

Genetic parameters of intra- and inter-specific hybrids of *Eucalyptus globulus* and *E. nitens*

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Abstract Intra-specific hybrids within *Eucalyptus nitens* and *E. globulus* were compared directly with inter-specific *E. nitens* × *globulus* using common parents. Diameter (age 2, 4, 6, 10 years) and Pilodyn (age 6 years) were used as indirect measures of growth and wood density, respectively. Genetic parameters were estimated for all cross types and traits. A direct comparison of the general combining ability with the general hybridising ability was made. Heterosis was estimated for intra- and inter-specific hybrids. The intra-specific hybrids in both species exhibit intermediate heritabilities and levels of additive genetic variance. The inter-specific F1 *E. nitens* × *globulus* exhibited high incidence of abnormalities at young ages and high levels of later age mortality. The mean performance of surviving inter-specific F1 hybrids was generally intermediate for all traits, to varying degrees, between the parental intra-specific crosses, and there is little evidence for significant heterosis. Different provenances of *E. globulus* may exhibit

different responses to hybridisation. In this case, the inter-specific F1 hybrids, using Taranna *E. globulus*, appear to perform worse on average than those using King Island provenance for growth traits. There is evidence that specific hybrid families are produced that outperform most of the pure species families for one or other of the traits examined; however, there is no reliable quantitative genetic method of predicting which parents should be used.

Keywords Genetic parameters · Eucalypts · F₁ hybrids

Introduction

Eucalypts are the most widely planted hardwood genus in the world (Eldridge et al. 1993). Their rapid expansion into new environments, combined with their ability for inter-specific hybridisation (Griffin et al. 1988; Potts and Wiltshire 1997), has led to the development of many commercial hybrids. Many early selections were often from sporadic hybrids, occurring in seed collections derived from native stands or exotic species trials (see Eldridge et al. 1993). There is now increasing interest in specifically breeding hybrids (Martin 1989; Nikles 1992; Nikles and Griffin 1992; Shelbourne 2000; Vigneron 1991; Vigneron 1995; Vigneron and Bouvet 2000), particularly F₁'s, although the rationale and the genetics of hybrid populations are poorly understood.

There are several reports of superiority of inter-specific F₁ hybrids of *Eucalyptus* mostly from India (Paramathma et al. 1997; Venkatesh and Sharma 1976, 1977a,b, 1979; Venkatesh and Thapliyal 1993), Brazil (Bison et al. 2006; Blake and Bevilacqua 1995; Campinhos and Ikemori 1977, 1989; Kageyama and Kikuti 1989; Wright 1997), Congo (Vigneron and Bouvet 2000; Wright 1997) and South

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Africa (Darrow 1995; Wright 1997). However, intra-specific controls are often absent or of poor accuracy (i.e. open-pollinated or unrelated to the F_1 's). This lack of adequate controls makes it difficult to assess whether differences between hybrid and pure species is simply a result of removing inbreeding effects. The question remains whether comparable genetic parameters and gains could have been achieved simply through removing inbreeding effects through wide intra-specific outcrossing and selection within species (Eldridge et al. 1993).

Such fundamental information is necessary if F_1 hybrid production is to proceed beyond haphazard crossing so that rigorous strategies can be developed for breeding improved hybrids. A key issue is whether reciprocal or simple recurrent selection schemes are most appropriate for breeding superior F_1 hybrids (Baradat et al. 1994; Bison et al. 2006; Bouvet and Vigneron 1996; Dungey et al. 2000b; Kerr et al. 2000; Nikles 1992; Nikles and Griffin 1992; Shelbourne 2000).

Differentiation of these breeding strategies depends on whether the best pure species selections also produce the best hybrid combinations or whether F_1 hybrid performance is unrelated to the general combining ability (GCA) of the parent in pure species combination. Nikles and Newton (1991) raise the concept of general hybridising ability (GHA) as a measure of the 'additive' performance of a trait in hybrid combination. As to which strategy is most suitable will, to a large extent, depend on the correlation between GCA and GHA estimates (tropical pine hybrids—Nikles and Newton 1991; Powell and Nikles 1996) and, more precisely, the genetic correlation between pure species and hybrid performance (Dieters and Dungey 2000; Newman and Reverter 2000) and their relative variability in the pure species and hybrid populations, respectively. Similarly, predictability of which parental combination will produce the best F_1 hybrids for deployment, whether by seed (full-sib families) or clonal propagation, will dependent upon the magnitude of specific combining effects in hybrid crosses, termed specific hybridising ability (SHA; Nikles and Newton 1991).

Eucalyptus globulus is a forest tree native to southeastern Australia (Dutkowski and Potts 1999; Jordan et al. 1993). It is the premier eucalypt for the Kraft pulping process because of its high pulp yield and wood density (Greaves and Borralho 1996; Greaves et al. 1997), so it is widely planted in temperate regions of the world (e.g. Australia, California, Chile, China, Italy, Portugal and Spain) for pulpwood production (Borralho 1992; Eldridge et al. 1993; Tibbits et al. 1997), but plantations are confined to relatively frost free areas (Tibbits et al. 1991a, 1997). The more frost tolerant species, *Eucalyptus nitens*, is often used as a replacement for *E. globulus* in plantations on colder sites (Tibbits et al. 1989, 1997; Tibbits and Hodge 2001, 1991a).

While there is certainly the opportunity to improve density, growth and frost resistance by exploiting the genetic variation within both *E. globulus* (Dutkowski and Potts 1999) and *E. nitens* (Tibbits and Hodge 1998), there is considerable interest in developing hybrids between these two species (Espejo et al. 1995; Rojas Vergara et al. 2001; Tibbits et al. 1997; Volker 1995). Indeed, when a breeding or deployment objective of improved growth and increased density is considered, coupled with the opportunity to increase frost resistance, the hybrid of *E. nitens* and *E. globulus* has been proposed as an ideal combination.

This paper compares the performance and genetic parameters of inter-specific F_1 hybrids between *E. nitens* and *E. globulus* ssp. *globulus* and intra-specific crosses grown on the same site for growth at ages 2, 3, 4, 6 and 10 years and wood density, at 6 years of age at a single site. The crossing design is unique in studies of eucalypt hybrids to date, due to (1) the relatively large number of parents involved, (2) the maintenance of common parentage in pure species and hybrid crosses and (3) the generation of both inter-provenance and inter-specific hybrids. This design allowed the comparison of inter-specific F_1 hybrid performance without appreciable inbreeding in the pure species controls, estimates of additive and non-additive genetic variance for intra-provenance, inter-provenance and inter-specific crosses and a direct comparison of parental performance in hybrid and pure species combination. The present study extends the studies of the genetics of frost (Volker et al. 1994) and disease resistance (Dungey et al. 1997) in an inter-specific F_1 hybrid population of *E. nitens* \times *globulus*.

Materials and methods

Mating designs

A controlled crossing program was undertaken to generate intra- and inter-specific crosses of *E. globulus* and *E. nitens* with common parentage (Table 1). A virtually complete factorial crossing design was used for *E. globulus*. About 26 unselected male parents from native stands at Taranna (16 parents, T1 to T16) and King Island (10 parents, K17 to K26; see Volker and Orme 1988) were mated with seven selected female parents derived from the same provenances, 3 from King Island (Ka to Kc) and 4 from Taranna (Te to Th). The control-pollinated *E. nitens* \times *globulus* F_1 hybrids were derived from an incomplete factorial mating design using 14 of the 26 *E. globulus* male parents and 7 of 11 *E. nitens* parents (Ni to Ns). The control-pollinated *E. nitens* plants were derived from an almost complete half diallel mating of ten first generation parents from provenance, Toorongo (Victoria, Australia; see Pederick 1979).

Table 1 The number of progeny from each family planted at the West Ridgley trial for *E. globulus* intra- and interprovenance, *E. nitens* × *globulus* F₁ hybrids (both in factorial mating design) and *E. nitens* (incomplete half diallel mating design)

<i>E. globulus</i> male parents		T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	K17	K18	K19	K20	K21	K22	K23	K24	K25	K26
<i>E. globulus</i> female parents	K a	25	20	24	18	20	23	25	16	20	22	32	20	23		24	20	20	22	20	19	20	20	25	27	20	20
	K b	35	20	45	28	18	15	20	20	19	20	17	19	19	20	28	33	14	21	20	20	20	17	25	13	20	20
	K c	20	13			20	12	13	20	12	24	11	22	20	20	14	19	21	20	20	20	20	20	21	20	23	20
	T e	18	19	10		20	20	13	20	20	20	20	20	15	20	20	20	18		16							
	T f	23	20	20	20	20	20	20	23	20	20	20	20	22	20	14	20	31			23	20	20	20	19	28	15
	T g	18	20	20	15	20	20	20	20	20	20	25	19	20	20	20	20	25	20	20	20	28					
<i>E. nitens</i> female parents	T h	29	20	17		20		20	20	20	20	20	20	14	22		20	20	20	20	20	20	20	20	20	20	20
	N i																										
	N j																										
	N k					7	17			19	6	7					9				12	8				11	17
	N l				20	20					13										17	13				22	18
	N m	16			21	17				15	20				8						12				17	11	24
	N n				21	23					11	14	22		18					7					16	19	11
	N o				20	5				15	18	9			23					10					20	19	13
	N p	20					13																			20	20
	N s																										20
																											20

T Taranna *E. globulus*, K King Island *E. globulus*, N Toorong *E. nitens*

Field trial location and design

In July 1990, a trial was established on an ex-pasture site at West Ridgley, Tasmania (latitude, 41°09'N; longitude, 145°46'E; altitude, 185 m). Soil and climatic details are given in Dungey et al. (1997). The trial was established using a resolvable incomplete block design, otherwise known as an alpha design (Paterson and Williams 1976). There were 20 plots per incomplete block comprising 14 *E. globulus*, 3 hybrid and 3 *E. nitens* plots. Within each incomplete block, the *E. globulus*, *E. nitens* × *globulus* and *E. nitens* were planted in separate sub-blocks to minimise competitive effects between cross types. There were 15 incomplete blocks per replicate and 4 replicates in the trial. Trees from each family were planted in five tree line-plots and spaced at 3 × 3 m.

Measurement

Trials were measured at 2, 3, 4, 6 and 10 years from planting in the winter of each year. The diameter at breast height (1.3 m above ground level) over bark (DBHOB, mm) was measured, described as D2, D3, D4, D6 and D10. An indirect measure of density (Greaves et al. 1996; Raymond et al. 1998) was obtained using Pilodyn assessment followed the method described in Raymond and MacDonald (1998). At age 6 years, the first three healthy trees in each plot were assessed for Pilodyn penetration, described as P6.

Analysis

Analysis of the data was carried out using all surviving trees at each measurement, even those trees that could be described as deformed, non-vigorous individuals, dead trees were treated as missing values in the analysis. Age 10 data was included in the analysis, as it is important to demonstrate, in trials such as this, that results can be biased by mortality.

The data were analysed using univariate and multivariate individual tree mixed models with ASREML (Gilmour et al. 1999) as appropriate. ASREML fits the general mixed model

$$y = X\beta + Z\mu + \varepsilon \quad (1)$$

where y is a vector of observations, X is the design matrix for fixed effects β , Z is the design matrix for random effects $\mu \sim (0, \sigma^2 G)$ and $\varepsilon (0, \sigma^2 R)$ are residuals. ASREML has the ability to utilise multi-trait information in a genetic analysis with a relationship matrix (A) in the definition of G . A matrix of relationships (a pedigree) for each tree was used to identify the additive genetic effects (Gilmour et al. 1999). The model used to estimate cross type effects and levels (and significance) of mid-parent heterosis included replicate and cross type (TT, KK, TK and KT, NT, NK and NN; see Table 2) as fixed effects. The inter-provenance crosses TK and KT were treated as a single cross type. The random effects were the additive genetic effects of individuals and their parents (female and male), the female by male interaction effects within cross types, the incomplete block within replicate and the plot effects.

Pooled genetic parameters for *E. globulus* overall were estimated by fitting the same model but excluding crosses involving *E. nitens*. Parameters within only the inter-specific F_1 hybrid crosses were estimated with the same model with two levels of cross type (NT and NK). The cross type effect was excluded from the model for estimating genetic parameters separately for *E. nitens* and the three *E. globulus* cross types (TT, KK, pooled TK and KT). The female by male interaction estimated either SCA in pure species crosses or SHA in F_1 hybrids. Narrow sense heritability (h^2) was calculated as:

$$h^2 = \frac{\sigma_{\text{add}}^2}{\sigma_{\text{add}}^2 + \sigma_{\text{SCA}}^2 + \sigma_{\text{plot}}^2 + \sigma_{\text{res}}^2} \quad (2)$$

where σ_{add}^2 , σ_{SCA}^2 , σ_{plot}^2 and σ_{res}^2 are the additive, SCA (or SHA in the case of the F_1 hybrids), plot and residual

Table 2 Cross type least squares means for DBHOB at age 2, 3, 4, 6 and 10 years (D2, D3, D4, D6 and D10) and Pilodyn penetration at age 6 years (P6) at the West Ridgley site

Species	Cross type	Trait					
		D2	D3	D4	D6	D10	P6
<i>E. globulus</i> intra-provenance	TT	68.3 (2.0)	110.6 (3.0)	129.2 (3.5)	161.4 (4.4)	192.8 (5.8)	12.8 (0.2)
	KK	73.7 (1.8)	117.7 (2.4)	140.6 (3.1)	181.2 (4.6)	226.9 (7.1)	13.9 (0.2)
<i>E. globulus</i> inter-provenance	KT, TK	71.9 (1.7)	115.0 (2.6)	136.6 (3.0)	176.1 (3.8)	221.2 (4.9)	13.4 (0.2)
<i>E. globulus</i> (combined)	TT, KK, KT, TK	70.9 (1.7)	114.0 (2.5)	134.7 (3.1)	171.4 (4.1)	211.2 (5.3)	13.3 (0.2)
<i>E. nitens</i> × <i>globulus</i> F_1 hybrid	NT	62.4 (1.9)	96.2 (3.0)	116.5 (3.4)	165.2 (4.3)	223.4 (5.8)	13.5 (0.2)
	NK	75.4 (2.7)	118.4 (4.2)	146.3 (4.7)	193.4 (5.8)	239.8 (7.1)	13.9 (0.2)
<i>E. nitens</i> × <i>globulus</i> (combined)	NT, NK	66.1 (1.8)	102.5 (2.9)	124.9 (3.4)	174.1 (4.3)	230.2 (5.7)	13.6 (0.2)
<i>E. nitens</i>	NN	77.2 (2.3)	126.4 (3.5)	151.7 (4.0)	190.1 (5.1)	225.3 (6.5)	13.7 (0.2)

Units are in millimetres for all traits, standard errors are shown in brackets. Cross types are *E. globulus* intra- and inter-provenance crosses, *E. globulus* CP crosses combined, *E. nitens* × *globulus* F_1 hybrid (split by provenance of *E. globulus* male parent and combined) and *E. nitens*

variances, respectively. An estimate of relative significance of dominance (assumes no higher order genetic interactions such as epistasis) was calculated as

$$d^2 = \frac{4\sigma_{SCA}^2}{\sigma_{add}^2 + \sigma_{SCA}^2 + \sigma_{plot}^2 + \sigma_{res}^2} \quad (3)$$

The denominator in Eqs. 2 and 3 is the phenotypic variance (σ_p^2).

Coefficients of variation such as coefficient of additive variation (CV_A) and coefficient of phenotypic variation (CV_P) were calculated using the appropriate variance component and least square means as:

$$CV_x = \left(\sqrt{\sigma_x^2} / \mu_x \right) \quad (4)$$

where CV_x is coefficient of variation of parameter x expressed as a percentage, σ_x^2 is the variance component and μ_x is the least squares mean.

F_1 hybrid heterosis was calculated as the difference between hybrid mean performance and the mean of the parental lines, i.e. mid-parent heterosis (Mayo 1987).

$$H(1,2) = F_1 - \left(\frac{(P_1 + P_2)}{2} \right) \quad (5)$$

where $H_{(1,2)}$ is the estimate of heterosis for the hybrid between species or provenances 1 and 2, F_1 is the mean for the trait in the F_1 hybrid (within species or between species) and P_1 and P_2 are the trait means for each trait in the parental species or provenances. This value was also expressed as a percentage of the mid-parent value. In this case, heterosis was calculated for intra-specific F_1 hybrids in *E. globulus* (i.e. crosses between Taranna and King Island provenance with KT and TK treated as one cross type) and for inter-specific F_1 hybrids (*E. nitens* \times *E. globulus*) where the provenance of the *E. globulus* parents was differentiated into Taranna (NT) and King Island (NK). The tests of significance of the deviation of the F_1 from the mid-parent value were undertaken using a family model (replicate, incomplete block within replicate, male, female, male by female interaction as random terms) with the contrast option in PROC MIXED of SAS Version 8.

Genetic correlations and associated standard errors between traits within cross types were estimated using bivariate analyses with ASREML. The genetic correlations between the performance of parents in pure breed and hybrid combination were determined also using ASREML as follows. In the analyses, a trait measured in a different cross type was treated as different trait (i.e. D2 for TT was treated as a separate trait to D2 for TK, etc.). This approach was adopted for both intra- (TK and KT) and inter-specific hybrids (NT and NK) and was done for all the growth and Pilodyn measurements. The genetic correlation between

pure species and hybrid performance is a direct estimate of the correlation of GCA and GHA described earlier. This genetic correlation is estimated with pedigree linkages using either the common male parents for the inter-specific hybrid or common male and female parents for the intra-specific hybrids. The analyses were undertaken in two stages. First, within *E. globulus*, using the inter-provenance hybrids (TK and KT treated as one cross type) and intra-provenance crosses (TT and KK) as separate cross types and therefore, separate traits in bivariate individual tree mixed model analysis, excluding plot and SCA effects. Second, within *E. globulus*, cross-types were treated as fixed effects to pool the *E. globulus* data into a single trait, with the multi-variate individual tree model analysis including *E. nitens* and *E. nitens* \times *E. globulus* (NT and NK treated as separate cross-types) as separate traits and excluding plot and SCA effects from the model. In this case, genetic correlation refers to the correlation of genetic effects within cross types.

Results

Means at the cross type level

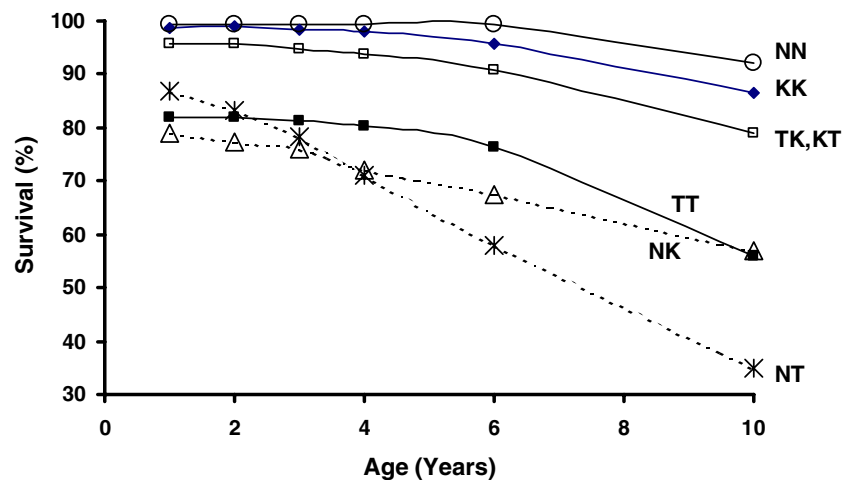
The growth (Table 2) and survival (Fig. 1) of *E. nitens* was better than *E. globulus* at this site, with its superiority increasing with age (Fig. 1, Table 2). Within *E. globulus*, KK grew better (Table 1) and had better survival (Fig. 1) than TT at all ages. Survival of the *E. globulus* inter-provenance hybrids (TK, KT) was effectively intermediated between KK and TT (Fig. 1). Survival of the inter-specific hybrids (NT, NK) was markedly less than any of the *E. globulus* or *E. nitens* pure species crosses (TT, KK, KT, TK and NN) by age 6 years (Fig. 1). Cross types involving Taranna parents (TT, NT, TK and KT) had lower survival (Fig. 1) and reduced vigour (Table 2) at all ages compared with KK and NN, and the survival of TT crosses by age 10 was as low as the NK inter-specific hybrids (Fig. 1).

At the family level, survival was highly variable at age 6 years, particularly in the F_1 hybrids where families ranged from 0 to 100% (data not presented). This was mainly due to specific males, which consistently produced inviable families in hybrid combination. The *E. nitens* female parents appeared to be more consistent in their production of viable hybrid progeny.

Heterosis

TK (and KT) exhibited reduced mid-parent heterosis for growth (2 to 3%), which increased with age to be significant ($P < 0.05$) by age 4 years (Table 3); however, the mean growth performance never exceeded the mean of

Fig. 1 Survival of cross types (*E. globulus* intra-provenance (TT, KK), *E. globulus* inter-provenance (TK, KT), *E. nitens* × *globulus* (NT, NK) and *E. nitens* (NN)) expressed as percentage of number of trees planted in 1990



the better intra-provenance cross, KK (Table 2). The poorer growth performance of TT compared with KK is also reflected in the growth performance of NT compared with NK. NT showed significant negative mid-parent heterosis for D2, D3, D4 and D6 (Table 3). However, at age 10 years, after significant mortality among slower growing individuals (Fig. 1), the mean growth of survivors in this cross type was not significantly different from the better performing cross type NN (Table 2). In contrast, heterosis for growth of NK was not significantly different from the mid-parent value and ranged from 0 to 6% across ages (Table 3). It should be noted that the mean diameter of the surviving F₁ hybrids (NT and NK) will be biased upward through reduced competition arising from the high mortality in the hybrid sub-blocks. This effect will be accentuated by the increased mortality between age 6 and 10 years (Fig. 1), which would result in relatively higher mean growth performance of survivors (Table 2), especially among poorer surviving cross types. This would be due to reduced competition and increased mortality of slower growing trees.

There were large differences in P6 between the two *E. globulus* provenances, with King Island provenance having greater Pilodyn penetration, hence lower density, than the Taranna provenance (Table 2). The mean P6 in *E. nitens* (NN) was comparable to the King Island provenance (KK) (Table 2). In the inter-provenance (TK and KT) and inter-specific F₁ hybrid crosses involving Taranna *E. globulus* (NT), the mean Pilodyn penetration was intermediate between the means of the parental populations (Table 2) and did not differ significantly from the mid-parent value (Table 4). In the inter-specific F₁ hybrid crosses involving King Island *E. globulus* (NK), the mean was slightly below the less dense King Island *E. globulus* (Table 2) but was not significantly different from either parent or the mid-parent value (Table 3).

Variances

The phenotypic coefficients of variation (CV_P) for growth traits were similar for *E. nitens* and *E. globulus* across all ages, although in *E. nitens* CV_P tends to increase with age,

Table 3 Mid-parent heterosis for intra-specific hybrid (H_{TK}) and inter-specific hybrids (H_{NT} and H_{NK}), expressed in mm and percent of mean diameter of the mid parent (%).

Hybrid type	Trait					
	D2	D3	D4	D6	D10	P6
Intra-specific						
H _{TK}	0.9(1%) ^{ns}	0.8(1%) ^{ns}	1.7(1%)*	4.8(3%)*	11.3(5%)**	0(0%) ^{ns}
Inter-specific						
H _{NT}	-10.4(-14%)***	-22.3(-19%)***	-24.0(-17%)***	-10.6(-6%)***	14.3(7%)*	0.2(2%) ^{ns}
H _{NK}	0(0%) ^{ns}	-3.7(-3%) ^{ns}	0.1(1%) ^{ns}	7.7(4%) ^{ns}	13.7(6%) ^{ns}	0.1(2%) ^{ns}

^{ns} Not significant

**P*≤0.05, significance of deviation of hybrid mean from mid-parent value

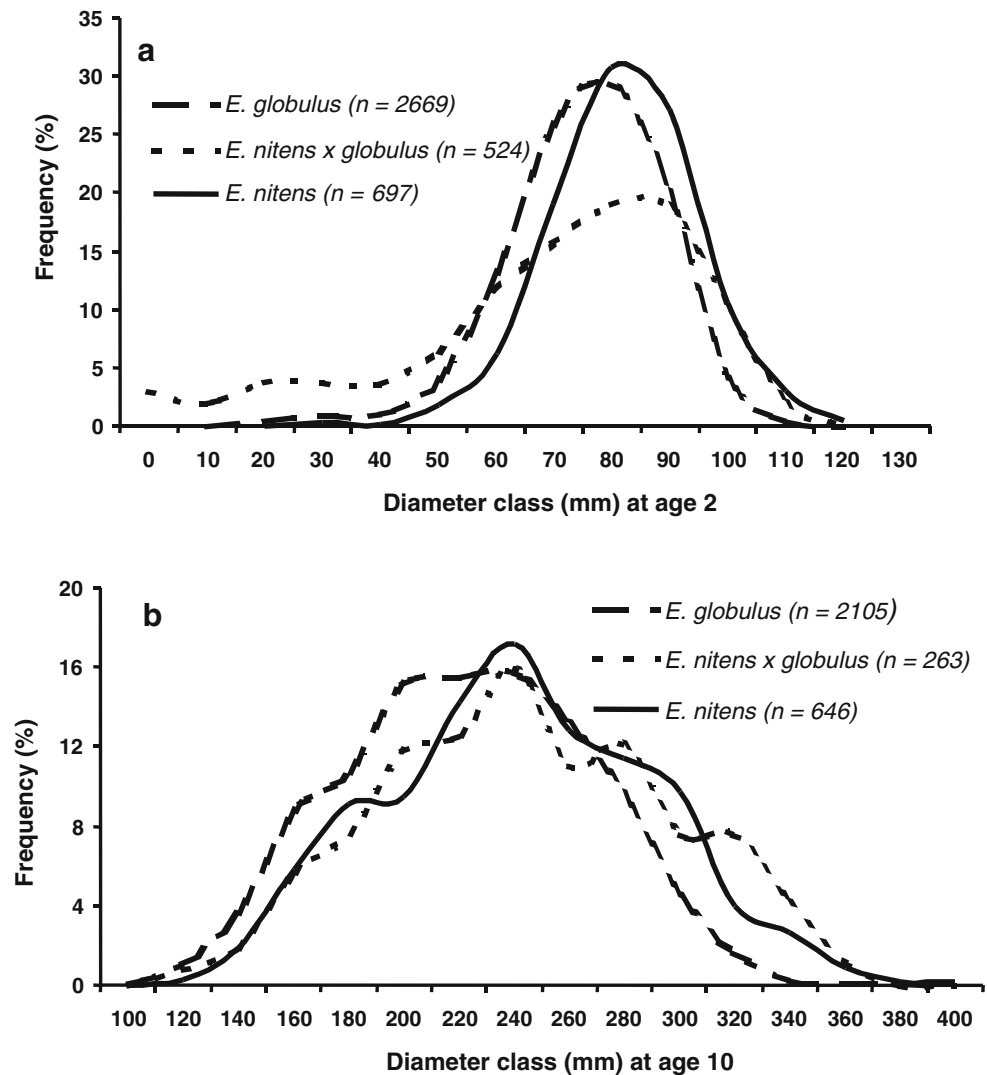
***P*≤0.01, significance of deviation of hybrid mean from mid-parent value

****P*≤0.001, significance of deviation of hybrid mean from mid-parent value

Table 4 Coefficients of variation (%) for traits D2, D3, D4, D6, D10 and P6 in *E. globulus*, *E. nitens* and F₁ hybrids. CV_A is the coefficient of additive variation and CV_P is the coefficient of phenotypic variation.

Trait	Component	<i>E. globulus</i>	<i>E. nit</i> × <i>glo</i>	<i>E. nitens</i>
D2	CV _A	8	27	7
	CV _P	18	34	16
D3	CV _A	6	29	9
	CV _P	16	37	14
D4	CV _A	7	28	10
	CV _P	17	37	15
D6	CV _A	7	19	14
	CV _P	18	29	19
D10	CV _A	6	14	17
	CV _P	20	22	22
P6	CV _A	6	5	4
	CV _P	11	12	11

while in *E. globulus*, it remains relatively constant in all cross types. (Table 4). The phenotypic variation in growth of the *E. nitens* × *globulus* F₁ hybrid population was markedly higher (at least 50%) than either pure species at ages 2 to 6 years contributed by higher components for additive, SCA and residual variances (not shown). The range of variation in the growth of the F₁ hybrids covered the extremes in growth exhibited by the pure species at all ages (Fig. 2). Due to mortality among slower growing individuals, the *E. nitens* × *globulus* F₁ hybrid SCA variance was reduced to zero, and residual variance was more similar to the pure species cross types by age 10 years (data not shown). This increased variation for D2 to D6 in the *E. nitens* × *globulus* F₁ hybrid was not a scale effect, as it was also reflected in a higher CV_P (Table 4) and was largely due to the higher level of poor performing, “abnormal” phenotypes. These abnormalities are reflected in the marked tail on the left-hand side of the frequency distribution for D2 in *E. nitens* × *globulus* F₁ hybrids

Fig. 2 Frequency distribution of DBHOB for *E. nitens*, *E. globulus* and *E. nitens* × *globulus* at **a** age 2 (D2), and **b** 10 (D10) years (n =number of trees surviving at time of measurement)

(Fig. 2a). Despite high levels of mortality among these individuals, the tail on the distribution still persists in D6 (not shown) but by age 10 has largely disappeared (Fig. 2b) in line with mortality of suppressed trees, which led to a marked reduction in CV_P (Table 4).

Genetic parameters

The heritability of growth traits in TT was moderate, at around $h^2=0.29\pm0.12$ in D2 decreasing to $h^2=0.18\pm0.08$ at age 10 (Table 5). In KK, the heritability was lower, with $h^2=0.15\pm0.09$ in D2 decreasing to $h^2=0.07\pm0.06$ at D10 (Table 5). The proportion of additive genetic variance expressed in TK and KT is intermediate to that found in either parental population as indicated by the intermediate heritabilities at all ages (Table 5), consistent with intermediate levels of additive genetic variation. While standard errors were high, d^2 in TT at early ages declined to virtually zero by age 6 years, whereas d^2 in KK, KT and TK tended to increase with age but remained low and not statistically different from zero (Table 5).

Trends over time in heritability of growth differed considerably between the two species and the F_1 hybrid populations (Table 5). The trend for *E. globulus* overall was for the heritability of diameter within cross types (within TT, KK, TK and KT) to drop from a moderate value of $h^2=0.19\pm0.06$ for D2 to $h^2=0.10\pm0.03$ for D10; these were statistically significant at all ages (Table 5). Diameter heritabilities for *E. nitens* were initially similar to *E. globulus* but markedly increased with time from $h^2=0.23\pm0.13$ for D2 to $h^2=0.56\pm0.20$ for D10 (Table 5). The diameter heritability for the inter-specific F_1 hybrid was high at all ages and slightly lower than *E. nitens* at ages 6 and 10 (Table 5), although differences were not significant. This was a direct reflection of increased additive genetic differences between the parents when in hybrid combination, where CV_A was higher in the inter-specific *E. nitens* \times *globulus* F_1 hybrids than the pure species

crosses for ages 2 to 6 years (Table 4). At age 10 years, CV_A in the *E. nitens* \times *globulus* F_1 hybrids has shown a marked decrease relative to pure species cross types (Table 4). In addition, the hybrids show a high coefficient of phenotypic variation (CV_P ; Table 4), which reflects the wide spread of individuals in the diameter distributions (Fig. 2), especially at early ages, in comparison to either of the parental species.

Dominance effects (d^2 ; Table 5), estimated from SCA effects among full-sib families, were TT and *E. globulus*-overall CP crosses for D2 and D3 but not for any other *E. globulus*, *E. nitens* nor the F_1 hybrid traits and cross types. This was partly a reflection of the small number of parents involved in the *E. globulus* intra-specific; *E. nitens* \times *globulus* and *E. nitens* cross types. d^2 accounted for between 0 and 39% of the total variance in growth in the pure species crosses and, while relatively stable with age in *E. globulus* overall, tended to decrease with age in *E. nitens* as the heritability increased (Table 5). In the inter-specific F_1 hybrids, d^2 for growth was quite high for ages 2 to 6 years but became zero at age 10 years (Table 5). This may be a reflection of mortality among slower growing individuals between ages 6 and 10 years, especially in the NT population (Fig. 1).

P6 h^2 was higher for *E. globulus* overall ($h^2=0.29\pm0.07$) than for *E. nitens* ($h^2=0.14\pm0.10$), with the hybrid intermediate ($h^2=0.20\pm0.11$; Table 5), although these latter two estimates were not significantly different from zero. P6 exhibited little or no d^2 in *E. globulus* and the F_1 hybrid population. The d^2 value was comparable to the h^2 estimate in *E. nitens* (Table 5), although neither was significantly different from zero.

Correlation between growth and Pilodyn

Genetic and phenotypic correlations between D6 and P6 for *E. globulus* overall, *E. nitens* and the F_1 hybrids at this site are shown in Table 6. The genetic correlation (r_g) ranged

Table 5 Heritability (h^2) and dominance ratio (d^2) (and standard errors) in intra- and inter-provenance crosses of *E. globulus*, combined analysis of all crosses in *E. globulus*, inter-species hybrid *E. nitens* *globulus* and within species crosses of *E. nitens* for D2, D3, D4, D6, D10 and P6

Species	Cross type		D2	D3	D4	D6	D10	P6
<i>E. globulus</i>	TT	h^2	0.29 (0.12)	0.27 (0.12)	0.28 (0.11)	0.24 (0.09)	0.18 (0.08)	0.30 (0.12)
		d^2	0.33 (0.13)	0.39 (0.14)	0.19 (0.10)	0.07 (0.08)	0	0.03 (0.10)
	KK	h^2	0.15 (0.09)	0.09 (0.07)	0.10 (0.07)	0.10 (0.07)	0.07 (0.06)	0.33 (0.17)
		d^2	0.06 (0.11)	0.08 (0.11)	0.10 (0.12)	0.08 (0.10)	0.18 (0.12)	0.12 (0.16)
	TK, KT	h^2	0.20 (0.07)	0.14 (0.06)	0.16 (0.06)	0.17 (0.07)	0.13 (0.06)	0.25 (0.09)
		d^2	0	0	0	0.05 (0.06)	0.03 (0.07)	0.02 (0.09)
	Overall	h^2	0.19 (0.06)	0.16 (0.05)	0.18 (0.05)	0.17 (0.05)	0.10 (0.03)	0.29 (0.07)
		d^2	0.12 (0.05)	0.14 (0.05)	0.05 (0.04)	0.08 (0.04)	0.08 (0.05)	0.04 (0.05)
	<i>E. nitens</i> \times <i>globulus</i>	h^2	0.61 (0.22)	0.59 (0.23)	0.60 (0.21)	0.42 (0.23)	0.47 (0.17)	0.20 (0.11)
		d^2	0.36 (0.24)	0.47 (0.27)	0.25 (0.19)	0.52 (0.28)	0	0.02 (0.14)
<i>E. nitens</i>		h^2	0.23 (0.13)	0.40 (0.18)	0.44 (0.18)	0.52 (0.19)	0.56 (0.20)	0.14 (0.10)
		d^2	0.12 (0.12)	0.13 (0.11)	0.14 (0.11)	0.10 (0.09)	0	0.13 (0.15)

Table 6 Genetic (r_g) and phenotypic (r_p) correlations between D6 and P6 with standard errors in brackets, for *E. globulus* (overall), *E. nitens globulus* and *E. nitens*

Species	r_g	r_p
<i>E. globulus</i>	0.19 (0.23)	0.19 (0.03)
<i>E. nitens</i> × <i>globulus</i>	−0.05 (0.45)	−0.01 (0.09)
<i>E. nitens</i>	0.81 (0.26)	0.13 (0.07)

from −0.05 to 0.81, but only the phenotypic correlation in *E. globulus* and the genetic correlation in *E. nitens* was significantly different from zero. The strong genetic correlation between D6 and P6 in *E. nitens* suggests that selection for faster growth will lead to a reduction in wood density. On the other hand, there appears to be no genetic correlation between P6 and D6 in the inter-specific *E. nitens* × *globulus* F₁ hybrid (Table 6), which suggests that selection in one trait is unlikely to have any effect on the performance of the other trait in the hybrid.

Correlation between intra- and inter-specific performance

The estimates of genetic correlation between the inter-specific hybrids and the pure species (i.e. GCA vs GHA) for growth at all ages and P6 were not significantly different from zero in all cases, except for D10 in *E. globulus* and *E. nitens*, where the correlations were -1.12 ± 0.16 and 0.65 ± 0.28 , respectively (Table 7). There was a trend for the genetic correlation between the *E. nitens* and the *E. nitens* × *globulus* F₁ hybrid growth to increase with age, from 0.35 for D2 to 0.67 for D6. In contrast, the correlation between the *E. globulus* and *E. nitens* × *globulus* for growth performance was much lower for these traits at 0.26 for D2 decreasing to 0.16 for D6 (Table 7). The poor correlation with *E. globulus* occurred despite significant levels of additive genetic variation in the pure *E. globulus* overall at all ages; however, the heritabilities for growth in *E. globulus* were lower than those recorded for *E. nitens* (Table 5). Despite the independence between variances and covariances in the model, the magnitude of the inter-specific correlation seems to be related to the expression of additive genetic variance in the pure species

parental population, particularly in the case of the increase in heritability for growth with age in *E. nitens* (Table 5).

The genetic correlation of parental values for P6 in interspecific crosses was positive but not significantly different from zero in *E. globulus* (0.60 ± 0.39) and *E. nitens* (0.68 ± 0.47 ; Table 7). This high interspecific vs hybrid genetic correlation with the *E. globulus* parents for P6 is consistent with the general trend across traits for the correlation to become increasingly positive with increasing heritability in the pure species crosses. The *E. nitens* population exhibited no significant additive genetic variation for P6, whereas significant levels were detected in *E. globulus* (Table 5). However, for the same pure species heritability (e.g. *E. globulus* D2 vs. P6), the genetic correlation for P6 was higher than that observed for D2.

In contrast to the poor inter-specific correlation involving *E. globulus*, there was a very high level of genetic correlation between the parental performance in *E. globulus* intra-provenance crosses and the corresponding inter-provenance (intra-specific) hybrids for growth at all ages and P6 (Table 7).

Discussion

Inter-specific F₁ hybrid performance

There are many reports of superior performance of inter-specific F₁ hybrids of *Eucalyptus* (de Assis 2000; Potts and Dungey 2001; Potts et al. 2000; Verryn 2000; Vigneron and Bouvet 2000); however, this does not appear to be the case for the *E. nitens* × *globulus* F₁ hybrid or for many other hybrid combinations involving *E. nitens* (Tibbits 2000) or *E. globulus* (Lopez et al. 2000; Potts et al. 2000). In the present case, the inter-specific F₁ *E. nitens* × *globulus* exhibited high incidence of abnormalities at young ages (Potts et al. 1992) and high levels of later age mortality. Such restrictions in the *E. nitens* × *globulus* F₁ hybrid has also been reported by Espejo et al. (1995). Similarly, inviability is a consistent feature in many other eucalypt hybrid combinations, particularly involving species from the section *Maidenaria*, to which both *E. nitens* and *E.*

Table 7 Genetic correlation (and standard errors) of GCA and GHA for intra- and inter-specific F₁ hybrids

Species	D2	D3	D4	D6	D10	P6
Genetic correlation of GCA with GHA within <i>E. globulus</i>						
<i>E. globulus</i> (TT)	0.72 (0.17)	0.79 (0.18)	0.94 (0.12)	0.93 (0.13)	0.97 (0.20)	1.15 (0.06)
<i>E. globulus</i> (KK)	0.72 (0.31)	0.60 (0.43)	0.99 (0.19)	0.91 (0.21)	0.93 (0.27)	0.94 (0.20)
Genetic correlation of GCA with GHA for each parental species with inter-specific F ₁ hybrids						
<i>E. globulus</i>	0.26 (0.35)	0.10 (0.40)	0.12 (0.34)	0.16 (0.46)	−1.12 (0.16)	0.60 (0.39)
<i>E. nitens</i>	0.35 (0.50)	0.69 (0.36)	0.45 (0.45)	0.67 (0.46)	0.65 (0.28)	0.68 (0.47)

Within *E. globulus*, the intra-species hybrid cross types TK and KT were pooled in the analysis as one cross type.

globulus belong (de Assis 2000; Potts and Dungey 2001). However, even higher levels of inviability have been reported in wider inter-specific crosses, and there appears to be a greater tendency towards such incompatibility in hybrids with increasing taxonomic distance (Griffin et al. 1988; Griffin et al. 2000; Potts and Dungey 2001).

Although the causes for such abnormalities to occur may be several, the results show that its degree can vary considerably and be parent specific. Where high mortality occurred, the surviving individuals in all crosses were of normal phenotype and often relatively vigorous. This effect has been noted in other studies with *Eucalyptus* (de Assis 2000; Perrow (MacRae) and Cotterill 2000; Tibbits 2000), suggesting parents may be heterozygous or polymorphic for factors causing abnormal or unsuccessful progeny. In operational breeding programs, it has been demonstrated that effective selection is still possible despite these disadvantages, provided crossing is undertaken at a large scale (Griffin et al. 2000). Deployment success is predicated on being able to mass produce the selections through vegetative propagation of selected individuals. Mass control-pollination is not an option because of the risk of high within family variance in the seedling performance.

In this study, the mean performance of surviving inter-specific F₁ hybrids of *E. nitens* × *globulus* for growth (D2 to D10) and P6 was generally intermediate, to varying degrees, between the parental intra-provenance crosses. On average, there was a tendency for the surviving inter-specific F₁ hybrids to perform better than the mid-parent value and even the better parent mean at later ages, particularly for crosses involving the King Island *E. globulus*. However, this was rarely statistically significant and was likely to be an artefact of the less competitive environment under which the surviving F₁ hybrids were growing compared with the parental controls, where mortality was relatively minor (especially in *E. nitens*). The distribution of D2 in the F₁ hybrids was considerably more skewed than in either parent species, showing a clear excess of trees with very slow growth. With time, abnormal trees died out, leaving a slight tail still evident at age 6 and a more normal distribution for the hybrids by age 10. Therefore, there is little evidence for significant heterosis at the cross type level in the surviving inter-specific hybrids. Similar conclusions are reached from other hybridisation programs involving species from the section *Maidenaria*. In most cases, the inter-specific F₁ hybrid mean was intermediate, or often below, the mid-parent value (Cauvin et al. 1987; Dungey et al. 1997; Lopez et al. 2000; Potts et al. 1992, 2000; Tibbits 2000). However, this mean response does not exclude the fact that some inter-specific F₁ hybrid individuals or families were outstanding. There was one outstanding inter-specific F₁ hybrid family observed, particularly for growth and survival, although its wood

density was below average. Other F₁ families with above average growth and survival and low wood density generally had a King Island *E. globulus* parent.

The evidence presented in this study shows that different provenances may exhibit different responses to hybridisation. In this case, the inter-specific F₁ hybrids, using Taranna *E. globulus*, appear to perform worse on average than those using King Island provenance. In this case, three out of ten male Taranna parents had very poor survival in the F₁ progeny, while all King Island parents showed good survival. This may indicate a provenance difference in barriers against hybridisation, but further provenances need to be sampled to verify this hypothesis. Similar results were observed for frost tolerance traits (Volker et al. 1994) where Taranna provenance *E. globulus* used in inter-specific hybrids showed poorer mean performance than where King Island parents were used.

A key point in assessing hybrid performance is defining the test environment (Martin 1989; Nikles and Griffin 1992). It has been shown that expression of hybrid superiority is often highly dependent on the environmental effects that may limit performance of one or other of the pure species parents (Nicholas 1987; Potts and Dungey 2001). The most common reason to breed hybrids would appear to be to provide suitable genotypes for planting in areas, which are marginal for one or both of the parental species in terms of environmental limitations, e.g. frost, drought, waterlogging, wind prone sites, nutritional limitations, pests and diseases (Dungey and Potts 2002; Potts et al. 2000; Vigneron and Bouvet 2000), or to combine economically important traits (e.g. high growth, good form, high wood density, long fibre length) in a single organism. In some cases, hybrids are desired to achieve a combination of environmental adaptability and economic trait improvements, as in this study.

In the present case, the site was clearly more favourable for *E. nitens* in terms of survival and growth of the survivors, and *E. globulus* was not subject to extreme frost damage, as it would be at higher altitudes in the same area (Potts et al. 2000). Despite this, there were still families from all cross types that showed favourable combinations of high growth and low Pilodyn (high wood density). At this site, there was no indication of any inter-specific F₁ hybrids with character combinations, which could not be found by exploiting the range of genetic variation within the pure species crosses. Potts et al. (2000) have shown that, with increasing altitude in this area, *E. globulus* growth is severely retarded compared to *E. nitens*. It is unlikely the F₁ hybrid might significantly out-perform the more frost sensitive *E. globulus* in terms of frost resistance (Tibbits et al. 1991b; Volker et al. 1994), and given the results, it is also unlikely that the F₁ hybrid would outperform or even be equal to *E. nitens* in growth at

higher altitudes. The inter-specific F_1 hybrids are likely to show at least slightly improved wood properties, compared to *E. nitens* for eucalypt kraft pulp production if high density *E. globulus* is used as a parent. However, *E. nitens* shows very high growth performance across a wide range of altitudes in this area (Potts et al. 2000). It is therefore likely to be less efficient to find genotypes of inter-specific *E. nitens* \times *globulus* F_1 hybrids with comparable growth to *E. nitens* and superior wood properties than simply exploiting genetic variation in wood properties within *E. nitens* (Tibbits and Hodge 1998).

There are two issues for consideration in comparing intra-species crosses with inter-species hybrids. Firstly, as demonstrated, there is genetic variation within species at the within and between provenance level that can be exploited. Secondly, heterosis exhibited in inter-provenance crossing may provide just as much gain as can be achieved with inter-specific F_1 hybridisation. This result emphasizes the importance of using the best pure species crosses as controls to assess the comparative value of producing hybrids from both an economic and biological perspective (Eldridge et al. 1993).

In this study, the inter-specific F_1 hybrids, exhibited high levels of abnormality or unsuccessful progenies and, at best, the performance of the surviving hybrids was no better than the parental species. In contrast, there was some evidence for mid-parent heterosis in growth for inter-provenance crosses of *E. globulus*, which appeared to be increasing with age. Evidence for heterosis in inter-provenance crossing has been reported in several forest tree species (Harfouche et al. 2000; Johnston et al. 2001; Schmidting and Nelson 1996). This is possibly a reflection of removal of mild inbreeding effects within provenances (Hardner et al. 1996). Nevertheless, this heterosis did not result in progeny of inter-provenance crosses outperforming progeny of the faster growing intra-provenance crosses from King Island in this study, although on average, the wood density would be improved.

Genetic parameters

In *E. globulus* intra-provenance crosses, it appears that King Island has lower levels of additive genetic variance for growth traits than Taranna as indicated through the CV_A and the heritability, although larger sample sizes are required to verify this result. Current models used for genetic evaluation assume homogeneous additive genetic variance across populations within a species (Dutkowski et al. 1997). Consistent with the expectations from quantitative genetic models (Falconer and MacKay 1996; Lo et al. 1993), the intra-specific hybrid exhibits intermediate heritabilities and intermediate levels of additive genetic variance. Taranna has moderate h^2 for growth, which decreases

slightly with time, whereas d^2 is less and relatively constant. Later age growth in King Island has low h^2 and d^2 indicating very low levels of genetic variation for diameter growth in this provenance. The inter-provenance crosses demonstrate a relatively constant d^2 while h^2 decreases with time. When viewed overall, *E. globulus* shows decreasing h^2 for growth over time and low but relatively stable d^2 . Other reports on age trends of genetic variance components in forest trees show a pattern of decreasing d^2 with age for height growth traits (Balocchi et al. 1993; Dieters et al. 1995; Harfouche and Kremer 2000; King et al. 1998; Kremer 1981). The generally lower d^2 in the inter-provenance crosses are consistent with their expression in intra-provenance crossing being due to inbreeding and deleterious gene effects.

Hardner and Tibbits (1998) found decreasing h^2 and greater levels of d^2 with increasing age for *E. nitens* diameter growth traits, whereas in this case, h^2 of diameter growth increased and d^2 decreased with age. In the former case, standard errors were much higher in comparison to the estimated genetic parameters.

Although there are a few reports of genetic parameters for inter-specific hybrid populations (Bouvet and Vigneron 1995, 1996; Dungey et al. 2000a; Gwaze et al. 2000; Rezende and de Resende 2000), there is a general lack of pure species controls. This means that there is little information on whether hybrid populations behave similarly to pure species populations and conform to current quantitative genetic models.

In this study, the phenotypic performance and genetic parameters indicate that the behaviour of the inter-specific F_1 hybrid population differs markedly from the inter- and intra-provenance crosses within species. This is reflected by the fact that the CV_A and h^2 for growth are highly inflated compared to the pure species controls with common parentage. In contrast, the inter-provenance F_1 hybrids had a level of additive genetic variation in the intra-specific F_1 hybrid population intermediate between that exhibited in the two intra-provenance populations, which is expected under an infinitesimal gene model (Lo et al. 1993). The correlation between additive genetic effects (GCA) in the *E. nitens* pure species and its hybrid population was moderately high, whereas the correlation between genetic effects in *E. globulus* and its hybrids was low and, in one case, strongly negative. This contrasts with the comparison of *E. globulus* intra-specific hybrids with within provenance crosses, which was strongly positive. In all cases, the correlations had very high standard errors and should be interpreted with caution. This result argues for completely different expression of genetic variation in the inter-specific hybrid population, at least for genes affecting growth.

In contrast to growth, more typical quantitative genetic behaviour of the inter-specific hybrid population was

observed for P6 in the present study. The evidence to support this includes (1) levels of additive variation in the hybrid population were comparable to those in the pure species population and (2) the correlation of genetic effects expressed in the *E. globulus* and *E. nitens* pure species crosses is positively correlated with that expressed in the hybrid population. In this case, selection of *E. globulus* and *E. nitens* parents with high wood density would be expected to result in hybrids with higher than average wood density; however, due to the large standard error associated with the genetic correlation estimates, this hypotheses requires further testing.

The correlation between pure and hybrid performance has been examined in a number of forest species (Dieters and Dungey 2000; Dungey and Nikles 2000; Nikles and Newton 1991; Powell 1993; Schneck and Langner 2000; Tibbits 2000; Vigneron and Bouvet 2000), including eucalypts, but sample size in virtually all cases is small. Specifically, what is important to breeders is the correlation of the GCA of parents in pure species to their GHA, as this will support effective recurrent selection in the pure species. Although under less robust field test designs, correlation varied between species and traits, poor GCA/GHA correlations occurred in this study, particularly for growth. Other reported correlations between pure *E. urophylla* breeding values for growth and its hybrids were stronger in *E. urophylla* × *grandis* with a correlation of 0.63 and *E. urophylla* × *pellita* equal to 0.83, using a F₁ factorials grown in Congo (Vigneron and Bouvet 2000). As expected, a strong correlation between the *E. urophylla* GHA values estimated from the two different hybrid combinations (0.64) was also reported. In South Africa, Verryen (2000) also reports a positive, but not-significant correlation (0.65) between previously estimated GCA of *E. grandis* parents and their GHA in *E. grandis* × *saligna* F₁ hybrid trial.

The poor genetic correlation between pure species and inter-specific hybrid growth, particularly in the *E. globulus* parents, observed in the present study could arise if (1) different genes are the determinants of a trait, such as growth, in the hybrid population compared to those in one or other parental population such as genes determining disease resistance (Vigneron and Bouvet 2000), (2) hybrid combinations are influenced more by non-additive than additive genetic effects (Dieters and Dungey 2000), or (3) other genetic factors such as chromosomal structural differences impact on hybrid performance. This result is consistent with the theoretical treatment (Gordon 1999), showing that hybrid populations are profoundly different from a random mating population and that the estimates of additive genetic variance in pure and hybrid populations are not theoretically comparable. Bouvet and Vigneron (1996) similarly note that results concerning additive and dominance variance in hybrid populations must be treated with

caution. Most of these possible non-additive inter-specific interactions appear to be deleterious, as some parents show high levels of inviability and poor growth in inter-specific hybrid combination, which cannot be predicted from knowledge of classical quantitative genetic models.

The high level of abnormalities observed in the nursery and at a young age in the hybrids (Dungey 1991; Potts et al. 1992) suggests that genetic mechanisms other than those expected under an infinitesimal gene effect model, may be operating in the hybrid population. These abnormalities were either lethal or have reduced the growth to such an extent that the individuals concerned were not able to survive competition from neighbouring trees. The problem was not confined only to major abnormalities. Bouvet and Vigneron (1996) reported a level of abnormalities around 10% for *E. urophylla* × *grandis*, which complicated analysis and interpretation of genetic effects. These problems also affected the analysis in the present study. The average family performance was reduced and family variance was considerably inflated at early stages in the inter-specific hybrids as evidenced by high CV_A. Once the less vigorous and deformed trees died, there was a corresponding effect on family performance through decreased competition at later ages, as a result of gaps amongst the hybrid plots. For these effects to result in such a marked increase in heritability for growth, they occurred only within a few families and never in others, causing heritability to decrease with time. This suggests a strong genetic basis to inter-specific hybrid performance, as suggested by Baril et al. (1997a,b) in an *E. urophylla* × *E. grandis* hybrid.

Implication for making choices in breeding and deployment

The implications of varying levels of GHA compared with GCA for different traits or parental species has implications for hybrid breeding strategy. In the case presented in this paper, it appears that wood density is a trait that behaves as predicted according to classical quantitative genetic theory in intra-/inter-provenance and inter-specific crosses. This reflects the strong genetic control of this trait. However, it becomes clear from the results that as the level of additive genetic variance is reduced, so too is the ability of a species to express its genetic merit in a predictable manner in a inter-specific hybrid combination.

The result also illustrates the importance of accounting for provenance or race effects for growth and Pilodyn penetration (wood density). Despite the fact that *E. globulus* produces a denser wood than *E. nitens*, the differences depend on the specific *E. globulus* races compared. In our study, trees from King Island were less dense (higher Pilodyn) than Toorongu *E. nitens*, whereas trees from Taranna *E. globulus* were about 10% denser.

Trees from King Island grew significantly better (about 10% also) than Taranna, so the overall merit of each cross type depends on the relative importance given to volume and wood density in the breeding objective.

In eucalypts, the relative value given to wood density in breeding for Kraft pulp production is marginally higher than for volume, but differences are small and depend on the cost structure, discount rate and selection criteria (Greaves et al. 1997). Therefore, the use of *E. nitens* × *globulus* F₁ hybrid would need to show significantly improved wood quality and growth compared to *E. nitens* to be useful in Tasmania. The indications are that there is no significant genetic correlation between growth and density in the inter-specific *E. nitens* × *globulus* F₁ hybrid.

Proposed and commercially used strategies for breeding eucalypt hybrids have been reviewed (Shelbourne 2000; Verry 2000). The two main strategies that have historically dominated the hybrid breeding literature are reciprocal recurrent selection (RRS; Comstock et al. 1949; Hyun 1976) and recurrent selection (RS). If the performance of the hybrids can be predicted easily from the performance of parents in the pure-breeds, then RS is the simplest alternative. However, as noted by Potts and Dungey (2001), RRS has obvious advantages where tests of both pure species are not possible (Vigneron and Bouvet 2000) or if there is a poor correlation between performance of parents in hybrid and pure species combinations. A RRS strategy, which is the most appropriate given the lack of parental predictability (low correlation of GCA with GHA) would require the removal of parents, which produce inter-species F₁ hybrid families with a propensity to produce abnormal phenotypes with low vigour and/or poor form. This strategy adds significant cost and time to a breeding program, which limits the achievement of gain per unit time. However, as classical quantitative genetic theory does not appear to explain the behaviour of inter-specific hybrids, there is doubt as to whether the normal measures of inheritance such as narrow sense heritability can be interpreted in the same way as applied to intra-specific crosses (Gordon 1999), and genetic gains would be more difficult to predict.

Nikles and Griffin (1992) pointed out that hybrids are used either because of heterosis or complementarity between species. In the present case, the inter-specific hybrid demonstrates little heterosis and limited complementarity. It must be considered that the inter-specific hybrid would be required to demonstrate a significant advantage over the parent species to warrant the breeding and propagation effort required to produce a deployment population. *E. nitens* × *globulus* is difficult to propagate by vegetative means, such as cuttings or tissue culture. Given the low level of heterosis and unreliability of prediction of hybrid performance demonstrated in this study, it would be

unwise to adopt a seed based strategy at least for the first generation hybrids. Some gain may be possible through initial screening of parents already established in pure species breeding arboreta for traits such as wood density and superior rooting ability. There will be significant progeny testing required, determining the worth of particular parents within species for generating inter-specific hybrids.

In this study, the hybrids did not show any clear advantage over either of the parental species, and more progress could probably be made by concentrating effort on improvement within species rather than through a hybrid program. There is no evidence that the hybrid combines high wood density of *E. globulus* with fast growth of *E. nitens* to an extent where there is a significant difference between the hybrid and *E. nitens*. The hybrid is not significantly different in frost resistance from the least resistant parent (*E. globulus*).

There is evidence, in this study, that specific hybrid families are produced that outperform most of the pure species families for one or other of the traits examined. This confirms that it is possible to discover such families and individuals, which could be exploited; however, there is no reliable quantitative genetic method of predicting which parents will produce outstanding inter-specific F₁ hybrid combinations. The hybrid combination of *E. nitens* × *globulus* therefore does not appear to demonstrate any clear advantages to the tree breeder due to the unpredictable performance of progeny and difficulty with production and propagation.

The present study demonstrates the importance of understanding the fundamental genetic parameters behind the performance of hybrid, which are commonly used in forestry. There are many examples of successful hybrid combinations of eucalypts and other genera used commercially around the world. These have often been exploited by way of vegetative propagation. Despite the size of many of these commercial hybrid programs, very little work has been done on the basic genetic parameters of the hybrids or their parental species. Consequently, there is little information available that allows evaluation of merit for potential parents or the prediction of gain in inter-specific hybrid breeding programs. This does not bode well for future genetic improvement of F₁ hybrid taxa.

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