c}y\infty}^2 = 1$ and is the clonal mean heritability for an infinite number of locations and blocks, $\sigma_{\bar{c}y\infty} = \sigma_{cy}$ and is the standard deviation of the clonal phenotypic variance for an infinite number of locations and blocks, and

$$E = H_{\bar{c}x}^2 \sigma_{\bar{c}x} / \sigma_{cy} \tag{2}$$

if it is assumed that intensity of selection is the same at an early age (i_x) and at the same age under maximum genetic gain (i_y). However, two components, $\sigma_{\bar{c}x}^2$ and $H_{\bar{c}x}^2$, change due to the variable numbers of locations and blocks.

Determining optimal selection age

The efficiency of early selection for MAI was calculated using the ratio of indirect selection at different ages (G_x) to maximum genetic gain at 6 years age ($G_{\max 6}$). Selection efficiency was calculated for a variable number of locations up to 10 and a maximum number of 12 blocks per location for each selection age.

Genetic gain at rotation age based on early selection or based upon selection for a different trait is defined as indirect genetic gain as expressed by Falconer (1993). Selection efficiency of early selection is the proportion of gain from indirect selection with respect to the gain from selection at rotation age and is estimated as:

$$E = G_x / G_{\max 6} = i_x H_{\bar{c}x} H_{\bar{c}y} r_{xy} \sigma_{\bar{c}y} / i_y H_{\bar{c}y\infty}^2 \sigma_{\bar{c}y\infty} \tag{3}$$

and

$$E = H_{\bar{c}x} H_{\bar{c}y} r_{xy} \sigma_{\bar{c}y} / \sigma_{cy}$$

if it is assumed that intensities of selection are the same (i) at selection and rotation age and $G_{\max 6}$ is the gain from selection based on an infinite number of blocks and an infinite number of locations. Note that $H_{\bar{c}y\infty}^2$ equals 1 and $\sigma_{\bar{c}y\infty}^2 = \sigma_{cy}^2$.

In order to demonstrate the concept of DSE regarding optimal selection age, the following assumptions were made: (1) rotation age is equal to 6 years; (2) propagation time in clonal gardens including the rooting phase is 2 years; (3) realization of benefits from testing and clonal selection are equivalent to selection age plus 8 years (2 years for bulking up in step 2 and 6 years after planting until harvest); (4) the 8 year period for commercial clonal propagation is sufficient to accomplish breeding and to produce rooted cuttings for testing; (5) genetic parameters are stable over generations; and (6) all genetic variation is due to additive effects.

To determine the optimal age of selection, an analysis was conducted to maximize the discounted benefits from an infinite number of rotations of early selection. This is similar to the selection efficiency used previously (McKeand 1988; White and Hodge 1992; Balocchi et al. 1994) except that this method accounts for the benefits in perpetuity. Discounted selection efficiency (DSE) was obtained as the product of selection efficiency (E) and a discounting factor for perpetual generations (Klemperer 1996). The discounting factor (D) is based on the general formula used in forestry to estimate the present value (V_0) of perpetual periodic series of harvesting revenues (p) per acre, using a discount rate (i) at the end of every rotation of t years, and expressed as (Klemperer 1996):

$$V_0 = p / \left[(1+i)^t - 1\right] \tag{4}$$

so that, genetic gains obtained at either early age or rotation age are adjusted by the discount factor, with t equivalent to selection age plus 8 years for propagation and harvesting of the material.

Table 2 Mean values and broad-sense heritabilities, parentheses, for survival, height and MAI in the three environments for ages 1 through 6 years

Trait	Years	Environment		
		Target	Guachicona	Maravillas
Survival (%)	1	95.1 (0.05)	84.4 (0.03)	94.8 (0.05)
	2	93.1 (0.13)	81.6 (0.40)	82.3 (0.17)
	3	92.6 (0.12)	80.0 (0.41)	77.0 (0.26)
	4	91.9 (0.14)	77.8 (0.39)	76.0 (0.26)
	5	91.4 (0.12)	72.6 (0.50)	72.8 (0.24)
	6	89.9 (0.10)	65.9 (0.48)	71.6 (0.23)
Height (m)	1	4.0 (0.23)	3.3 (0.36)	1.4 (0.16)
	2	10.2 (0.17)	8.1 (0.46)	5.2 (0.16)
	3	15.6 (0.11)	12.4 (0.46)	8.3 (0.08)
	4	20.4 (0.12)	15.4 (0.54)	12.1 (0.10)
	5	24.2 (0.14)	17.2 (0.52)	15.2 (0.07)
	6	26.2 (0.19)	19.4 (0.52)	17.1 (0.09)
MAI (m^3 ha^{-1} yr^{-1})	1	0.0	0.0	0.0
	2	19.0 (0.14)	7.6 (0.44)	2.9 (0.18)
	3	35.9 (0.14)	16.7 (0.43)	9.4 (0.21)
	4	49.9 (0.17)	21.8 (0.50)	18.2 (0.22)
	5	56.5 (0.20)	23.3 (0.49)	23.8 (0.19)
	6	56.5 (0.22)	24.4 (0.52)	25.0 (0.21)

Discounted selection efficiency is calculated as follows:

$$\mathrm{DSE} = (\mathrm{E})(\mathrm{D})$$

and

$$\mathrm{DSE} = \left(\frac{H_{\bar{c}x}H_{\bar{c}y}r_{xy}\sigma_{\bar{c}y}}{\sigma_{cy}}\right)\left[\frac{(1+i)^{y+8}-1}{(1+i)^{x+8}-1}\right], \qquad (5)$$

where E is defined as the selection efficiency in Equation 3, D is the discounting factor, i is the interest rate (5%, 10%, 15%, 20%), x is the early selection age (2, 3, 4, 5 years), and y is the age at time of harvest (6 years).

Results and discussion

Means and broad-sense heritabilities

Means and broad-sense heritabilities are given in Table 2 for survival, height and MAI for the three environments and for ages 1 through 6 years. The mean values demonstrate the high growth rate and survival present in the target environment while the mean values for Guachicona and Maravillas are much poorer and very similar.

Although the mean values for growth and survival are similar for Guachicona and Maravillas, the heritabilities are quite disparate with Guachicona having moderate to high heritabilities for growth and survival. Both Maravilas and the target environment have heritabilities that are generally low to moderate. The values for heritability and means for growth and survival traits tend to underscore the differences among the three environments.

Genetic correlations

Age–age genetic correlations

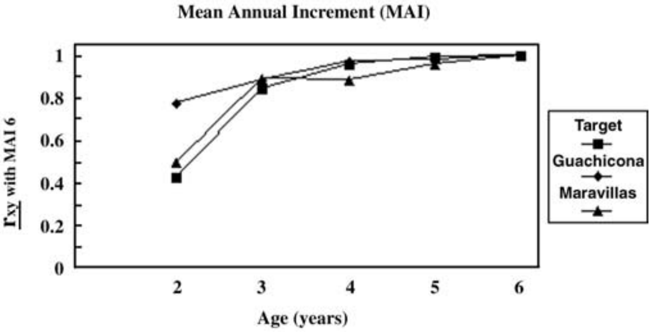

Fig. 1 Genetic correlations (r_{xy}) for mean annual increment (*MAI*) at different ages with MAI at 6 years in clonal trials of *E. grandis* for three environments

The genetic correlations for MAI at different ages with MAI at rotation age (MAI6) were low for Maravillas and the target environment at 2 years ($r_{xy} < 0.5$) but were high for all three environments at 3 years ($r_{xy} > 0.8$) and thereafter (Fig. 1). High age–age genetic correlations ($r_{xy} > 0.70$) for diameter (DBH) between years 1 and 5 had been reported for *E. urophylla* in China (Wei and Borralho 1998). High genetic correlations ($r_{xy} > 0.88$) for diameter (DBH) between 2.5 years and 6.5 years were obtained for *Eucalyptus cloeziana* in Brasil (Marques et al. 1996).

In a similar fashion, strong genetic correlations ($r_{xy} > 0.95$) were also found for the sectional area at 4 years with the sectional area at 8, 13 and 18 years for *E. globulus* in Portugal (Borralho et al. 1992a). Differences between these previous studies and the present estimates of genetic correlations for MAI at 2 years in this study might be associated with the effect of including survival in our response variable (since MAI incorporates survival) and with the reaction of diameter growth to this survival.

The genetic correlations between height at 3 years (HT3) and height at 6 years (HT6) were high at Guachicona ($r_{xy} = 0.94$) and the target environment ($r_{xy} = 0.77$),

Table 3 Trait–trait genetic correlations between height (HT), mean annual increment (MAI), and wood density (WD) of clonal trials of *E. grandis* in three different environments at 3 and 6 years

Environment	Trait				
	HT 3	HT 6	MAI 3	MAI 6	WD 3
Target					
HT 6	0.77				
MAI 3	0.80	0.75			
MAI 6	0.64	0.87	0.84		
WD 3	0.14	–0.05	–0.04	0.0	
WD 6	0.0	0.06	0.03	–0.08	0.95
Guachicona					
HT 6	0.94				
MAI 3	0.80	0.73			
MAI 6	0.83	0.84	0.88		
WD 3	0.04	0.00	–0.03	–0.06	
WD 6	–0.04	0.02	–0.07	–0.06	0.71
Maravillas					
HT 6	0.51				
MAI 3	0.74	0.19			
MAI 6	0.68	0.60	0.89		
WD 3	0.45	0.04	0.49	0.40	
WD 6	0.27	–0.06	0.21	0.16	0.90

but only moderate at Maravillas (r_{xy} = 0.51) (Table 3). High age–age genetic correlation for height ($r_{xy} > 0.78$) between years 1 and 5 had been reported for *E. urophylla* (Wei and Borralho 1998). Comparable genetic correlations for height between year 4 and years 8, and 13 in *E. globulus* (Borralho et al. 1992a) were also high (r_{xy} = 0.77) at all ages except at year 1 (r_{xy} = 0.44).

Wood density showed very high genetic correlations between 3 and 6 years age in the target environment (r_{xy} = 0.95) and in Maravillas (r_{xy} = 0.90), and a somewhat smaller correlation in Guachicona, r_{xy} = 0.71. Similar, genetic correlations (r_{xy} = 0.93) for wood density between years 3 and 6 had been reported for *E. nitens* in Australia (Greaves et al. 1997).

Trait–trait correlations

Genetic correlations between height and the target trait, and mean annual increment at 6 years (MAI6), are presented in Fig. 2. In general the genetic correlations tended to increase with age except at Maravillas, the colder environment, where the genetic correlation between HT and MAI6 decreased after the 4th year.

Genetic correlations between height and MAI at the same age, either at 3 or 6 years, were high and positive, r_{xy} = 0.80 to 0.87, in the target environment and Guachicona, but moderate in Maravillas, r_{xy} = 0.74 to 0.60 (Table 3). This is in agreement with the genetic correlations for height from years 1 to 6 with the sectional area at 8 years, which were high (r_{xy} = 0.77) at all ages, except at year 1 (r_{xy} = 0.44) for *E. globulus* in Portugal (Borralho et al. 1992b). The genetic correlations between height and wood density either at the same or different years were almost zero in the target environment and Guachicona, but moderate to low in Maravillas.

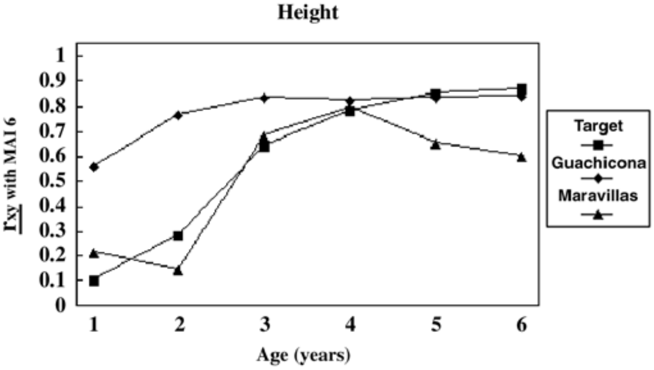

Fig. 2 Genetic correlations (r_{xy}) for height at different ages with MAI at 6 years in clonal trials of *E. grandis* for three environments

Published reports on trait–trait correlations of clonal material of *E. grandis* are very scarce and most studies on the subject are related to *E. grandis* hybrids (Bouvet and Bailleres 1995) or *E. grandis* from seedling origin (Malan 1988, 1991). These studies agree that genetic correlations between growth traits and wood density for *E. grandis* and its hybrids were of moderate to large magnitude but negative. However, our study and others from *Eucalyptus* species of seedling origin showed different results indicating that the genetic correlations between growth traits and wood density are either low or nil in most cases (Borralho et al. 1992b; Greaves et al. 1997; Wei and Borralho 1997; Tibbits and Hodge 1998).

Optimal selection ages for *Eucalyptus* species, managed in a short-rotation, have been reported as 12 months for height and DBH in *E. urophylla* (Wei and Borralho 1998), 2.5 years for DBH in *E. cloeziana* (Marques et al. 1996) and 3.0 years for *Eucalyptus* hybrids (Bouvet 1991). In our study, the higher genetic correlations of height and MAI at 3 years with MAI at 6 years compared to the lower correlations between 2 years and 6, coupled with the small increase in broad-sense heritabilities over time, would indicate that 3 years is the minimum biological age for selection. Furthermore, the high genetic correlations for wood density between 3 and 6 years suggests that age 3 is very suitable for selection on one trait or on a combination of traits based on a selection index including wood and growth traits.

Standard parameter estimates

The linear regression for the modeling of individual tree heritability (H^2) using the observed values as the dependent variable (Table 4) and age as the independent variable gave a good fit to the data (R^2_{adj} = 0.90) indicating a significant age effect (p = 0.01). Due to the fluctuation of the type B genetic correlation from age 2 to age 6 for MAI, the fit of the linear regression for this parameter was weak (R^2_{adj} = 0.41) and the independent variable

Table 4 Standard genetic parameter estimates for mean annual increment (MAI) to be used in the simulation. The variance components σ^2_c, σ^2_{cs}, σ^2_e are variances due to clonal effects, clone by location interaction effects and residual effects in the target environment, respectively. Variance components are expressed as a fraction of a phenotypic variance sum to unity due to data standardization. The value H^2 is the broad-sense individual heritability (Equation 1), r_B is the type *B* genetic correlation and r_{xy} is the genetic correlation between MAI at each age and MAI at 6 years

Age	Variance components estimates			Standard parameter estimates		Observed parameter values		
	σ^2_c	σ^2_{cs}	σ^2_e	H^2	r_B	H^2	r_B	r_{xy}
2	0.1301	0.1074	0.7625	0.13	0.55	0.14	0.58	0.44
3	0.1518	0.1159	0.7323	0.15	0.57	0.14	0.53	0.84
4	0.1735	0.1223	0.7042	0.17	0.59	0.17	0.58	0.96
5	0.1953	0.1270	0.6777	0.20	0.61	0.20	0.61	0.99
6	0.2170	0.1300	0.6530	0.22	0.62	0.22	0.64	1.00

was not significant. However, for the small range of ages used, the predicted values increase smoothly indicating a higher type B genetic correlation (less clone by location interaction) as trees get older, a more reasonable option than considering stable correlations across ages.

We also investigated the possibility of estimating age–age correlations using the logarithmic transformation of Lambeth (1980) based on the general formula developed for several conifer species:

$$r_p = 1.02 + 0.308 \log_e(\text{younger age}/\text{older age}). \quad (18)$$

However, the predicted phenotypic correlation for MAI at 2 years with MAI at rotation age was higher (r_p = 0.68) than the observed value (r_{xy} = 0.43). Even if it were assumed that the phenotypic correlation is equal to the genetic correlation, Lambeth's formula overestimates the observed value by 50%.

Another approach for obtaining smoothed age–age correlations, a simple linear regression on the observed values of the genetic correlations, showed a weak fit to the data (R^2_{adj} = 0.63) and a significant effect of age at *p*-value = 0.07. However, the predicted genetic correlation for MAI between year 2 and 6 (r_{xy} = 0.59) was not close to the observed value (r_{xy} = 0.43). Therefore, it was decided to use the observed age–age correlations given that no appropriate models were found and the abrupt change from year 2 to 3 may be real and closer to the true values. Thus the standard parameter estimates used in the simulation study to determine the optimal number of locations and blocks for clonal tests and optimal selection ages are presented in Table 4.

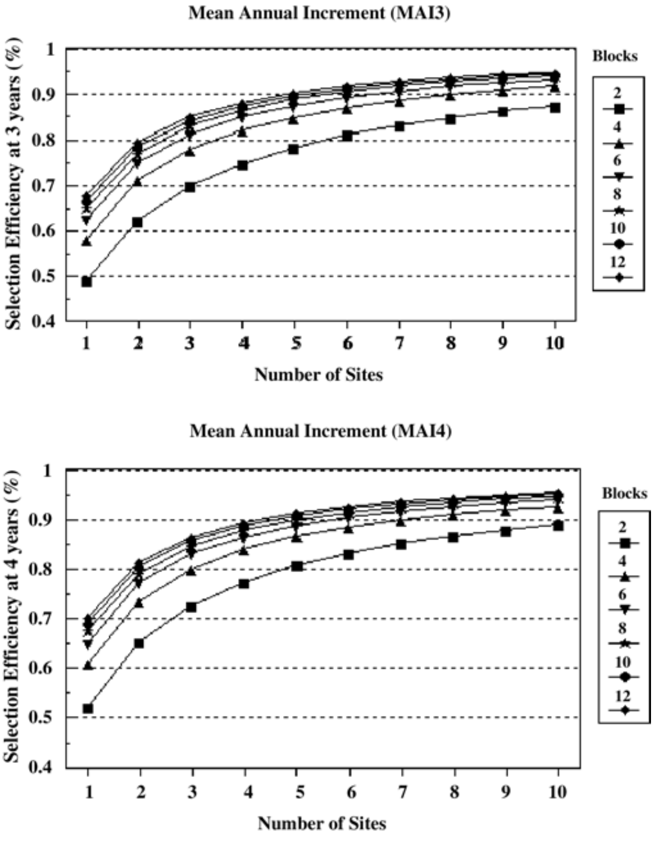

Fig. 3 Selection efficiency for mean annual increment (*MAI*) of direct selection at 3 and 4 years with respect to maximum gain at the same age achievable from an infinite number of sites and blocks. Genetic parameters used to conduct these simulations were from Table 4

Optimal test designs

Selection efficiencies for MAI at 3 and 4 years with respect to the maximum gain achievable at those ages assuming an infinite number of locations and blocks are presented in Fig. 3. In a single-tree plot design, 90% selection efficiency is obtained from each of the following combinations of: (1) five locations and 12 blocks per location, (2) six locations and six blocks, (3) eight locations and four blocks, and (4) ten locations and two blocks by selecting at 3 years age. For a fixed number of ramets, increasing the number of locations and decreasing the number of blocks per location, generally, results in higher selection efficiencies.

The increase in efficiency of selection is associated with the increase of the clonal mean heritability, $H^2_{\bar{c}x}$ (Equation 2), due to the increment in the number of locations and ramets per clone. Similar responses in the efficiency of progeny and clonal testing have been reported previously (Shaw and Hood 1985; Russell and Libby 1986; White and Hodge 1992).

All the studies reviewed pointed out that maximum gains are achievable with a low number of ramets per clone or trees per family on a given location allowing the testing of a large number of genotypes for deployment or breeding screening. Selection of an optimal number of locations and clones for the same efficiency of selection ultimately depends on biological considerations, political regulations and economical or logistic constraints to carry over the program goals. For predetermined selection efficiencies between 80 and 90%, a test design spread on six locations with six blocks per location (a total of 36 ramets per clone) seems to be a good option. This provides an acceptable number of locations to test for genotype by environment interaction, if present, and a sufficient number of ramets to buffer against mortality.

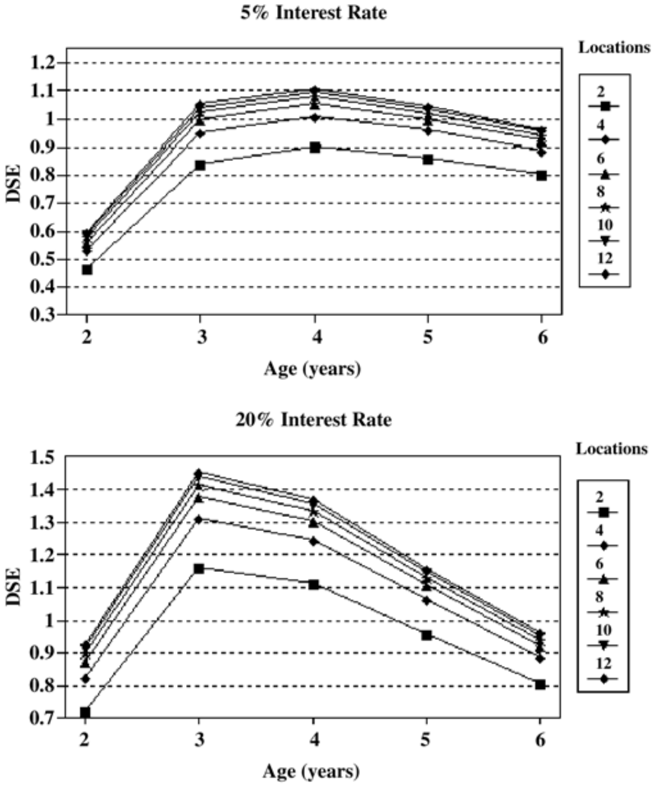

Fig. 4 Effect of discounted selection efficiency at perpetuity (DSE from Equation 5) on selection age using a discount rate of 5% and 20% for a randomized complete block design with single-tree plots and a fixed number of six blocks from age 2 to 6 in clonal trials of *E. grandis*. The time to realize the benefits is 14 years corresponding to a 6 year rotation plus 8 years for propagation and harvesting

Optimal selection age

Discounted selection efficiency values (DSE), based on interest rates of 5%, 10%, 15% and 20%, were higher than those commonly reported in the literature for this type of analysis (McKeand 1988; Balocchi et al. 1994). These interest rates include the risk of uncertainty of investments in the forestry business under the scenario of inflationary economies, a common scenario where this tropical species is planted.

Discounted selection efficiency based on a fixed number of six blocks per location indicated that the optimum selection age decreased with increasing interest rates (Fig. 4). At a 5% interest rate the discounted selection efficiency (DSE) reach its maximum at 4 years, being only 3% higher than DSE at 3 years for a variable number of locations. At the other interest rates (10%, 15% and 20%), DSE is higher at 3 years age and its absolute magnitude increases with the interest rate.

Comparable results were obtained for *Pinus elliottii* indicating that selection efficiency is increased by increasing the interest rate used in the discounted selection efficiency (White and Hodge 1992). Similar results were found with *Pinus taeda* where the lowest optimum selection age (6 years) was for selection among full-sib families based on the total genetic component and the higher interest rates used in the study (Balocchi et al. 1994).

As the efficiency of indirect selection is a function of the heritabilities of the traits and the genetic correlation between them, MAI seems to be a better predictor of MAI at 6 years than height. Mean annual increment (MAI) had higher age–age correlations at all ages (Fig. 1 and 2) and higher heritabilities showing a steady increase from year 2 to 6 in the target environment.

Studies determining discounted selection efficiency are usually based on existing data from a single generation (McKeand 1988; White and Hodge 1992; Balocchi et al. 1994) or based on simulations for a few generations (Kang 1985; Newman and Williams 1991). This is probably due to the fact that turnover of generations of coniferous species limits the availability of genetic parameters over multiple generations. On the other hand, the quantitative genetic theory to estimate genetic gains over several generations of selection, taking into account changes in genetic parameters due to directional selection, has not been developed (Kang 1985; Wu 1998), leading to the debatable assumption of stable genetic parameters over time.

Even though several generations of directional selection are expected to alter the genetic variances (Bulmer 1980), this effect may be counteracted by the infusion of new genes in each breeding cycle, increasing the genetic variability in the breeding population. Furthermore, higher heritabilities and more precise genetic correlations should be obtained as improved test designs are developed and clonal tests are established with better control of the environmental factors.

Although the advantages of early selection are more attractive to long rotation species (Magnussen 1989) and the precise timing of the early selection is not as critical as for short-rotation species (Borralho et al. 1992a), its determination is still important if economical considerations are taken into account. It should be noted that in this study discounted selection efficiency (DSE) at perpetuity was compared on the basis of gain per generation by compounding each rotation's cash flows to rotation-end into one net value, *p* (Equation 4).

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