PROSPECTS FOR GENETIC IMPROVEMENT OF *EUCALYPTUS CLADOCALYX* IN WESTERN AUSTRALIA*

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ABSTRACT

Sugar gum (*Eucalyptus cladocalyx* F. Muell.) plantations can produce high-value timber over a medium-length rotation in the 400- to 600-mm rainfall zone of southern Australia. We evaluated growth and tree form in sugar gum family trials on three sites in Western Australia. The trials contained 42 open-pollinated families originating from wild collections in the southern Flinders Ranges and Kangaroo Island (wild families) and four planted stands. Height and stem diameter were assessed at 3.5 and 5.5 years and stem volume was calculated. Branch size and stem straightness were scored at 3.5 years and axis persistence was assessed at 5.5 years. Mixed model equations were fitted to estimate heritability ($\hat{h}^2$) for all traits, genetic correlations between traits (Type A), and between sites (Type B), and age-age correlations for growth parameters.

Progeny from planted stands outperformed those from the wild for stem volume and straightness. Those of Kangaroo Island displayed the largest branches and poorest axis persistence. Estimates of narrow-sense within provenance heritability for stem volume at the three sites ranged from 0.40 to 0.47 and were similar at 3.5 and 5.5 years. The mean $\hat{h}^2$ estimate was 0.11 for branch size, 0.29 for stem straightness, and 0.21 for axis persistence. Genetic correlations for growth traits between ages 3.5 and 5.5 were extremely high, the weakest being 0.96. Genetic correlations between growth and form traits were generally positive (i.e., favourable) but not statistically significant. Genetic correlations between sites for growth and stem straightness were

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not significantly different from unity. Our results suggest that selection and breeding of superior individuals from high-ranking families could yield significant gains in growth and modest gains in stem straightness. A single breeding population may suit a wide range of sites in Western Australia given the lack of genotype × site interaction.

Keywords: variance components; heritability; tree improvement; breeding; genotype-environment interaction; correlation; *Eucalyptus cladocalyx*

INTRODUCTION

Sugar gum is endemic to South Australia, where it occurs in three disjunct regions: Kangaroo Island, the southern Flinders Ranges, and on the Eyre Peninsula (Boland *et al*. 1984). It produces timber of high density, strength, and durability in the medium rainfall zone (400 to 600 mm) of southern Australia (e.g., Blakemore 2004). It also coppices readily and is tolerant of a wide range of soils. Introductions, predominantly from the southern Flinders Ranges, were made to other areas of southern Australia from the 1870s onwards. This resulted in a population in western Victoria established as plantation blocks and farm windbreaks.

In 1999 sugar gum was included in a collaborative breeding programme to improve growth and form by ALRTIG (Australian Low Rainfall Tree Improvement Group). Early results collated from ALRTIG partners' pre-existing trials revealed provenance differences in growth and form (Bird & Jackson 2006; Bush *et al*. 2005; Harwood & Bush 2002) which has allowed recommendation of best-bet provenances and development of seed production areas and seed stands. These results also guided the formation of ALRTIG's base breeding populations, which were established as a set of 12 provenance-progeny trials throughout southern Australia in 2001. Six of these trials contain around 100 families, while the remainder, including the three reported on here, contain a smaller subset of the same families.

The provenance-progeny trials allow for validation of the provenance recommendations made by ALRTIG and for estimation of genetic parameters. Developing breeding strategies to maximise genetic gain for commercially important traits is particularly dependent on three such parameters: (1) within-provenance heritability ($\hat{h}^2$); (2) "Type-A" genetic correlations between traits; and (3) "Type-B" genetic correlations between sites.

Narrow-sense heritability ($\hat{h}^2$) is a measure of the genetic determination over a trait and is an important determinant of genetic gain from direct selection on a target trait (Lynch & Walsh 1998).

Type-A genetic correlations relate different traits and are important when multiple breeding objectives are desired. For sugar gum, we would be seeking to improve tree form and growth traits. The genetic correlations between these traits will

provide a valuable indication of the potential for concurrent selection on form and growth (Wu & Matheson, 2002).

Type-B genetic correlations are those between measures of a single trait in different environments (Burdon 1977; Yamada 1962) and have been used as a measure of genotype-×-site (G × E) interaction in numerous studies (e.g., Costa e Silva *et al.* 2006; Pswarayi *et al.* 1997; Woolaston *et al.* 1991). The presence of G × E can greatly affect realised gains from tree improvement and may result in the need to breed for genotypes that are stable across environments (Eberhart & Russell 1966), or to regionalise breeding and/or deployment populations (Costa e Silva *et al.* 2006; Hodge 1996).

The current study was undertaken to determine the prospects for genetic improvement of sugar gum growth and form in Western Australia. Our objectives were to: (a) evaluate genetic material sourced from wild and planted stands; (b) estimate narrow-sense heritability of growth and form traits along with genetic correlations between these traits; and (c) assess the importance of genotype-×-environment interactions across three diverse planting sites.

MATERIALS AND METHODS

Experimental Material

In this study we examined a subset of three provenance-progeny trials established in Western Australia comprising 42 open-pollinated families at each site (Table 1). The families were from a total of 10 seed sources; however, these could be grouped to represent two distinct wild regions-of-provenance as shown by

TABLE 1–Details of the 42 families in our experiment

Region-of-provenance group	Seed source	Selection method	Families
S. Flinders Ra.	Wirrabara State Forest	Random (ex wild)	4
S. Flinders Ra.	Wilmington	Random (ex wild)	2
S. Flinders Ra.	Mt. Remarkable	Random (ex wild)	2
Kangaroo Island	Flinders Chase National Park	Random (ex wild)	7
Kangaroo Island	Cygnet River	Random (ex wild)	3
Kangaroo Island	American River	Random (ex wild)	3
Planted Stand	Kersbrook SPA	Phenotypically selected mother and pollen parents	10
Planted Stand	Majorca	Phenotypically selected mother	5
Planted Stand	Mt. Burr	Phenotypically selected mother	4
Planted Stand	Lismore	Phenotypically selected mother	2

McDonald *et al*. (2003): southern Flinders Ranges (eight families), and Kangaroo Island (12 families). Families from Lismore, Majorca, and Mt Burr were all from phenotypically selected mother trees in planted stands that very probably originated from the southern Flinders Ranges. The Kersbrook SPA families were from southern Flinders Ranges mothers situated in a rogued seed production area that also included a small proportion of Kangaroo Island pollen parents. These phenotypically selected materials had been placed in a "planted stand" region-of-provenance group (22 families). The ALRTIG breeding populations did not contain any material from the Eyre Peninsular, as earlier provenance trials had demonstrated inferior growth and form.

Seed was supplied by ALRTIG and identified by mother identity code. Seedlings were raised at State Flora Nursery, Murray Bridge, South Australia, before being transported to Albany, Western Australia, for sorting and planting.

Test Sites and Experimental Design

Three field trials were located on sites in southern Western Australia that represented a possible commercial planting area for sugar gum. We have identified the sites by name of the nearest town, although the trial coordinates were precise; Kojonup (34° 3′ S 117° 9′ E), Wellstead (34° 39′ S 118° 18′ E), and Esperance (33° 42′ S 122° 9′ E). Soil conditions were determined by excavation to 3 m. The Kojonup trial was established on gritty duplex (sand/loam) with weathered granite regolith at around 2 m. The Wellstead and Esperance trials were on deep sandy soils, with grey and yellow colour, respectively. The climate from June 2001 to March 2007 was estimated at each test site by spatial interpolation of daily records from nearby weather stations (Jeffrey *et al*. 2001). Mean annual rainfall was about 500 mm at all three sites, and pan evaporation was greatest at Esperance (around 1700 mm; Table 2). The Kojonup site experiences the highest maximum temperatures in summer and the lowest minimum temperatures throughout the year (Table 2), although even this site experienced only 2 nights colder than freezing during the trial period, with the lowest temperature estimated to be –1°C.

Trials were established in winter 2001 by conventional hand planting. Sites were ripped to 700 mm soil depth, and mounded in rows 5 m apart. Spacing was 2.5 m between trees within rows, giving an initial stocking of 800 stems/ha. Each trial comprised five complete replicates, each containing two incomplete blocks (20 × 84 m), with five-tree family row plots in randomised incomplete block designs. A broad-spectrum fertiliser mix was incorporated into the mounds prior to planting at the Kojonup and Wellstead sites, and this consisted of N (4.6 kg/ha), P (6.0 kg/ha), K (5.0 kg/ha), S (5.6 kg/ha), Mn (3.0 kg/ha), Cu (0.75 kg/ha), Mg (0.75 kg/ha), Zn (0.75 kg/ha), and B (0.25 kg/ha). A combination of knock-down and pre-emergent herbicide was used to create weed-free planting sites. A year after

TABLE 2–Average seasonal rainfall, pan evaporation, maximum temperature, and minimum temperature at the three test sites from June 2001 to March 2007

		Summer	Autumn	Winter	Spring	Annual
Rainfall (mm)	Kojonup	43	150	167	159	495
	Wellstead	77	152	167	168	539
	Esperance	76	129	166	166	515
Pan evaporation (mm)	Kojonup	575	300	118	382	1325
	Wellstead	597	326	138	419	1426
	Esperance	656	383	191	528	1694
Maximum temperature (°C)	Kojonup	27.9	22.9	15.2	19.5	21.5
	Wellstead	24.4	22.2	16.2	19.1	20.5
	Esperance	26.3	23.7	17.7	21.2	22.3
Minimum temperature (°C)	Kojonup	12.1	10.5	5.7	7.5	8.9
	Wellstead	13.5	12.1	7.3	9.1	10.5
	Esperance	14.7	12.8	7.9	10.0	11.4

planting Wellstead and Esperance sites received N (9.5 kg/ha), P (12.0 kg/ha), K (10.0 kg/ha), S (9.5 kg/ha), Mn (3.0 kg/ha), Ca (2.8 kg/ha), Cu (1.5 kg/ha), Mg (1.5 kg/ha), Zn (1.5 kg/ha), and B (0.5 kg/ha). All sites received follow-up herbicide to control grass competition.

Assessments

Tree height was measured with a hypsometer (Vertex III, Haglöf, Sweden) and diameter at breast height (dbh) using a tape at ages 3.5 and 5.5 years. Stem volume was estimated as V = 1/3 × basal area at breast height × height. A subjective score was assigned to each tree for stem straightness (1 to 6 straightest) and branch size (1 to 6 smallest) at 3.5 years. Axis persistence was assessed at 5.5 years by assigning scores 1 to 6, where 1 indicates forking at the base, 2 indicates forking in the lowest quarter, 3 indicates forking in the second quarter, 4 indicates forking in the third quarter, 5 indicates forking in the uppermost quarter, and 6 indicates no forking. Subjective scores were assigned by a single assessor within each trial and the distribution of scores approximated the normal distribution.

Statistical Analyses and Genetic Models

ASReml version 2.0 (VSN International, Hemel Hempstead, UK) was used to solve univariate and multivariate mixed models by restricted maximum likelihood methods (Gilmour *et al.* 2002). Multivariate analyses were undertaken using data from individual test sites to estimate heritabilities and Type-A correlations between traits. Families were modelled as nested within regions-of-provenance. Type-B genetic correlations were determined by treating different sites as different traits,

and a single analysis was undertaken for each trait. The analyses were all conducted within the framework of the general linear mixed model:

$$\mathbf{y = Xb + Zu + e} \quad [1]$$

where **y** is the vector of observations on n traits, **b** and **u** are vectors of fixed and random effects (respectively), **X** and **Z** are incidence matrices for fixed and random model terms, and **e** is a vector of random residual terms. The vector **b** contained sub-vectors for fixed effects of replicate and region-of-provenance effects, and **u** contained sub-vectors for the random effects of incomplete blocks, plots, and families. Blocks and plots were modelled without covariance, while family effects were modelled with covariance to determine genetic correlations. The error vector **e** was modelled with covariance between traits for single-site analyses (i.e., Type A). The variance-covariance matrices relating to family effects of multi-site analyses were at first unstructured so as to provide Type B genetic correlations. Covariances were subsequently constrained to a single value for all three combinations of sites and further to a covariance of 1.0. One-tailed likelihood ratio tests were then applied to determine whether different pairs of sites had significantly different genetic correlations and whether genotype × environment interaction was statistically significant (Stram & Lee 1994).

Narrow-sense heritability was estimated for each site and trait:

$$\hat{h}^2 = \frac{2.5\sigma^2_f}{\sigma^2_f + \sigma^2_P + \sigma^2_B + \sigma^2_e}, \quad [2]$$

where σ^2_f is the variance of half-sib families, σ^2_P is the variance due to plots, σ^2_B is the variance due to incomplete blocks, σ^2_e is the error variance, and 2.5 represents a coefficient of relationship of 0.4 assuming an average outcrossing rate of 70% (Volker *et al.* 1990). The standard errors of 2 were calculated using a first-order Taylor series expansion to approximate the variance of a ratio of variances implemented in ASReml (Gilmour *et al.* 2002; Lynch & Walsh,1998).

RESULTS

Region-of-provenance Effects

Seedlings originating from phenotypic selections from planted stands were consistently greater in stem volume between 3.5 and 5.5 years than those from wild seed sources, even though seedlings from Kangaroo Island displayed equal or greater height at Kojonup and Esperance (Table 3). Diameter at breast height and stem volume of seedlings from Kangaroo Island increased more rapidly between the 3.5 and 5.5 year measurements than those from South Flinders (Table 3). Seedlings from Kangaroo Island displayed substantially heavier branching and poorer axis persistence across the three sites than did those originating from planted stands or the southern Flinders Ranges (Fig. 1A and 1C). Kangaroo Island seedlings were also significantly less straight at two sites (Fig. 1B).

TABLE 3–Average tree height, diameter at breast height (dbh), and stem volume of progeny from Planted Stands, South Flinders Provenance, and Kangaroo Island Provenance at three test sites; Kojonup, Wellstead, and Esperance. Standard errors are in parentheses.

	Kojonup			Wellstead			Esperance		
	Planted stands	South Flinders	Kangaroo Island	Planted stands	South Flinders	Kangaroo Island	Planted stands	South Flinders	Kangaroo Island
Height (m)									
3.5 years	6.72 (0.12)	6.17 (0.18)	6.97 (0.15)	6.81 (0.12)	6.31 (0.19)	6.36 (0.16)	8.09 (0.17)	7.44 (0.26)	8.25 (0.22)
5.5 years	8.53 (0.2)	7.92 (0.26)	9.11 (0.24)	8.79 (0.15)	8.00 (0.23)	8.17 (0.20)	10.38 (0.35)	9.47 (0.42)	10.26 (0.39)
Dbh (mm)									
3.5 years	107 (2)	96 (3)	90 (3)	104 (2)	92 (3)	82 (3)	124 (3)	112 (4)	110 (3)
5.5 years	134 (2)	119 (3)	120 (3)	131 (2)	116 (4)	109 (3)	147 (4)	130 (5)	136 (4)
Volume (dm^3)									
3.5 years	21.3 (0.9)	16.2 (1.3)	16.3 (1.2)	20.1 (1.7)	15.2 (1.1)	12.7 (1.0)	35.0 (1.6)	27.1 (2.4)	29.0 (2.0)
5.5 years	41.7 (1.9)	31.9 (2.8)	36.8 (2.5)	41.6 (1.5)	30.5 (2.3)	28.1 (2.0)	62.6 (3.5)	47.3 (4.8)	55.7 (4.3)

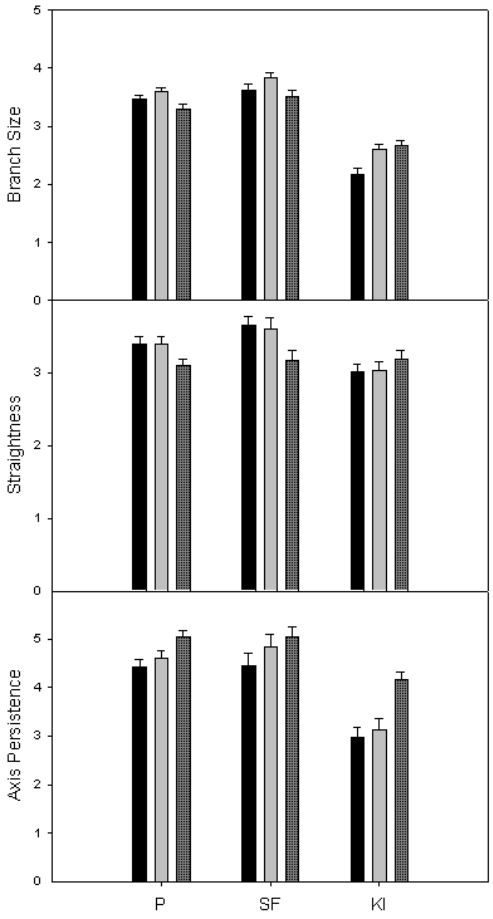

FIG. 1–Average scores for branch size, stem straightness, and axis persistence of progeny from planted stands ("P"), South Flinders region-of-provenance ("SF"), and Kangaroo Island region-of-provenance ("KI") on three test sites: Kojonup (black bars), Wellstead (light grey bars), and Esperance (dark grey bars). Error bars are standard errors.

Heritability Estimates

Heritability estimates for tree height ranged from 0.55 to 0.85 across sites and the two measurement times, whereas those for diameter at breast height were lower, but still high, ranging from 0.41 to 0.44 (Table 4). Those for stem volume ranged from 0.40 to 0.47 and estimates were remarkably consistent between 3.5 and 5.5 years. Heritabilities varied between sites from 0.16 to 0.50 for stem straightness, from 0.19 to 0.23 for axis persistence, and from 0.03 to 0.17 for branch size (Table 4).

Correlations between Traits within Each Site

Genetic correlations between the 3.5 and 5.5 year measures of growth were very high, the lowest being 0.96 for height at Esperance (Table 5). Form traits were not consistently correlated with growth traits, although stem straightness was positively correlated with early height growth at Wellstead and Esperance (Type-A correlation around 0.41; Table 5). There was also a significant and favourable

TABLE 4–Coefficient of variation (CV), variance components and narrow-sense heritability for each trait and site, with standard errors in parentheses

	Kojonup		Wellstead		Esperance	
Height 3.5 yr						
CV	0.16		0.20		0.18	
Phenotypic variance	0.97	(0.07)	0.80	(0.07)	1.50	(0.13)
Additive variance	0.54	(0.15)	0.68	(0.17)	1.18	(0.30)
Residual variance	0.70	(0.04)	0.49	(0.03)	0.93	(0.05)
Heritability	0.55	(0.12)	0.85	(0.15)	0.78	(0.14)
Height 5.5 yr						
CV	0.15		0.14		0.17	
Phenotypic variance	1.54	(0.15)	1.24	(0.11)	3.01	(0.47)
Additive variance	0.92	(0.25)	0.98	(0.26)	1.76	(0.46)
Residual variance	0.85	(0.05)	0.74	(0.04)	1.25	(0.07)
Heritability	0.60	(0.13)	0.79	(0.14)	0.58	(0.14)
Dbh 3.5 yr						
CV	0.24		0.29		0.25	
Phenotypic variance	376.90	(23.97)	351.90	(22.25)	658.80	(41.11)
Additive variance	164.90	(46.83)	151.50	(42.94)	268.90	(78.26)
Residual variance	305.35	(15.71)	290.88	(14.88)	550.68	(28.44)
Heritability	0.44	(0.10)	0.43	(0.10)	0.41	(0.10)
DBH 5.5 yr						
CV	0.19		0.20		0.22	
Phenotypic variance	564.00	(35.56)	523.10	(33.17)	931.00	(60.40)
Additive variance	239.40	(68.68)	228.70	(64.27)	380.10	(109.50)
Residual variance	465.70	(25.99)	436.16	(22.05)	751.78	(39.22)
Heritability	0.42	(0.10)	0.44	(0.10)	0.41	(0.10)
Volume 3.5 yr						
CV	0.51		0.61		0.52	
Phenotypic variance	71.60	(4.68)	55.83	(3.45)	226.10	(14.29)
Additive variance	33.74	(9.37)	22.41	(6.47)	96.23	(27.56)
Residual variance	58.09	(2.98)	46.83	(2.40)	186.95	(9.67)
Heritability	0.47	(0.11)	0.40	(0.10)	0.43	(0.10)
Volume 5.5 yr						
CV	0.44		0.45		0.50	
Phenotypic variance	292.70	(19.27)	218.00	(13.66)	792.10	(52.83)
Additive variance	136.40	(38.48)	90.50	(26.18)	324.00	(92.21)
Residual variance	228.63	(11.95)	179.08	(9.25)	616.88	(32.06)
Heritability	0.47	(0.11)	0.42	(0.10)	0.41	(0.10)
Branch size						
CV	0.32		0.25		0.31	
Phenotypic variance	0.72	(0.04)	0.48	(0.03)	0.86	(0.05)
Additive variance	0.12	(0.05)	0.01	(0.02)	0.11	(0.05)
Residual variance	0.62	(0.04)	0.40	(0.02)	0.80	(0.04)
Heritability	0.17	(0.07)	0.03	(0.04)	0.12	(0.06)
Straightness						
CV	0.28		0.27		0.35	
Phenotypic variance	0.78	(0.05)	0.83	(0.06)	1.25	(0.07)
Additive variance	0.12	(0.05)	0.42	(0.12)	0.26	(0.10)
Residual variance	0.63	(0.04)	0.65	(0.04)	1.13	(0.06)
Heritability	0.16	(0.07)	0.50	(0.11)	0.21	(0.07)
Axis persistence						
CV	0.51		0.51		0.34	
Phenotypic variance	3.78	(0.20)	4.08	(0.22)	2.54	(0.14)
Additive variance	0.72	(0.26)	0.94	(0.35)	0.52	(0.21)
Resi**ta**dual variance	3.54	(0.20)	3.49	(0.20)	2.16	(0.13)
Heritability	0.19	(0.07)	0.23	(0.08)	0.21	(0.08

TABLE 5–Type-A genetic correlations between tree height (HT), diameter at breast height (dbh), stem volume (VOL) at ages 3.5 and 5.5 years, and branch weight, stem straightness, and axis persistence at Kojonup, Wellstead, and Esperance trials. Standard errors of estimates are presented in parentheses and significant correlations (alpha=0.05) are in bold.

	dbh3.5	VOL3.5	HT5.5	dbh5.5	VOL5.5	Branching	Straightness	Axis persistence
Kojonup								
HT3.5	**0.84 (0.07)**	**0.94 (0.03)**	**1.01 (0.01)**	**0.86 (0.06)**	**0.93 (0.04)**	0.02 (0.27)	0.20 (0.27)	0.11 (0.23)
dbh3.5		**0.96 (0.02)**	**0.73 (0.10)**	**0.99 (0.01)**	**0.94 (0.03)**	**0.51 (0.23)**	0.21 (0.28)	0.29 (0.22)
VOL3.5			**0.79 (0.08)**	**0.97 (0.02)**	**0.99 (0.01)**	0.30 (0.24)	0.17 (0.28)	0.27 (0.21)
HT5.5				**0.73 (0.10)**	**0.83 (0.07)**	–0.01 (0.24)	0.22 (0.23)	0.00 (0.14)
dbh5.5					**0.97 (0.01)**	**0.46 (0.21)**	0.39 (0.22)	0.37 (0.20)
VOL5.5						0.33 (0.22)	0.38 (0.22)	0.35 (0.20)
Branching							**0.49 (0.24)**	0.33 (0.26)
Straightness								0.43 (0.25)
Wellstead								
HT3.5	**0.92 (0.05)**	**0.96 (0.03)**	**0.98 (0.01)**	**0.91 (0.04)**	**0.92 (0.04)**	0.32 (0.68)	**0.40 (0.18)**	0.10 (0.21)
dbh3.5		**0.97 (0.02)**	**0.90 (0.05)**	**0.99 (0.01)**	**0.96 (0.02)**	0.20 (0.68)	0.30 (0.20)	0.12 (0.22)
VOL3.5			**0.91 (0.04)**	**0.95 (0.02)**	**0.99 (0.01)**	0.33 (0.71)	0.22 (0.21)	0.15 (0.22)
HT5.5				**0.89 (0.05)**	**0.92 (0.04)**	0.04 (0.40)	0.19 (0.18)	0.10 (0.21)
dbh5.5					**0.96 (0.02)**	0.07 (0.43)	0.32 (0.18)	0.16 (0.22)
VOL5.5						0.14 (0.45)	0.19 (0.19)	0.19 (0.22)
Branching							–0.34 (0.47)	0.43 (0.51)
Straightness								0.12 (0.22)
Esperance								
HT3.5	**0.94 (0.04)**	**0.99 (0.02)**	**0.96 (0.02)**	**0.94 (0.04)**	**0.95 (0.03)**	–0.30 (0.26)	**0.42 (0.21)**	0.21 (0.22)
dbh3.5		**0.97 (0.02)**	**0.93 (0.04)**	**1.00 (0.01)**	**0.95 (0.02)**	–0.24 (0.28)	**0.45 (0.23)**	0.27 (0.23)
VOL3.5			**0.93 (0.04)**	**0.96 (0.02)**	**0.98 (0.01)**	–0.30 (0.27)	0.39 (0.23)	0.35 (0.23)
HT5.5				**0.95 (0.04)**	**0.97 (0.03)**	–0.30 (0.23)	0.34 (0.20)	0.32 (0.21)
dbh5.5					**0.96 (0.02)**	–0.28 (0.24)	**0.53 (0.19)**	0.39 (0.22)
VOL5.5						–0.33 (0.23)	**0.43 (0.20)**	**0.51 (0.20)**
Branching							0.34 (0.26)	–0.11 (0.31)
Straightness								0.40 (0.24)

genetic correlation between branch thickness and diameter at breast height at Kojonup (Type A correlation 0.51 with diameter at breast height 3.5, and 0.46 with diameter at breast height 5.5; Table 5). At Esperance, axis persistence and stem straightness were positively related to volume at 5.5 years (Type-A correlations of 0.51 and 0.43, respectively; Table 5).

Genotype x Environment Interaction

Type-B correlations between pairs of sites were very high for growth traits and stem straightness, ranging upwards of 0.87 (for volume at 5.5 years between Kojonup and Esperance; Table 6). Log likelihood did not decrease significantly for these traits when genetic correlations were constrained to a single value across the three pairs of sites and in six out of seven cases we could demonstrate that the correlation was not significantly different to 1.0 (Table 6). Type-B correlations for axis persistence were very high for pairs of sites involving Wellstead but significantly lower (0.78) for Kojonup-Esperance (Table 6). The lowest and least precise Type-B correlations were estimated for branch thickness. A single genetic correlation of 0.50 was determined for this trait (Table 6).

DISCUSSION

Our results suggest good prospects for improving sugar gum growth and stem straightness by selection and breeding, and it appears that single breeding and deployment populations could be developed for a wide range of sites in south Western Australia. We found that progeny of phenotypically selected mothers outperformed those of both wild regions-of-provenance for growth, which demonstrates the gains made by selection of superior trees in planted stands for both breeding and deployment. This effect was most pronounced at Wellstead, the poorest yielding site. On the other hand, progeny from planted stands were comparable with southern Flinders Ranges material for the three form traits we assessed (*see* Fig. 1). Bush *et al*. (2005), and Bird & Jackson (2006) found that collections of Kangaroo Island provenance outperformed those of southern Flinders Ranges for growth but were considerably poorer in form. Our findings support this earlier work from Victoria and South Australia, suggesting that provenance effects on growth and form may be stable across southern Australia.

We estimated heritabilities of between 0.40 and 0.85 for growth traits (*see* Table 4). These are substantially higher than previous estimates of 0.21 and 0.25 for diameter and height at a 28-month measure of ALRTIG's Bordertown (South Australia) progeny trial (Harwood *et al*. 2007) and are generally higher than those for growth traits in other eucalypt species (e.g., Table 18.4 in Eldridge *et al*. 1993). Heritability estimates for form traits were generally low-to-moderate although heritability for stem straightness was high at Wellstead. Harwood *et al*. (2007) estimated a heritability of 0.21 for axis persistence at the ALRTIG Bordertown trial.

TABLE 6–Type-B genetic correlations between three sites for growth and form traits under three covariance conditions, assuming a different correlation for each pair of sites ("Three Correlations"), one correlation for each pair of sites ("One Correlation"), and a correlation of 1 which implies no genotype × environment interaction ("Correlation=1"). Likelihood ratio tests of the difference in log likelihood of the models ΔLogL) were used to determine the simplest model, for which the correlation(s) are presented in bold.

Trait	Sites	One Correlation		Three Correlations			Correlation=1	
		Corr	(se)	ΔLogL	Corr	(se)	ΔLogL	Corr
HT3.5	Kojonup-Esperance	0.94	(0.07)					
	Kojonup-Wellstead	0.94	(0.07)	0.02	**0.93**	**(0.05)**	1.39*	
	Wellstead-Esperance	0.93	(0.06)					
HT5.5	Kojonup-Esperance	0.94	(0.06)					
	Kojonup-Wellstead	0.93	(0.06)	0.59	0.96	(0.04)	0.44	**1.00**
	Wellstead-Esperance	1.00	(0.04)					
dbh3.5	Kojonup-Esperance	0.95	(0.09)					
	Kojonup-Wellstead	1.00	(0.08)	0.08	0.97	(0.06)	0.08	**1.00**
	Wellstead-Esperance	0.98	(0.08)					
dbh5.5	Kojonup-Esperance	0.91	(0.09)					
	Kojonup-Wellstead	0.98	(0.07)	0.57	0.97	(0.05)	0.21	**1.00**
	Wellstead-Esperance	1.00	(0.07)					
VOL3.5	Kojonup-Esperance	0.90	(0.10)					
	Kojonup-Wellstead	1.00	(0.09)	0.37	0.93	(0.07)	0.49	**1.00**
	Wellstead-Esperance	0.92	(0.10)					
VOL5.5	Kojonup-Esperance	0.87	(0.10)					
	Kojonup-Wellstead	0.98	(0.08)	0.50	0.93	(0.06)	0.73	**1.00**
	Wellstead-Esperance	0.94	(0.09)					
Branching	Kojonup-Esperance	0.45	(0.31)					
	Kojonup-Wellstead	0.37	(0.53)	0.48	**0.50**	**(0.26)**	1.78*	
	Wellstead-Esperance	0.97	(0.70)					
Stem straightness	Kojonup-Esperance	1.07	(0.20)					
	Kojonup-Wellstead	0.94	(0.16)	0.38	0.92	(0.10)	0.37	**1.00**
	Wellstead-Esperance	0.91	(0.14)					
Axis persistence	Kojonup-Esperance	**0.78**	**(0.20)**					
	Kojonup-Wellstead	**1.16**	**(0.12)**	2.26*				
	Wellstead-Esperance	**1.04**	**(0.16)**					

* Indicates statistically significant ΔLogL by likelihood ratio test

An important assumption in our models is that the families are nested as families within sub-populations (42 families within three regions-of-provenance). This logical grouping is supported by the regional genetic divergence study of McDonald *et al.* (2003) and has positive pragmatic implications given the relatively small number of families included. Though there are 10 seed sources represented in these trials, the sample of families within each is too small to make reliable estimates of provenance (or seed source) performance. A larger ALRTIG trial testing 133 families at Bordertown allows a comparison of the effect of assuming families nested within provenance *versus* families nested within region-of-provenance using the grouping chosen in this paper. Indications are that heritability of growth traits is approximately 20% higher when subpopulations are defined as regions-of-provenance rather than discrete provenances (ALRTIG unpubl. data) indicating that this may well be a source of upwards bias in our study. This highlights the well-known issue of estimating heritability from small samples.

We assumed a coefficient of relationship (r) of 1/2.5, which is usual for wild populations of eucalypts (Eldridge *et al.* 1993) where a significant proportion of inbreeding is normal. Results from a recent allozyme study on sugar gum confirm that inbreeding is common in this species, with a mean multilocus outcrossing rate t_m of 0.57 (McDonald *et al.* 2003). Moreover, outcrossing rates have been shown to be highly variable between families (McDonald *et al.* 2003) and this could account for the unusually high $\hat{h}^2$ and Type-B genetic correlations (Griffin & Cotterill 1988; Hodge *et al.* 1996). Hodge *et al.* (1996) suggested that differential inbreeding depression among native stand open-pollinated families could be responsible for inflated h^2 estimates as well as under-estimation of genotype-×-environment interaction in *E. globulus*. Single-site estimates of h^2 can be inflated by genotype-×-environment interaction (Comstock & Moll 1963) although the high Type-B genetic correlations between our three sites negate this possibility.

Selection amongst progeny for deployment and further breeding is an important purpose of progeny testing. The optimum time of selection depends on changes in heritability and genetic correlations over time (Borralho *et al.* 1992). Our assessments at ages 3.5 and 5.5 years could both be considered early in the context of a potential 20-year rotation for sugar gum producing small sawlogs. Nevertheless, we have shown that h^2 estimates for growth traits are generally stable over this period and that additive genetic correlations between 3.5 and 5.5 years are extremely high. These results indicate that selections at age 3.5 would have been almost identical to those made at 5.5 years, but would have been obtained 2 years earlier. The trials have now been thinned, and it will be interesting to observe the ongoing trends in genetic correlations and variances.

Type-A genetic correlations between commercially important traits were favourable, though generally non-significant (*see* Table 5). This suggests that selection on a key

trait (e.g., volume) should not produce indirect losses in other commercial traits, but neither should genetic correlations be relied upon to achieve indirect gains. Rather, it appears that simultaneous selection on multiple traits might result in the most rapid gains in profitability of sugar gum (Cotterill & Dean 1990).

Our very high estimates of Type-B genetic correlations for growth and stem straightness indicate a lack of G × E for these traits across the three test sites. Although our test sites span 480 km, they were similar in climate and soil texture and it is possible that the inclusion of sites with markedly different temperature, water availability, or soil texture might have resulted in significant G × E. For example, Costa e Silva *et al*. (2006) explained significant G × E in *E. globulus* across Australia by differing responses to contrasting site water relations during summer, and Wu & Ying (2001) explained G × E in *Pinus contorta* Loudon across Canada by mean annual temperature. It is unclear why the sugar gum growth was substantially better at Esperance than at Kojonup and Wellstead. As part of a separate study we drilled beneath the Esperance trial when it was 6 years old and found fresh groundwater at 18 m, but we know very little about the rooting depth of sugar gum and it is uncertain if the trees were able to access this groundwater.

CONCLUSIONS

The planted stands represented in our trial are currently being used as seed production areas and our results support previous findings (e.g. Bird & Jackson, 2006; Bush et al., 2005) that these stands are likely to be a better source of seed than wild collections. We recognise that our study is limited by the small sample of families and inadequate representation of all provenances. Nevertheless, it is an important first regional assessment of the potential for genetic improvement in sugar gum. We have determined good prospects for rapid realisation of genetic gain in growth and stem straightness as heritability appears high and correlations between traits and sites in Western Australia are favourable.

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