THE GENETIC ARCHITECTURE OF A *EUCALYPTUS GLOBULUS* FULL-SIB BREEDING POPULATION IN AUSTRALIA

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ABSTRACT

Genetic parameters were estimated for diameter at breast height (DBH), height and core basic density (CBD) from ten second-generation control-pollinated *Eucalyptus globulus* progeny trials in Australia. Using multi-site analysis we aimed, firstly, to determine a suitable linear model to fit to the data and, secondly, to determine the relative importance of additive and non-additive genetic effects. A model with heterogeneous additive and error variances was used for all traits. The individual site heritabilities averaged 0.12 for DBH, 0.11 for height and 0.44 for CBD. Over all sites, the ratios of SCA (specific combining ability) and subrace to additive genetic variance for DBH (0.25 and 0.5) and height (0.30 and 0.25) were significantly greater than zero, but not for CBD (0.08 and 1.00). Inter-site additive genetic correlations were 0.71 for DBH, 0.72 for height and 1.07 for CBD, and all were not significantly different from 1. This study suggests that, for early growth, levels of dominance are comparable to additive genetic effects in this breeding population and there are significant genetic differences between subraces. In contrast, for CBD most genetic variation was additive and significant differences between subraces could not be detected with the small sample.

Keywords: *Eucalyptus globulus,* model testing, non-additive genetic effects, diameter at breast height, height, core basic density

INTRODUCTION

Eucalyptus globulus is one of the most widely planted hardwood species in the world for the production of pulpwood due to its short-rotation length and favorable pulping qualities (BROWN, 2000; POTTS *et al.*, 2004). It is native to south-east Australia (BROOKER 2000) and it is grown in plantations in many temperate countries (ELDRIDGE *et al.* 1993), with breeding programs in Australia (TIBBITS *et al.* 1997; MCRAE *et al.*, 2001), Chile (SANHUEZA & GRIFFIN, 2001), China (ZANG *et al.* 1995), Portugal (BORRALHO *et al.* 1992; ARAÚJO *et al.* 1997), Spain (SORIA & BORRALHO 1997; SORIA *et al.* 1998), Uruguay (BALMELLI *et al.*, 2001) and Argentina (LOPEZ *et al.*, 2002). Knowledge of genetic parameters is important in running breeding programs and essential for breeding value prediction. A good understanding of genetic variation and co-variation of economically important traits is needed, along with an understanding of the expression of these variations in different environments. Many studies have estimated genetic parameters for *E. globulus*, but most are based on open-pollinated progeny tests (reviewed in LOPEZ *et al.*, 2002). Unpredictable and differential inbreeding in open-pollinated progeny means that the accuracy of such estimates has been questioned, particularly for growth traits (HARDNER & POTTS 1995; POTTS *et al.* 1995; HODGE *et al.* 1996; VOLKER 2002). Estimates based on fully pedigreed progeny tests in different environments are necessary to improve the accuracy of genetic parameter estimates and enable accurate prediction of genetic merit for breeding and deployment.

A key issue in accurate genetic parameter estimation and breeding value prediction is the identifica-

tion of the most appropriate genetic model (COSTA E SILVA *et al.* 2005). This is particularly challenging when evaluating information across multiple trials and ages, and where the genetic connection between trials is less than complete. This is often the case in programs implementing a 'rolling front' breeding strategy, which combines information across locations, years, generations, and pedigree groups in regular genetic evaluation (BORRALHO & DUTKOWSKI 1996). In Australia, the TREEPLAN® system has been implemented by the Southern Tree Breeding Association (STBA) to undertake such large-scale genetic evaluation of *E. globulus* and *Pinus radiata* (KERR *et al.*, 2002; MCRAE *et al.*, 2004). In the TREEPLAN® model, measurements on different sites are mapped to the same selection criterion and transformed to have a common additive genetic variance. They are thus effectively assumed to have a unit inter-site correlation. Genotype by environment (G×E) interaction and age-to-age correlations for growth are accommodated by having selection criteria that reflect different site types and age classes (KERR *et al.*, 2002). Individual site estimates of the additive genetic variance are used to scale the data on each site. Specific combining ability (SCA) variance is effectively assumed to be constant across sites for each selection criterion. As the first of the second generation breeding trials of *E. globulus* have reached evaluation age, these assumptions can now be tested using full-sib progeny grown in a variety of environments.

A number of second-generation control-pollinated progeny trials of *E. globulus* have been established in southern Australia since 1997 as a part of the STBA breeding program (JARVIS *et al.* 1995; MCRAE *et al.*, 2001, 2004). The parents of the progeny in these trials were selected from base population trials established using open-pollinated seed collected from parents in a number of subraces (DUTKOWSKI & POTTS 1999). While these early second-generation trials are small in size, genetic links exist among them through common families, parents and grandparents. This paper aims firstly, to identify an appropriate evaluation model for the analysis of these progeny trials and secondly, to provide early estimates of genetic parameters in the second-generation breeding population of *E. globulus* using this model.

MATERIALS AND METHODS

Trial design and genetic materials

The data used in this analysis came from ten full-sib *E. globulus* control-pollinated progeny trials established by the STBA in Victoria, Tasmania and Western Australia from 1997 to 2001 (Table 1). All trials are resolvable row column designs produced using the program cycDesign (WILLIAMS *et al.* 2002). There were 11 replicates of one-tree plots in trial STBGL126, 5 replicates of three-tree row-plots in trial STBGL121, and 5 replicates of two-tree row-plots in the other trials. The numbers of plot-rows per replicate varied from 5 to 8, the number of plot-columns per replicate varied from 5 to 12, and the number of plots per replicate varied from 30 to 96.

The trials were all second-generation trials. Some open-pollinated families were included in these trials as controls but they were excluded from this analysis as variation in outcrossing rates may bias parameter estimation (HODGE *et al.* 1996). The parents of the families in the trials had two sources: the first were STBA first generation individuals selected from all STBA member base population trials on a combined index of DBH (diameter at breast height, 1.3 m) and Pilodyn penetration (an indirect measure of wood density), and the second were eleven first generation trees from the Strzelecki Ranges race (DUTKOWSKI & POTTS 1999) which had been phenotypically selected for growth in a provenance trial. These non-STBA trees were highly ranked in the orchard and were from a highly ranked race. The control-pollination (CP) families included two types of crosses: crosses between STBA first generation males and females and crosses between STBA first generation males and the non-STBA females. Ninety-five percent of the families were inter-race F_1 crosses.

Families and parents were spread across sites to provide linkage between trials (Table 2). The number of families and parents in common was quite low for some pairs of trials. Linkages at the sub-race level were better as only 12 subraces were presented overall and each trial contained at least nine.

There were 5,584 CP trees planted in the trials and 93% survived. Three performance traits were measured: height (m), diameter at breast height (DBH; cm) and core basic density (CBD; $kg \cdot m^{-3}$). There were 3,141 height observations from 6 trials, 3,820 DBH observations from 9 trials and 516 core basic density observations (one tree per plot) from 3 trials. The age at measurement ranged from 14 to 32 months for height, 22 to 57 months for DBH, and 43 to 47 months for core basic density. For trees with multiple stems, only data from the largest stem were included. Observations of dead trees and those field coded 'reject' were treated as missing values.

Table 1. Trial information.

	Trial (STBGL_)										
	100	101	102	107	108	109	114	115	121	126	All trials
Year of establishment	1997	1997	1998	1998	1998	1998	1999	1999	2001	2001	
Geographical region	Vic	WA	Tas	Tas	WA	Vic	Vic	Vic	WA	WA	
Latitutde (South)	38° 12'	33° 56'	41° 10'	43° 10'	34° 49'	37° 30'	37° 18'	37° 47'	34° 43'	34° 16'	
Longitude (East)	146° 26'	116° 16'	145° 51'	146° 51'	118° 3'	140° 51'	141° 1'	143° 51'	117° 52'	116° 1'	
Design features											
No. of replicates	5	5	5	5	5	5	5	5	5	11	
No. of plot-rows/replicate	7	6	6	8	7	8	6	5	8	8	
No. of plot-columns/replicate	5	6	5	7	10	7	6	9	11	12	
No. of plots/replicate	35	36	30	56	70	56	36	45	88	96	
No. of trees/plot	2	2	2	2	2	2	2	2	3	1	
Spacing (m × m)	3.6 × 2.8	4.0 × 2.0	4.0 × 2.0	4.0 × 2.5	5.0 × 2.0	4.0 × 2.2	4.0 × 2.1	4.0 × 2.0	4.25 × 1.9	5.0 × 1.9	
Genetic materials											
No. of subraces	9	9	9	9	10	10	10	10	9	12	12
No. of grand-parents	17	17	19	22	24	21	28	31	53	70	78
No. of parents	27	27	25	41	43	38	38	47	92	116	150
No. of families	37	36	30	56	64	56	36	45	98	167	337
No. of crosses/parent†	2.7 (1–6)	2.7 (1–5)	2.4 (1–6)	2.7 (1–6)	3.0 (1–6)	2.9 (1–6)	1.9 (1–5)	1.9 (1–5)	2.1 (1–6)	2.9 (1–13)	8.3 (1–29)
No. of progeny/parent†	21 (1–53)	21 (1–46)	20(10–53)	26 (5–58)	30(10–60)	27 (7–58)	18 (5–50)	18 (6–50)	27 (3–78)	18 (1–98)	74 (2–267)
No. of trees/family†	8 (1–10)	8 (1–10)	9 (5–10)	10 (5–10)	9 (8–10)	9 (5–10)	10 (5–10)	9 (6–10)	13 (3–15)	6 (1–11)	17 (1–66)
Observations											
Total CP trees	288	289	255	530	657	520	342	425	1231	1047	5584
Survival (%) [a]	92 (24)	77 (43)	96 (34)	97 (26)	91 (57)	88 (30)	88 (45)	96 (32)	97 (22)	97 (14)	93
No. of DBH observations [a]	254 (43)	197 (43)	223 (34)	468 (47)	554 (57)	437 (30)	243 (45)	358 (32)	1086 (22)	–	3820
DBH mean (SD) (cm)	104 (22)	130 (21)	90 (14)	83 (19)	141 (35)	67 (20)	125 (19)	82 (14)	67 (9)	–	91 (34)
No. of height observations [a]	–	–	244 (21)	497 (26)	597 (27)	450 (30)	–	359 (32)	–	994 (14)	3141
Height mean (SD) (m)	–	–	1.77 (0.45)	3.18 (0.91)	7.1 (1.46)	6.92 (1.47)	–	6.99 (0.89)	–	2.64 (0.81)	4.60 (2.43)
No. of CBD observations [a]	164 (44)	214 (43)	138 (47)	–	–	–	–	–	–	–	516
CBD mean (SD) ($kg \cdot m^{-3}$)	491 (30)	466 (31)	520 (45)	–	–	–	–	–	–	–	488 (41)

† Range given in parentheses. [a] Months of age at measurement given in parentheses. DBH = diameter at breast height, CBD = core basic density; Vic = Victoria, WA = Western Australia, TAS = Tasmania.

Table 2. Families (below diagonal) and parents (above diagonal) in common among the trials analysed.

STBGL_	100	101	102	107	108	109	114	115	121	126
100		27	29	20	19	17	11	15	13	15
101	29		26	20	17	17	11	15	13	15
102	29	21		19	19	16	12	16	14	16
107	7	10	3		39	39	18	25	18	26
108	7	10	4	48		38	20	24	19	26
109	6	9	3	48	47		19	25	17	26
114	1	3	0	4	6	4		33	24	33
115	4	6	3	6	10	5	27		25	37
121	3	4	2	4	4	4	3	4		83
126	0	0	0	2	5	3	5	6	53	

Multi-site analysis

Genetic model

Variance components were estimated with a multi-site linear random-effects model by using restricted maximum likelihood as implemented in the computer package ASREML (GILMOUR *et al.*, 2002). The model fitted was:

$$\begin{bmatrix}\mathbf{y}_1\\ \vdots\\ \mathbf{y}_n\end{bmatrix} = \mathbf{X}_t\mathbf{t} + \begin{bmatrix}\mathbf{Z}_{b_1}\mathbf{b}_1\\ \vdots\\ \mathbf{Z}_{b_n}\mathbf{b}_n\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{c_1}\mathbf{c}_1\\ \vdots\\ \mathbf{Z}_{c_n}\mathbf{c}_n\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{r_1}\mathbf{r}_1\\ \vdots\\ \mathbf{Z}_{r_n}\mathbf{r}_n\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{p_1}\mathbf{p}_1\\ \vdots\\ \mathbf{Z}_{p_n}\mathbf{p}_n\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{sr_1}\mathbf{sr}_1\\ \vdots\\ \mathbf{Z}_{sr_n}\mathbf{sr}_n\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{add_1}\mathbf{add}_1\\ \vdots\\ \mathbf{Z}_{add_n}\mathbf{add}_n\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{sca_1}\mathbf{sca}_1\\ \vdots\\ \mathbf{Z}_{sca_n}\mathbf{sca}_n\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \vdots\\ \mathbf{e}_n\end{bmatrix} \quad [1]$$

where all effects apart from the mean and site were treated as random effects (each with its own variance); $\mathbf{y}_i$ is the vector of individual tree data (DBH, height or core basic density) in site i (i = 1 to n, where n is the number of sites); $\mathbf{t}$ is the vector of fixed site effects; and, for each site i, $\mathbf{b}_i$ is the vector of replicate effects; $\mathbf{c}_i$ is the vector of plot-column effects; $\mathbf{r}_i$ is the vector of plot-row effects; $\mathbf{p}_i$ is the vector of plot effects for the sites with multiple tree measurements per plot; $\mathbf{sr}_i$ is the vector of subrace effects; $\mathbf{add}_i$ is the vector of additive genetic effects of individual trees; $\mathbf{sca}_i$ is the vector of effects for specific combining ability (SCA); and $\mathbf{e}_i$ is the vector of residuals. $\mathbf{X}_t$, $\mathbf{Z}_{b_i}$, $\mathbf{Z}_{c_i}$, $\mathbf{Z}_{r_i}$, $\mathbf{Z}_{p_i}$, $\mathbf{Z}_{sr_i}$ $\mathbf{Z}_{add_i}$, and $\mathbf{Z}_{sca_i}$ are incidence matrices relating the observations to the effects in the model. The plot effect was removed from the model for core basic density and was not fitted for height in site 126 as only single-tree plots were planted at this site. The subrace effect was fitted as a random term rather than fixed (as in a genetic groups model, QUAAS 1981) due to the small amount of data available and imbalance in crossing and site representation (FOULLEY *et al.* 1992; KENNEDY & TRUS 1993), as well as to allow control of the subrace to additive variance (see below). The design matrix for the subrace effects (z_{sr_i}) was constructed manually so as to reflect the maternal and paternal subrace contributions to each observation.

Each random effect was assumed to be normally distributed, with a mean of zero and a variance-covariance matrix which is the Kronecker product of the inter-site variance-covariance matrix **G** and either a numerator relationship matrix (**A**) (HENDERSON 1984) for the additive genetic effects, or an identity matrix **I** for all other effects. The inter-site matrix **G** can be expressed as the product of a diagonal matrix of standard deviations **D** and a symmetric matrix **C** of correlations.

$$\mathbf{G} = \mathbf{DCD} = \begin{bmatrix}\sigma_1 & 0 & \dots & 0\\ 0 & \sigma_2 & \dots & 0\\ \vdots & \vdots & \dots & \vdots\\ 0 & 0 & \dots & \sigma_n\end{bmatrix}\begin{bmatrix}1 & r_{12} & \dots & r_{1n}\\ r_{21} & 1 & \dots & r_{2n}\\ \vdots & \vdots & \dots & \vdots\\ r_{n1} & r_{n2} & \dots & 1\end{bmatrix}\begin{bmatrix}\sigma_1 & 0 & \dots & 0\\ 0 & \sigma_2 & \dots & 0\\ \vdots & \vdots & \dots & \vdots\\ 0 & 0 & \dots & \sigma_n\end{bmatrix} \quad [2]$$

where σ_i is the standard deviation in site i, and r_{ij} are the corresponding correlations between site i and site j. As inter-site correlations for design features and residuals were assumed to be zero, **C** was defined as **I** for these effects, which is the equivalent of **G** being the direct sum of each site's variance-covariance matrix for each effect. The additive genetic variance is denoted as σ^2_{add}, SCA variance as σ^2_{sca}, subrace variance as σ^2_{sr}, plot variance as σ^2_p and error variance as σ^2_e. The additive genetic correlation is denoted as r_{add}, the SCA correlation as r_{sca} and the subrace correlation as r_{sr}.

Tests of hypotheses and model comparison

In order to test the significance of the homogeneity of variances across sites for the genetic effects, a base model was used that assumed the design features, additive genetic and error variances were heterogeneous. A few more complex models were used to (i) test the homogeneity of variances across sites by adding or dropping model restrictions and (ii) test inter-site correlations, either by setting these correlations (r_{ij} in equation 2) arbitrarily or by estimating them. Models 1 or 2 in Table 3 are those against which the Log Likelihood was compared when sequentially adding or dropping variance and correlation restrictions by using a two-tailed, p degree of freedom, likelihood ratio test (LRT), where p is the difference between the number of parameters estimated. Model 3 in Table 3 was used to estimate a uniform inter-site correlation for the additive genetic, SCA and subrace effects. Attempts were made to estimate all inter-site correlations amongst trials but the model failed to converge. This was likely to be due to the low degree of pedigree connection amongst some trials (Table 2). The deviation of the uniform across-site correlations from 1 was tested using a two-tailed, one degree of freedom, likelihood ratio test. Models 4 and 5 (Table 3) assumed that σ^2_{sca} and σ^2_{sr} were each a constant ratio of σ^2_{add}, where η and λ were the constants. A range of combinations of η and λ were tested to find the combination of values leading to the maximum Log Likelihood. The significance of each ratio was then tested with a one-tailed LRT after fixing one of these ratios to zero and finding the value of the other ratio that produced the maximum log likelihood. Inter-site correlations for subrace and SCA effects (r_{sr} and r_{sca}) were forced to be 1 in these models. In model 4, the inter-site additive genetic correlations (r_{add}) were also forced to be 1. In model 5, r_{add} was forced to be one between sites from the same geographical region and to 0.7 between sites from different geographical regions (see Table 1), based on the patterns of inter-state correlations for diameter growth found by BORRALHO *et al.* (1995). Model 5 is analogous to the model used in TREEPLAN® for growth, except that subrace was treated as random. The TREEPLAN® model used for core density is analogous to Model 4. The Akaike Information Criterion (AIC, Akaike 1973) was used to compare models 4 and 5 with the other models, a larger AIC indicating better model fit to the data. The AIC was calculated as:

$$h_i^2 = \frac{\sigma^2_{add_i}}{\sigma^2_{add_i} + \sigma^2_{sca_i} + \sigma^2_{p_i} + \sigma^2_{e_i}}$$

$$AIC = 2 \times (LogL - \rho) \quad [3]$$

where LogL is the log likelihood value of the model and ρ is the number of parameters estimated.

Heritability and dominance ratio

Variance components, heritability and dominance ratios were estimated with model 5, unless the AIC value indicated that there was a substantially better model. The significance of variances for each site was tested with a one-tailed LRT test, with one degree of freedom, by separately fixing each site variance to zero. Constant ratios across sites of SCA or subrace variances to the additive variance were tested against zero, also with a one-tailed LRT test with one degree of freedom. The heritability (h_i^2) and dominance ratio (d_i^2 for each site *i* were calculated as

Table 3. Constraints applied to models for which the likelihood analysis could converge to allow the testing of variance homogeneity (Models 1 and 2) and estimate across site correlations (Model 3). Additionally, models 4 and 5 are given for comparison, and they refer to models where the SCA and subrace variances are in a constant ratio η or λ to the additive variance respectively.

Model	σ^2_e	σ^2_{add}	σ^2_{sca}	σ^2_{sr}	r_{add}	r_{sca}	r_{sr}
1	H	H	U	U	1	1	1
2	H	H	H	H	1	0	0
3	H	H	U	U	k_1	k_2	k_3
4	H	H	$\eta\sigma^2_{add}$	$\lambda\sigma^2_{add}$	1	1	1
5*	H	H	$\eta\sigma^2_{add}$	$\lambda\sigma^2_{add}$	0.7[a] and 1.0[b]	1	1

Note: H – heterogeneous variances across sites; U – homogeneous variances across sites; k_1, k_2, k_3 – uniform across-site correlations estimated for [a] between regions and [b] within regions. *Analogous to the model used in TREEPLAN® for growth.

$$h_i^2 = \frac{\sigma^2_{add_i}}{\sigma^2_{add_i} + \sigma^2_{sca_i} + \sigma^2_{p_i} + \sigma^2_{e_i}} \quad [4]$$

$$d_i^2 = \frac{4\sigma^2_{sca_i}}{\sigma^2_{add_i} + \sigma^2_{sca_i} + \sigma^2_{p_i} + \sigma^2_{e_i}} \quad [5]$$

The plot term was excluded from the denominator for basic density as only one tree was sampled per plot.

RESULTS

Tests of hypothesis

Tests for the hypothesis that variances were homogeneous across-sites are shown in Table 4. The additive variance was heterogeneous across sites for growth traits but not for core basic density. The SCA variance was heterogeneous for all traits, and the subrace variance was only heterogeneous for height. The error variance was heterogeneous across sites for all traits as assuming homogeneity led to models with the lowest AIC values for all traits examined (Table 4).

Table 4. Significance probability from two-tailed likelihood ratio tests applied to test variance homogeneity across sites. Variance estimates were tested one at a time by dropping or adding constraints for the parameter in question in model 1 for DBH and CBD, and in model 2 for height. The degrees of freedom (DF) used for significance testing are indicated for each trait.

Variance	DBH	Height	CBD
σ^2_{add}	<0.001	0.003	0.756
σ^2_{sca}	0.035	<0.001	0.017
σ^2_{sr}	0.170	<0.001	0.458
σ^2_{e}	<0.001	<0.001	0.008
DF	8	5	2

Common estimates for inter-site additive genetic correlations, obtained by using model 3 (Table 3) were high (0.71 for DBH, 0.72 for height and 1.07 for core basic density) and they were not significantly different from 1 (Table 5). Inter-site correlations of SCA and subrace effects for DBH and core basic density were also not significantly different from 1. However, in many cases, r_{sr} and r_{sca} exceeded the theoretical limit of 1 and were estimated with large standard error, which means that the data used poorly estimates these correlations. Nevertheless, inter-site correlations of SCA and subrace effects for height were significantly different from 1 but not from zero, suggesting that there are G×E for these effects in this case.

Model comparison

The AIC of model 4 was the same as that of model 5 for DBH and core basic density (Table 6). This suggests that additive genetic correlations for DBH and core basic density can be treated the same within and between regions. Despite highly significant heterogeneity in σ^2_{add} ($P < 0.001$) for DBH with only slight heterogeneity in σ^2_{sca} ($P < 0.05$) and none for σ^2_{sr} (Table 4), no significant change in the fit (as indicated by the AIC) was obtained by treating σ^2_{sr} and σ^2_{sca} homogeneous as in model 1, as opposed to a constant ratio of σ^2_{add} as in models 4 and 5 (Table 6). However, for height, allowing for heterogeneous variances across sites and non-additive inter-site correlations of 0 (model 2) led to a better model fit than all the other models tested on the basis of the AIC (Table 6). The zero across-site correlations for non-additive effects are consistent with the non-additive G×E detected for height (Table 5).

Genetic parameters

Diameter at breast height (DBH)

Genetic parameters for DBH estimated using model 5 are shown in Table 7. The additive variance for DBH was significant in 7 of the 9 sites, with h^2 ranging from 0.05 to 0.25 and averaging 0.12. The ratio of σ^2_{sca} to σ^2_{add} of 0.25 was highly significantly different from zero ($P<0.001$; Table 8), so the d^2 of 0.12 was the same as h^2. The ratio of σ^2_{sr} to σ^2_{add} of 0.50 was also significantly ($P<0.01$) different from zero (Table 8).

Estimates of σ^2_{add} from single-site and multi-site analyses were compared for DBH to exemplify the improvement in parameter estimation resulting from greater data availability due to the linkage from the same families as well as the common parents and relatives across sites. Multi-site analysis led to a lower estimated standard error of the additive variance estimates (Table 7). Significant additive genetic variance was found in 7 of 9 sites in the multi-site analysis but in only one site in the single-site analysis. Estimates of additive genetic variance

Table 5. Estimates of uniform inter-site correlations (standard error) from model 3 for subrace (r_{sr}), additive (r_{add}) and SCA (r_{sca}) effects, and significance probabilities of their deviation from zero and one, following two-tailed likelihood ratio tests.

Trait	Hypothesis test	r_{sr}	r_{add}	r_{sca}
DBH		1.02 (0.20)	0.71 (0.16)	2.23 (2.30)
	H_0: r = 1, H_1: r≠ 1	p = 0.371	p = 0.527	p = 1.000
	H_0: r = 0, H_1: r≠ 0	p = 0.655	p < 0.001	p = 0.237
Height		0.0 (0.16)	0.72 (0.14)	0.02 (0.11)
	H_0: r = 1, H_1: r≠ 1	p = 0.001	p = 0.393	p < 0.001
	H_0: r = 0, H_1: r≠ 0	p = 1.000	p = 0.003	p = 1.000
CBD		–0.16 (0.55)	1.07 (0.21)	1.06 (0.09)
	H_0: r = 1, H_1: r≠ 1	p = 0.209	p = 0.313	p = 1.000
	H_0: r = 0, H_1: r≠ 0	p = 1.000	p < 0.001	p = 0.424

Note: Genetic correlation estimates were unbounded, hence, two-tailed likelihood ratio tests were used.

Table 6. The change of log likelihood (ΔLogL) and Akaike Information Criterion (AIC) relative to model 1 and the number of parameters estimated (*r*) for the models detailed in Table 3 for DBH, height and core basic density.

Model	DBH			Height			Core basic density		
	ΔlogL	ρ	ΔAIC	ΔlogL	ρ	ΔAIC	ΔlogL	ρ	ΔAIC
1	0	20	0	0	14	0	0	8	0
2	9	36	–15	13	24	7	4	12	–1
3	2	23	–2	–1	17	–8	3	11	–1
4	0	20	0	–16	14	–31	0	8	1
5[a]	0	20	0	–15	14	–30	0	8	1

[a] Analogous to TREEPLAN®.

of DBH were obtained in trials STBGL102, STBGL107 and STBGL114 with the multi-site analysis while no additive variance was detected in these sites with the single-site analysis. This shows that multi-site analysis can improve estimates of variance components, compared to single-site analysis, although the additive variances in trials STBGL102 and STBGL107 were not significantly different from zero in the multi-site analysis.

Tree height

The genetic parameters for height are reported with model 5 (Table 9) for comparison with DBH, as well as for the best model for height (model 2; Table 10). With model 5 the additive variance for height was significantly different from zero on only 3 of the 6 sites with h^2 estimates ranging from 0 to 0.26 and averaging 0.11. The ratio of σ^2_{sca} to σ^2_{add} of 0.3 and the ratio of σ^2_{sr} to σ^2_{add} of 0.25 were significant (P<0.01; Table 8). With the best model (model 2), σ^2_{add} was significant on the same 3 sites, with h^2 ranging from 0.002 to 0.24 and also averaging 0.11 (Table 10). SCA variance was significantly different from zero in 2 of the 6 sites, with d^2 ranging from 0 to 0.39 and averaging 0.26. Subrace variance was only significantly different from zero in one site. The average dominance ratio was over double the average heritability when estimated using model 2, but only 1.2 times the additive when estimated as a constant ratio with model 5.

Core basic density

The additive variance of core basic density estimated with model 5 was significantly different from zero in all three sites examined with h^2 ranging from 0.30 to 0.55 and averaging 0.44 (Table 11). The ratios of $\sigma^2_{sca}/\sigma^2_{add}$ (0.08) and $\sigma^2_{sr}/\sigma^2_{add}$ (0.13) were not significantly different from zero (Table 8).

DISCUSSION

This analysis found that there were heterogeneous

Table 7. Variance component estimates and h^2 of DBH for each trial estimated with model 5 which assumed heterogeneous σ^2_{add} and σ^2_e, constant ratios of σ^2_{sca} and σ^2_{sr} to σ^2_{add} ($\eta = 0.25$, $\lambda = 0.5$) and inter-site correlations of 1 within regions and 0.7 between regions. The column effect was not fitted in the model as its variance was at the lower boundary of the parameter space in all trials.

Trial STBGL_	Multisite							Single-site
	$\sigma^2_b \pm$ se	$\sigma^2_r \pm$ se	$\sigma^2_p \pm$ se	$\sigma^2_{add} \pm$ se †	$\sigma^2_{sca} = \sigma^2_{add} \times \eta$	$\sigma^2_e \pm$ se	$h^2 \pm$ se	$\sigma^2_{add} \pm$ se
100	0	4 ± 10	14 ± 51	60 ± 33**	15	378 ± 62	0.13 ± 0.06	65 ± 81^{ns}
101	28 ± 27	0.5 ± 8	0	106 ± 50*	27	297 ± 49	0.25 ± 0.09	83 ± 70^{ns}
102	0	1.3 ± 4	21 ± 24	13 ± 10^{ns}	3	166 ± 27	0.07 ± 0.05	0
107	4 ± 6	37 ± 23	70 ± 24	7 ± 5^{ns}	2	252 ± 25	0.02 ± 0.02	0
108	0	29 ± 24	0	254 ± 61**	64	715 ± 65	0.25 ± 0.05	129 ± 132^{ns}
109	41 ± 32	13 ± 11	52 ± 25	21 ± 10**	5	262 ± 28	0.06 ± 0.03	27 ± 35^{ns}
114	6 ± 9	13 ± 13	0	16 ± 12*	4	312 ± 31	0.05 ± 0.03	0
115	49 ± 36	11 ± 8	20 ± 13	17 ± 7**	4	111 ± 15	0.11 ± 0.05	26 ± 18^{ns}
121	3 ± 2	0	6 ± 3	9 ± 3***	2	57 ± 4	0.12 ± 0.03	13 ± 6*
Average	15	13	20	56	14	283	0.12	38

† Significance testing was conducted by fixing additive variance of the site tested to zero, and fixing variances of SCA and subrace to the values expected under the constant ratios of additive variance estimated in the original analysis. A one-tailed likelihood ratio test was used.

Table 8. Constant ratios of σ^2_{sca} to σ^2_{add} and σ^2_{sr} to σ^2_{add} across sites that led to the highest log likelihood value in model 5 and significance test against a ratio of zero (one-tailed likelihood ratio test with 1 degree of freedom).

Trait	$\eta = \sigma^2_{sca}/\sigma^2_{add}$	$\lambda = \sigma^2_{sr}/\sigma^2_{add}$
DBH	0.25***	0.50**
Height	0.30**	0.25**
Core basic density	0.08^{ns}	0.13^{ns}

additive variances across sites for diameter at breast height and height, but not for core basic density. In addition, for all traits, the changes in AIC with models 4 and 5 were similar indicating that there is no difference between forcing the additive genetic inter-site correlation to be 1 (model 4), and forcing within region correlations to be 1 and between region correlations to be 0.7 (model 5). This suggests the regional structuring of the site-correlation is not relevant in this case and unnecessarily downgrades information from other regions. However, it should be noted that a recent study of large open-pollinated progeny trials suggests that stratification of sites on the basis of drought risk may be superior to the current regional stratification (COSTA E SILVA *et al.* 2006). Our results showed that model 5 was not a

Table 9. Variance component estimates and h^2 of height for each trial in the model 5 assuming heterogeneous σ^2_{add} and σ^2_e, constant ratios of σ^2_{sca} and σ^2_{sr} to σ^2_{add} ($\eta = 0.3$, $\lambda = 0.25$) and inter-site correlations of 1 within regions and 0.7 between regions.

Trial (STBGL_)	$\sigma^2_b \pm$ se	$\sigma^2_r \pm$ se	$\sigma^2_c \pm$ se	$\sigma^2_{add} \pm$ se †	$\sigma^2_{sca} = \sigma^2_{add} \times \eta$	$\sigma^2_e \pm$ se	$h^2 \pm$ se
102	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01ns	0.01	0.13 ± 0.05	0.13 ±0.07
107	0.18 ± 0.06	0.09 ± 0.11	0.01 ± 0.01	0.00 ± 0.001ns	0.00	0.38 ± 0.06	0.00 ± 0.001
108	0.06 ± 0.05	0.05 ± 0.03	0.00 ± 0.001	0.52 ± 0.13**	0.16	1.34 ± 0.08	0.26 ± 0.06
109	0.26 ± 0.23	0.08 ± 0.07	0.01 ±0.02	0.15 ± 0.07**	0.05	1.71 ± 0.18	0.08 ± 0.04
115	0.21 ± 0.16	0.02 ± 0.02	0.02 ± 0.02	0.06 ± 0.001***	0.02	0.49 ± 0.04	0.11 ± 0.05
126	0.29 ± 0.22	0.01 ± 0.01	0.01 ± 0.01	0.03 ± 0.01ns	0.01	0.39 ± 0.02	0.07 ± 0.02
Average	0.17	0.045	0.01	0.13	0.04	0.65	0.11

† Significance testing was conducted by fixing additive variance of the trial tested to zero, fixing variances of SCA and subrace to the values under the constant ratios. A one-tailed likelihood ratio test was used.

Table 10. Variance component estimates, h^2 and d^2 of height for each trial in the best model (model 2) assuming σ^2_{add}, σ^2_{sca}, σ^2_{sr} and σ^2_e are heterogeneous and r_{add}= 1, r_{sca}= r_{sr} =0.

Trial (STBGL_)	$\sigma^2_{sr} \pm$ se †	$\sigma^2_{add} \pm$ se †	$\sigma^2_{sca} \pm$ se †	$\sigma^2_e \pm$ se	$h^2 \pm$ se	$d^2 \pm$ se
102	0.01 ± 0.03^{ns}	0.02 ± 0.02^{ns}	0.01 ± 0.01^{ns}	0.14 ± 0.02	0.12 ± 0.13	0.24 ± 0.26
107	0.05 ± 0.06^{ns}	0.001 ± 0.01^{ns}	$0.06 \pm 0.03^{***}$	0.55 ± 0.04	0.002 ± 0.001	0.39 ± 0.16
108	$0.90 \pm 0.56^{**}$	$0.29 \pm 0.18^{**}$	0.09 ± 0.07^{ns}	1.28 ± 0.13	0.17 ± 0.10	0.22 ± 0.18
109	0.07 ± 0.15^{ns}	$0.23 \pm 0.09^{**}$	0.16 ± 0.09^{ns}	1.32 ± 0.17	0.13 ± 0.10	0.37 ± 0.19
115	0.00 ± 0.00^{ns}	$0.14 \pm 0.06^{***}$	0.0004 ± 0.01^{ns}	0.45 ± 0.06	0.24 ± 0.10	0.003 ± 0.01
126	0.01 ± 0.01^{ns}	0.005 ± 0.01^{ns}	$0.03 \pm 0.005^{***}$	0.30 ± 0.02	0.01 ± 0.02	0.36 ± 0.11
Average	0.17	0.11	0.06	0.67	0.11	0.26

† Significance testing was conducted by fixing the variance component of the trial tested to zero and comparing the change in the Log Likelihood value. A one-tailed likelihood ratio test was used.

Table 11. Variance component estimates and h^2 of core basic density for each trial from model 5 which assumed heterogeneous σ^2_{add} and σ^2_e, constant ratios of σ^2_{sca} and σ^2_{sr} to σ^2_{add} (η = 0.08, λ = 1.0) and inter-site correlations of 1 within regions and 0.7 between regions. The column effect was not fitted in the model as its variance was at the lower boundary of the parameter space at all sites. The plot effect was not fitted as only one tree per plot was measured.

Trial (STBGL_)	$\sigma^2_b \pm$ se	$\sigma^2_r \pm$ se	$\sigma^2_{add} \pm$ se	$\sigma^2_{sca} = \sigma^2_{add} \times \eta$	$\sigma^2_e \pm$ se	$h^2 \pm$ se
100	0 ± 0	0 ± 0	$388 \pm 138^{***}$	31	292 ± 93	0.55 ± 0.11
101	72 ± 60	0 ± 0	$344 \pm 118^{***}$	28	347 ± 83	0.48 ± 0.07
102	0 ± 0	167 ± 145	$502 \pm 226^{***}$	40	1108 ± 213	0.30 ± 0.09
Average	24	56	411	33	582	0.44

good model for estimating variance components and genetic parameters for early age height. In the hypothesis tests, SCA variances and subrace variances were heterogeneous across sites and inter-site correlations for SCA and subrace effects were not different from zero. Model 5 treats the SCA and subrace variances as constant ratios of the additive genetic variance, which means that it assumes homogeneity of these two variance components across sites. Moreover, it assumes inter-site correlations of unity within regions for SCA and subrace effects. Model 5 therefore does not match the heterogeneity and inter-site correlations in the real height data. This result suggests that height breeding values calculated by using variance components obtained in a model like model 5 are not precise and that a model similar to model 2 should be used.

Our study indicates that within the STBA second generation breeding population there are not only genetic differences between subraces for growth (as suggested by significant σ^2_{sr} / σ^2_{add} for DBH and height), but also small but significant additive genetic variation within sub-races available for selection. The latter variation is reflected in our average estimates of individual-site, narrow-sense heritabilities for growth traits (DBH h^2 = 0.12; height h^2 = 0.11). However, our CP mean heritability estimates are approximately half the average of the many values reported from open-pollinated progeny trials of this species (DBH h^2 = 0.21; height h^2 = 0.21 – LOPEZ *et al.*, 2002). Most of these OP estimates are derived from base population trials. While this discrepancy could represent erosion of additive genetic variation for growth in the second generation breeding population following selection (BULMER 1971; GEA *et al.* 1997), it is more likely that it represents inaccuracy in estimating additive genetic variance and initial breeding values using open-pollinated progenies (POTTS *et al.* 1995; HODGE *et al.* 1996). Indeed, direct comparison of OP and CP heritabilities derived from *E. globulus* families of common parentage indicated that OP heritabilities for growth are virtually double the estimates obtained from full-sib families (HODGE *et al.* 1996; VOLKER, 2002). This is consistent with the general comparison, and our CP narrow-sense heritability estimates for DBH are virtually identical to those reported by other authors using different populations of *E. globulus* at the single-site (VOLKER 2002 – h^2 = 0.12; COSTA E SILVA *et al.* 2004 – h^2 = 0.08) and across-site (VOLKER 2002 – h^2 = 0.06 to 0.10; COSTA E SILVA *et al.* 2004 – h^2 = 0.10) levels.

This consistency suggests that, as a rule of thumb, about 10% of the phenotypic variation for growth (DBH and height) within sub-races of *E. globulus* is likely to be due to additive genetic effects.

The exploitation of heterosis is a common objective of plant breeding programs (MAYO 1987; BROWN *et al.* 1990; FALCONER & MACKAY 1996). Specific combining ability (SCA) has been used as a measure of heterosis (KRALJEVIC-BALALIC *et al.* 1976; OETTLER *et al.*, 2003). SCA is of interest as superior performance in the combination of specific female and male parents can be used in deployment. Identification of elite full-sib families and use of these families in commercial deployment has been applied as a strategy for exploiting heterotic (or SCA) effects and avoiding inbreeding depression in plant breeding (KNIGHT 1979; HECKER & HELMERICK 1985). Significant dominance (or SCA) variation has been reported for growth traits in various populations of *E. globulus*. Studies of two-year stem volume in an inter- and intra-race factorial of *E. globulus* grown across different sites in Australia have reported significant across-site SCA variance (VAILLANCOURT *et al.* 1995 – $d^2 = 0.14$, $h^2 = 0.07$; HODGE *et al.* 1996 – inter-race $d^2 = 0.15$, $h^2 = 0.02$, intra-race $d^2 = 0.05$, $h^2 = 0.08$). However, no significant SCA variance for 6-year DBH was found in an across-site analysis of the same trials (VOLKER, 2002), nor in an analysis of 4-year DBH of 6 cloned CP progeny trials of *E. globulus* in Portugal (COSTA E SILVA *et al.*, 2004). Nevertheless, in the former case, significant individual site estimates of SCA variation were obtained (average across 5 sites $d^2 = 0.14$, $h^2 = 0.12$ – VOLKER, 2002), but these effects were not stable across sites.

The significant $\sigma^2_{sca}/\sigma^2_{add}$ ratio in the present study suggests that there is significant dominance variance in the STBA breeding population for growth. The dominance variation is of similar importance to the additive genetic variation (Table 8), but consistent with the results of VOLKER (2002), there is the suggestion that the dominance variation may be less stable in its expression across sites than the additive genetic variation, at least for early age height (Table 5). If this instability proves widespread, the capturing of dominance effects for growth would require targeting specific sites. At the individual site level, our estimates of the dominance ratio for growth (DBH $d^2 = 0.12$ as derived from the ratio of SCA to additive variance, height $d^2 = 0.26$) are at the higher end of the estimates reported in the literature. It should be noted that about 95% of the families in our population were derived from crossing parents from different subraces, and there is little power to separate SCA effects into inter- and intra-subrace components. Some previous studies have separately estimated SCA for inter- and intra-subrace crosses (VAILLANCOURT *et al.* 1995; HODGE *et al.* 1996; VOLKER, 2002), but families from the same landrace were used by COSTA E SILVA *et al.* (2004). HODGE *et al.* (1996) did report higher dominance effects within inter-subrace crosses than within intra-subraces crosses which, if repeatable, could explain the significant dominance variation detected in the present population. However, it may also be due to our dominance effects including interactive effects derived from crossing between different combinations of subraces as well as inter-race crossing *per se*. Several lines of evidence suggest that at least the later effect is important. Firstly, progeny derived from crossing between proximal trees in native forests exhibit reduced growth compared to those from geographically distant crosses (HARDNER *et al.* 1998). Secondly, the growth of inter-subrace hybrids has been reported to significantly exceed the mid-parent value estimated from intra-subrace crosses in two independent studies of *E. globulus* (VOLKER 2002; LOPEZ *et al.* 2003). While we do not as yet have a measure of how important such heterotic effects are relative to the additive genetic differences between subraces, such inter-subrace F_1 heterosis is to a large extent already captured in the mean performance of this breeding population but we can not estimates its importance as few intra-race crosses were undertaken. However, as only the additive subrace effects are accounted for in our models, our estimates of SCA include differences in the interactive effects between parents from different sub-races. Such effects are unlikely to be large in this breeding population as our estimates of dominance for DBH are comparable to the intra-race average reported by VOLKER (2002).

The importance of non-additive effects in the control of growth in *E. globulus* may be underestimated in all studies to date due to their failure to account for mortality at earlier ages in the life cycle. While mortality was too low in our trials to warrant formal quantitative analysis, it was evident that high mortality was restricted to specific families and mortality itself is likely to have a large non-additive genetic component (LI, unpubl. data). Mortality in *E. globulus* is strongly size-dependent (CHAMBERS & BORRALHO 1996) and future analyses of non-additive effects for later age growth may be improved by combining survival and growth information. This will be important if age trends in the expression of non-additive genetic effects (*e.g.* BALOCCHI *et al.* 1993) are to be separated from mortality effects.

There has been no study investigating genetic parameters of core basic density in CP crosses in *E. globulus.* Pilodyn penetration has been used to measure wood density in many studies. In a study of

OP families comparing core basic density and pilodyn penetration (MUNERI & RAYMOND 1999), the h^2 of density assessed on cores ($h^2 = 0.63 \pm 0.11$) was 3.3 times that of Pilodyn penetration ($h^2 = 0.19$). In OP trials in general, the reported heritabilities of core basic density ranged from 0.50 to 1.00 and averaged 0.68 (BORRALHO *et al.* 1992; BORRALHO *et al.* 1993; MUNERI & RAYMOND 1999; LOPEZ *et al.*, 2002) while that of pilodyn ranged from 0.13 to 0.57 and averaged 0.33 (DEAN *et al.* 1990; MACDONALD *et al.* 1997; MUNERI & RAYMOND 1999; LOPEZ *et al.* 2002). It seems that heritability of pilodyn penetration reported by MUNERI and RAYMOND (1999) is atypically low and the h^2 of core basic density is probably more like twice that of Pilodyn penetration. Using this ratio, our average h^2 of core basic density (0.44) would equate to a h^2 for Pilodyn penetration of approximately 0.22. This is similar to the h^2 of Pilodyn penetration reported by VOLKER (2002, $h^2 = 0.25 \pm 0.07$) and COSTA E SILVA *et al.* (2004, $h^2 = 0.17 \pm 0.07$) in the only CP trials in which wood density has been reported to date for *E. globulus*.

Significant variation of growth and wood density between the subraces has been reported in a number of studies (KUBE *et al.* 1993; ALMEIDA *et al.* 1995; KUBE *et al.* 1995; DUTKOWSKI & POTTS 1999; LOPEZ *et al.* 2002; MIRANDA & PEREIRA 2002). In the current study significant subrace variance has been found for growth but not for wood density. All of the parents of individuals in the trials have been selected on a combined index of diameter at breast height and wood density (Pilodyn penetration). Because growth traits are less heritable and easily affected by inbreeding depression in an open-pollinated population (HODGE *et al.* 1996), selection on growth is probably not as efficient as that on wood density. Selection in the first generation may have lead to a decrease in the differences in wood density between subraces in the second generation due to elimination of many of the low density races as well as selection of the denser individuals within the lower density subraces where they are represented. Analysis of all data in the first and second generations together would be an approach to account for the impacts of selection in the first generation.

CONCLUSIONS

This study investigated the genetic architecture of diameter at breast height, height and core basic density in a *E. globulus* full-sib breeding population at multiple sites. As the study population involved a number of small trials, exploiting the pedigree connectivity between trials allowed improved accuracy of single-site parameter estimates and breeding value predictions. However, failure of the more complete multivariate models to converge made model fitting problematic, and the challenge was to find reduced models which best fitted the multivariate data. It was found that the model assuming heterogeneous additive and residual variances across sites and constant ratios of dominance and subrace variances to additive variance was an adequate model to estimate variance components and genetic parameters for diameter at breast height and core basic density but not for tree height. The fitting of the reduced multivariate models allowed significant additive genetic variance to be detected for the three traits examined. Significant SCA variance was only found for diameter at breast height and tree height, and subrace variance was highly significant only for tree diameter.

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