The rejection of clones at age 3 and above should be based upon their current nursery performance e.g. rooting, survival, etc., in addition to the last available data of growth in field trial. Propagation of a given clone should be stopped if it gets rejected at any stage in selection process. The requirement of nursery space for progressively multiplying the germplasm of the selected sets of clones will be practically of the order of second year < third year < fourth year < fifth year, although number of selected clones will be in the opposite order. The above strategy is, therefore, operationally feasible.

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Age Trends of Heritabilities and Genotype-by-Environment Interactions for Growth Traits and Wood Density from Clonal Trials of *Eucalyptus grandis* HILL ex MAIDEN

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Abstract

Obtaining accurate and precise genetic parameter estimates is fundamental to determining breeding strategies, and for choosing genotypes for commercial propagation. Results for survival and growth from seven clonal genetic tests of *Eucalyptus grandis* in Colombia supported the a priori contention of sub-dividing them into three different environments for deployment and possibly breeding purposes. The genotype-by-environment interactions (GxE) for growth traits were moderate at six years of age in the target environment (5 sites representative of 95% of the *E. grandis* planting area for the clonal program). Therefore, it is recommended to breed and select for clones that perform well across the range of sites within the target environment. The clonal rankings for growth traits at the two extreme sites differed markedly between these two distinct environments, and between each extreme environment and the five sites in the target environment. Thus, the extreme environments require separate clonal test locations and deployment populations. Broad sense heritabilities for survival, individual tree volume and mean annual increment (MAI) tended to increase over time for the three environments, but the trends for height were quite different among environments. The broad sense heritabilities for mean wood density declined with age, but GxE interaction for wood density was low indicating that clonal rankings were stable among the five sites within the target environment. The estimation of genetic gains by two methods, predicted clonal values and the classical formula, gave similar results and showed great potential for increasing productivity in the target environment through selection of the top clones.

Key words: Eucalyptus grandis, genetic parameters, clonal forestry, genetic gain.

Introduction

In the last twenty years, there has been increasing interest on the part of many *Eucalyptus* breeding programs around the world in developing clonal forestry to enhance both plantation productivity and product uniformity (LAMBETH *et al.,* 1989; DENISON and KIETZKA, 1993; BERTOLUCCI *et al.,* 1995; ARAUJO *et al.,* 1997). In this context, the estimation of basic genetic parameters is crucial in determining the best strategies for clonal breeding and testing and in predicting genetic gains from deploying the best clones (BURDON, 1992; WHITE, 1996).

In the case of *Eucalyptus grandis*, there are few reports in the literature regarding genetic parameters for growth and wood quality traits of clonal material (KAGEYAMA and KIKUTI, 1989; IKEMORI, 1990; LAMBETH *et al.,* 1994). In general, broad sense heritabilities have shown moderate genetic control for growth traits (H^2=0.22 to 0.41) and wood density (H^2=0.30). However, some of these heritability estimates are based on a single genetic test and therefore may be upwardly biased by the presence of genotype-by-environment interaction if the GxE interaction variance is larger than zero (COMSTOCK and MOLL, 1963; HODGE and WHITE, 1992). There are no estimates from multiple sites over many ages, and given the importance of *E. grandis* in world plantations, such estimates are needed.

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Genotype-by-environment interaction (GxE) in forest tree species arises when the relative performance of genetic entries is not consistent in different environments. When GxE is present, breeders either develop separate breeding or propagation populations for each site type or select genotypes that perform well across many sites (McKeand *et al.,* 1990).

Given the fact that both the tree improvement and the clonal deployment programs for *E. grandis* in Smurfit Carton de Colombia are recent, genotype-by-environment interaction of clones has been incompletely tested. Preliminary estimates in Colombia come from a three-year-old clonal trial of 27 clones planted on two sites for which GxE for growth traits was non-existent (both sites had good soil quality, Lambeth *et al.,* 1994). Other values of type B genetic correlations for clonal material were estimated at one year of age (Endo and Wright, 1993), but the trials were too young to provide reliable estimates. Results in the literature are incomplete and surprisingly few are from well-designed clonal tests in multiple locations.

The objective of this study was to obtain unbiased estimates of genetic parameters for growth traits and wood density from clonal trials assessed from one through six years (rotation age for *E. grandis* in Colombia). These results included: (1) estimates of and trends in broad-sense heritabilities (H^2); (2) estimates of genotype-by-environment interaction (GxE) for each trait; and (3) predicted genetic gains at six years of age. The results of this study provide reliable estimates of age trends for these important traits and give useful insights for planning breeding and clonal deployment programs in Colombia and other countries where *E. grandis* is planted.

Materials and Methods

Field Establishment and Test Design

Of the seven sites selected for the trial, five sites represent the target environment (95% of the planting area) for forestry plantations of *E. grandis* in Colombia (Arcadia, Cedral, Indostan, La Tulia and Suiza, *Table 1*). The other two tests are on marginal sites with extreme environmental conditions where *E. grandis* is operationally planted on a limited basis (Guachicona and Maravillas, *Table 1*). The test at Guachicona is at low elevation and is hot and dry. The test at Maravillas is at high elevation and is the coldest of the seven tests. The assessment of productivity and genetic expression across the range of environments represented by these seven sites provides valuable information for management decisions.

The 65 clones for this test series were selected from among 460 clones present in the first clonal test series in which most clones were only tested at a single location. Mass propagation of the 65 clones was done at the "Restrepo" nursery, Department of Valle, and the management of the sprouts, cuttings and rooted plants was similar to operational clones in the nursery. Site preparation and cultural practices were basically the same at all sites and followed the standard practices applied by the operational plantation program (details in Osorio, 1999).

The experimental design at each location was a randomized complete block design with variable numbers of blocks per test and a 6-tree row plot per clone per block at a spacing of 3 m x 3 m. The numbers of clones and blocks in each test were related to the quantity of ramets available from each clone and to the relative importance of clonal testing in certain plantation areas (Cedral), areas close to the mill (Guachicona), or highly productive areas (Suiza). The study is unbalanced with 27 clones common to all seven sites and almost all clones planted on at least three sites.

Data Collection

Survival, height and diameter were measured at ages one through six and wood density at three and six years. Total height was measured with a telescopic pole at ages one and two and with a hypsometer from years three through six. Diameter at breast height (DBH) was assessed at ages two through six using diameter tapes. Basic wood density was sampled by randomly selecting three trees from each clone in each block and extracting, at breast height, 5 mm wood increment cores. Basic wood density was estimated by the water volume displacement method (ASTM, 1969).

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

$$\text{Individual Tree Volume } (m^3) = 0.024 + 0.335\ D^2H \quad (1)$$

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 as $m^3\ ha^{-1}\ yr^{-1}$ (Osorio,1999).

Data Editing and Standardization

Prior to analyses, editing of the data was performed to remove measurement or recording errors. The identification of potential outliers and influential measurements was conducted by building a linear regression for height and diameter at each site using PROC INSIGHT (SAS®, 1993). This procedure allowed the plotting of all observations and provided useful information on diagnostic measurements for outliers (Myers, 1990) as well as their effects on the moments of the distribution i.e., mean, error variance, skewness, and kurtosis (Sorensen and White, 1988). In all, less than 2% of the observations were deleted from the data based not only on their statistical information, but also on the physical and biological observations supplied at the time of measurements.

Table 1. – Site name and location, number of blocks and clones, and climatic conditions of seven clonal test of *Eucalyptus grandis* in Smurfit Carton de Colombia.

Location	Latitude (N)	Longitude (O)	Altitude (m)	Mean Annual Rainfall (mm)	Mean Annual Temperature (°c)	Blocks (No)	Clones (No)
Arcadia	2° 29'	76° 40'	1750	2155	18.3	6	29
Cedral	4° 42'	75° 40'	1850	2820	17.0	8	64
Guachicona	3° 34'	76° 28'	950	1052	24.0	2	65
Indostan	4° 15'	75° 47'	1750	2414	18.3	6	29
Maravillas	4° 20'	75° 38'	2400	2340	13.0	6	29
La Tulia	4° 22'	76° 20'	1970	2000	17.0	5	30
Suiza	3° 49'	76° 28'	1560	1156	18.9	8	64

The data were also examined for any factors affecting the performance of individual trees. The most relevant factor affecting growth was the stem breakage of trees due to the strong winds during the dry seasons at "Arcadia", "Cedral", and "Maravillas". Broken-topped trees resumed growth soon after the damage occurred and only a few died. Preliminary analyses including or excluding broken-topped trees gave similar estimates for all growth and wood density traits; therefore, results reported include all trees.

In order to remove scale effects and help to create homogeneous variance structures across tests, the square root of the block phenotypic variance was used to standardize all continuous traits before the analyses (FALCONER, 1993; WHITE, 1996). For each growth and wood density trait, each measurement was divided by the phenotypic standard deviation of its corresponding block producing a transformed variable with phenotypic variance of one.

Analyses of Survival, Growth Traits and Wood Density

Prior studies of the performance of *E. grandis* (CANNON, 1982; EASLEY and LAMBETH, 1989) and analyses of all pair-wise test combinations of this data (OSORIO, 1999) showed that the two extreme sites, "Guachicona" and "Maravillas", were distinctly different from the other five sites, which represent the target environment (*Table 1*). This situation led to the use of a multivariate analysis that considers each response variable as three traits: (1) a "target environment", defined by five sites; (2) "Guachicona"; and (3) "Maravillas".

Estimates of variance components, for survival (%), total height (m), individual tree volume (m^3), MAI (m^3 ha^{-1} $year^{-1}$) and wood density (g cm^{-3}), were obtained from the multivariate computer program MTDFREML (BOLDMAN *et al.,* 1993). MTDFREML uses restricted maximum likelihood (REML) to estimate variance components based on residuals calculated after fitting the fixed effects of the model by generalized least squares (SEARLE *et al.,* 1992). REML estimation is the preferred choice in animal breeding (HENDERSON, 1984) and it has also proven to have better poperties for unbalanced data than other estimators in forest genetic tests (HUBER *et al.,* 1994).

Multivariate methods allow simultaneous estimation of variances and covariances of different traits in a closed system, yielding empirically unbiased estimates of type B genetic correlations for unbalanced data with heterogeneous variances (LU, 1999). Moreover, for multivariate models, MTDFREML provides estimates of variance and covariance components that are constrained within the parameter space, facilitating their interpretation and practical applications (LU, 1999). For the derivative-free method, the solution for variance or covariance components occurs when the putative global maximum of the log likelihood function is found. At least two sets of starting values were used in each analysis to check convergence of the estimates.

In this study, survival was analyzed based on 0/1 scores, without transformation, given that enough evidence has been produced to support the fact that REML analysis on 0/1 data provides satisfactory results (BANKS *et al.,* 1985; WESTFALL, 1987; HUBER, 1993; DIETERS *et al.,* 1996; LOPES, 1998).

Variance components estimated for each response variable included s^2_{ci}, s^2_{bscl}, s^2_{cs1}, s^2_{bci} and s^2_{ei} which are the components for clone (traits 1 through 3, i = 1 through 3), block within site by clone (trait 1), clone by site (trait 1), block by clone (traits 2 and 3), and residual effects (traits 1 through 3), respectively. The covariance of clonal effects ($s_{c(ij)}$) between traits "i" and "j" was obtained as a measure of the genetic covariance between traits.

The statistical analysis of each variable followed the multivariate mixed model, in matrix form:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 \\ 0 & X_2 & 0 \\ 0 & 0 & X_3 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 \\ 0 & Z_2 & 0 \\ 0 & 0 & Z_3 \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \\ c_3 \end{bmatrix} + \begin{bmatrix} N_1 \\ 0 \\ 0 \end{bmatrix} [d_1] + \begin{bmatrix} Q_1 \\ 0 \\ 0 \end{bmatrix} [p_1] + \begin{bmatrix} 0 & 0 \\ W_2 & 0 \\ 0 & W_3 \end{bmatrix} \begin{bmatrix} t_2 \\ t_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix} \quad (2)$$

Details of the multivariate model used for each response variable are in the Appendix. In addition to covariance components, MTDFREML provides estimates of broad-sense individual heritabilities for the target environment (trait 1, pooled over 5 sites), and for the extreme environments traits (traits 2 and 3), for each response variable analyzed according to the following equations:

Target Environment (trait 1), (pooled sites):

$$H^2 = \frac{\sigma^2_{c1}}{\sigma^2_{c1} + \sigma^2_{bsc1} + \sigma^2_{cs1} + \sigma^2_{e1}} \quad (3)$$

Extreme Environments (traits 2 and 3), (single-site analyses):

$$H^2 = \frac{\sigma^2_{c2or3}}{\sigma^2_{c2or3} + \sigma^2_{bc2or3} + \sigma^2_{e2or3}} \quad (4)$$

The heritability estimates for growth characteristics for traits 2, "Guachicona", and 3, "Maravillas " (Eq. 4) are upwardly biased by the presence of genotype-by-environment interaction (COMSTOCK and MOLL, 1963).

Estimates of heritabilities for survival were obtained from analysis of 0/1 data using MTDFREML and transformed to the liability scale. The liability scale reduces the influence of the incidence on the genetic parameter estimates facilitating the comparison of estimates from tests with different mean incidences (DEMPSTER and LERNER, 1950; Gianola, 1982; LOPES, 1998). The following equation was used for this purpose:

$$H^2 = H^2_{0/1} \frac{p(1-p)}{z^2} \quad (5)$$

where:

$H^2_{0/1}$ is the heritability on the observed binomial scale, p is the mean incidence of survival and z is the height of the ordinate at the threshold corresponding to the incidence in the trial (DEMPSTER and LERNER, 1950).

Genetic Correlations

Two methods were used to estimate the type B genetic correlations either within or between traits. The type B genetic correlation (r_B) among the five sites composing the target environment was calculated with the estimates of variance components obtained from MTDFREML following YAMADA (1962):

$$r_B = \frac{\sigma^2_{c1}}{\sigma^2_{c1} + \sigma^2_{cs1}} \quad (6)$$

where:

r_B is the type B genetic correlation, variance components as previously defined.

The type B genetic correlation between any two of the defined environmental traits was calculated as

$$r_B = \frac{\sigma_{cij}}{\sqrt{\sigma^2_{ci} * \sigma^2_{cj}}} \qquad (7)$$

where:

r_B is the type B genetic correlation between traits "i" and "j", variance components as previously defined.

Estimation of Genetic Gains

Genetic gains for individual tree volume and mean annual increment were estimated for the target environment by two methods at six years. The first method used the predicted genetic merit of the clones obtained from the MTDFREML analyses. These "clonal values" were predicted using Best Linear Unbiased Prediction (BLUP), which considers "clonal values", as random effects to be predicted rather than fixed effects to be estimated (HENDERSON, 1984; WHITE and HODGE, 1988).

The predicted clonal values obtained from standardized data were back transformed to percentage gains in the measurement units by first multiplying by the square root of the mean phenotypic variance ($\sqrt{s^2_p}$) across all blocks, dividing by the phenotypic mean ($\bar{x}p$) of the target environment and multiplying by 100. Gains were estimated by selecting the best one of the 67 clones tested and successively increasing by one the number of selections until all 67 were selected. This results in 67 different gains predictions at decreasing levels of selection intensity.

The second method to predict genetic gains from clonal selection was made according to FALCONER (1993), using the respective heritability of clonal means:

$$\text{Gain (\%)} = (H^2_{\bar{c}} * i * \sigma_{p\bar{c}})(100/\bar{x}_p) \qquad (8)$$

$H^2_{\bar{C}}$ is broad sense heritability based on clone means,

i is the intensity of selection,

$s_{p\bar{c}}$ is the square root of the phenotypic variance of clonal means,

and broad sense heritability of clonal means is calculated based on the clonal phenotypic standard deviation and expressed as:

$$H^2_{\bar{c}} = \frac{\sigma^2_{c1}}{\sigma^2_{c1} + \frac{\sigma^2_{cs1}}{s} + \frac{\sigma^2_{bsc1}}{bs} + \frac{\sigma^2_{e1}}{bsn}} \qquad (9)$$

where:

variance components are as previously defined; and

s = number of sites, r = number of blocks per site and n = harmonic mean of the number of ramets per plot.

Results and Discussion

Average Trends in Survival and Growth

Average survival (%) over the six years for the target environment was high and much better than survival at either of the extreme sites ("Guachicona" or "Maravillas", *Figure 1*). The survival results of the target environment are in agreement with all previous clonal studies located in representative areas of operational plantings, which had survival greater than 90% at half-rotation (LAMBETH *et al.,* 1994). At the "Maravillas" site the poor survival is a reflection of the poor adaptability of the species to lower temperatures at high elevations, where cold-tolerant *Eucalyptus* species perform better (NEWMAN, 1981; CANNON, 1982; EASLEY and LAMBETH, 1989).

Mortality at "Guachicona" was very high in the first year (16%), increased steadily for the next two years and increased sharply in the fourth year. Mortality at this site is associated with the hot and dry climate and the long-term agricultural practices (irrigation and fertilization) which increased the pH in this alluvial soil (about pH 6.5).

All growth traits (total height, individual tree volume, and mean annual increment) followed a consistent pattern, with clones performing better in the target environment, followed by "Guachicona" and "Maravillas", respectively (*Figure 1*). Height and individual tree volume increased through time over the six years; however, MAI reached a plateau in the target environment at five years.

The growth of clones of *E. grandis* in the target environment through 6 years, for both individual tree volume (0.33 m^3) and MAI (58 $m^3\ ha^{-1}\ yr^{-1}$), is in line with other estimates of productivity of the species in the tropics (IKEMORI, 1990; ZOBEL, 1993; DARROW, 1995). However, the estimates for growth at "Guachicona" and "Maravillas" are marginal having less than half of the growth of the target environment. It would be possible to increase the productivity of *E. grandis* in these sites by hybridizing the species with some other *Eucalyptus* species, such as *E. camaldulensis* and *E. globulus,* that have shown better adaptability and performance in "Guachicona" and "Maravillas", respectively (CANNON, 1982; LADRACH, 1987).

Trends of Broad Sense Heritabilities

Survival

Broad sense heritability for survival is reported in the underlying continuous scale after transformation (*Figure 2*), while estimates based on 0/1 data and the percentage of incidence for the trait in the different environments are presented in *table 2.*

Heritability for survival at the "Guachicona" site tended to increase with age and was under strong genetic control after the second year (H^2 = 0.40 to 0.50). The heritability for survival at "Maravillas" steadily increased during the first three years. From this point forward the heritability stabilized exhibiting moderate genetic control (H^2 = 0.26). On the other hand, herit-

Table 2. – Average survivel (%), and broad sense heritabilities based on 0/1 data and on the liability scale for clonal tests in the three different environments.

Test Age	Guachicona			Maravillas			Target Environment		
	Survival (%)	H^2 (0/1)	H^2 Liability	Survival (%)	H^2 0/1	H^2 Liability	Survival (%)	H^2 0/1	H^2 Liability
1	84.35	0.014	0.032	94.77	0.011	0.047	95.07	0.011	0.049
2	81.53	0.190	0.403	82.30	0.079	0.170	93.13	0.035	0.128
3	80.00	0.202	0.412	76.97	0.136	0.261	92.61	0.035	0.124
4	77.81	0.202	0.393	76.04	0.135	0.255	91.93	0.044	0.145
5	72.56	0.280	0.500	72.80	0.133	0.239	91.35	0.038	0.120
6	65.90	0.286	0.478	71.65	0.132	0.234	89.85	0.036	0.104

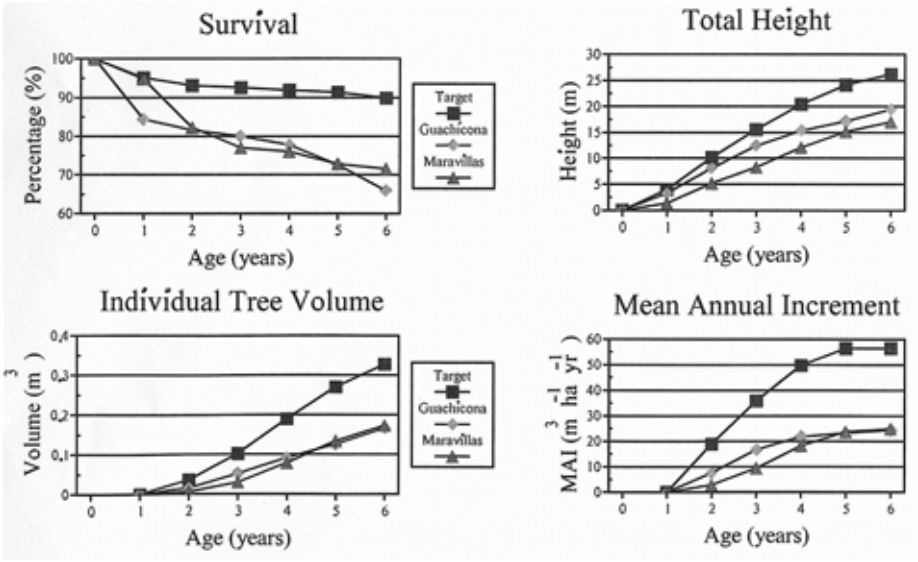

Figure 1. – Trends of average survival, height, individual tree volume and mean annual increment (MAI) of *Eucalyptus grandis* across six years after planting for three environments.

ability of survival in the target environment was, in general, low increasing during the first two years and thereafter remaining almost constant between 0.10 and 0.15.

There are very few published estimates of heritabilities for survival for *E. grandis*. At a very young age, 1.25 years, narrow sense heritability for survival in Florida in the binomial scale (h^2 = 0.09) was within the range of broad sense heritabilities for six of these seven clonal trials H^2 = 0.02 to 0.10 (ROCKWOOD *et al.,* 1989). On the contrary, estimates of the heritability of survival on the underlying scale, for open pollinated families of *E. globulus* spp. *globulus* in areas where frost damage was the main cause of mortality (54–12%), had high heritabilities varying from h^2 = 0.32 to 0.57 at 4 to 5 years of age (CHAMBERS *et al.,* 1996).

While the single-site H^2 estimates for "Guachicona" and "Maravillas" are upwardly biased compared to estimates from the target environment (pooled analysis, 5 tests), the higher values in the extreme environments may also reflect genetic differences in adaptation. Within the target environment, the high mean survival (90% at a rotation age of 6 years) and the low H^2 (about 0.1), taken together, indicate that: (1) *E. grandis* is well adapted to these conditions; and (2) Survival is not an important trait for the selection program in this environment.

Growth traits

As a general result, broad sense heritabilities for growth traits were higher at the "Guachicona" site than for either "Maravillas" or the target environment (*Figure 2*). Differences in heritabilities across traits were associated with changes in the magnitude of the variance components. Lower environmental variation was observed for all growth traits at "Guachicona", a flat site, versus the other sites located on gentle slopes

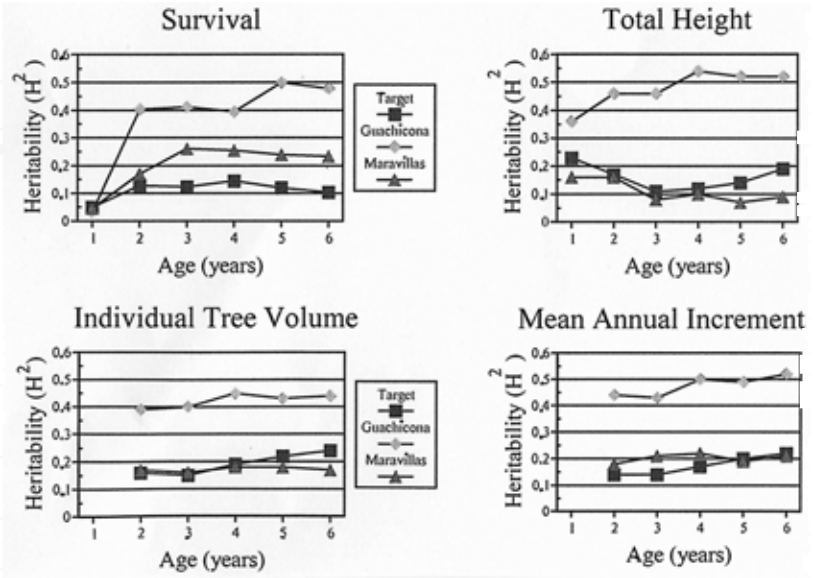

Figure 2. – Trends of broad sense heritabilities (H^2) for survival, height, individual tree volume and mean annual increment (MAI) of *Eucalyptus grandis* across six years after planting for three environments.

in the mountains, probably due to a better layout of the trial in the field or a more positive response to intensive management practices.

Broad sense heritability for total height was markedly different for "Guachicona" compared to the other sites. At "Guachicona" the heritability increased during the first four years and then stabilized at a very high level $H^2 = 0.5$. At "Maravillas" and the target environment the heritability decreased until the third year, and then it leveled off at "Maravillas", but increased until rotation age at the target environment.

Broad-sense heritability estimates for individual tree volume and MAI, were moderate and showed similar trends in the target environment. The estimates slightly decrease or remain constant until year three and thereafter they gradually increased until rotation age. These estimates of broad sense heritabilities for growth traits are lower than those obtained in previous clonal trials (LAMBETH *et al.,* 1994) because, in the latter, the estimates at each age were averages of single-site analyses.

It seems that when mortality is high as in "Guachicona" and "Maravillas", clonal differences in MAI are exacerbated and the heritability estimates for MAI are slightly higher than those estimates of volume at each particular site. On the contrary, the heritability estimates for volume and MAI in the target environment were of similar magnitude due to the relative lack of a mortality effect.

Genotype-by-Environment Interaction

Preliminary analyses of total height (m), individual tree volume (m^3), and MAI ($m^3\ ha^{-1}\ year^{-1}$) using data from all possible pairs of sites supported the a priori notion of considering the target environment (5 sites), "Guachicona", and "Maravillas" as three distinct traits (OSORIO, 1999). Moreover, the genetic correlations derived from the multivariate analyses among "traits" using MTDFREML, are measurements of the GxE interaction among these three site groupings (*Table 3*).

The genetic correlations for MAI at age 6 indicated a type B genetic correlation of zero between the target environment and either of the other two sites, and a negative correlation ($r_B = -0.49$) between "Guachicona" and "Maravillas". Low to moderate type B genetic correlations among the three traits were found for height and individual tree volume. The negative type B genetic correlation between "Guachicona" and "Maravillas" provides further substantiation that growth responses in these environments may be due to different gene loci.

Genotype-by-environment interaction among the five sites within the target environment over the years was moderate as indicated by the type B genetic correlation of approximately 0.6 for both individual tree volume and MAI (*Figure 3*). The type B genetic correlation decreased from the first until the third year and thereafter increased until rotation age. The type B genetic correlation for total height was high in the first year, and then fluctuated between 0.50 and 0.64 in the remaining years.

Wood Density

Mean values of wood density were very similar for "Maravillas" and the target environment, but both were lower than density values at "Guachicona" (*Figure 4*). With the exception of the latter, the results compare favorably with other published estimates of wood density at the same age (VAN WYK, 1990;

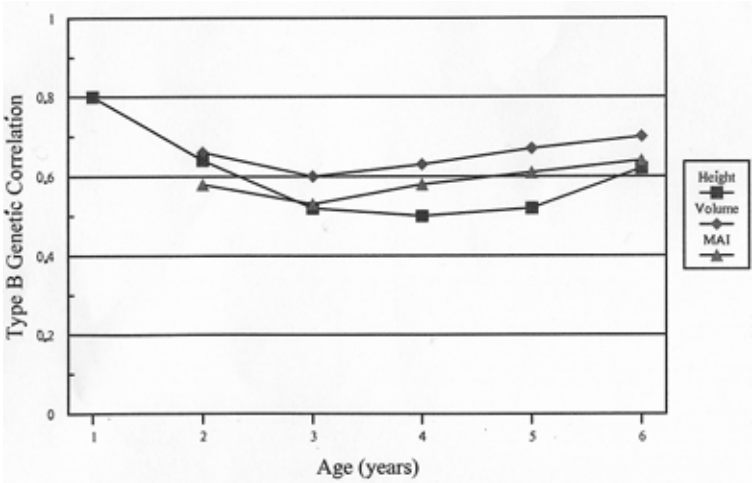

Figure 3. – Trends of type B genetic correlations for growth traits of *Eucalyptus grandis* at five locations representing the target environment across six years after planting.

Table 3. – Broad-sense heritabilites and genetic correlations among environments treated as different "traits" in the multivariate analyses (1 = target environment, 2 = Guachicona and 3 = Maravillas), for growth variables and wood density analyzed at six years of age.

Trait	Height [1] Trait			Volume Trait			MAI Trait			Wood Density Trait		
	1	2	3	1	2	3	1	2	3	1	2	3
1	0.19			0.24			0.22			0.35		
2	0.21	0.52		0.54	0.44		0.02	0.52		0.63	0.29	
3	0.20	0.56	0.09	0.34	0.65	0.17	0.01	-0.49	0.21	0.88	0.81	0.41

[1]) Broad-sense heritabilities on diagonals and genetic correlations (r_B) among "traits" below diagonals.

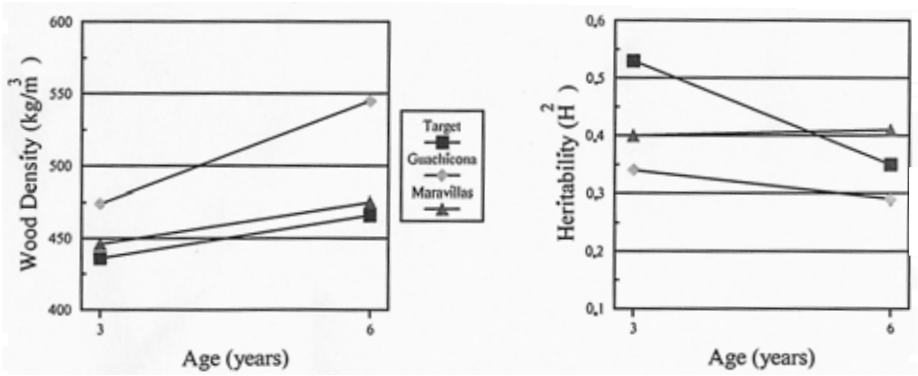

Figure 4. – Trends of average basic wood density and broad sense heritabilities for clonal trials of *Eucalyptus grandis* at two ages in three environments.

WANG and YANG, 1995; DENISON and KIETZKA, 1993). The high values of wood density at "Guachicona" may be related to the factors limiting growth at the site (ZOBEL *et al.,* 1987).

Trends in the heritabilities of wood density showed a different pattern for each environment (*Figure 4*). Broad-sense heritability for wood density was stable in "Maravillas", but it decreased in both "Guachicona" and the target environment over time. Broad-sense heritability in the target environment was high at three years and consistent with other reported estimates of wood density in Eucalyptus (MALAN, 1991). However, the estimate decreased at six years as the clonal variance decreased and the within plot variance increased.

Wood density heritabilities for "Guachicona" and "Maravillas" were of moderate genetic size (*Figure 4*).The large type B genetic correlations of wood density (*Table 3*) among the three groups of sites (the target environment, "Guachicona" and "Maravillas") indicated very little GxE. Thus wood density could be considered as one trait across all three environments although some clonal rankings change between the target environment and "Guachicona".

The genotype-by-environment interaction of wood density within the target environment was unimportant (r_B = 0.90) at three and six years of age indicating that clonal rankings remain nearly constant across all sites in this environment. These results coincide with previous studies (BHAT *et al.,* 1990) which revealed very little differences in the genetic control of wood properties of *E. grandis* between geographical regions. Nevertheless, MALAN and VERRYN (1996) reported changes in wood density ranks with small changes in the environment, for 9 out of 25 *E. grandis* clones.

Genetic Gains

The estimates of genetic gains from clonal selection for mean annual increment and individual tree volume at six years showed high genetic gains for intensities of selection above i = 1.0, *i.e.* proportions less than 25 clones out of 67, p = 0.37, (*Figure 5*). Differences between clonal gain estimates derived from predicted clonal values and from the classical formula are related to the advantages of BLUP, which adjusts all predictions to reflect unbalance in the data and actual distribution of the clonal predictions in the extremes. In the standard formula the assumption is made that all clonal means have the same heritability and equal representation in all tests; and clonal values have a normal distribution. Deviation from expectations of a normal distribution, especially in the highest ranking or lowest ranking clonal values, can cause difference in the gains predictions from these two methods. Even with these differences, the two approaches resulted in very similar predicted gains at all selection intensities.

Conclusions

Differences in survival, growth rates and type B genetic correlations from the multivariate analyses support the contention of sub-dividing the seven sites into three different environments, a target environment (five sites), "Guachicona" and "Maravillas". These groups of sites are representative of the *E. grandis* planting area of the company. The target environment representing the main planting region, and the two extreme sites represent marginal planting areas for distinctly different reasons: (1) "Guachicona" is a hot-dry, low-elevation site; and (2) "Maravillas" is a cold high-elevation site.

The low type B genetic correlation between the two extreme sites for survival suggested that survival may be controlled by different genes in these two different edaphoclimatic conditions. Further, the continued decline in survival over time indicates the poor adaptability of the species to the particular environmental conditions at either site.

Broad sense heritabilities for survival, individual tree volume and mean annual increment (MAI) tended to increase over time for the three environments, but the trends for height were quite different among the three environments. Mean annual increment (MAI) seems the most appropriate variable to be used as an indicator of growth and genetic parameters since it incorporates both mortality and growth rate providing a better indicator for operational clonal plantings across diverse environments.

The genotype-by-environment interaction (GxE) for growth traits at six years age was moderate (r_B=0.6 to 0.7) among the five sites within the target environment. Furthermore, the clonal rankings for MAI at the two extreme sites differed markedly both between those sites and between each of the two extreme sites and the target environment. Thus, all three environments will require separate clonal test locations and deployment populations for growth traits.

The trends of broad sense heritabilities for mean wood density were unexpected. Heritabilities tended to stay constant or decrease over time for the three environments. GxE interaction of wood density was low (r_B=0.9) indicating that clonal rankings were very stable among the five sites within the target environment. Overall, wood density could be considered a single trait across all three environments.

The estimates of genetic gains for clonal selection by the two methods (predicted clonal values and the classical gains for-

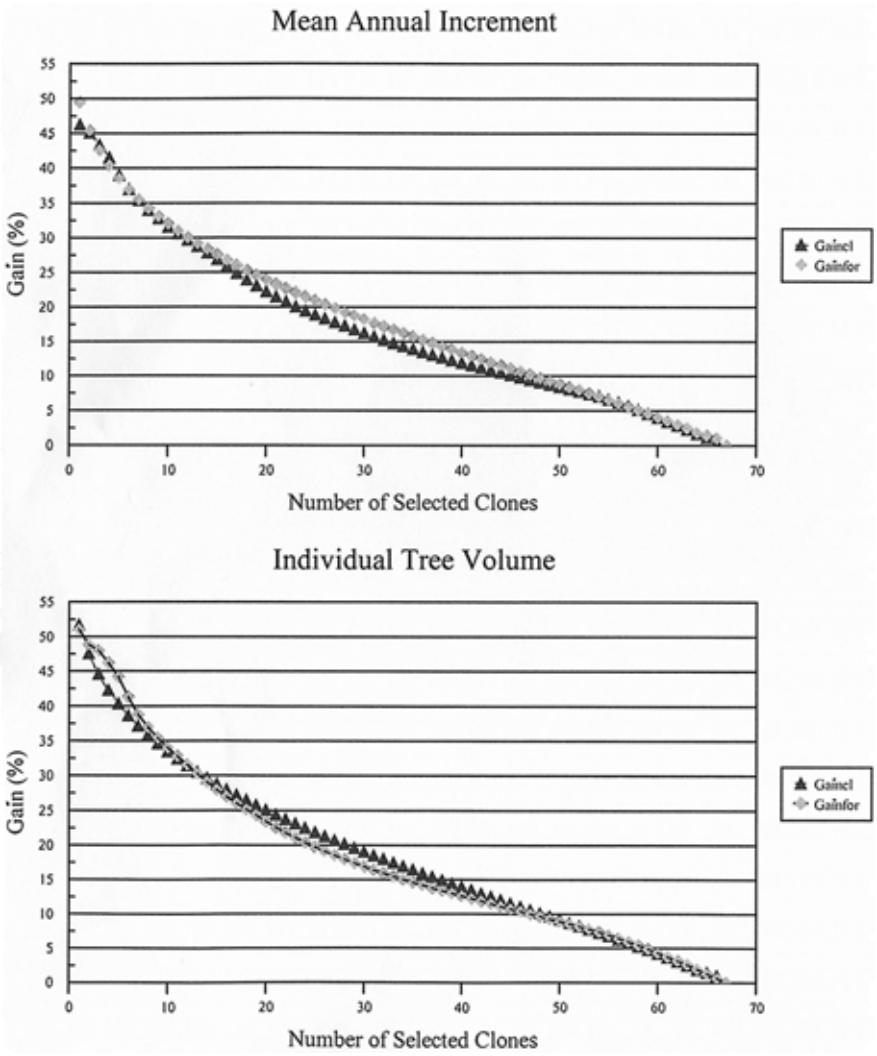

Figure 5. – Clonal genetic grains in mean annual increment (MAI) and individual tree volume, in the target environment, estimated by using predicted clonal values and the standard formula. Each gain estimate is computed by selecting the best additional clone out of a total of 67 until all clones are selected. Gaincl stands for gain computed from predicted clonal values and Gainfor refers to gain computed from the standard formula (FALCONER, 1993).

mula) were similar and showed the great potential available to increase productivity in the target environment through clonal selection. However, the method of gains based on clonal values estimated with BLUPs should provide more precise estimates due to the proper accounting for data imbalance.

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Appendix

The statistical analysis of each variable followed the multivariate mixed model, in matrix form (see Materials and Methods for definitions of variance components):

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 \\ 0 & X_2 & 0 \\ 0 & 0 & X_3 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 \\ 0 & Z_2 & 0 \\ 0 & 0 & Z_3 \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \\ c_3 \end{bmatrix} + \begin{bmatrix} N_1 \\ 0 \\ 0 \end{bmatrix} [d_1] + \begin{bmatrix} Q_1 \\ 0 \\ 0 \end{bmatrix} [p_1] + \begin{bmatrix} 0 & 0 \\ W_2 & 0 \\ 0 & W_3 \end{bmatrix} \begin{bmatrix} t_2 \\ t_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix} \quad (10)$$

where:

y = vector of observations corresponding to three traits, remembering that each trait is measured on a separate set of ramets for clones in a different environment. Observations in the target environment are trait 1 (subscript 1), in the "Guachicona" environment are trait 2 (subscript 2), and in the "Maravillas" environment are trait 3 (subscript 3).

b = vector of fixed effects for site and block effects for trait 1, and block fixed effects for traits 2 and 3.

c = vector of random clonal effects corresponding to traits 1, 2, and 3 of length equal to three times the total number of clones distributed as MVN~(0, C). C = $\mathbf{c} \quad I_c$ where I_c is the identity matrix (unrelated clones) of dimensions equal to the total number of clones and $\mathbf{c}$ is the among traits covariance matrix (3x3) as

$$\begin{bmatrix} \sigma^2_{c1} & \sigma_{c12} & \sigma_{c13} \\ \sigma_{c21} & \sigma^2_{c2} & \sigma_{c23} \\ \sigma_{c31} & \sigma_{c32} & \sigma^2_{c3} \end{bmatrix} \otimes I_c = \mathbf{C}. \quad (11)$$

d_1 = vector of the uncorrelated random effects for clone by site interactions, and d_1 is N~(0, D). D is a square matrix $s^2_{cs} I_k$) and has dimensions to the total number of combinations of clone by site (cs) for trait 1, i.e. only present in the model for trait 1.

p_1 = vector of the uncorrelated random effects for block within site by clone interactions and p is N~(0, K). K is a square matrix ($\sigma^2_{bsc} I_k$) and has dimensions equivalent to total number of combinations of block within site by clone (*bsc*) for trait 1, i.e. only present in the model for trait 1.

t = matrix of the uncorrelated random effects for block by clone interactions, and t is MVN~(0, T). T is a block-diagonal square matrix and has dimensions equal to the total number of blocks by clone combinations (*bc*) for traits 2 (n2) and 3 (n3), *i.e.* only present in the model for traits 2 and 3. The only non-zero elements for T are along the diagonal. Elements t_{11} through $t_{n2,n2}$ are s^2_{bc2} and elements $t_{n2+1,n2+1}$ through $t_{n2+n3,n2+n3}$ are s^2_{bc3}.

e = vector of random residual effects for traits i = 1, 2, and 3 and e is MVN~(0, R). R is a square matrix and has dimensions equal to the sum of the numbers of observations for traits 1 (n1), 2 (n3) and 3 (n3). R is block diagonal with the only non-zero elements occurring on the diagonal (no covariances among the error terms since the traits were not measured on the same observational units). The first n1 observations along the diagonal equal to s^2_{e1}, the next n2 observations equal to s^2_{e2}, and the final n3 observations equal to s^2_{e3}.

The variance for observations (**V**) is:

$$\mathrm{Var}\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \mathbf{ZCZ'} + \mathbf{NDN'} + \mathbf{QKQ'} + \mathbf{WTW'} + \mathrm{R} = \mathbf{V} \qquad (12)$$

where:

X, Z, N, Q and **W** are incidence matrices relating records to the fixed, clonal and uncorrelated random effects, described in sub-matrix form in the Appendix, Equation 1. **X, Z, N, Q** and **W** have dimensions equivalent to (*nxp*) where n = the total number of observations corresponding to traits 1, 2 and 3 and p is the number of levels for the modeled effects.

Allozyme Variation and Mating System of Coastal Populations of *Pinus koraiensis* SIEB. et ZUCC. in Russia

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Summary

Based on the analysis of 26 allozyme loci, levels of gene variation were ascertained in coastal populations of Korean pine. On average, 55.4% loci were polymorphic, the number of alleles per locus was 1.84, the expected heterozygosity was 0.176, and the observed heterozygosity was 0.177. On average, the heterozygote deficiency was characteristic for Korean pine populations (F_{IS}=0.012). The most diversity was found within populations (F_{ST}=0.016). Genetic distances between populations were small (D_N=0.003). Level of gene flow was 16.96 migrants per generation. Multilocus outcrossing estimates ranged from 0.751 to 0.986 indicating mating system differences in coastal populations of Korean pine.

Key words: Pinus koraiensis, coastal populations, allozymes, genetic variation, mating system.

Introduction

The Korean pine, *Pinus koraiensis* SIEB. et ZUCC., with many species of deciduous broad-leaved trees and other conifers, form the broad-leaved Korean pine mixed forests of the Russian Far East. Selective harvesting and fires have repeatedly stressed most of the forests. At present, clear cuttings of broad-leaved Korean pine mixed forests are illegal. However, the harvest of the broad-leaved Korean pine forests is occurring without authorization because of demand for pine and hardwood timber. For this reason, the broad-leaved Korean pine forestlands are decreasing (KORYAKIN and ROMANOVA, 1996). Thus, there is a need to emphasize conservation of Korean pine genetic resources.

Knowledge of the level and distribution of genetic variation, both within and among population, facilitates the conservation of gene resources (BROWN, 1978; MILLAR and LIBBY, 1991). Recently, the results of genetic variation studies of Korean pine populations in the Russian Far East (KRUTOVSKII et al., 1995; POTENKO and VELIKOV, 1998) and South Korea (KIM et al., 1994) have been reported. Differences in levels of genetic variation, within and among the population in different parts of Korean pine's natural range, were observed (POTENKO and VELIKOV, 1998). Greater variation was found in South Korean populations, with less occurring in the north-west part of natural range in Russia. Additionally, the measurements of mating systems showed a high proportion of outbreed progeny in three earlier studied Korean pine populations (POLITOV and KRUTOVSKII, 1994; KRUTOVSKII et al., 1995). All previously analyzed populations in Russia represented the internal range of naturally occurring Korean pine.

Marginal populations of some conifer species tend toward to lower heterozygosity than central population (BERGMANN and GREGORIUS, 1979; YEH and LAYTON, 1979; GURIES and LEDIG, 1982; HAWLEY and DEHAYES, 1994), which might be expected because of isolation and restricted gene flow, and because marginal populations frequently owe their origin to colonizing events and suffer from the bottleneck of the founder effect (LEDIG, 1986).