

## GENETIC PARAMETERS ESTIMATES, SELECTION INDICES AND PREDICTED GENETIC GAINS FROM SELECTION OF *EUCALYPTUS GLOBULUS* IN CHILE

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### ABSTRACT

Genetic parameters for growth, survival, frost damage and pilodyn penetration (as a proxy for wood density) were estimated with four-year-old data from six progeny tests of *Eucalyptus globulus* Labill. ssp. *globulus* (*E. globulus*) planted in south-central Chile. The progeny tests included 289 open-pollinated families collected from mass-selected plus trees in the Colcura landrace plantations located in the coastal regions of central Chile. Individual heritabilities were moderate to moderately high for mean annual increment in volume per tree (MAIV), frost resistance and pilodyn ( $h^2 = 0.25, 0.26$  and  $0.34$ , respectively); whereas estimates for survival on an underlying (continuous) scale and for height were lower ( $h^2 = 0.17$  and  $0.19$ , respectively). Type B genetic correlations for all traits across three different sites (coast, central valley, and Andean foothills) were moderate, except for MAIV in the foothills compared to coast and central valley ( $r_B = 0.18$ ). Genetic correlations among traits resulted in favorable associations among MAIV, frost resistance and survival, whereas a slightly unfavorable genetic correlation was found between MAIV and pilodyn ( $r_A = 0.14$ ).

A selection index was developed in order to optimize genetic gains on MAIV and pilodyn, simultaneously. With index weights of 0.3 for MAIV and 0.7 for pilodyn, a genetic gain of approximately 24 % for MAIV and 4 % for pilodyn can be expected from backward selection of the top 20 % of the parents (*i.e.*, selecting the top 60 out of 289 parents based on the index). A favorable correlated response in frost resistance and survival can be expected from selection on volume.

**Keywords:** *E. globulus*, heritability, genetic correlation, index selection, genetic gain, wood density.

### INTRODUCTION

One of the most extensively planted *Eucalyptus* species in the world, Tasmanian blue gum (*Eucalyptus globulus* Labill. ssp. *globulus*) occupies approximately 230,000 ha of plantations in Chile (INFOR 1997). The species is used in the pulp and paper industry because of its fast growth and high pulp yield (ELDRIDGE *et al.* 1993, TIBBITS *et al.* 1997). Many organizations in Chile have already commenced breeding programs to improve the growth, yield and fiber quality of the species (GRIFFIN 1993, JAYAWICKRAMA *et al.* 1993). Information on heritabilities and genetic variation for use in breeding programs is primarily obtained through the analysis of field trials (GRIFFIN 1993, ELDRIDGE *et al.* 1993, WHITE 1996).

This study utilizes data from field trials of the breeding program of the forestry company Forestal y Agrícola Monteáguila S.A. (FAMASA). FAMASA operates in central Chile with the primary goal of

producing high quality pulpwood from *Eucalyptus* species. Company lands are located in region VIII of the country (lat. 37° S) with about 21,000 ha of *Eucalyptus globulus* plantations located in three main planting sites: the Pacific coastal area, the central valley and the Andean foothills. The overall area has predominantly warm temperate climate, with mean annual temperature ranging from about 11 to 15 °C and annual rainfall varying from 500 to 2000 mm·year<sup>-1</sup> (TIBBITS *et al.* 1997). The elevation ranges from 0 to 450 m.a.s.l. and soil types are clays, sandy clays and volcanic ashes (Turmao soil type).

*E. globulus* is rather sensitive to cold temperatures (GRIFFIN 1993, TIBBITS *et al.* 1997). Comparing the three main areas in the company lands, the coastal farms are predominantly free of frosts. The central valley and the Andean foothills experience temperatures down to -10 °C during the winter, and, especially in the central valley, frosts are accentuated in depressions due to the lack of air circulation. In the absence of

frosts, survival rates for *E. globulus* above 90% can be easily achieved under standard operational silviculture. Growth rates on milder sites for *E. globulus* approach 25 to 30 m<sup>3</sup>·ha<sup>-1</sup>·yr<sup>-1</sup> and rotation ages range from 8 to 10 years (JAYAWICKRAMA *et al.* 1993, TIBBITS *et al.* 1997). Therefore, the primary traits of interest to assess in plantation species for pulpwood production in Chile are wood density and stem volume, together accounting for 95 % of the potential gain possible by selection (GREAVES *et al.* 1997) and frost resistance, due to its influence over survival and adaptation.

Breeding values represent the genetic worth of an individual judged by its individual performance and the mean genetic merit of its relatives (FALCONER & MACKAY 1996). Predictions of breeding values can be used to rank families, to identify the best genotypes for clonal and seedling seed orchards, and to make deployment decisions in operational plantations (WHITE 1996). Consequently, in order to maximize genetic gains in any breeding program, accurate and precise predictions of breeding values are critical (WHITE & HODGE 1987, WHITE 1996). Following breeding value prediction, the optimal procedure for selection is to combine breeding value predictions from various traits into a selection index to select genotypes projected to yield maximum genetic gains in the aggregate trait (COTTERILL & DEAN 1990, FALCONER & MACKAY 1996).

Using FAMASA data from 289 parents and more than 20,000 of their offspring planted in six tests, the specific objectives of this paper are to: (1) Estimate genetic parameters for MAIV (Mean annual increment in volume per tree), pilodyn (a proxy for wood density), frost resistance and survival; (2) Predict breeding values for 289 *E. globulus* selections and offspring; and (3) Use these parameter estimates and breeding value predictions to develop selection indices; and (4) Estimate genetic gain from various types and intensities of selection.

## MATERIALS AND METHODS

### Trial Sites and Design

This study used four- and five-year-old data from six progeny tests planted with seedlings from 289 open-pollinated families of *E. globulus* (Table 1). These 289 selections were made from the local Chilean land race from 15,000 ha of plantations growing along the Chilean coast (lat. 37° S). The 289 selections were felled and open-pollinated seed was collected. The origin of the seed used to establish these land race plantations is unknown.

Open-pollinated progeny from these selections were tested in two consecutive years and two disconnected sets of trials. Set one consists of 149 families established in 1990 at two test locations, whereas set two consists of 140 families established in 1991 at four test locations. Consequently, the two sets provide independent parameter estimates since they come from: (1) A different sample of families; (2) Different years of planting; and (3) Different test locations.

The statistical design used in all trials is an alpha-lattice with four-tree row plots and six replications per site (PATTERSON & WILLIAMS 1976).

Growth and quality traits were measured on all tests. Measurements were recorded as height (*HT*) in meters, diameter at breast height (*DBH*) in centimeters, and survival (*SURV*) as 0–1 binary values. Two trees in each plot of four trees were selected on phenotype and measured for pilodyn (*PILO*) in mm of penetration in the stem at 1.37 m height, having previously removed the bark at the point of assessment. Pilodyn penetration was used as an indicator of wood density since prior studies suggest that the relationship between pilodyn and basic density is linear, and genetic and phenotypic correlations for *Eucalyptus* species are generally high (GREAVES *et al.* 1995, RAYMOND & MACDONALD 1998). Frost damage (*FR*) was assessed at age two on

**Table 1.** Description of six progeny trials containing 289 *E. globulus* families (Fams) in two disconnected sets of experiments located in three distinct edapho-climatic regions.

Test	Set	Site	Soil Type	Age (years)	Fams (#)	Annual rainfall	Altitude (m.a.s.l.)	Frosts* (No·yr <sup>-1</sup> )
2	1	Coast	Clay	5	149	1330 mm	250	0
102	1	Valley	Trumao	5	149	1741 mm	360	66
1	2	Coast	Clay	4	140	1330 mm	120	0
101	2	Valley	Clay	4	140	1308 mm	310	43
103	2	Valley	Trumao	4	140	1741 mm	340	66
201	2	Foothills	Trumao	4	140	2255 mm	400	94

\* Data contributed by Forestal y Agrícola Monteáguila S.A. Source: 1993–1995 data and meteorological records (unpublished).

3 tests located in areas where freezing temperatures most frequently occur (central valley and foothills). The response variable was percentage of foliage damaged by frost, with interval increments of 20 % used to obtain measurements of 0, 20, 40, 60, 80, or 100 % (100 % being equivalent to death from frost damage).

HT and DBH were measured after the fourth (Set 2) and fifth (Set 1) growing seasons and used to compute individual tree volume outside bark per tree as:

$$VOL (m^3) = 0.785*(DBH^2) * (1.37+0.33 * (HT -1.37)) \quad [1]$$

where  $-VOL (m^3)$  is the individual tree volume in cubic meters;  $DBH$  is the diameter at breast height in meters; and  $HT$  is the height of the tree in meters. Assuming stem growth as a cylinder below  $DBH$  and a cone above  $DBH$ , this function has been used in the absence of other more specific functions (LAMBETH *et al.* 1983, HODGE *et al.* 1996).

To account for family survival, mean annual increment for volume ( $MAIV$ ) on a per hectare basis was calculated for each tree as:

$$MAIV (m^3 ha^{-1} \cdot yr^{-1}) = ((VOL * Survival) * Trees ha^{-1})/Age \quad [2]$$

Where  $VOL$  is the individual tree volume from Equation 1;  $Survival$  is the family mean survival per test, as a decimal equivalent of percent;  $Trees ha^{-1}$  is the number of trees per hectare at time of planting; and  $Age$  is the measurement age in years. The distribution for  $MAIV$  was verified robust to the normality assumption.

Data were edited and cleaned prior to the statistical analysis. Observations lying outside the normal range were eliminated since they inflate error variances, and result in misleading estimates (SORENSEN & WHITE 1988). Outliers were eliminated on the basis that suspected runts were due to selfing, and selfs violate the genetic assumptions of half-sib tests (SORENSEN & WHITE 1988). Deleted measurements accounted for less than 1 % of the observations for five tests and less than 3 % of the data for one test.

## Statistical Analysis

### Single-site analysis to estimate genetic parameters

Single-site analyses were conducted on each test location for the traits height,  $MAIV$ , frost, survival and pilodyn. The goal was to obtain accurate estimates of variance components and single-site narrow sense heritability ( $h_B^2$ ) for all traits. First, the 289 selections had originated from five different locations in the central coast; so single site F-tests were conducted to

determine the significance of seed source effects for  $MAIV$  and frost damage using SAS Proc Mixed (SAS Institute Inc. 1996). The analysis showed no significant effects due to seed sources; therefore seed source effects were removed from the linear model for estimating variance components.

Using variance component estimates from SAS Proc Mixed (SAS Institute Inc. 1996), single-site (biased) heritabilities were calculated according to the formula:

$$h_B^2 = 3.3 * \sigma_f^2 / \sigma_f^2 + \sigma_{fr}^2 + \sigma_w^2 \quad [3]$$

where:  $h_B^2$  is the estimated individual tree heritability for each trait; 3.3 is an approximation to  $1/(2 * \Phi_{xy})$ , where  $\Phi_{xy}$  is the coefficient of coancestry; and would be four if open-pollinated families were true half-sib families (SQUILLACE 1974, BORRALHO 1994, FALCONER & MACKAY 1996);  $\sigma_f^2$  is the family variance component estimate;  $\sigma_{fr}^2$  is the replicate by family interaction variance component estimate; and  $\sigma_w^2$  is the residual variance component estimate (FALCONER & MACKAY 1996).

These  $h_B^2$  estimates are called single-environment or biased heritabilities because  $\sigma_f^2$  in the numerator is upwardly biased since it is measured in only one environment. Thus, the additive genetic variance is confounded with the genotype by environment interaction (COMSTOCK & MOLL 1963).

Since survival was measured on a binary scale 0–1, which is dependent on the incidence of a trait (GIANOLA 1982, LOPES 1998), heritability estimates were converted to the continuous underlying scale ( $h_{UND}^2$ ) assuming a threshold model by DEMPSTER & LERNER (1950) to facilitate comparison among sites with different mean incidences:

$$h_{UND}^2 = h_{B(0,1)}^2 p(1-p) / c^2 \quad [4]$$

where:  $h_{UND}^2$  is the transformed individual narrow-sense heritability on the underlying continuous scale;  $h_{B(0,1)}^2$  is the individual narrow-sense heritability on the binary scale (no transformation);  $p$  is the average percentage of survival per site; and  $c$  is the ordinate of the normal density function at the average survival incidence.

Paired-site and across-site analyses were performed for the traits  $MAIV$ , frost damage, height, pilodyn and survival to estimate: (1) Narrow sense heritabilities for each trait ( $h^2$ ); (2) Type B genetic correlations to measure family by location interaction for each trait ( $r_B$ ); and (3) Genetic correlations among traits ( $r_{xy}$ ). Prior to these analyses, frost damage,  $MAIV$ , height and pilodyn were standardized by dividing each tree's measurement by the replicate phenotypic standard deviation, in order to remove scale effects due to tests and reduce heterogeneity of variance (VISSCHER *et al.*

1991, FALCONER & MACKAY 1996, WHITE 1996). For the trait survival measured as a binary 0–1 score, no standardization to stabilize variances was performed and data were analyzed without transforming the observations. This followed recommendations from previous studies by HUBER (1993) and LOPES (1998) that suggest that REML estimates on 0–1 scores, not transformed, provide satisfactory estimates.

SAS Proc Mixed was used to obtain REML estimates of variance components for  $h^2$  and  $r_B$  for all traits (LITTELL *et al.* 1996, SAS Institute Inc. 1996). The model for the analysis was:

$$Y_{ijklm} = m + T_i + R(T)_{ij} + b(TR)_{ijk} + f_j + Tf_{il} + f(RT)_{ijl} + w_{ijklm} \quad [5]$$

where:  $Y_{ijklm}$  is the observed phenotype of the  $m^{\text{th}}$  individual of the  $l^{\text{th}}$  family from the  $k^{\text{th}}$  block nested within the  $j^{\text{th}}$  replicate at the  $i^{\text{th}}$  test location;  $m$  is the overall mean;  $T_i$  is the fixed effect of the  $i^{\text{th}}$  test;  $R(T)_{ij}$  is the fixed effect of the  $j^{\text{th}}$  replicate nested within the  $i^{\text{th}}$  test;  $b(TR)_{ijk}$  is the random effect of the  $k^{\text{th}}$  block nested within the  $j^{\text{th}}$  replicate in the  $i^{\text{th}}$  test,  $\sim \text{NID}(0, \sigma_{b(TR)}^2)$ ;  $f_j$  is the random effect of the  $j^{\text{th}}$  family,  $\sim \text{NID}(0, \sigma_f^2)$ ;  $Tf_{il}$  is the random effect of the interaction between the  $l^{\text{th}}$  family and the  $i^{\text{th}}$  test location,  $\sim \text{NID}(0, \sigma_{fT}^2)$ ;  $f(RT)_{ijl}$  is the random effect of the interaction between the  $j^{\text{th}}$  replicate within the  $i^{\text{th}}$  test and the  $l^{\text{th}}$  family,  $\sim \text{NID}(0, \sigma_{f(RT)}^2)$ ;  $w_{ijklm}$  is the residual,  $\sim \text{NID}(0, \sigma_w^2)$ ; and  $i = 1, \dots, 2$ ;  $j = 1, \dots, 6$ ;  $k = 1, \dots, 13$ ;  $l = 1, \dots, 149$ ;  $m = 1, 2, 3, 4$  for Set 1; and  $i = 1, \dots, 4$ ;  $j = 1, \dots, 6$ ;  $k = 1, \dots, 15$ ;  $l = 1, \dots, 140$ ;  $m = 1, 2, 3, 4$  for Set 2.

Individual-tree narrow sense heritabilities were calculated for each trait using variance components from both the paired-wise and the pooled analysis of all tests within a set as:

$$h^2 = 3.3 * \sigma_f^2 / (\sigma_f^2 + \sigma_{fT}^2 + \sigma_{f(RT)}^2 + \sigma_w^2) \quad [6]$$

where all terms are defined in Equation 5. Across-site type B genetic correlations among tests were calculated using the formula (YAMADA 1962, FALCONER & MACKAY 1996):

$$r_B = \sigma_f^2 / (\sigma_f^2 + \sigma_{fT}^2) \quad [7]$$

where  $r_B$  is the estimated type B genetic correlations for each trait measured in a group of sites based on the variance components obtained from SAS Proc Mixed (SAS Institute Inc. 1996); and all remaining terms were previously defined in Equation 5.

Across-site genetic correlations among pairs of traits were calculated using the computer program MTDFREML (BOLDMAN *et al.* 1993). Type A genetic

correlations refer to the analysis of different traits measured on the same individual trees. Across-site genetic correlations among pair of traits were obtained according to the formula:

$$r_{A,xy} = \sigma_{A,xy} / (\sigma_{A,x}^2 \cdot \sigma_{A,y}^2)^{1/2} \quad [8]$$

where:  $r_{A,xy}$  is the estimated type A genetic correlation among two different traits  $x$  and  $y$  measured on the same individuals, based on the variance components and covariances obtained from the multivariate computer program MTDFREML (BOLDMAN *et al.* 1993);  $\sigma_{A,xy}$  is the additive genetic covariance between the two traits  $x$  and  $y$ ;  $\sigma_{A,x}^2$  is the additive genetic variance of trait  $x$ ; and  $\sigma_{A,y}^2$  is the additive genetic variance of trait  $y$  (YAMADA 1962, FALCONER & MACKAY 1996).

Variance components from SAS Proc Mixed were used as starting points to obtain covariances and genetic and environmental correlations from MTDFREML (BOLDMAN *et al.* 1993). In order to maintain the 3.3 weight over the family variance, all variances used as priors in MTDFREML were held constant while permitting the program to iterate for covariances to obtain the correlation estimates.

#### *Selection Indices and Genetic Gain*

Genetic parameters can be used to predict breeding values and to estimate genetic gain from selection. Breeding values represent the genetic worth of an individual judged by the mean genetic merit of its progeny or other relatives (FALCONER & MACKAY 1996). Given that Best Linear Unbiased Predictions, or BLUP, (HENDERSON 1975, HENDERSON 1984) is a preferred method for prediction of breeding values, BLUP estimates were obtained using the set of computer programs MTDFREML (BOLDMAN *et al.* 1993).

When more than one trait is measured, breeding values from multiple traits are aggregated into a selection index. The selection index of aggregated genetic merit is a linear combination of the BLUP of breeding values for the traits of interest, so that selection is based solely on a particular index as if it were a single cumulative trait (WHITE & HODGE 1989, COTTERILL & DEAN 1990, FALCONER & MACKAY 1996). Due to the absence of appropriate economic values, we used the Monte Carlo methodology to construct selection indices (COTTERILL & DEAN 1990, BORRALHO *et al.* 1993). Changing the relative weights of each combination of traits caused the predicted genetic gains to change, and the set of weights that yielded the most desirable genetic gains were used for developing selection schemes. Genetic gains were calculated for each scheme to discriminate among strategies of selection for

the highest genetic gains.

The resulting values for the index on breeding values for MAIV and pilodyn in percent, were calculated by the formula:

$$I_{MCi} = a * BV_{maiv}(\%) + b * BV_{pilo}(\%) \quad [9]$$

where:  $I_{MCi}$  = resulting value for the index given a combination  $i$  of weights, by the Monte Carlo approach;  $a$  = weighting coefficient assigned to the breeding value of MAIV;  $b$  = weighting coefficient assigned to the breeding value of PILO;  $BV_{maiv}(\%)$  = breeding value prediction for MAIV expressed as percentages over the adjusted mean of the population for the coastal and valley areas; and  $BV_{pilo}(\%)$  = breeding value prediction for PILO expressed as percentages over the adjusted mean of the population; with  $a + b = 1$ ; and using increments of magnitude 0.1;  $i = 0$  to 11.

In this manner we obtained a set of indices ( $I_{MCi}$ ), by systematically reducing the emphasis in one trait, and simultaneously relocating that weight to the second. Subsequently, genetic gains for each combination of weights in the selection indices were calculated and expressed as percent gains in pilodyn and MAIV by selection based on the index. The resulting gains from each trait were then reconverted to percent maximum gains to determine which index coefficients yield the maximum gain possible in each trait, and how they vary when the index weights change.

## RESULTS AND DISCUSSION

### General Trends in Means across Tests

The most severe mortality was observed in those tests located at colder sites, tests 102 and 201 (Table 2). Test 102 was located in a particularly cold spot, without

much air circulation, which accentuated the effect of low temperatures. These results are consistent with observations in the field that suggest that low temperatures are the main cause for mortality. In coastal sites where low temperatures are mild and soils are more fertile, operational plantings can reach over 96 to 98 % survival. Test 101, as an example, located on a milder site in the central valley had 96 % survival.

Height means per site remained relatively stable across tests within sets (9.1 to 15.2 m in Table 2). In contrast, MAIV is calculated on basis of annual growth and is a function of survival and individual tree volume. Thus, mortality, height and diameter at breast height (DBH) all influence test means for MAIV. The highest MAIV observed occurred in the test with the largest individual tree volume and excellent survival (test 2).

Test 1 had the lowest mean for pilodyn and also the lowest values for MAIV and height. This suggests that lower pilodyn penetration (a proxy for higher wood density) can be associated with slower growth, as indicated by BORRALHO *et al.* (1993), DEAN *et al.* (1991), and MACDONALD *et al.* (1997).

### Single-site Estimates of Heritability

Heritabilities for survival were low to moderate across all tests ( $h_B^2 = 0.04$  to  $0.32$  in the binary scale) and increased by transformation to the underlying liability scale ( $h_{B(UND)}^2 = 0.11$  to  $0.54$ ). For *E. globulus*, CHAMBERS *et al.* (1995) found almost the same ranges of heritability both in the binary and underlying scales ( $h_B^2 = 0.06$  to  $0.39$  and  $h_{B(UND)}^2 = 0.13$  to  $0.57$ ). Values of heritability for Test 102 were apparently seriously affected by low survival (35 %) as shown in Table 2. This low survival was presumably caused by severe frosts, as seen by an average percent frost damage of about 75 % for the trees planted at that test location.

**Table 2. Single-site estimates of narrow-sense heritabilities ( $h_B^2$ ) for six progeny tests of *E. globulus* at ages four and five, and underlying heritability ( $h_{B(UND)}^2$ ) for survival.**

Test	Survival (%)		Frost (%)		Height (m)		MAIV(m <sup>3</sup> .ha <sup>-1</sup> .yr <sup>-1</sup> )		Pilodyn (mm)	
	Mean	$h_{B(UND)}^2$	Mean	$h_B^2$	Mean	$h_B^2$	Mean	$h_B^2$	Mean	$h_B^2$
1	72.9	1.00	NA	NA	9.1	0.31	7.7	0.54	11.6	0.43
2	90.7	0.11	NA	NA	15.2	0.23	21.8	0.37	12.6	0.50
101	95.6	0.50	NA	NA	10.6	0.25	12.0	0.25	12.8	0.43
102	35.0	0.31	74.4	0.24	12.1	0.18	9.2	0.9*	12.7	0.22
103	86.9	0.43	31.9	0.51	10.9	0.44	14.6	0.65	12.6	0.36
201	67.5	0.54	68.9	0.36	9.9	0.08	12.8	0.82	12.3	0.41
Average	74.8	0.48	58.4	0.37	11.3	0.25	13.0	0.59	12.4	0.39

(\*) =  $h_B^2$  for MAIV on test 102 was changed from 1.56 to 0.90 (an estimate from MTDFREML (BOLDMAN *et al.* 1993)).

These heritability estimates for survival and frost tolerance are appreciable indicating that some families were better adapted to colder sites.

Single-site individual heritabilities for growth traits were low to moderate, with values ranging from  $h_B^2 = 0.1$  to  $h_B^2 = 0.4$  for height (Table 2). Heritability estimates for MAIV ( $h_B^2 = 0.25$  to  $h_B^2 = 0.9$ ) were higher than normally observed for individual tree volume estimates. VERGARA and GRIFFIN (1997) obtained  $h_B^2 = 0.17$  for averaged single site individual tree volume. MAIV heritability values may be inflated because: (1) MAIV is the product of two positively correlated traits (since volume and survival have genetic correlations of 0.91 to 1 (Table 4)); (2) The impact of survival on the heritability of MAIV comes from a family heritability not individual tree heritability (since the family survival is multiplied by tree volume in equation 2). Family heritabilities are calculated by dividing variances in the denominator of Equation 4 by the number of trees within family contributing to the estimates. As an example, individual heritability for survival was  $h_B^2 = 0.19$  in the binary scale for test 102, whereas family heritability for survival at the same test used in MAIV calculations was  $h_B^2_{family} = 0.53$ . Heuristically, all trees in the same family in a test share the same value for survival in calculation of MAIV. Thus, families with good survival tend to separate from those with poor survival. This could increase the family variance and partially explain the relatively high heritabilities in MAIV compared to individual tree volume.

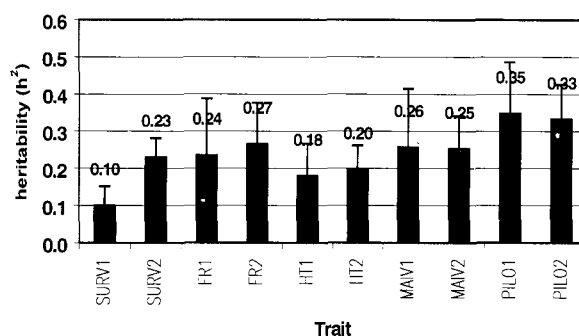
Heritabilities for pilodyn ranged from moderate to high (0.22 to 0.5), though heritability was notably lower for Test 102.

### Paired-site and Across-site Estimates of Genetic Parameter

#### Heritability

Individual heritabilities for *HT*, *MAIV* and *FR* showed moderate values whereas estimates for *PILO* were higher (Figure 1). Heritability estimates reported by VERGARA & GRIFFIN (1997) for the same population suggest that pilodyn ( $h^2 = 0.30$ ) has a much higher heritability than individual tree volume ( $h^2 = 0.14$ ) and frost ( $h^2 = 0.14$ ); although the magnitude of their estimates was slightly lower than those reported here.

Survival heritability values were  $h^2 = 0.06$  to  $h^2 = 0.11$  for Sets 1 and 2, respectively, for the non-transformed scores. Values in the underlying scale increased slightly to  $h^2 = 0.10$  and  $h^2 = 0.23$  for Sets 1 and 2, respectively (Figure 1). These values are much lower than those reported by CHAMBERS *et al.* (1996) in open-



**Figure 1.** Estimated individual-tree narrow-sense heritabilities ( $h^2$ ) from pooled analysis across tests within a set, and 95% confidence intervals on  $h^2$  estimates for survival (*SURV* on the underlying continuous scale), frost damage (*FR*), height (*HT*), mean annual increment on volume (*MAIV*) and pilodyn (*PILO*). Numbers 1 and 2 indicate the set for the two independent sets of families and locations.

pollinated families of *E. globulus* at four to five years of age (from  $h^2 = 0.19$  to  $h^2 = 0.57$  in the underlying scale).

Frost damage heritability was moderate with estimates of  $h^2 = 0.24$  to  $h^2 = 0.27$ . These values are lower than those for open-pollinated families found by VOLKER *et al.* (1994) ( $h^2 = 0.53$  to  $0.61$ ), although they used the electrical conductivity method to evaluate frost resistance. VERGARA & GRIFFIN (1997) in contrast, found heritabilities of about  $h^2 = 0.14$  for frost damage. Individual narrow-sense heritabilities for *HT* were slightly higher than estimates by VOLKER *et al.* (1990), DEAN *et al.* (1991) and BORRALHO *et al.* (1992b), which ranged from 0.12 to 0.22 for *E. globulus* open-pollinated families in Portugal and Tasmania. DEAN *et al.* (1991) found values of  $h^2$  to be about 0.21 for pilodyn and VOLKER *et al.* (1990) reported 0.19  $h^2$  for volume. These are slightly lower than estimates reported in the present study, although the assumed coefficients of relationship vary among studies.

For the combined analysis, heritability estimates for *MAIV* were  $h^2 = 0.26 \pm 0.158$  and  $h^2 = 0.25 \pm 0.088$  for Sets 1 and 2, respectively, with 95% confidence intervals as estimated by Taylor Series approximate methods (HUBER *et al.* 1992). These values approach previous estimates by VOLKER *et al.* (1990), DEAN *et al.* (1991) and BORRALHO *et al.* (1992b, 1992c) for growth of about  $h^2 = 0.06$  to  $h^2 = 0.29$ . VERGARA & GRIFFIN (1997) estimated individual volume heritability of  $h^2 = 0.14$ , approximately half of the estimates for *MAIV* in this study. The larger estimates of  $h^2$  for *MAIV* in this study may be due to (1) Inflated additive variance due to the fact that survival and volume are positively correlated and *MAIV* is the product of these two traits; (2) Good family survival in a test increases substantially the individual *MAIV* for those families in the test

inflating the additive variance since all family members share a common value for survival in calculation of MAIV; and (3) Estimates of heritability for these open-pollinated families might be over-estimated due to effects of selfing and neighborhood inbreeding (POTTS *et al.* 1995, HODGE *et al.* 1996).

The estimates of heritability for MAIV and PILO ( $h^2 = 0.35 \pm 0.139$  and  $h^2 = 0.33 \pm 0.093$  for Sets 1 and 2, respectively) suggest significant heritability for growth and wood density, and reinforce the opportunities to obtain significant gains from selection on these traits. Heritabilities for pilodyn penetration from paired-site and grouped-site analysis varied little, ranging from  $h^2 = 0.28$  to  $h^2 = 0.42$ , about the same range of  $h^2 = 0.28$  to  $h^2 = 0.41$  found by MACDONALD *et al.* (1997). Nevertheless, MUNERI & RAYMOND (2000), BORRALHO *et al.* (1992c) and DEAN *et al.* (1991) found much higher heritabilities for wood density. This suggests higher sampling errors for pilodyn than those for wood density, probably associated with smaller area of wood core sampled by the pilodyn and the pilodyn methodology in general. Still, other reports indicate a high genetic and phenotypic correlation between pilodyn and wood density and high efficiency of pilodyn for indirect selection to increase wood density (MUNERI & RAYMOND 2000, GREAVES *et al.* 1995).

The standard errors of estimates for heritability based on the combined analysis ranged between 0.03 and 0.08; and their magnitudes approximate those by BORRALHO *et al.* (1992a, 1995) and ARAUJO *et al.* (1996). These relatively low error variances are due to the large set of parents under analyses and the large number of offspring. Among sets, the magnitudes of the standard errors of heritability were lower for Set 2, because these estimates come from a larger sample of families and from more test locations (four in Set 2, two in Set 1).

#### Genotype by environment interactions

Genotype by environment interaction was significant ( $p = 0.05$ ) for the traits SURV and MAIV, but not for HT, PILO nor FR (FR was not assessed at all sites).

Type B genetic correlations among tests for MAIV varied depending on the location of the tests (Table 3). For tests located in the coast or valley,  $r_B$  values were moderate ( $r_B = 0.48$  to  $0.59$ ), indicating some genotype by environment interaction for MAIV. However, tests in these two regions compared with the mountain foothills, had higher genotype by environment interaction ( $r_B = 0.18$  coast- foothills and  $r_B = 0.40$  valley-foothills). For this reason and considering the particular characteristics of the foothills sites, MAIV here was considered two separate traits MAIV<sub>CV</sub> (Mean annual increment on volume for the coastal and valley sites) and MAIV<sub>M</sub> (Mean annual increment for the Andean foothill test).

These results differ from those reported by VERGARA & GRIFFIN (1997), where they found little genotype by environment interaction for pilodyn, volume and frost; and volume was treated as just one trait across all sites. This might be explained by the fact that they used individual tree volume estimates instead of MAIV, so that differences in family survival rankings across sites did not contribute to gxe in their study.

Type B genetic correlations ( $r_B$ ) for pilodyn among sites were very stable and above 0.70, indicating little gxe. This is primarily true for height, but survival displayed a pattern more similar to MAIV, being differentiated as a separate trait in the mountain tests.

#### Trait-trait genetic correlations

Genetic correlations help determine the importance of acclimation for the species in this range of environments and help make inferences about indirect re

**Table 3. Type B genetic correlations across sites and sets at ages four (set two) and five (set one) for survival (SURV), frost damage (FR), height (HT), mean annual increment on volume (MAIV) and pilodyn (PILO).**

Group of Sites	Type B genetic correlation ( $r_B$ ) per Trait				
	SURV	FR	HT	MAIV	PILO
Valley-Valley	0.71	NA	0.77	0.59	0.92
Coast-Valley (*)	0.36	NA	0.69	0.48	0.86
Valley-Mountains	0.32	0.62	0.67	0.40	0.78
Coast-Mountains	0.19	NA	0.50	0.18	0.70
Coast-Valley-Mountains	0.30	NA	0.68	0.45	0.82

(\*) Includes sets one and two, since set one (tests 2–102) occupy solely regions coast and valley for  $r_B$  estimates. The rest of the correlations pertain only to set one.

**Table 4.** Trait-trait genetic correlations ( $r_{A(x,y)}$ ) across sites within sets at ages four (set two) and five (set one) for survival (SURV), frost damage (FR), height (HT), mean annual increment on volume (MAIV) and pilodyn (PILO).

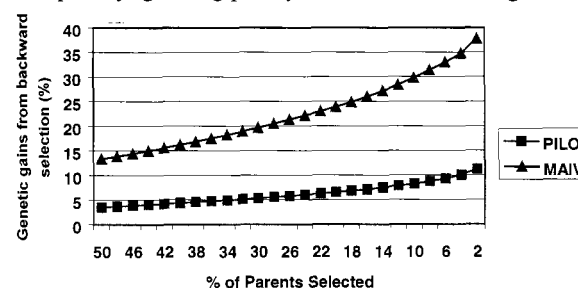
		SET 1 (above diagonal)					
		PILO	MAIV <sub>CV</sub>	MAIV <sub>M</sub>	HEIGHT	FROST	SURV <sub>C</sub>
SET 2 (below diagonal)	PILO		0.13		0.15	-0.23	-0.12
	MAIV <sub>CV</sub>	0.22			0.90	-1.00	1.00
	MAIV <sub>M</sub>	0.09	0.46*				
	HEIGHT	0.11	1.00	0.94		-1.00	0.54
	FROST	0.07	-0.83	-0.61	-0.95		-1.00
	SURV <sub>CV</sub>	0.12	0.91		0.77	-0.85	
	SURV <sub>M</sub>	0.11		1.00	0.68	-1.00	0.43*

sponses in a trait from selection on another trait (Table 4). The primary factor influencing acclimation is the tolerance to low temperatures. Frost resistance and survival were closely associated, with genetic correlations very close to  $-1$  ( $r_{A(x,y)} = -0.85$  to  $-1$ ). Moreover, survival appears to be very highly associated with MAIV, with correlations ranging about  $r_{A(x,y)} = 1$  (as survival was used in the calculation for MAIV this is to be expected). Therefore, selection on MAIV seems attractive since it suggests favorable correlated responses in frost resistance and survival. These results were consistent with those reported by CHAMBERS & BORRALHO (1997), where they recommend selection combining survival and volume over volume per tree alone, in order to achieve substantially higher gains. Survival is a very important trait for selection if the goal is to maximize productivity on a per hectare basis, and its importance increases in sites where mortality (or adaptation) becomes more relevant (CHAMBERS & BORRALHO 1997).

The correlation between MAIV and PILO is of special interest in this type of analysis since productivity and density are the most important traits affecting selection for pulp production (BORRALHO *et al.* 1993, GREAVES *et al.* 1997). Genetic correlations obtained from MAIV and PILO penetration were generally unfavorable (slightly positive), estimated as  $r_{A(x,y)} = 0.13$  for Set 1 in the coastal-valley sites, and  $r_{A(x,y)} = 0.22$  and  $0.09$  for the coastal-valley areas and foothills in Set 2, respectively. These correlations for MAIV and PILO agree with previous studies by MACDONALD *et al.* (1997) that found a genetic correlation  $r_{A(x,y)} = 0.25$  between pilodyn and diameter. BORRALHO *et al.* (1993) and DEAN *et al.* (1991) also reported slightly negative genetic correlations between volume and basic density ( $-0.10$ ) or pulp yield ( $-0.05$ ).

### Selection Indices and Genetic Gain

Predicted genetic gains for MAIV and pilodyn were used to explore the amount of genetic gain expected solely from backward selection on a single trait. This refers to selecting the top fraction of parents (out of 289) based solely on MAIV breeding values, while completely ignoring pilodyn and *vice versa* (Figure 2).



**Figure 2.** Percent genetic gains for the traits mean annual increment on volume (MAIV) and pilodyn (PILO) expected from backward selection of varying fractions of parental genotypes from the 289 plus-tree selections of *Eucalyptus globulus* in the Colcura landrace population.

Even though heritabilities are higher for the trait pilodyn ( $h^2 = 0.35$  and  $0.33$  for Sets 1 and 2, respectively), if selection is to be made on a single trait, greater genetic gains, in percentage terms, can be expected from selection solely on volume (Figure 2). This may be caused by the broader phenotypic range observed for MAIV. Therefore, if expected genetic gains on pilodyn are desirable, more weight should be placed on the pilodyn breeding values than the relative weights necessary to make comparable gains in MAIV.

If all emphasis is placed on MAIV (coefficient  $b$  in equation in Equation 10 is set to zero such that no weight is placed on PILO), then selecting the top 10% of the parents for MAIV will result in a negative re-



sponse from pilodyn (–33 %) and selecting the top 50 % of the parents results in –13 % in *PILO*. The negative genetic correlation between these two traits results in much lower responses in one trait when increasing the emphasis on the second trait, and this effect is exacerbated at higher selection intensities.

The range of favorable genetic gains for both traits fluctuates between 0.4 to 0.9 weight on pilodyn (index weights a:b for MAIV: pilodyn = 0.6 : 0.4 to 0.1 : 0.9). Any set of weights in between these values is feasible depending on desirability, and will result in a positive outcome from selection for both traits. Within this range, predicted genetic gains for both traits are positive. Therefore, the most profitable weights in between this range will depend on biological and also economic considerations; although the relationships between the traits and the economic models for costs and incomes need to be clearly defined (COTTERILL & DEAN 1990, BORRALHO *et al.* 1992c, GREAVES *et al.* 1997).

## CONCLUSIONS

Individual narrow-sense heritabilities for pilodyn across sites were moderate to high, which is consistent with previous estimates for the same trait and species (MACDONALD *et al.* 1997) (Figure 1). Pilodyn, as an estimator of density, had the highest individual heritabilities. This implies that individual tree mass selection on pilodyn can be expected to produce substantial genetic gain, since phenotypic measurements on individual trees contain more information about underlying genetic values than traits with lower heritabilities (given other parameters are held constant). The next most heritable trait under analysis is MAIV, followed by frost, then height with moderate to low heritability values. Finally, survival had the lowest heritability, with lower estimates than previous studies by CHAMBERS *et al.* (1996).

Genotype by environment interaction was important for survival and MAIV, whereas family by test interaction effects were not significant for pilodyn. Family rankings for pilodyn were relatively stable across sites (Table 3).

Coastal and Valley areas correlate moderately to low on average for all traits; however, when the Andean foothills test is included, correlations for MAIV decrease substantially, suggesting that we should consider this as a distinct edapho-climatic zone with respect to the productivity of *E. globulus*. Consequently, MAIV for the foothills test was treated as a separate trait from MAIV in the coastal and valley tests. However, these results must be considered preliminary because there was only a single test planted in the foothills area. Additional testing is necessary to clearly define the association between these sites and the Andean foot-

hills.

Since the correlations between frost damage and growth are close to 1, greater volume is genetically associated with less damage due to low temperatures. It can be suggested that risk of frost damage is marginally lower in families that are genetically fast growing in these environments. Frost damage and MAIV are therefore favorably correlated, which indicates that selection for MAIV will also result in gains on frost resistance. These results directly impact the traits to be used for selection indices. By selection for MAIV, it is possible to make gains in two important traits: faster growth potential and better survival due to cold tolerance.

Wood density, as estimated by pilodyn, and MAIV are slightly unfavorably correlated. This will have a detrimental effect during the process of selection, since improving one trait is expected to result in an unfavorable response from the second trait. However, those correlations are very small ( $r_B < 0.20$ ), therefore their impact is expected to be relatively small.

Given the favorable genetic correlations among the traits MAIV, survival and frost, it seems reasonable for tree breeding purposes to develop a selection index based only on MAIV and pilodyn (COTTERILL & DEAN 1990). With this index, substantial genetic gains are possible for backward, forward and combined selection.

Finally, the real challenge for the breeder will be to set the appropriate economic weights for the breeding objectives to ensure that it maximizes the value of obtaining all these genetic parameters.

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