GENETIC VARIATION AND INTER-TRAIT CORRELATIONS IN *EUCALYPTUS GLOBULUS* BASE POPULATION TRIALS IN ARGENTINA

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ABSTRACT

Genetic variation and inter-trait correlations were examined in a base population of *Eucalyptus globulus* established on four sites in Argentina. The genetic material included 223 open pollinated seed lots from 11 Australian localities and 52 open pollinated and control pollinated seed lots from European and South American land races. Survival, growth, bark thickness, tree form, transition to adult foliage and Pilodyn penetration were assessed, at different ages up to 4-years. Average single site individual narrow-sense heritabilities were low for forking (0.03), survival (0.05) and form (0.10); intermediate for growth (0.27) and relative bark thickness (0.32); and high for Pilodyn penetration (0.48) and transition to adult foliage (0.60). There was strong positive genetic correlation between the same trait measured at different sites (> 0.70) and ages (> 0.64). In general, the genetic correlations between growth and other traits were not statistically significant (Pilodyn penetration –0.04, fork 0.06, proportion of adult foliage 0.06, bark thickness –0.02). Correlations amongst subrace effects were generally consistent with the family within subrace genetic correlations, but to some extent lower and less significant. Other estimates of genetic parameters reported for *E. globulus* were generally consistent with the present study. The limitations on parameter estimates from open pollinated progeny trials are discussed.

Key words: *Eucalyptus globulus*, heritability, genetic correlation, genetic variation, genotype x environment interaction, tree breeding.

INTRODUCTION

Eucalyptus globulus is a forest tree native to south-eastern Australia and variously given specific (BROOKER 2000) or sub-specific status (*E. globulus* ssp. *globulus*; KIRKPATRICK 1975). It is the premier pulpwood *Eucalyptus* species and is grown in plantations in many temperate countries around the world (ELDRIDGE *et al.* 1993). It is in various stages of domestication in many countries such as Australia (TIBBITS *et al.* 1997), Chile (SANHUEZA & GRIFFIN 2001; GUTIÉRREZ *et al.* 2001), China (ZANG *et al.* 1995), Portugal (ARAÚJO *et al.* 1997), Spain (SORIA & BORRALHO 1998) and Uruguay (BALMELLI *et al.* 2001). Genetic parameters are required to optimise breeding and deployment strategies, as well as estimate breeding values and gains from selection (WHITE 1996; BORRALHO 2001). To determine the response to selection, it is important to know how much of the phenotypic variation in a given trait is under genetic control (heritability). It is also important to understand the extent to which the expression of the genetic variation is stable across different ages (age to age genetic correlations) and different sites (as an indication of genotype x environment interaction), as well as the genetic correlations existing amongst different traits to predict the response to selection in a multivariate sense (FALCONER & MACKAY 1996).

Most studies of genetic parameters in *E. globulus* have focused on growth (e.g. POTTS & JORDAN 1994b; BORRALHO *et al.* 1995; HODGE *et al.* 1996; BALMELLI *et al.* 2001) and its association with a few key traits such as survival (CHAMBERS *et al.* 1996), wood density (BORRALHO *et al.* 1992b; MACDONALD *et al.* 1997; MUNERI & RAYMOND 2000), flowering precocity (CHAMBERS *et al.* 1997), form (VOLKER *et al.* 1990) and vegetative phase change (IPINZA *et al.* 1994; JORDAN *et al.* 2000). These studies differ in analytical

technique, statistical model, genetic material studied and/or test environment.

The present study reports the genetic parameters for the first pedigreed *E. globulus* trials grown in Argentina. These trials combine both native stand seed lots from Australia and land race material from around the world to construct a large base population for breeding this species in Argentina (LOPEZ *et al.* 2001b). We examined the level of genetic control and genetic correlations for eight traits covering growth, wood density, form, bark thickness and vegetative phase change. The expression of genetic variation in these traits is examined across four sites, as well as the change with age up to 4-years.

MATERIALS AND METHODS

Plant material and trials

The four sites studied are located in the Buenos Aires Province, Argentina, within the traditional *E. globulus* planting zone (defined in LOPEZ *et al.* 2001c). The trials are identified as BALC (lat. 37° 45' S long. 58° 17' W), BOSC (lat. 38° 39' S long. 59° 04' W), MANU (lat. 37° 53' S long. 59° 56' W) and VOCA (lat. 38° 28' S long. 59° 06' W) and vary in average annual rainfall from 850 to 1008 mm and average annual minimum temperature from –5.8° to –3.3 °C (see LOPEZ *et al.* 2001b). The trials included a total of 14,925 trees from 276 seed lots. Two hundred and twenty three open pollinated (OP) families and one bulk collection were from 11 native stand localities in Australia and 52 seed lots were from land races from Portugal, Spain, Chile and Argentina. The land race seed lots included 37 OP families and 10 control pollinated (CP) families, as well as 5 bulk collections of varying levels of genetic improvement. The number of families (i.e. seed lots) per trial ranged from 220 to 275. Full details of the distribution of families across collection localities are given in LOPEZ *et al.* (2001b).

The trials comprised 15 replicates per family of single-tree-plots. Families were arranged in sets of 20 to 25, based on their geographic provenance. Sets were randomly allocated to a position in the trial and families within each set were randomly arranged in each replicate of the set. Spacing was 3 m × 3 m in all trials.

Measurements

Measurements were made of growth, adult foliage, Pilodyn penetration, bark thickness, form and survival. Stem diameter (cm) over bark was assessed at breast height (1.3 m) at 2 (DBH2), 3 (DBH3) and 4 (DBH4) years after planting. Total height (cm) was measured at 1 (HT1) and 2 (HT2) years. The proportion of adult foliage was assessed at age 2 (ADFO), while tree form (FORM; 1 worst – 4 best) was assessed at age 3 (MANU and VOCA) or 4 (BALC and BOSC). These last two variables were measured on an ordered 4-point scale (details in LOPEZ *et al.* 2001b). Bark thickness (BTHI) and Pilodyn penetration (PILO) were measured (mm) only in BALC and BOSC at age 4. The variable BARK used for analysis is the percentage of DBH4 that was effectively bark for each individual tree. The presence of forks at age 2 (FORK) was assessed in the same 2 trials approximately 2 months after light hail damage. Survival (SURV) was determined based on the oldest assessment for each trial (i.e. age 4 for BALC and BOSC and age 3 for MANU and VOCA).

The general set of data used for analysis was from all those trees that were alive at measurement; however, isolated outliers (usually runts) were rejected. At MANU approximately 25 % of trees suffered damage by cows at an early age and were excluded from the analysis.

Analyses

For each trial, an incomplete block design was imposed *a posteriori* (see ERICSSON 1997; FU *et al.* 1999). The incomplete block size used for each trial was that which maximised the model likelihood for the oldest diameter measurement (DUTKOWSKI *et al.* 2002). Variance components for each trait were estimated with an individual tree mixed model, using restricted maximum likelihood implemented with ASReml (GILMOUR *et al.* 2001). The model fitted was:

$$\mathbf{y} = \mathbf{X}\,\mathbf{b} + \mathbf{Z}_A\,\mathbf{a} + \mathbf{Z}_C\,\mathbf{c} + \mathbf{e} \qquad [1]$$

where: $\mathbf{y}$ is the vector of individual tree data; $\mathbf{b}$ is the vector for all the fixed effects (overall mean, subrace as defined by the classification of DUTKOWSKI & POTTS (1999) or land race (LOPEZ *et al.* 2001b), and pollination type -open pollinated or control pollinated); $\mathbf{a}$ is the vector of unobservable additive genetic effects of individual trees; $\mathbf{c}$ is the vector for the random effects of the incomplete blocks and $\mathbf{e}$ is the vector of residuals. $\mathbf{X}$, $\mathbf{Z}_A$ and $\mathbf{Z}_C$ are incidence matrices relating the observations to the fixed and random effects in the model. Model 1 was fitted for both univariate and bivariate analyses and in both cases, the expected mean and variances of the parameters are:

$$\begin{bmatrix} y \\ a \\ c \\ e \end{bmatrix} N \left(\begin{bmatrix} Xb \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} V & Z_A G_A & Z_C G_c & R \\ G_A Z_A & G_A & 0 & 0 \\ G_c Z_c & 0 & G_C & 0 \\ R & 0 & 0 & R \end{bmatrix} \right) \quad [2]$$

where $\mathbf{V} = \mathbf{Z}_A \mathbf{G}_A \mathbf{Z'}_A + \mathbf{Z}_C \mathbf{G}_C \mathbf{Z'}_C + \mathbf{R}$, $\mathbf{G}_A = \mathbf{A} \otimes \mathbf{G}_o$ where $\mathbf{A}$ is the numerator relationship matrix, $\mathbf{G}_o$ is the additive genetic covariance matrix, and $\otimes$ is the Kronecker product, $\mathbf{G}_C = \mathbf{I} \otimes \mathbf{G}_{Co}$ where $\mathbf{I}$ is an identity matrix, $\mathbf{G}_{Co}$ is the incomplete block covariance matrix and $\mathbf{R} = \mathbf{R}_t \otimes \mathbf{I}$ where $\mathbf{R}_t$ is the trait residual covariance matrix. For the univariate case, some of these matrices (e.g. $\mathbf{G}_o$, $\mathbf{R}_t$) collapse to scalars (e.g. σ^2_a, σ^2_e). The additive relationship matrix $\mathbf{A}$ was modified to account for an assumed 30% selfing rate, which increases the sib additive coefficient of relatedness (r) from 0.25 to 0.4 and the parent-offspring relatedness from 0.25 to 0.4 as well (DUTKOWSKI *et al.* 2001). The few bulk seed samples were included in the relationship matrix with missing male and female pedigree information. A binomial model was fitted to presence/absence traits (SURV, FORK) with a probit transformation. The significance of random effects was tested using a likelihood ratio test (SEARLE 1971).

To compare the absolute levels of additive genetic variation across traits, the coefficients of additive genetic variance were calculated as:

$$CV_a = 100 \frac{\sigma_a}{\bar{x}} \quad [3]$$

where: σ_a is the within subrace additive genetic standard deviation calculated from the univariate model and $\bar{x}$ is the population mean (after HOULE 1992). Single site, narrow-sense heritabilities (h^2) were calculated as:

$$h^2_{op} = \frac{\sigma^2_a}{\sigma^2_a + \sigma^2_e} \quad [4]$$

where: σ^2_a is the additive genetic variance within subraces and σ^2_e is the error variance component in [2]. The error term includes the specific combining effect from the few controlled crossed families. The standard errors of estimates were calculated by ASReml from the average information matrix, using a standard truncated Taylor series approximation (GILMOUR *et al.* 2001). Genetic differences between subraces were tested with the F-statistics using an error degree of freedom derived from the family within subraces term. Subrace least square means and their standard errors were also estimated in ASReml. Pearson's correlation coefficients amongst these subraces least square means were estimated using the PROC CORR procedure in SAS (version 8).

Pairwise genetic correlations and their standard errors were estimated using a bivariate model that was extended from the univariate model. Whether correlations were significantly different from zero or not was determined with a likelihood ratio test.

RESULTS AND DISCUSSION

Expression of genetic effects

The genetic variation was partitioned into fixed subrace effects and random additive genetic variation within subrace. The estimates presented in this study are dominated by open pollinated native stand families (82 %) but also integrated information from open pollinated (14%) and control pollinated (4%) land race families. All traits showed significant subrace differentiation, except survival at MANU (Table 1). The patterns of differentiation at the subrace level are discussed by LOPEZ *et al.* (2001b), therefore this paper focuses on the genetic variation of families within subraces.

Statistically significant levels of additive genetic variation within subraces were detected for all traits except survival, where significant variation was only detected at VOCA (Table 1). However the magnitude of the additive variance was scale dependent and in the case of growth, increased with the measurement mean. The ability of traits to respond to selection can be compared by the coefficient of additive genetic variance (CV_A) that measures levels of additive genetic variation while accounting for scale and size effects (HOULE 1992). The CV_A was close to 10% for most traits, except for the proportion of adult foliage, which was greater than 40% at all sites (Table 1). In a review of the magnitude of the coefficient of additive genetic variation across a large number of quantitative traits in a variety of forest tree species, CORNELIUS (1994) reported median values for height and diameter growth of 9%, consistent with the average obtained in the present study.

The magnitude of the genotype x environment interaction on trait expression can be gauged by the genetic correlation between the same trait measured at different sites. Such correlations could be partitioned into the correlation of subrace effects (r_s) and the correlation of additive genetic effects within subraces (r_g). The subrace correlations across sites were strong and positive for most traits (Table 3), indicating stability of subraces performance for the traits observed. Genetic correlations within subraces were also high (Table 4), and in general slightly higher than the subrace correlations.

Table 1. The overall means with standard deviation (sd), additive genetic variance (x) with their significance (Sig.) and coefficient of additive genetic variation (CV_A in % units), within subrace heritabilities (h^2) with their standard errors (s.e.) and the F values and significance of the subrace effects (F) for the 34 variables measured across the four trials. Significance of effects are noted as ns = not significant; * $P < 0.05$; ** $P < 0.01$ and *** $P < 0.001$; NT = could not be tested. "n" represents the number of data for each trait included in the analysis. The traits HT (height, cm), DBH (diameter at breast height, cm), PILO (pilodyn penetration, mm), BARK (bark thickness, %), FORM (stem form), ADFO (adult foliage, proportion), FORK (presence of fork, binary) and SURV (survival, binary) are followed by a number which represents the age of measurement in years. Note that n in DBH3 at BALC and BOSC are smaller that DBH4 due to exclusion of data at age 3.

Trait	Site	*n*	Mean	s.d.	Additive genetic		Heritability		Subrace effect	
					σ^2_a	CV_A	h^2	s. e.	F	Sig.
HT1	BALC	3694	128	6.1	278***	13	0.22	0.03	3.5	***
	BOSC	3216	159	6.3	360***	12	0.36	0.05	13.6	***
HT2	BALC	3676	523	18.8	2717***	10	0.24	0.04	6.7	***
	BOSC	3186	539	14.7	1587***	7	0.22	0.04	10.0	***
	VOCA	3838	564	15.2	2970***	10	0.23	0.03	15.5	***
	MANU	2778	483	12.6	992***	7	0.11	0.03	12.4	***
DBH2	BALC	3626	7.32	0.31	0.671***	11	0.23	0.03	6.0	***
	BOSC	3160	9.64	0.32	0.848***	10	0.29	0.04	7.7	***
	VOCA	3671	8.50	0.27	0.944***	11	0.25	0.04	9.4	***
	MANU	2614	6.61	0.16	0.139***	6	0.09	0.03	10.5	***
DBH3	BALC	3199	11.03	0.41	1.217***	10	0.27	0.04	4.2	***
	BOSC	2927	13.20	0.44	1.656***	10	0.33	0.05	3.7	***
	VOCA	3744	12.02	0.36	1.854***	11	0.27	0.04	8.5	***
	MANU	2820	9.27	0.25	0.427***	7	0.12	0.03	4.4	***
DBH4	BALC	3592	12.54	0.45	1.964***	11	0.33	0.04	3.0	**
	BOSC	3122	16.55	0.54	2.696***	10	0.35	0.05	2.3	*
PILO	BALC	3511	13.03	0.26	0.798***	7	0.43	0.05	11.6	***
	BOSC	3103	13.44	0.31	1.027***	8	0.52	0.06	7.0	***
BARK	BALC	3508	8.22	0.31	0.953***	12	0.33	0.04	21.9	***
	BOSC	3094	8.34	0.34	1.008***	12	0.31	0.04	13.5	***
FORM	BALC	3517	3.14	0.13	0.091***	10	0.14	0.03	12.0	***
	BOSC	3101	2.47	0.14	0.091***	12	0.09	0.03	13.1	***
	VOCA	3744	3.00	0.11	0.071***	9	0.07	0.02	14.4	***
	MANU	2820	2.72	0.13	0.091***	11	0.09	0.03	7.0	****
ADFO	BALC	3679	0.23	0.04	0.026***	71	0.65	0.06	7.8	***
	BOSC	3198	0.24	0.05	0.029***	69	0.64	0.06	5.3	***
	VOCA	3544	0.46	0.04	0.043***	46	0.62	0.06	10.3	***
	MANU	2665	0.43	0.05	0.034***	43	0.54	0.06	5.8	***
FORK	BALC	3679	0.25		0.044NT		0.04	0.02	6.0	***
	BOSC	3182	0.48		0.035NT		0.03	0.02	4.4	***
SURV3	VOCA	3769	0.91		0.153***		0.13	0.03	2.3	*
	MANU	3432	0.88		0.036 ns		0.03	0.04	1.6	ns
SURV4	BALC	3592	0.96		0.026 ns		0.02	0.07	3.1	***
	BOSC	3123	0.95		0.022 ns		0.02	0.07	2.0	*

Table 2. Individual narrow-sense heritability estimates (h^2) for growth traits of *Eucalyptus globulus* open pollinated families from single sites or the sites average when multiple sites are reported. The coefficient of relationships (r) used in the estimation are given and the heritabilities have been standardised to a common basis of $r = 0.4$ (h^2_{op}) for comparison. Where r is not given these are treated as $r = 0.4$. The traits dbh (diameter at breast height), ht (height) and vol (volume) are followed by a number which represents the age of measurement in years. The group effect represents the inclusion (Yes) or not (No) in the statistical model of a fix effect to account for the provenance, subrace, race or other group effect. Number of families (No. of families) and number of sites (No. of sites) tested, and type of population (Pop. type) refers to whether land race (L) or dominantly Australian native stand (*N*) families have been tested.

Trait	h^2	r	h^2_{op}	Group effect	No. of families	Pop. type	No. of sites	Country	Source of reference and year
dbh ?	0.15	–	0.15	No	560	L & N	5 +	Portugal	ARAUJO *et al.* (1997)
dbh2	0.14	0.35	0.12	Yes	224	N	1	Chile	IPINZA *et al.* (1994)
dbh3	0.17	0.35	0.15	Yes	224	N	1	Chile	IPINZA *et al.* (1994)
dbh3	0.13	0.40	0.13	No	89	N	3	Uruguay	BALMELLI *et al.* (2001)
dbh4	0.10	0.54	0.14	No	20	N	4	Australia, VIC	WOOLASTON *et al.* (1991)
dbh4	0.13	0.35	0.11	Yes	224	N	1	Chile	IPINZA *et al.* (1994)
dbh4	0.24	0.40	0.24	No	589	N	14	Australia	BORRALHO *et al.* (1995)
dbh4	0.39	0.25	0.24	Yes	594	N	5	Australia, TAS	BORRALHO & POTTS (1996)
dbh4	0.26	0.40	0.26	Yes	569	N	5	Australia, TAS	MACDONALD *et al.* (1997)
dbh4	0.28	0.40	0.28	Yes	474	N	5	Australia, TAS	DUTKOWSKI *et al.* (1997)
dbh5	0.14	0.40	0.14	Yes	260	N	14	Spain	SORIA *et al.* (1997)
dbh5	0.12	0.40	0.12	No	89	L	3	Uruguay	BALMELLI *et al.* (2001)
dbh5	0.21	0.40	0.21	Yes	70	N	3	Australia	MUNERI & RAYMOND (2001)
dbh6	0.24	0.40	0.24	Yes	45	N	1	Australia, TAS	VOLKER *et al.* (1990)
ht ?	0.25	–	0.25	No	560	L & N	5 +	Portugal	ARAUJO *et al.* (1997)
ht1	0.23	0.33	0.19	No	20	L	1	Portugal	BORRALHO *et al.* (1992)
ht2	0.06	0.54	0.08	No	20	N	4	Australia, VIC	WOOLASTON *et al.* (1991)
ht2	0.20	0.35	0.18	Yes	224	N	1	Chile	IPINZA *et al.* (1994)
ht2	0.18	0.33	0.15	No	20	L	1	Portugal	BORRALHO *et al.* (1992)
ht3	0.20	0.35	0.18	Yes	224	N	1	Chile	IPINZA *et al.* (1994)
ht3	0.12	0.40	0.12	No	89	L	3	Uruguay	BALMELLI *et al.* (2001)
ht4	0.17	0.35	0.15	Yes	224	N	1	Chile	IPINZA *et al.* (1994)
ht4	0.51	0.25	0.32	Yes	594	N	5	Australia, TAS	BORRALHO *et al.* (1996)
ht4	0.29	0.33	0.24	No	20	L	1	Portugal	BORRALHO *et al.* (1992)
ht5	0.17	0.40	0.17	Yes	260	N	14	Spain	SORIA *et al.* (1997)
ht5	0.10	0.40	0.10	No	89	L	3	Uruguay	BALMELLI *et al.* (2001)
ht6	0.12	0.40	0.12	Yes	45	N	1	Australia, TAS	VOLKER *et al.* (1990)
ht6	0.34	0.33	0.28	No	27	L	1	Portugal	BORRALHO *et al.* (1992)
ht8	0.29	0.33	0.24	No	43	L & N	1	Portugal	BORRALHO *et al.* (1992)
ht9	0.33	0.33	0.27	No	27	L	1	Portugal	BORRALHO *et al.* (1992)
vol?	0.22	–	0.22	No	560	L & N	5 +	Portugal	ARAUJO *et al.* (1997)
vol2	0.26	0.5	0.33	Yes	24	N	5	Australia	HODGE *et al.* (1996)
vol2	0.10	0.5	0.13	Yes	8	N	5	Australia	HODGE *et al.* (1996)
vol3	0.10	0.40	0.10	No	89	L	3	Uruguay	BALMELLI *et al.* (2001)
vol4	0.10	0.35	0.09	Yes	224	N	1	Chile	IPINZA *et al.* (1994)
vol4	0.38	0.40	0.38	Yes	549	N	1	Australia, TAS	POTTS & JORDAN (1994)
vol4	0.36	–	0.36	–	653	L & N	–	Chile	VERGARA & GRIFFIN (1997)
vol5	0.12	0.40	0.12	No	89	L	3	Uruguay	BALMELLI *et al.* (2001)
vol6	0.19	0.40	0.19	Yes	45	N	1	Australia, TAS	VOLKER *et al.* (1990)
vol9	0.18	–	0.18	–	–	–	1	Portugal	COTTERILL & BROLIN (1997)

[1] Heritabilities estimated by the authors for Australian native stand families have not been included in the average presented here as these were highly inflated due to inclusion of large provenance effects in the difference between families.

Table 3. Across site correlations between subrace least square means and their significance from zero. The significances are noted as ns = not significant; * $P < 0.05$; ** $P < 0.01$ and *** $P < 0.001$. The traits HT (height, cm), DBH (diameter at breast height, cm), PILO (pilodyn penetration, mm), BARK (bark thickness, proportion), FORM (stem form), ADFO (adult foliage proportion), FORK (presence of fork, binary) and SURV (survival, binary) are followed by a number which represents the age of measurement in years.

Trait	Site	BOSC	VOCA	MANU
HT1	BALC	0.56 ns		
HT2	BALC	0.85 ***	0.77 **	0.74 *
	BOSC		0.82 **	0.79 **
	VOCA			0.84 ***
DBH2	BALC	0.85 ***	0.64 *	0.72 *
	BOSC		0.69 *	0.88 ***
	VOCA			0.78 **
DBH3	BALC	0.77 **	0.57 ns	0.70 *
	BOSC		0.80 **	0.85 **
	VOCA			0.78 **
DBH4	BALC	0.84 **		
ADFO	BALC	0.96 ***	0.90 ***	0.95 ***
	BOSC		0.88 ***	0.96 ***
	VOCA			0.88 ***
FORM	BALC	0.83 **	0.89 ***	0.74 *
	BOSC		0.91 ***	0.80 **
	VOCA			0.54 ns
PILO	BALC	0.94 ***		
BARK	BALC	0.83 **		
FORK	BALC	0.42 ns		

High intra-population genetic correlations (r_g) are often associated with high inter-population (e.g. r_s) genetic correlations (ZENG 1987) as in the present case. However, this is not always the case in *E. globulus* (POTTS & JORDAN 1994a; JORDAN *et al.* 2000) and to some extent the patterns of subrace correlation will depend upon the pattern of subrace sampling. In contrast, the genetic correlations within subraces are likely to be more stable and reflect pleiotropy. The pooled estimates across different subraces would argue against an effect of linkage. In the present case, measurements of the same trait at different sites were genetically correlated at a level usually greater than 0.7 (Table 4) and, at least for most growth measurements, this was also the case at the subrace level. These results would argue that the same genes are being expressed at the different sites and that from a breeding perspective a single breeding population would be suitable for the range of sites tested.

Growth

Fast growth is one of the major objectives of eucalypt breeding programs around the world (GREAVES *et al.* 1997; BORRALHO 2001). Growth was under moderate genetic control in our trials. In general, single site heritability estimates for growth traits ranged from 0.09 to 0.36 (Table 1). The average heritability of four single trial estimates for diameter across ages was 0.25. Estimates from MANU were atypically low (0.09 to 0.12), but this poor expression of genetic variation for growth within subraces at this site was not reflected in the expression of subrace differences. Heritabilities for height ranged from 0.11 to 0.36.

A comparison with heritability estimates reported in the literature is complicated by the differences in environment, methodology of analysis (e.g. whether group effects are excluded or not), age of evaluation and the coefficient of relatedness (r) used. Table 2 lists the heritability for growth traits reported in other OP

Table 4. Across site genetic correlations ± standard errors derived from pairwise analyses. All correlations were significantly different from zero (* $P < 0.001$). The traits HT (height, cm), DBH (diameter at breast height, cm), PILO (pilodyn penetration, mm), BARK (bark thickness, proportion), FORM (stem form), ADFO (adult foliage proportion), FORK (presence of fork, binary) and SURV (survival, binary) are followed by a number which represents the age of measurement in years.**

Trait	Site	BOSC	VOCA	MANU
HT1	BALC	0.78 ± 0.07		
HT2	BALC	0.93 ± 0.07	0.85 ± 0.07	0.92 ± 0.12
	BOSC		0.94 ± 0.07	0.84 ± 0.12
	VOCA			0.92 ± 0.12
DBH2	BALC	0.85 ± 0.07	0.81 ± 0.07	0.89 ± 0.14
	BOSC		0.83 ± 0.07	0.91 ± 0.14
	VOCA			0.78 ± 0.14
DBH3	BALC	0.94 ± 0.06	0.89 ± 0.06	1.12 ± 0.10
	BOSC		0.93 ± 0.05	0.95 ± 0.11
	VOCA			0.90 ± 0.10
DBH4	BALC	0.89 ± 0.05		
ADFO	BALC	0.99 ± 0.02	0.97 ± 0.02	1.03 ± 0.02
	BOSC		0.96 ± 0.03	1.00 ± 0.03
	VOCA			1.01 ± 0.02
FORM	BALC	0.98 ± 0.14	0.98 ± 0.14	0.70 ± 0.18
	BOSC		1.12 ± 0.19	0.98 ± 0.21
	VOCA			0.84 ± 0.22
PILO	BALC	0.89 ± 0.04		
BARK	BALC	0.88 ± 0.06		
FORK	BALC	0.77 ±0.35		

studies of *E. globulus* after standardising the coefficient of relationship to 0.4 to allow a better comparison between studies. Our average heritability (0.25) for tree diameter across sites and ages was close to the heritabilities reported for most Australian trials (BORRALHO et al. 1995, 0.24; MACDONALD *et al.* 1997, 0.26; MUNERI & RAYMOND 2000, 0.21). Other studies (WOOLASTON et al. 1991; IPINZA *et al.* 1994; ARAÚJO *et al.* 1997; SORIA *et al.* 1997) reported much lower heritabilities for diameter (0.11 to 0.15). The average narrow-sense heritability for diameter, weighted by the number of families included in each of the studies reviewed in Table 2 (including our study) is 0.21. This value could suffice as standard value for the OP heritability of diameter growth in *E. globulus*.

The average heritability for height (0.23) across the four Argentinian trials was similar to that for diameter and equivalent to the weighted average of reported estimates for height (0.23) given in Table 2. While tree volume was not studied in the present case, the weighted average heritability for volume ($h^2 = 0.28$) in Table 2 was of the same magnitude as those reported from other *Eucalyptus* species, such as *E. urophylla* and *E. grandis* ($h^2 = 0.31$ and 0.29, respectively) (reviewed in REZENDE & DE RESENDE 2000).

There was a consistent increase in heritability estimates for diameter with age in all four Argentinian trials (Table 2). This trend has been previously reported in other forest tree species (as reviewed in WEI & BORRALHO 1996), including *E. globulus* (BORRALHO *et al.* 1992a). Size-dependent mortality (CHAMBERS *et al.* 1996) or selective thinning may mask such age trends in the expression of genetic variation by reducing the amount of genetic variation (WEI & BORRALHO 1998). However, this is unlikely to be important in the present case. Mortality was low (Table 1) and when accounted for using a multivariate analysis combining fourth year diameter with first year height measurements, the heritability of fourth year diameter only marginally increased over the univariate estimate (e.g.

Table 5. Subrace least square mean correlations between the different traits within sites. The significances are noted as ns = not significant; * $P < 0.05$; ** $P < 0.01$ and *** $P < 0.001$. The traits HT (height, cm), DBH (diameter at breast height, cm), PILO (pilodyn penetration, mm), BARK (bark thickness, proportion), FORM (stem form), ADFO (adult foliage, %), FORK (presence of fork, binary) and SURV (survival, binary) are followed by a number which represents the age of measurement in years.

Site	Trait	HT2	DBH2	DBH3	DBH4	PILO	BARK	FORM	ADFO	FORK
BALC	HT1	0.80 **	0.65 *	0.70 *	0.69 *	−0.67 *	0.77 **	0.04 ns	0.29 ns	0.18 ns
	HT2		0.81 **	0.70 *	0.71 *	−0.66 *	0.68 *	0.11 ns	0.20 ns	−0.34 ns
	DBH2			0.92 ***	0.92 ***	−0.53 ns	0.74 **	−0.19 ns	−0.19 ns	−0.13 ns
	DBH3				0.96 ***	−0.54 ns	0.84 **	−0.06 ns	−0.24 ns	0.00 ns
	DBH4					−0.62 *	0.79 **	−0.08 ns	−0.22 ns	−0.02 ns
	PILO						−0.71 *	−0.50 ns	0.00 ns	0.20 ns
	BARK							0.15 ns	−0.26 ns	−0.05 ns
	FORM								0.21 ns	−0.31 ns
	ADFO									0.26 ns
BOSC	HT1	0.87 ***	0.80 **	0.74 **	0.46 ns	−0.50 ns	0.69 *	−0.41 ns	0.42 ns	0.54 ns
	HT2		0.90 ***	0.78 **	0.76 **	−0.54 ns	0.62 *	−0.22 ns	0.34 ns	0.49 ns
	DBH2			0.90 ***	0.88 ***	−0.40 ns	0.62 *	−0.46 ns	0.09 ns	0.57 ns
	DBH3				0.72 *	−0.38 ns	0.64 *	−0.58 ns	−0.20 ns	0.33 ns
	DBH4					−0.33 ns	0.44 ns	−0.24 ns	−0.03 ns	0.45 ns
	PILO						−0.66 *	−0.23 ns	−0.24 ns	−0.23 ns
	BARK							−0.19 ns	0.04 ns	0.28 ns
	FORM								0.24 ns	−0.49 ns
	ADFO									0.48 ns
VOCA	HT2		0.93 ***	0.92 ***				−0.06 ns	0.50 ns	
	DBH2			1.00 ***				−0.22 ns	0.41 ns	
	DBH3							−0.22 ns	0.37 ns	
	FORM								0.00 ns	
	SURV3	0.15 ns	−0.11 ns	−0.15 ns				0.20 ns	0.14 ns	
MANU	HT2		0.88 ***	0.89 ***				0.03 ns	0.56 ns	
	DBH2			0.94 ***				0.02 ns	0.40 ns	
	DBH3							−0.14 ns	0.35 ns	
	FORM								0.18 ns	

at BALC, 0.33 and 0.35 and BOSC, 0.35 and 0.36, respectively).

There were very strong age-age correlations in the expression of genetic variation both within (r_g; Table 6) and between subraces (r_s; Table 5). As would be expected, the magnitude of this genetic correlation declined with increasing age interval. However, even at the greatest interval, the correlations were still highly significant and the genetic correlations (r_g) between 1 year height and the 4 year diameter were greater than 0.6. While subrace effects were less strongly correlated across ages than the genetic effects within subraces, in most cases these correlations were high and statistically significant. While these trials are still relatively young, a strong genetic correlation (r_g >0.7) between height at age 2 years and later age sectional area measurements (8–18 years) has been reported by BORRALHO *et al.* (1992a) for *E. globulus*. Sectional area estimates at age 4 years were also highly correlated (r_g > 0.95) with later age measurements taken close to rotation age of between 8 and 18 years. These results argue that selection for later age growth could occur as early as 2 years, but BORRALHO *et al.* (1992a) argue that the optimal age for selection is four years or, if expressed in terms of average tree size, 8m of height.

Despite the environmental differences between trials (LOPEZ *et al.* 2001b), growth was strongly correlated across sites for all pair-wise comparisons (r_g > 0.78). Growth on the different sites can thus be considered the same trait because family performance was stable and the genotype by environment interaction was very small (BURDON 1977). Comparable within race genetic correlations across sites were reported by MACDONALD *et al.* (1997) for 4 year-old diameter of *E. globulus* across five sites in Tasmania (averaged 0.80 cf 0.91 for comparable ages in the present study). In another Australian study, MUNERI & RAYMOND (2000) reported similar genetic correlation between two sites

Table 6. Genetic correlations (± standard errors) between different traits within sites derived from pairwise bivariate analyses. The significance of the difference of correlation from zero was noted as ns = not significant; * $P < 0.05$; ** $P < 0.01$ and *** $P < 0.001$. The traits HT (height, cm), DBH (diameter at breast height, cm), PILO (pilodyn penetration, mm), BARK (bark thickness, proportion), FORM (stem form), ADFO (adult foliage proportion), FORK (presence of fork, binary) and SURV (survival, binary) are followed by a number which represents the age of measurement in years.

Site	Trait	HT2	DBH2	DBH3	DBH4	PILO	BARK	FORM	ADFO	FORK
BALC	HT1	0.88 ± 0.03 ***	0.84 ± 0.03 ***	0.80 ± 0.04 ***	0.82 ± 0.04 ***	–0.07 ± 0.0 ns	0.04 ± 0.10 ns	0.18 ± 0.12 ns	0.00 ± 0.10 ns	0.08 ± 0.18 ns
	HT2		0.89 ± 0.02 ***	0.87 ± 0.03 ***	0.88 ± 0.03 ***	–0.09 ± 0.10 ns	–0.02 ± 0.11 ns	0.36 ± 0.11***	–0.01 ± 0.09 ns	0.20 ± 0.18 ns
	DBH2			0.99 ± 0.01 ***	0.98 ± 0.01 ***	0.00 ± 0.11 ns	0.06 ± 0.10 ns	0.19 ± 0.12 ns	–0.13 ± 0.09 ns	0.06 ± 0.17 ns
	DBH3				1.00 ± 0.00 ***	0.01 ±0.10 ns	0.09 ± 0.10 ns	0.23 ± 0.11***	–0.06 ± 0.09 ns	0.06 ± 0.17 ns
	DBH4					–0.02 ± 0.09 ns	0.11 ± 0.09 ns	0.25 ± 0.11***	–0.02 ± 0.09 ns	0.09 ± 0.16 ns
	PILO						–0.46 ± 0.08***	–0.19 ± 0.11 ns	–0.04 ± 0.08 ns	0.08 ± 0.15 ns
	BARK							0.13 ± 0.11 ns	0.08 ± 0.08 ns	0.07 ± 0.16ns
	FORM								0.15 ± 0.10 ns	–0.40 ± 0.16***
	ADFO									0.47 ± 0.14***
BOSC	HT1	0.77 ± 0.05 ***	0.79 ± 0.04 ***	0.68 ± 0.06 ***	0.64 ± 0.06 ***	–0.13 ± 0.09 ns	0.10 ± 0.10 ns	–0.03 ± 0.14 ns	0.18 ± 0.09***	0.26 ± 0.19 ns
	HT2		0.85 ± 0.03 ***	0.83 ± 0.04 ***	0.81 ± 0.04 ***	–0.12 ± 0.10 ns	–0.16 ± 0.11ns	0.38 ± 0.13***	0.27 ± 0.09***	–0.09 ± 0.21 ns
	DBH2			0.98 ± 0.01 ***	0.93 ± 0.02 ***	–0.01 ± 0.10 ns	–0.04 ± 0.10 ns	0.01 ± 0.14 ns	0.05 ± .09 ns	0.09 ± 0.20 ns
	DBH3				0.98 ± 0.01 ***	0.03 ± 0.10 ns	–0.16 ± 0.10 ns	0.14 ± 0.14 ns	–0.02 ± 0.09 ns	–0.11 ± 0.20 ns
	DBH4					0.05 ± 0.10 ns	–0.17 ± 0.10 ns	0.14 ± 0.14 ns	0.11 ± 0.09 ns	–0.02 ± 0.19 ns
	PILO						–0.42 ± 0.08***	–0.06 ± 0.13 ns	0.04 ± 0.09 ns	0.34 ± 0.18 ns
	BARK							–0.20 ± 0.14 ns	–0.05 ± 0.09 ns	0.02 ± 0.19 ns
	FORM								0.33 ± 0.12***	–0.79 ± 0.18***
	ADFO									0.11 ± 0.18 ns
VOCA	HT2		0.94 ± 0.01 ***	0.92 ± 0.02 ***				0.30 ± 0.13***	0.21 ± 0.08***	
	DBH2			0.98 ± 0.01 ***				0.35 ± 0.13***	0.14 ± 0.08 ns	
	DBH3							0.26 ± 0.13 ns	0.17 ± 0.08***	
	FORM							0.11 ±0.16 ns	0.01 ± 0.13 ns	
	SURV3	0.81 ± 0.05 ***	0.60 ± 0.08 ***	0.41 ± 0.12 ***					0.31 ± 0.09***	
MANU	HT2		0.80 ± 0.07 ***	0.70 ± 0.10 ***				0.45 ± 0.20***	0.16 ± 0.13 ns	
	DBH2			0.93 ± 0.03 ***				0.32 ± 0.22 ns	–0.03 ± 0.13 ns	
	DBH3							0.42 ± 0.19***	–0.01 ± 0.13 ns	
	FORM								–0.01 ± 0.14 ns	

in Victoria (0.76) but growth at these sites was poorly correlated with a third site in Tasmania (0.12 and 0.29). The correlation of subrace performance across sites was also usually strong, but of lower significance than the genetic correlations (Table 3). In contrast, more variable race correlations were reported by MACDONALD *et al.* (1997), which in one case was even of different sign to the additive genetic correlations within races, suggesting the Tasmanian sites were more divergent than those in the present study.

Survival

There is interest in including survival as a selection criterion in *E. globulus* breeding programs where the aim is to maximise productivity on a per hectare basis (CHAMBERS *et al.* 1996; CHAMBERS & BORRALHO 1997; TORO *et al.* 1998). This is particularly important in more extreme environments where mortality due to drought or frost may have an economical impact. In the present case, survival was high (>88 %), and had the lowest heritability of all traits. The heritability of survival averaged less than 0.05 and only at one site was this significantly different from zero (VOCA, 0.13). CHAMBERS *et al.* (1996) reported that heritability for *E. globulus* survival ranged from 0.19 to 0.57 in sites in Australia and Portugal, with sites most affected by drought having lower heritabilities for survival than those affected by frost. While subtle differences in survival were detected between subraces at all but one Argentinian site, the trials were not subject to major stress during the period studied and genetic variation in factors affecting survival was poorly expressed.

Pilodyn penetration

After growth, wood density is the second most important selection trait included in *E. globulus* breeding programs aimed at pulpwood production (BORRALHO *et al.* 1993; BORRALHO 2001). Wood density is often measured indirectly in such programs using Pilodyn penetration due to the lower assessment cost. Pilodyn penetration is inversely related to wood density (MUNERI & RAYMOND 2000). In the two trials assessed, Pilodyn penetration was much more heritable than growth (0.43 and 0.52). These single site heritabilities were higher than those reported by MACDONALD *et al.* (1997; 0.28 to 0.41) and particularly MUNERI & RAYMOND (2000; 0.13 to 0.27).

Pilodyn penetration was highly genetically correlated (r_g = 0.89 ± 0.04) across the two sites assessed. This correlation was close to the average (0.91) from a study of five trials established in Tasmania which included more than 500 families (MACDONALD *et al.* 1997) and slightly higher than the average (0.82) across site genetic correlations reported by MUNERI & RAYMOND (2000) for over 70 families on three Australian trials. The correlation between subrace Pilodyn penetration across the two Argentinian sites was very high (r_s = 0.94). MACDONALD *et al.* (1997) also reported high correlations in race performance across sites for Pilodyn penetration (average 0.79). These regular reports of high genetic correlations in Pilodyn penetration across sites at both the genetic and subrace/race levels clearly indicate little genotype x environment interaction occurs for wood density in *E. globulus*, consistent with the findings of MUNERI & RAYMOND (2000).

Bark thickness

Relative bark thickness may not only affect estimates of under-bark volume, but may be of adaptive significance, affecting the susceptibility or recovery of trees from damage by pests (e.g. *Phoracantha semipunctata* – SORIA & BORRALHO 1998; *Perga affinus* – DUTKOWSKI & POTTS 1999; JORDAN *et al.* 2002) or environmental stress (e.g. drought – DUTKOWSKI & POTTS 1999). Estimates of heritability for relative bark thickness were significant but moderate (0.33 and 0.31) and highly significant differences were observed between subraces (Table 1). The genetic correlation of bark thickness across sites was high both within (0.88) and between (0.83) subraces. DUTKOWSKI *et al.* (1997) and KELLY (1997) reported similar estimates of within race heritability. The latter author also notes that relative bark thickness remained fairly constant across ages (4; 5 and 8 years of age), sites (5 in Tasmania and 1 in Spain) and measurement technique.

Tree form

Forking and tree form are not commonly included in eucalypt breeding programs as primary selection traits when the objective is pulpwood production (BORRALHO *et al.* 1993; GREAVES *et al.* 1997; WEI & BORRALHO 1999). However, such traits may be important for solid wood objectives (RAYMOND 2000). In the Argentinian trials, the early forking observed after hail was poorly heritable (0.03 and 0.04) and the trees recovered after a few months. However, this damage did appear to have impact on later age form (4 years) as the genetic correlation between the presence of forks at 2 years and tree form assessed at age 4 years was significant and negative at both sites (–0.40 and –0.79). Poor form appeared to at least partly arise from the forking early in establishment. However, the heritability of form on the four sites was also low (0.07 to 0.14). VOLKER *et al.* (1990)

reported higher heritability (0.22 ± 0.07) for form from a trial assessed at age 8. However in both studies, the heritability of tree form was lower than estimates for growth. Despite the low heritability for forking and form, the genetic expression of these traits was highly correlated across sites, at least within subraces (Table 4; form 0.70; forking 0.77).

Vegetative phase change

In heteroblastic species such as *Eucalyptus globulus*, the timing of transition from juvenile to adult foliage type is important as the leaf types differ in numerous physiological and anatomic characteristics. In the case of *E. globulus*, many pests are adapted to one or another type of foliage (e.g. LAWRENCE *et al.* 2002; STEINBAUER 2001), and variation in the timing of the transition may affect performance (JORDAN *et al.* 2000). The proportion of adult foliage was the most heritable of all traits in the present study, averaging 0.60. High heritability estimates for this ontogenetic trait were similarly reported in a base population trial of *E. globulus* in Tasmania (height to phase change $h^2 = 0.67 \pm 0.13$; JORDAN *et al.* 1999) and for other eucalypt species (WILTSHIRE *et al.* 1998). Despite the lower heritability reported by IPINZA *et al.* (1994; height to phase change $h^2 = 0.30$), the timing of the transition to adult foliage seems clearly to be under strong genetic control in eucalypts. In addition, the relative timing of this transition appears to be extremely stable across environments. The very high genetic correlations between (0.92) and within (0.99) subraces for the proportion of adult foliage in the canopy, implies there is no environment interaction affecting the expression of this ontogenetic trait (see also JORDAN *et al.* 2000).

Inter-trait correlations

The genetic correlation between two traits will determine how selection operating on one trait will affect genetic variation in another (i.e. correlated selection – FALCONER & MACKAY 1996). A positive genetic change in one trait could affect other traits in the population in an adverse or favourable manner depending upon the strength and direction of their genetic correlations.

Within races, genetic variation in growth was effectively independent of genetic variation in the proportion of adult foliage in the canopy, the level of forking, Pilodyn penetration and relative bark thickness (Table 6). The only exceptions involved specific growth correlations with vegetative phase change. There was a low, but significant positive correlation of early growth with the proportion of adult foliage at two sites. This is indicative of the general trend observed at the environmental and genetic level by JORDAN *et al.* (2000) for fast growth to result in more rapid transition to adult foliage. This trend was also evident in the genetic correlation with four-year diameter reported by IPINZA *et al.* (1994), but not for their earlier age measurements. There was no significant association between growth and the transition to adult foliage at the subrace level in the present study, although such a correlation was reported for a disease damaged site in Tasmania where early phase change resulted in better growth (JORDAN *et al.* 2000).

Survival was genetically correlated with growth traits at VOCA (Table 5). VOCA was the only trial where there was a significant genetic basis to variation in survival within subraces (Table 1) and, as with growth, survival was also correlated with the proportion of adult foliage, but not with form. The correlation estimates between survival and growth were within the top range of those reported previously (CHAMBERS *et al.* 1996) and indicate mortality was size dependent due to the death of genetically slower growing plants. However, these significant genetic correlations (r_g) were not evident at the subrace level (r_s; Table 5).

There was a general tendency for good form to be genetically correlated with fast growth at all sites (Table 6). This association was not detected at the subrace level (Table 5) but a similar trend was also reported by VOLKER *et al.* (1990) in *E. globulus* where good tree form was weakly genetically associated with fast growth (r_g for height 0.43, diameter 0.07 and volume 0.13). Regardless of whether this trend is a scoring artifact or a true biological tendency, the genetic correlation is clearly in a direction favourable for breeders.

There was a tendency for trees with genes for thicker bark to also have denser wood. The correlation between the relative bark thickness and Pilodyn penetration was highly significant at both sites assessed ($r_g = -0.46$ to -0.42; Table 6). This trend was also evident at the subrace level (Table 5) and has also been observed in trials in Tasmania (DUTKOWSKI & POTTS 1999), where it was suggested to be a pleiotropic relationship reflecting from the joint origin of wood and bark in the cambium.

A knowledge of the genetic relationship between growth and wood density is important for breeding programs. An adverse correlation, as observed in some *Pinus* species (e.g. BURDON & LOW 1992), can markedly retard progress in selection toward a fast growing, high density ideotype required to optimise pulp yield per hectare. Within sites in the present study, Pilodyn penetration was genetically independent of diameter

within subraces (average r_g ~ 0.00; Table 6) and slightly positive when across site correlations are also considered (average r_g ~ 0.09; LOPEZ *et al.* 2001a). Other studies reported positive genetic correlations between growth and Pilodyn penetration (0.04, 0.18 and 0.85 MUNERI & RAYMOND 2000; average of 5 sites 0.26 MACDONALD *et al.* 1997; 0.19 VOLKER unpubl. data) and slightly negative associations between growth and basic density (MUNERI & RAYMOND 2000), but rarely were these correlations significantly different from zero. At the subrace level, there was a tendency for faster growth to be associated with lower Pilodyn penetration (i.e. denser wood) in the present study (Table 5). At the race level this association was highly variable across sites in the study of MACDONALD *et al.* (1997), but the combined correlation was also slightly negative (–0.19). Regardless, the very low correlations between growth and Pilodyn penetration within the total population in Argentina when both genetic and sub-race effects are combined suggest that the traits can be improved independently (LOPEZ *et al.* 2001a).

Limitation of parameter estimates

As most eucalypt species are only in the early stages of domestication, the majority of the genetic parameters reported to date are derived from open pollinated progeny trials (ELDRIDGE *et al.* 1993; POTTS & WILTSHIRE 1997) and *E. globulus* is no exception (Table 2). However, the accuracy of these parameter estimates has been questioned, particularly for growth (GRIFFIN & COTTERILL 1988; POTTS *et al.* 1995). Eucalypts have a mixed mating system (HARDNER & POTTS 1995; POTTS & WILTSHIRE 1997) and inbreeding depression for growth after selfing is severe (HARDNER & POTTS 1995; HARDNER *et al.* 1996; LOPEZ *et al.* 2000). Bi-parental inbreeding may also be significant in wild populations (HARDNER *et al.* 1998; SKABO *et al.* 1998). Variation in the levels of outcrossing in the open pollinated progeny may thus impact considerably on their growth performance (HARDNER & POTTS 1995; BORRALHO & POTTS 1996; BURGESS *et al.* 1996). Hence, heritability for growth estimated from open pollinated progenies can be inflated and not reflect the true additive genetic variation amongst parents where the expression of inbreeding depression is variable (HODGE *et al.* 1996). It has also been argued that the stability of inbreeding depression may result in overestimation of the strength of the additive genetic correlation in growth across ages and sites (POTTS *et al.* 1995; HODGE *et al.* 1996).

Varied results have been found when comparing estimates of heritability and breeding values derived from open pollinated and control pollinated progeny of the same *E. globulus* parents, even when adjusted as in the present study. Breeding values derived from native stand open pollinated progeny have been shown to be significantly correlated with those derived from controlled crosses for traits such as susceptibility to *Mycosphaerella* sp. fungus attack (DUNGEY *et al.* 1997), Pilodyn penetration (VOLKER unpublished) and height to vegetative phase change (JORDAN *et al.* 1999). Heritability estimates derived for these traits have been comparable in the both cross types. In contrast, heritability estimates derived from native stand open pollinated progeny were highly inflated for growth traits, and breeding values derived from open and control pollination were poorly correlated (GRIFFIN & COTTERILL 1988; HODGE *et al.* 1996; P. VOLKER unpublished data). Such differences may be due to variation in inbreeding and not accounting for non-additive genetic effects (i.e. maternal or specific combining ability). Indeed, the specific combining effects for growth in *E. globulus* appear to be relatively high, at least comparable to additive genetic effects (HODGE *et al.* 1996; VAILLANCOURT *et al.* 1995; P. VOLKER unpublished data). Non-random outcrossing with a few male parents may thus also bias breeding values derived from open pollinated progeny.

Most *E. globulus* breeding programs are moving to controlled pollinated assessment after first generation improvement, stimulated by the development of new single-visit pollination procedures (HARBARD *et al.* 1999; WILLIAMS *et al.* 1999). Such full pedigree control will allow more accurate estimation of genetic parameters, the possibility of separating additive from non-additive genetic effects, and improved accuracy in the prediction of genetic merit for breeding and deployment.

CONCLUSIONS

Heritabilities estimated for most traits were consistent with other studies. Survival, forking and form were poorly heritable. Growth and relative bark thickness were under moderate genetic control, whereas Pilodyn penetration and vegetative phase change were under strong genetic control. Genetic variation in most traits was strongly correlated across sites, indicating low genotype by environment interaction. Age-age genetic correlations for growth were also high. However, the possibility that these genetic parameters, particularly for growth, are inflated by inbreeding depression cannot be dismissed. Growth traits were in general genetically independent from other key objective traits at the within and between subrace levels.

The significant genetic variation detected for both growth and Pilodyn, coupled with their genetic independence, would argue that considerable progress can

be made in improvement of this base population for pulpwood production in Argentina. A strong genetic correlation across ages and sites suggests that early selection for growth and a single breeding population is possible with little loss of genetic gain.

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LITERATURE CITED

ARAÚJO, J. A., LEMOS, L., RAMOS, A., FERREIRA, J. G. & BORRALHO, N. M. G. 1997: The RAIZ *Eucalyptus globulus* breeding program: A BLUP rolling-front strategy with a mixed clonal and seedling deployment scheme. *In:* Proc. of the IUFRO Conference on Silviculture and Improvement of Eucalypts. Salvador, Bahia, Brasil. EMBRAPA, Colombo. pp. 371–376.

BALMELLI, G., RESQUIN, F. & TRUJILLO, I. 2001: Estimación de parámetros genéticos para características de crecimiento y productividad en *Eucalyptus globulus* en Uruguay. *In:* Proc. of the IUFRO International Symposium on Developing the Eucalypt of the Future. INFOR, Valdivia, Chile.

BORRALHO, N. M. G. 2001: The purpose of breeding is breeding for a purpose. *In:* Proc. of the IUFRO International Symposium on Developing the Eucalypt of the Future. INFOR, Valdivia, Chile.

BORRALHO, N. M. G., COTTERILL, P. P. & KANOWSKI, P. J. 1992a: Genetic control of growth of *Eucalyptus globulus* in Portugal. II. Efficiencies of early selection. *Silvae Genetica* **41**: 70–77.

BORRALHO, N. M. G., KANOWSKI, P. J. & COTTERILL, P. P. 1992b: Genetic control of growth of *Eucalyptus globulus* in Portugal I. Genetic and phenotypic parameters. *Silvae Genetica* **41**: 39–45.

BORRALHO, N. M. G., COTTERILL, P. P. & KANOWSKI, P. J. 1993: Breeding objectives for pulp production of *Eucalyptus globulus* under different industrial cost structures. *Canadian Journal of Forest Research* **23**: 648–656.

BORRALHO, N. M. G., JARVIS, S. F. & POTTS, B. M. 1995: Multivariate restricted maximum likelihood estimation of genetic parameters for diameter at 3 to 5 years in the *Eucalyptus globulus* base population in Australia. *In:* Eucalypt Plantations: Improving Fibre Yield and Quality. CRCTHF–IUFRO Conference. (Ed. B.M. Potts, N.M.G. Borralho, J.B. Reid, R.N. Cromer, W.N. Tibbits and C.A. Raymond.) Hobart, Tasmania. CRC for Temperate Hardwood Forestry. pp. 230–232.

BORRALHO, N. M. G. & POTTS, B. M. 1996: Accounting for native stand characteristics in genetic evaluations of open pollinated progeny from *Eucalyptus globulus* base population. *New Forests* **11**: 53–64.

BROOKER, M. I. H. 2000: A new classification of the genus *Eucalyptus* L'Her. (Myrtaceae). *Australian Systematic Botany* **13**: 79–148.

BURDON, R. D. 1977: Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. *Silvae Genetica* **26**: 168–175.

BURDON, R. D. & LOW, C. B. 1992: Genetic survey of *Pinus radiata*. 5: wood properties: variation, heritabilities, and interrelationships with other traits. *New Zealand Journal of Forestry Science* **22**: 228–245.

BURGESS, I. P., WILLIAMS, E. R., BELL, J. C., HARWOOD, C. E. & OWEN, J. V. 1996: The effect of outcrossing rate on the growth of selected families of *Eucalyptus grandis*. *Silvae Genetica* **45**: 97–101.

CHAMBERS, P. G. S. & BORRALHO, N. M. G. 1997: Importance of survival in short-rotation tree breeding programs. *Canadian Journal of Forestry Research* **27**: 911 –917.

CHAMBERS, P. G. S., BORRALHO, N. M. G. & POTTS, B. M. 1996: Genetic analysis of survival in *Eucalyptus globulus* ssp. *globulus*. *Silvae Genetica* **45**: 107–112.

CHAMBERS, P. G. S., POTTS, B. M. & TILYARD, P. 1997: The genetic control of flowering precocity in *Eucalyptus globulus* ssp. *globulus*. *Silvae Genetica* **46**: 207–214.

CORNELIUS, J. 1994: Heritabilities and additive genetic coefficients of variation in forest trees. *Canadian Journal of Forest Research* **24**: 372–379.

DUNGEY, H. S., POTTS, B. M., CARNEGIE, A. J. & ADES, P. K. 1997: *Mycosphaerella* leaf disease: Genetic variation in damage to *Eucalyptus nitens*, *E. globulus* and their F_1 hybrid. *Canadian Journal of Forest Research* **27**: 750 –759.

DUTKOWSKI, G. W. & POTTS, B. M. 1999: Geographical patterns of genetic variation in *Eucalyptus globulus* ssp. *globulus* and a revised racial classification. *Australian Journal of Botany* **47**: 237–263.

DUTKOWSKI, G. W., POTTS, B. M. & BORRALHO, N. M. G. 1997: Revised racial classification of *Eucalyptus globulus* ssp. *globulus* and the importance of including race in analysis of progeny trials. *In:* Proc. of the IUFRO Conference on Silviculture and Improvement of Eucalypts. Salvador, Bahia, Brasil. EMBRAPA, Colombo. pp. 322–329.

DUTKOWSKI, G. W., GILMOUR, A. R. & BORRALHO, N. M. G. 2001: Modification of the additive relationship matrix for open pollinated trials. *In:* Proc. of the IUFRO International Symposium on Developing the Eucalypt of the Future. INFOR, Valdivia, Chile.

DUTKOWSKI, G. W., COSTA E SILVA, J., GILMOUR, A. R. & LOPEZ, G. A. 2002: Spatial analysis methods for forest genetic trials. *Canadian Journal of Forest Research, (in press)*.

ELDRIDGE, K., DAVIDSON, J., HARWOOD, C. & VAN WYK, G. 1993: Eucalypt Domestication and Breeding. Clarendon Press, Oxford, 288 pp.

ERICSSON, T. 1997: Enhanced Heritabilities and Best Linear Unbiased Predictors Through Appropriate Blocking of Progeny Trials. *Canadian Journal of Forest Research*

27: 2097–2101.

FALCONER, D. S. & MACKAY, T. F. C. 1996: Introduction to Quantitative Genetics. Addison Wesley Longman Limited, Edinburgh Gate, Harlow, England, 464 pp.

FU, Y. B., YANCHUK, A. D. & NAMKOONG, G. 1999: Incomplete block designs for genetic testing: some practical considerations. *Canadian Journal of Forest Research* **29**: 1871–1878.

GILMOUR, A. R., THOMPSON, R., CULLIS, B. R. & WELHAM, S. J. 2001: ASREML Reference Manual. Technical Report NSW Agriculture.

GREAVES, B. L., BORRALHO, N. M. G. & RAYMOND, C. A. 1997: Breeding objective for plantation eucalypts grown for production of kraft pulp. *Forest Science* **43**: 465–475.

GRIFFIN, A. R. & COTTERILL, P. P. 1988: Genetic variation in growth of outcrossed, selfed and open-pollinated progenies of *Eucalyptus regnans* and some implications for breeding strategy. *Silvae Genetica* **37**: 124–131.

GUTIÉRREZ, B., MOLINA, M., BALOCCHI, C. & DROPPELMANN, F. 2001: Desarrollo de una raza local de *Eucalyptus globulus* tolerante al frío. *In:* Proc. of the IUFRO International Symposium on Developing the Eucalypt of the Future. INFOR, Valdivia, Chile.

HARBARD, J. L., GRIFFIN, A. R. & ESPEJO, J. 1999: Mass controlled pollination of *Eucalyptus globulus*: a practical reality. *Canadian Journal of Forest Research* **29**: 1457–1463.

HARDNER, C. M. & POTTS, B. M. 1995: Inbreeding depression and changes in variation after selfing in *Eucalyptus globulus* ssp *globulus*. *Silvae Genetica* **44**: 46–54.

HARDNER, C. M., POTTS, B. M. & GORE, P. L. 1998: The relationship between cross success and spatial proximity of *Eucalyptus globulus* ssp. *globulus* parents. *Evolution* **52**: 614–618.

HARDNER, C. M., VAILLANCOURT, R. E. & POTTS, B. M. 1996: Stand density influences outcrossing rate and growth of open-pollinated families of *Eucalyptus globulus*. *Silvae Genetica* **45**: 226–228.

HODGE, G. R., VOLKER, P. W., POTTS, B. M. & OWEN, J. V. 1996: A comparison of genetic information from open-pollinated and control-pollinated progeny tests in two eucalypt species. *Theoretical and Applied Genetics* **92**: 53–63.

HOULE, D. 1992: Comparing evolvability and variability of quantitative traits. *Genetics* **130**: 195–204.

IPINZA, R. H., GARCÍA, X., APIOLAZA, L. A., MOLINA, M. P., CHUNG, P. & PARRA, P. 1994: Variación juvenil de un ensayo de procedencias y familias de *Eucalyptus globulus* subsp. *globulus* Labill, en la séptima región, Chile. *Ecología* **8**: 259–270.

JORDAN, G. J., POTTS, B. M. & WILTSHIRE, R. 1999: Strong, independent quantitative genetic control of vegetative phase change and first flowering in *Eucalyptus globulus* ssp. *globulus*. *Heredity* **83**: 179–187.

JORDAN, G. J., POTTS, B. M., CHALMERS, P. & WILTSHIRE, R. J. E. 2000: Quantitative genetic evidence that the timing of vegetative phase change in *Eucalyptus globulus* ssp. *globulus* is an adaptive trait. *Australian Journal of Botany* **48**: 561–567.

JORDAN, G. J., POTTS, B. M. & CLARKE, A. R. 2001: Susceptibility of *Eucalyptus globulus* ssp. *globulus* to sawfly (*Perga affinis* ssp. *insularis*) attack and its potential impact on plantation productivity. *Forest Ecology and Management* **160**: 189–199.

KELLY, C. M. 1997: Natural variation and genetic control of relative bark thickness in *Eucalyptus globulus* ssp. *globulus*. Unpublished BSHonours Thesis, University of Tasmania.

KIRKPATRICK, J. B. 1975: Geographical Variation in *Eucalyptus globulus*. Forestry and Timber Bureau, Bulletin 47 Australian Government Publishing Service, Canberra, 64 pp.

LAWRENCE, R., POTTS, B. M. & WHITHAM, T. G. 2002: Relative importance of plant ontogeny, host genetic variation, and leaf age for a common herbivore. *Ecology*, (*in press*).

LOPEZ, G. A., APIOLAZA, L. A., POTTS, B. M., DUTKOWSKI, G. W., GELID, P. & RODRIGUEZ TRAVERSO, J. M. 2001a: Genetic parameters for growth and pilodyn from *Eucalyptus globulus* in Argentina. *In:* Proc. of the IUFRO International Symposium on Developing the Eucalypt of the Future. (Ed. S. Barros). INFOR, Valdivia, Chile.

LOPEZ, G. A., POTTS, B. M., DUTKOWSKI, G. W. & RODRIGUEZ TRAVERSO, J. M. 2001b: Quantitative genetics of *Eucalyptus globulus*: Affinities of land race and native stand localities. *Silvae Genetica* **50**: 244–252.

LOPEZ, G. A., POTTS, B. M., RODRIGUEZ TRAVERSO, J. M. & GELID, P. 2001c: The performance of *Eucalyptus maidenii* provenances in Argentina. *In:* Proc. of the IUFRO International Symposium on Developing the Eucalypt of the Future. INFOR, Valdivia, Chile.

LOPEZ, G. A., POTTS, B. M. & TILYARD, P. A. 2000: F_1 hybrid inviability in *Eucalyptus*: the case of *E. ovata* x *E. globulus*. *Heredity* **85**: 242–250.

MACDONALD, A. C., BORRALHO, N. M. G. & POTTS, B. M. 1997: Genetic variation for growth and wood density in *Eucalyptus globulus* ssp. *globulus* in Tasmania (Australia). *Silvae Genetica* **46**: 236–241.

MUNERI, A. & RAYMOND, C. A. 2000: Genetic parameters and genotype-by-environmet interactions for basic density, pilodyn penetration and stem diameter in *Eucalyptus globulus*. *Forest Genetics* **7**: 317–328.

POTTS, B. M. & JORDAN, G. J. 1994a: Genetic variation in the juvenile leaf morphology of *Eucalyptus globulus* Labill. ssp. *globulus*. *Forest Genetics* **1**: 81–95.

POTTS, B. M. & JORDAN, G. J. 1994b: The spatial pattern and scale of variation in *Eucalyptus globulus* ssp. *globulus*: variation in seedling abnormalities and early growth. *Australian Journal of Botany* **42**: 471–492.

POTTS, B. M., VOLKER, P. W., HODGE, G. R., BORRALHO, N. M. G., HARDNER, C. H. & OWEN, J. V. 1995: Genetic s to the exploitation of base populations of *Eucalyptus globulus* ssp. *globulus*. *In:* Eucalypt plantations: Improving Fibre Yield and Quality, Proc. CRCT HF –IUFRO Conf., Hobart, 19–24 Feb. (Ed. B.M. Potts, N.M.G. Borralho, J.B. Reid, R.N. Cromer, W.N. Tibbits and C.A. Raymond.) Hobart, Tasmania. CRC for Temperate Hardwood Forestry. pp. 217–221.

POTTS, B. M. & WILTSHIRE, R. J. E. 1997: Eucalypt genetic and genecology. *In* Eucalypt Ecology: Individuals to Ecosystems. Ed. J. Williams and J. Woinarski.) pp.

56–91. Cambridge University Press, Cambridge.

RAYMOND, C.A. 2000: Tree breeding issues for solid wood production. *In:* Proc. of the IUFRO International Conference on The Future of Eucalypts for Wood Products. Launceston, Tasmania. Australia. pp. 265–270.

REZENDE, G. D. S. P. & DE RESENDE, M. D. V. 2000: Dominance effects in *Eucalyptus grandis*, *Eucalyptus urophylla* and hybrids. *In:* Proc. of the Symposium on Hybrid Breeding and Genetics. (Ed. H. S. D. Dungey, M. J. Dieters and D. G. Nikles,) Brisbane. Department of Primary Industries. pp. 93–100.

SANHUEZA, R. & GRIFFIN, A. R. 2001: FAMASA Fiber Yield Improvement Programme (F.Y.I.P.): 10 years experience breeding *Eucalyptus globulus*. *In:* Proc. of the IUFRO International Symposium on Developing the Eucalypt of the Future. INFOR, Valdivia, Chile.

SEARLE, S. R. 1971: Linear Models. John Wiley & Sons, New York, 532 pp.

SKABO, S., VAILLANCOURT, R. E. & POTTS, B. M. 1998: Fine-scale genetic structure of *Eucalyptus globulus* ssp. *globulus* forest revealed by RAPDs. *Australian Journal of Botany* **46**: 583–594.

SORIA, F., BASURCO, F., TOVAL, G., SILIO, L., RODRIGUEZ, M. C. & TORO, M. 1997: Bayesian estimation of genetic parameters and provenance effects for height and diameter of *Eucalyptus globulus* in Spain. *In:* Proc. of the IUFRO Conference on Silviculture and Improvement of Eucalypts. Salvador, Bahia, Brasil. EMBRAPA, Colombo. pp. 95–100.

SORIA, F. & BORRALHO, N. M. G. 1998: The genetics of resistance to *Phoracantha semipunctata* attack in *Eucalyptus globulus* in Spain. *Silvae Genetica* **46**: 365–369.

STEINBAUER, M. J. 2002: Oviposition preference and neonate performance of *Mnesampela privata* in relation to heterophylly in *Eucalyptus dunnii* and *E. globulus*. *Agricultural & Forest Entomology, (in press).*

TIBBITS, W. N., BOOMSMA, D. B. & JARVIS, S. 1997: Distribution, biology, genetics, and improvement programs for *Eucalyptus globulus* and *E. nitens* around the world. *In* Proc. of the 24th Biennial Southern Tree Improvement Conference, June 9–12 1997. *Edited by* T. White, D. Huber and G. Powell.) pp. 81–95. Southern Tree Improvement Committee, Orlando, Florida.

TORO, M. A., SILIÓ, L., RODRIGUEZ, M. C., SORIA, F. & TOVAL, G. 1998: Genetic analysis of survival to drought in *Eucalyptus globulus* in Spain. *In:* Proc. of the 6th World Congress on Genetics Applied to Livestock Production. pp. 499–502.

VAILLANCOURT, R. E., POTTS, B. M., WATSON, M., VOLKER, P. W., HODGE, G. R., REID, J. B. & WEST, A. K. 1995: Detection and prediction of heterosis in *Eucalyptus globulus*. *Forest Genetics* **2**: 11–19.

VOLKER, P. W., DEAN, C. A., TIBBITS, W. N. & RAVENWOOD, I. C. 1990: Genetic parameters and gains expected from selection in *Eucalyptus globulus* in Tasmania. *Silvae Genetica* **39**: 18–21.

WEI, X. & BORRALHO, N. M. G. 1996: A simple model to describe age trends in heritability in short rotation tree species. *In:* Proc. of the QFRI–IUFRO Conference Tree Improvement for Sustainable Tropical Forestry. (Ed. M. J. Dieters, A. C. Matheson, D. G. Nikles, C. E. Harwood and S. M. Walker.) Caloundra, Queensland, Australia. 1996. pp. 178–181.

WEI, X. & BORRALHO, N. M. G. 1998: Use of individual tree mixed models to account for mortality and selective thinning when estimating base population genetic parameters. *Forest Science* **44**: 246–253.

WEI, X. & BORRALHO, N. M. G. 1999: Objectives and selection criteria for pulp production of *Eucalyptus urophylla* plantations in South East China. *Forest Genetics* **6**: 181–190.

WHITE, T. 1996: Genetic parameter estimates and breeding value predictions: issues and implications in tree improvement programs. *In:* Proc. of the QFRI-IUFRO Conference Tree Improvement for Sustainable Tropical Forestry. (Ed. M. J. Dieters, A. C. Matheson, D. G. Nikles, C. E. Harwood and S. M. Walker.) Caloundra, Queensland, Australia. 1996. pp. 110–117.

WILLIAMS, D. R., POTTS, B. M. & BLACK, P. G. 1999: Testing single visit pollination procedures for *Eucalyptus globulus* and *E. nitens*. *Australian Forestry* **62**: 346–352.

WILTSHIRE, R. J. E., POTTS, B. M. & REID, J. B. 1998: Genetic control of reproductive and vegetative phase change in the *Eucalyptus risdonii–E. tenuiramis* complex. *Australian Journal of Botany* **46**: 45–63.

WOOLASTON, R., WHITEMAN, P. H. & CAMERON, J. N. 1991: Genetic analyses of four year diameter measures for *Eucalyptus globulus* growing across four sites in Victoria, Australia. *In:* Proc. of the IUFRO symposium on Intensive Forestry: The Role of Eucalypts. (Ed. A.P.G. Schönau.) Durban, South Africa. Southern African Institute of Forestry, Pretoria. pp. 371–381.

ZANG, D., WANG, H. & YOU, Y. 1995: Performance and selection of a 4-year *Eucalyptus globulus* seedling seed orchard in Yunnan, China. *In:* 'Eucalypt plantations: Improving Fibre Yield and Quality' Proc. CRCTHF – IUFRO Conf., Hobart, 19–24 Feb. (Ed. B. M. Potts, N. M. G. Borralho, J. B. Reid, R. N. Cromer, W. N. Tibbits and C. A. Raymond.) Hobart, Tasmania. CRC for Temperate Hardwood Forestry. pp. 226–229.

ZENG, Z.-B. 1987: Long-term correlated response, interpopulation covariation, and interspecific allometry. *Evolution* **42**: 363–374.