

Prospects for genetic improvement of *Eucalyptus cladocalyx* in Western Australia

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Sugar gum (*Eucalyptus cladocalyx* F. Muell.) produces high value timber over a medium-length rotation in the 400-600 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 contain 42 open-pollinated families originating from the southern Flinders Ranges and Kangaroo Island (wild families) and four planted stands. Height and 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 determine narrow-sense within-provenance heritability (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. Heritability estimates for stem volume ranged between sites from 0.40 to 0.47 and were similar at 3.5 and 5.5 years. The median h^2 estimate was 0.17 for branch size, 0.21 for stem straightness and 0.21 for axis persistence. Genetic correlations of growth traits between age 3.5 and 5.5 were extremely high, the weakest being 0.96. Type A genetic correlations between growth and form traits were generally positive (i.e. favourable) but not statistically significant. Type B genetic correlations were not significantly different to unity for growth or stem straightness. 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 \times site interaction.

Key Words

Eucalyptus cladocalyx, sugar gum, variance components, heritability, tree improvement, breeding, genotype-environment interaction, correlation

Introduction

Sugar gum (*Eucalyptus cladocalyx* F. Muell.) is endemic to South Australia, where it occurs in three disjunct regions: Kangaroo Island, the southern Flinders Ranges and on the Eyre Peninsula. 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 from the 1870s onwards. This resulted in a large population in western Victoria established as plantation blocks and farm windbreaks.

In 1999 sugar gum was included in a collaborative breeding program 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 and Jackson, 2006; Bush et al., 2005; Harwood and 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 (h^2); (2) 'Type-A' genetic correlations between traits, and; (3) 'Type-B' genetic correlations between sites.

Narrow-sense heritability (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 and 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 and 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-by-site ($G \times E$) interaction in numerous studies (e.g. Costa e Silva et al., 2006; Pswarayi et al., 1997; Woolaston et al., 1991). The presence of $G \times E$ can greatly impact upon realised gains from tree improvement and may result in the need to breed for genotypes that are stable across environments (Eberhart and 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 whether genotype x environment interactions are present between three diverse planting sites.

Materials and Methods

Experimental material

This study examines a subset of three provenance-progeny trials established in Western Australia comprised of 42 open-pollinated families at each site (Table 1). The families are from a total of 10 seed sources, however these can be grouped to represent two distinct wild regions-of-provenance as shown by McDonald et al. (2003): southern Flinders Ranges (8 families); and Kangaroo Island (12 families). Families from Lismore, Majorca and Mt Burr were all from phenotypically selected mothers in planted stands that very probably originated from the southern Flinders Ranges. The Kersbrook SPA families are from southern Flinders Ranges mothers situated in a rogued seed production area that also includes a small proportion of Kangaroo Island pollen parents. These phenotypically selected materials have been placed in a 'planted stand' region-of-provenance group (22 parents). The ALRTIG breeding populations do not contain any material from the Eyre Peninsular, as earlier provenance trials have 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 represent a possible commercial planting area for sugar gum. We have identified the sites by name of the nearest town, although the trial coordinates are 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). Rainfall was similar between the sites at around 500 mm annually, while pan evaporation was greatest at Esperance (around 1700 mm; Table 2). The Kojonup site experienced the greatest maximum temperatures in summer and the lowest minimum temperatures throughout the year (Table 2), although even this site only experienced two nights colder than freezing, with the lowest temperature estimated to be -1 °C.

Seedlings were established at 800 stems per hectare in winter 2001 by conventional hand planting. Sites were ripped to 700 mm, and mounded in rows 5 m apart. A broad-spectrum fertiliser mix was incorporated into the mounds (70 kg ha⁻¹) and a combination of knock-down and pre-emergent herbicide was used to create weed-free planting sites. Wellstead and Esperance sites were fertilised again after planting and all sites received follow-up herbicide to control grass competition. Each trial comprised five-tree row plots in randomised incomplete block designs with five complete replicates each containing two incomplete blocks (20 m x 84 m).

Assessments

Tree height was measured with a hypsometer (Vertex III, Haglöf, Sweden) and diameter at breast height (DBH) using a tape at age 3.5 and 5.5 years. Stem volume was estimated as $V = 1/3 \times \text{basal area at breast height} \times \text{height}$. 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:

$$[1] \mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

where \mathbf{y} is the vector of observations on n traits, \mathbf{b} and \mathbf{u} are vectors of fixed and random effects (respectively), \mathbf{X} and \mathbf{Z} are incidence matrices for fixed and random model terms and \mathbf{e} is a vector of random residual terms. The vector \mathbf{b} contained sub-vectors for fixed effects of replicate and region-of-provenance effects, and \mathbf{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 \mathbf{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 x environment interaction was statistically significant (Stram and Lee, 1994).

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

$$[2] \quad h^2 = \frac{2.5\sigma_f^2}{\sigma_f^2 + \sigma_p^2 + \sigma_B^2 + \sigma_e^2},$$

where σ_f^2 is the variance of half-sib families, σ_p^2 is the variance due to plots, σ_B^2 is the variance due to incomplete blocks, σ_e^2 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 h^2 estimates 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 and 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). DBH and stem volume of seedlings from Kangaroo Island grew more rapidly between the 3.5 and 5.5 year measurement 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 (Figure 1A and 1C). Kangaroo Island seedlings were also significantly less straight at two sites (Figure 1B).

Heritability estimates

Heritability estimates for tree height ranged from 0.55 to 0.85 across sites and the two measurement times, whereas those for DBH 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 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 genetic correlation between branch thickness and DBH at Kojonup (Type A correlation 0.51 with DBH3.5 and 0.46 with DBH5.5; 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 seed production. 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 Figure 1). Bush et al. (2005), and Bird and 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 and also suggest 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, Eldridge et al., 1994).

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 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 (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 are approximately 20% higher when subpopulations are defined as regions-of-provenance rather than discrete provenances (ALRTIG unpublished 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. 1994) where a high 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 of $t_m=0.57$ (McDonald et al., 2003). The high Type-B genetic correlations between our three sites negate the possibility that genotype-by-environment interaction has caused upward bias in our single-site estimates of h^2 (Comstock and Moll, 1963). Heritability estimates for form traits were generally low-moderate (see Table 4) although heritability for stem straightness was high at Wellstead. Harwood et al. (2007) estimated a heritability of 0.21 for axis persistence in a 28 month-old trial at Bordertown.

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 age 3.5 and 5.5 years could both be considered early in the context of a potential 20-year rotation for sugar gum. Nevertheless, we have shown that 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 two 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 and Dean, 1990).

Our very high estimates of Type-B genetic correlations for growth and stem straightness indicate a lack of $G \times E$ for these traits across the three test sites. Although our test sites span 480 km, they were relatively alike 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 $G \times E$. For example, Costa e Silva et al. (2006) explained significant $G \times E$ in *E. globulus* across Australia by site water relations during summer and Wu and Ying (2001) explained $G \times E$ in *Pinus contorta* across Canada by mean annual temperature. It is unclear why the sugar gum growth was substantially better at Esperance than 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. 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 and 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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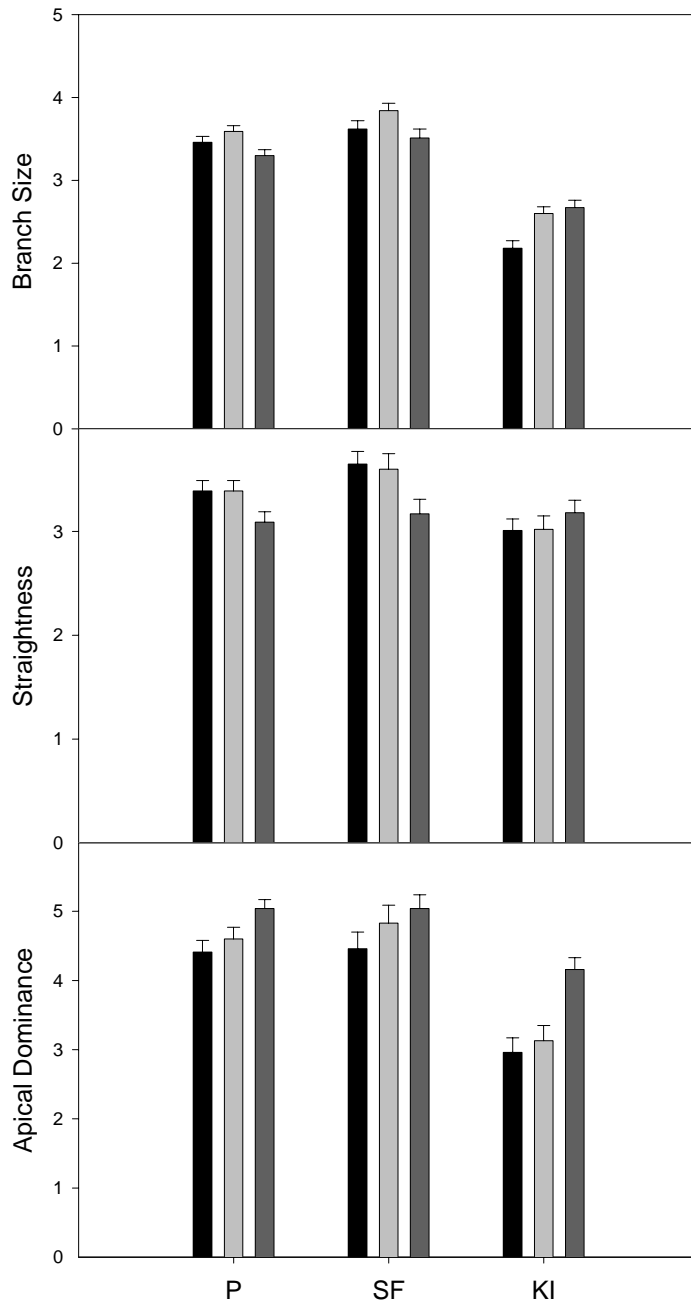


Figure 1. Average scores for branch size, stem straightness and axis persistence of progeny from planted stands (“P”), South Flinders region-of-provenance (“SF”) and Kangaroo Island region-of-provenance (“KI”) on three test sites: Kojonup (black bars), Wellstead (light grey bars) and Esperance (dark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

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	Cygnets 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

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

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
<i>Height (m)</i>									
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)
<i>DBH (mm)</i>									
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)
<i>Volume (dm³)</i>									
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)

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)
Branching						
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)
Residual 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 font.

Kojonup	DBH3.5	VOL3.5	HT5.5	DBH5.5	VOL5.5	Branching	Straightness	Axis Persistence
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	DBH3.5	VOL3.5	HT5.5	DBH5.5	VOL5.5	Branching	Straightness	Axis Persistence
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	DBH3.5	VOL3.5	HT5.5	DBH5.5	VOL5.5	Branching	Straightness	Axis Persistence
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)

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 x 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 font.

Trait	Sites	Three Correlations		One Correlation			Correlation=1	
		Corr	(se)	ΔLogL	Corr	(se)	ΔLogL	Corr
HT3.5	Kojonup-Esperance	0.94	(0.07)	0.02	0.93	(0.05)	1.39*	
	Kojonup-Wellstead	0.94	(0.07)					
	Wellstead-Esperance	0.93	(0.06)					
HT5.5	Kojonup-Esperance	0.94	(0.06)	0.59	0.96	(0.04)	0.44	1.00
	Kojonup-Wellstead	0.93	(0.06)					
	Wellstead-Esperance	1.00	(0.04)					
DBH3.5	Kojonup-Esperance	0.95	(0.09)	0.08	0.97	(0.06)	0.08	1.00
	Kojonup-Wellstead	1.00	(0.08)					
	Wellstead-Esperance	0.98	(0.08)					
DBH5.5	Kojonup-Esperance	0.91	(0.09)	0.57	0.97	(0.05)	0.21	1.00
	Kojonup-Wellstead	0.98	(0.07)					
	Wellstead-Esperance	1.00	(0.07)					
VOL3.5	Kojonup-Esperance	0.90	(0.10)	0.37	0.93	(0.07)	0.49	1.00
	Kojonup-Wellstead	1.00	(0.09)					
	Wellstead-Esperance	0.92	(0.10)					
VOL5.5	Kojonup-Esperance	0.87	(0.10)	0.50	0.93	(0.06)	0.73	1.00
	Kojonup-Wellstead	0.98	(0.08)					
	Wellstead-Esperance	0.94	(0.09)					
Branching	Kojonup-Esperance	0.45	(0.31)	0.48	0.50	(0.26)	1.78*	
	Kojonup-Wellstead	0.37	(0.53)					
	Wellstead-Esperance	0.97	(0.70)					
Stem Straightness	Kojonup-Esperance	1.07	(0.20)	0.38	0.92	(0.10)	0.37	1.00
	Kojonup-Wellstead	0.94	(0.16)					
	Wellstead-Esperance	0.91	(0.14)					
Axis Persistence	Kojonup-Esperance	0.78	(0.20)	2.26*				
	Kojonup-Wellstead	1.16	(0.12)					
	Wellstead-Esperance	1.04	(0.16)					

* indicates statistically significant ΔLogL by likelihood ratio test