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Genetic Variation for Growth and Wood Density in *Eucalyptus globulus* ssp. *globulus* in Tasmania (Australia)

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Summary

Genetic parameters for diameter and Pilodyn penetration were estimated for a 5 year-old *Eucalyptus globulus* ssp. *globulus* base population established across 5 sites in Tasmania (Australia). The model included race, family, plot, incomplete block and family-by-site interaction as random and replicate as fixed effects. Race effects were generally low for diameter and moderate for Pilodyn, with heritabilities across the 5 sites of $h^2 = 0.20$ and 0.30 respectively. For each trait, correlations between trials were generally high, suggesting that a combined analysis across sites should be appropriate. The genetic correlation between Pilodyn penetration and diameter was moderately unfavourable (averaged 0.25) whereas race correlations were low but favourable (–0.19).

Key words: heritability, genetic correlation, Pilodyn, REML.

FDC: 165.3; 232.1; 561.2; 812.31; 176.1 *Eucalyptus globulus*; (946).

Introduction

A number of genetic improvement programs using *Eucalyptus globulus* for pulpwood production have been initiated in the last few years in many countries, with breeding populations based mainly on ssp. *globulus* seed collected in native stands (*e.g.* Orme, 1977; Gardiner and Crawford, 1987, 1988). So far, published genetic parameters for a range-wide *E. globulus* ssp. *globulus* base population have included growth (Potts and Jordan, 1994b; Borralho *et al.*, 1995), frost tolerance (Volker *et al.*, 1994), leaf morphology (Potts and Jordan, 1994a), flowering time (Gore and Potts, 1995) and drought tolerance (Dutkowski, 1995). The genetics of wood density, albeit being identified as a key trait in pulpwood breeding (Borralho *et al.*, 1993; Greaves *et al.*, 1997a) has not been studied in great detail. Previous estimates were based on wood samples from a few families in a limited range of provenances (*e.g.* Dean *et al.*, 1990; Borralho et al., 1992b). The use of Pilodyn, a hand-held instrument which drives a steel pin into the wood with a known force, has been recommended as an effective method to measure wood density in standing trees (Sprague *et al.*, 1983; King *et al.*, 1988). In eucalypts, the relationship between Pilodyn penetration and wood density seems to be linear and relatively constant across sites, with phenotypic correlations generally above 0.7 (GREAVES *et al.*, 1996; RAYMOND and MACDONALD, 1996). Recent Pilodyn studies on young *E. nitens* progeny confirmed a high within provenance heritability ($h^2 = 0.65$) and genetic correlations with density close to one (GREAVES *et al.*, 1997b), suggesting that Pilodyn penetration and wood density should be intrinsically the same trait. An obvious advantage of the Pilodyn is that a large number of trees can be measured in a non-destructive way and at a reduced cost. Despite being an indirect method, the Pilodyn allows for more extensive and accurate studies on the genetic control of wood density across sites.

In this paper we will look at the relative importance of race and within race genetic variation, and estimate heritabilities and genetic correlations within and between sites for diameter and Pilodyn. The analysis is based on 5, 5-year old progeny trials of *E. globulus* established in northern Tasmania.

Material and Methods

The CSIRO collection

The genetic material used in this study was collected by the CSIRO Tree Seed Centre in 1987 and 1988, and includes 561 open pollinated (half-sib) families from typical *E. globulus* ssp. *globulus* and a few families from populations taxonomically intermediate between this subspecies and other mainland subspecies, in particular *pseudoglobulus* (see JORDAN *et al.*, 1994). The collection was grouped into 23 races, based on a modification of JORDAN's racial classification (JORDAN *et al.*, 1994), with the atypical race Wilson's Promontory (Victoria) being excluded from the analysis. The number of families in each race is given in *table 1.*

Trials

The 5 trials were established by North Forest Products in northern Tasmania. All sites were ripped and mounded before trees were planted at a spacing of 4 m x 2.5 m, with fertilizer being applied with each seedling at planting. The trials were established as a resolvable incomplete block design (PATTERSON and WILLIAMS, 1976), with 5 replicates each and between 21 and 28 incomplete blocks, with each block containing between 20 and 25 families in 2-tree plots.

Table 1. – Details of the race classification and number of families per race in the analysis.

Race	No. Families
Lavers Hill, Vic	6
West Otway Ranges, Vic	120
East Otway Ranges, Vic	41
Strzelecki, Vic	66
South Gippsland, Vic	12
Flinders Island	60
Cape Barren Island	44
Clarke Island	6
St Helens, Tas	11
NE Tasmania	24
Mayfield, Tas	5
Tasman Peninsula, Tas	10
Triabunna, Tas	9
SE Tasmania	52
Mt Dromedary, Tas	4
Jericho	5
South Tasmania	18
Dover	5
Recherche Bay	4
Port Davey	6
West Tasmania	29
King Island	32

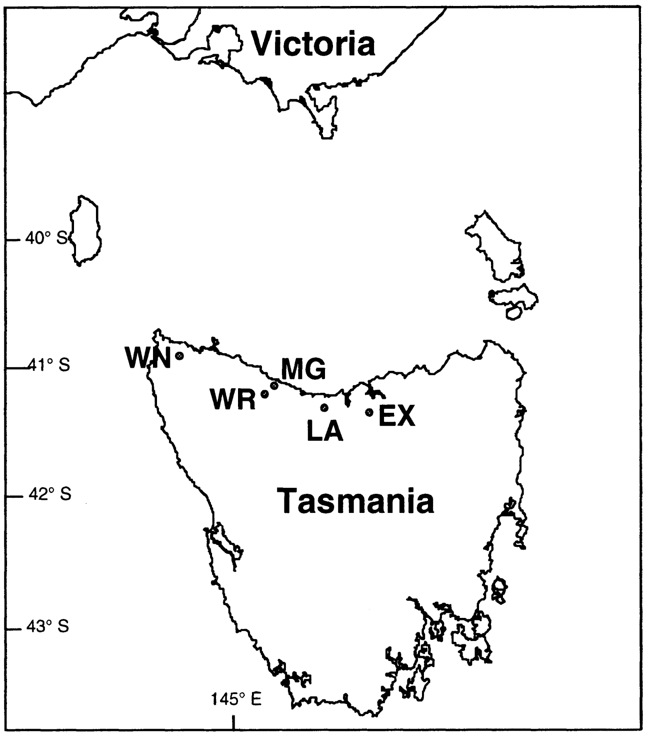

Figure 1. – Trial locations.

Measurements

Diameter at 1.3 m was measured on all trees at 4 years. Pilodyn penetration was measured at age 5½ years on half of the trees, in 2 of the 5 replicates at each site with 1 tree per plot and 2 measurements (averaged) per tree. Trees that were in the top 10% for diameter were also measured, irrespective of location. The equipment used for density assessment was a Pilodyn 6J Forest with a 2.5 mm striker pin (GREAVES et al., 1996).

Statistical analysis

Data for diameter and Pilodyn penetration were standardised by replicate within site variance, and site phenotypic variance, respectively so that total variance for each trait equals one. The analysis for diameter was based on the following model:

$$y = mean + SR + iblock + plot + race + fam + w \qquad [1]$$

where *SR* is the effect due to replicate within a site assumed fixed, *iblock* is the effect of the incomplete blocks, assumed random, *plot* is the effect due to plot, assumed random, *race* is the race effect, assumed random, *fam* is the family (or GCA) effect, assumed random and *w* is the residual variance. Pilodyn data was analysed using a simpler model:

$$y = mean + SR + race + fam + w \qquad [2]$$

In the across site analysis, a random term for the family-by-site interaction was also included. This term is likely to include the interactions between both the family within race and race with site. Narrow-sense heritabilities were calculated as

$$h^2 = \frac{2.5V_{fam}}{V_{fam} + V_{plot} + V_w} \qquad [3]$$

for the single site analysis, and

$$h^2 = \frac{2.5V_{fam}}{V_{fam} + V_{plot} + V_{fs} + V_w} \qquad [4]$$

for the across site analysis, where V_{fs} is the variance of the family-by-site effects. The coefficient of relationship between open pollinated sibs of *1/2.5* was used, assuming an average rate of outcrossing of 70%, after Volker *et al.* (1990). Race repeatability was calculated for each site as:

$$\rho = \frac{V_{race}}{V_{race} + V_{fam} + V_{plot} + V_w} \qquad [5]$$

and for the combined analysis as:

$$\rho = \frac{V_{race}}{V_{race} + V_{fam} + V_{plot} + V_{fs} + V_w} \qquad [6]$$

Genetic correlations were calculated as:

$$r_G = \frac{\mathrm{cov}(fam_1, fam_2)}{\sqrt{V_{fam_1} \cdot V_{fam_2}}} \qquad [7]$$

where cov (fam_1, fam_2) is the covariance between family effects at site 1 and 2. Race correlations were calculated as:

$$r_G = \frac{\mathrm{cov}(race_1, race_2)}{\sqrt{V_{race1} \cdot V_{race2}}} \qquad [8]$$

where cov ($race_1$, $race_2$) is the covariance between race effects at site 1 and 2, and V_{race} is the variance of race effects. Analyses were based on a multivariate REML algorithm, using program VCE version 3.1 (Groeneveld, 1995). Standard errors for the heritability estimates were calculated as (Becker, 1985):

$$\sigma_{h^2} = 2.5\sqrt{\frac{2(1-t)^2(1+(k-1)t)^2}{k(k-1)(s-1)}} \qquad [9]$$

where k is the number of offspring per family, s is the number of families and $t = h^2/2.5$. Standard errors of genetic correlations were approximated using Robertson's (1959) equation as:

$$\sigma_{r_G} = \frac{(1-r_G^{\,2})}{\sqrt{2}}\sqrt{\frac{\sigma_{h_x^2}\sigma_{h_y^2}}{h_x^2 h_y^2}} \qquad [10]$$

where r_G is the genetic correlation and σ_{h^2} is the standard error of the heritability. The likelihood ratio test was used to test the significance of the random effects.

Results and Discussion

Mean diameter growth and Pilodyn penetration in each trial are listed in *table 2*. Diameter changed markedly across trials, ranging from 12.9 cm in Massey Greene (MG) to half that size (6.5 cm) at Latrobe (LA). Pilodyn penetration seems to change according to growth rate, with fast growing sites, such as West Ridgley (WR) and Massey Greene (MG) having the lowest density (highest Pilodyn), and slow growing sites such as Woolnorth (WN), Latrobe (LA) and Exeter (EX), having higher wood density. A similar relationship between growth rate and wood density was found between contrasting plantation sites for *E. globulus* in Tasmania (Muneri, pers. comm.) and Victoria (Greaves, pers. comm.), but results from spacing (Ferrari and Scaramuzzi, 1982) and irrigation trials (Pereira and Araújo, 1990), where growth rates varied markedly, showed no apparent relationship between growth and wood density.

Table 2. – Overall trial means for diameter and Pilodyn in Woolnorth (WN), West Ridgley (WR), Massey Greene (MG), Latrobe (LA) and Exeter (EX), in northern Tasmania.

	Trial					
	WN	WR	MG	LA	EX	TOTAL
Diameter						
No parents	463	423	557	534	517	561
No records	4195	3367	5047	4766	4859	22477
Mean (cm)	7.52	10.78	12.94	6.50	6.85	
s.d.	3.53	3.18	3.37	2.02	2.22	
Pilodyn						
No parents	456	411	553	529	514	561
No records	1214	1024	1520	1392	1391	6572
Mean (mm)	12.26	13.81	13.44	11.82	12.75	
s.d.	1.71	1.81	1.89	1.59	1.68	

The range of mean Pilodyn penetration, between 11.8 mm at Latrobe (LA) and 13.8 mm at West Ridgley (WR), should correspond to differences in density of around 20 kg•m^{-3}, as approximated by Raymond and MacDonald's (1996) regression function1). This is only a 5% change from an expected mean at this age of around 500 kg•m^{-3}. Compared with the 2-fold increase in diameter between slow and fast growing sites, differences in wood density are therefore small.

Variance components for growth

Variance components for growth due to race, family within race, plot and residual effects are given in *table 3*. Race repeatability (the ratio between race variance and total variance, excluding that due to incomplete blocks) varied somewhat between trials. Woolnorth (WN) had the highest repeatability (ρ = 0.10), decreasing eastwards to Latrobe (LA) and Exeter (EX) where race effects were near zero. Pooled analysis also gave low race effects (repeatability of 0.04). Family-by-site interaction was significant but accounted for only 4% of the total variance (excluding block variance). Plot effects, a measure of family-by-replicate interaction, were not significant and were removed from the pooled analysis. Single-site heritabilities for diameter were low to moderate, ranging between 0.17 at Latrobe and 0.35 at Massey Greene. Within race heritability estimates seem to be related with growth rate: the 2 fast growing sites (WR and MG) had the highest heritabilities (h^2 = 0.34 and 0.35, respectively), and the slowest growing site (LA) had the lowest (h^2 = 0.17), a relatively small but significant difference, at the 5% level based on the LR test. The heritability from the combined analysis was h^2 = 0.20,

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1) DEN = 745.87 – 19.46 PIL (r^2 = 0.56)

Table 3. – Variance components for diameter (percentage variance in parenthesis), race repeatability and within race heritability (plus standard errors) on each site and across the 5 sites in Tasmania. Data from each replicate were standardised to have a phenotypic variance of one. Variance due to incomplete blocks is not presented.

Trial	V_{race}	V_{fam}	V_{plot}	$V_{fam.site}$	V_w	ρ	h^2 (s.e.)
WN	0.092 (10)	0.064 (7)	0.024 (3)	–	0.721 (80)	0.102	0.20 (0.04)
WR	0.046 (6)	0.098 (13)	0.001 (0)	–	0.629 (81)	0.059	0.34 (0.05)
MG	0.053 (6)	0.114 (13)	0.000 (0)	–	0.698 (81)	0.061	0.35 (0.04)
LA	0.019 (2)	0.056 (7)	0.062 (7)	–	0.706 (84)	0.023	0.17 (0.04)
EX	0.011 (1)	0.081 (10)	0.049 (6)	–	0.697 (83)	0.013	0.24 (0.04)
Combined	0.032 (4)	0.065 (8)	–	0.038 (4)	0.718 (84)	0.038	0.20 (0.02)

slightly lower than the average of all estimates, a consequence of the low family-by-site interaction.

Previous studies on the genetic control of growth in *E. globlus* (*e.g.* Volker *et al.*, 1990; Dean *et al.*, 1990; and Woolaston *et al.*, 1990, in Australia; and Borralho *et al.*, 1992a and b in Portugal) found heritabilities between 0.06 and 0.29, but assumptions on the coefficients of relationship varied between 0.33 and 0.54. Only recently, have heritabilities based on full pedigreed material been reported. Hodge *et al.* (1996) found a heritability of 0.08 based on a few parents from 2 provenances of *E. globulus* tested across 5 sites in Australia. Other estimates for growth based on full-sib trials, include $h^2 = 0.18$ from a 4 year-old trial in Tasmania (Peter Volker, pers. comm.), and $h^2 = 0.19$ and 0.28 across a range of full-sib trials (local land race) in Portugal (Araújo *et al.*, 1996). The across-site estimates of $h^2 = 0.20 \pm 0.02$ found here seems to confirm a significant, but relatively low heritability for growth in *E. globulus.*

Correlation between sites for growth

Genetic and race correlations for diameter across the 5 sites were generally high (*Table 4*), suggesting that diameter can be considered a single trait across the 5 trials. This is an encouraging result considering the large differences in growth rate observed amongst trials. Between site race correlations involving Latrobe were poorer, and on one occasion even negative (*Table 4*), although such estimates are likely to be of little significance as race effects at Latrobe were near zero and statistically not significant.

Table 4. – Race (below diagonal) and genetic correlations (above diagonal) for diameter between the 5 trials.

	WN	WR	MG	LA	EX
WN		0.690	0.816	0.662	0.702
WR	0.706		0.847	0.791	0.700
MG	0.452	0.919		0.970	0.916
LA	-0.443	0.227	0.334		0.884
EX	0.599	0.875	0.672	0.382	

Variance components for wood density

Table 5 lists the variance components due to race, family and residual effects for Pilodyn penetration. Overall, race repeatability (or the proportion of total variance explained by race effects) was greater for Pilodyn than for diameter, and significant at all sites, despite the incomplete statistical model used (*i.e.* no incomplete block effects were fitted due to reduced data). Woolnorth (WN) had the lowest race repeatability (p = 0.08) and Latrobe had the highest (p = 0.16) with a combined estimate of 0.11.

Heritability of Pilodyn penetration did not change much across the 5 sites, ranging between 0.28 and 0.41, with a combined estimate of 0.33 ± 0.03. Family-by-site effects were small but significant, accounting for only 3% of the total variance (*Table 5*). Previous heritability estimates published for wood density in *E. globulus* by Dean *et al.* (1990) and Borralho *et al.* (1992b) used wood discs, and varied between 0.4 and 0.8, values clearly above the range found here for Pilodyn. It is possible that Pilodyn, despite the high genetic and phenotypic correlation with wood density (Greaves *et al.*, 1997b), may have an intrinsic lower heritability than samples taken from cores or discs, for example due to greater sampling errors. The Pilodyn pin penetrates up to 2 growth rings, hence sampling only 2 consecutive years. Cores or disks sample 7 or more rings. If measurements of wood density across rings have a low repeatability, cores and disks will provide a more

Table 5. – Variance components for Pilodyn penetration (percentage variance in parenthesis), race repeatability and within race heritability (plus standard errors) on each site and across the 5 sites in Tasmania. Data from each replicate were standardised to have a phenotypic variance of 1.

Trial	V_{race}	V_{fam}	$V_{fam.site}$	V_w	ρ	h^2 (s.e.)
WN	0.079 (12)	0.100 (11)	–	0.799 (78)	0.081	0.28 (0.11)
WR	0.123 (14)	0.134 (13)	–	0.678 (73)	0.132	0.41(0.12)
MG	0.156 (15)	0.143 (11)	–	0.720 (73)	0.153	0.41 (0.11)
LA	0.141 (20)	0.099 (13)	–	0.632 (67)	0.162	0.34 (0.11)
EX	0.139 (19)	0.109 (12)	–	0.715 (69)	0.144	0.33 (0.11)
Combined	0.102 (11)	0.114 (12)	0.024 (3)	0.718 (75)	0.106	0.33 (0.03)

accurate estimate of wood density. However, a recent study by GREAVES *et al.* (1997b) found both genetic and phenotypic correlations of density between rings to be near one, suggesting little advantage of sampling more rings. Alternatively, family effects estimated in DEAN *et al.* (1990) and BORRALHO *et al.* (1992b) studies may have been inflated because race effects were ignored. Interestingly, the lower estimate by BORRALHO *et al.* (1992b) of 0.44 was from a local land race progeny trial, whereas in the multi-provenance trial, with families from King Island, Otway Ranges and Flinders Island, the heritability estimate was $h^2 = 0.80$. Similarly, in DEAN *et al.* (1990), where families were from a range of provenances, the heritability was $h^2 = 0.77$.

Providing Pilodyn penetration is a reliable indicator of wood density in eucalypts, the results found here may suggest that a large proportion of the observed variation in density is between races. Heritability and genetic variation for wood density within a race seems to be considerably smaller than initially thought.

Table 6. – Race (below diagonal) and genetic correlations (above diagonal) for Pilodyn penetration between the 5 trials.

	WN	WR	MG	LA	EX
WN		0.997	0.860	0.917	0.876
WR	0.970		0.895	0.931	0.891
MG	0.984	0.993		0.875	0.844
LA	0.502	0.656	0.563		0.995
EX	0.689	0.805	0.729	0.972	

Correlation between sites for density

Genetic and race correlations of pilodyn across sites are listed in *table 6*. Genetic correlations were consistently very high (average r_G of 0.91), suggesting Pilodyn can be considered the same trait across all sites. Race correlations were also very high but, as with growth, lower estimates were found between the trials at Woolnorth and Latrobe ($r_{race} = 0.50$). These 2 trials, Woolnorth in the far NW and Latrobe in the north-east, are probably the most contrasting in terms of rainfall. Otway Ranges and the 2 North Eastern Tasmanian races were the main cause of this low correlation, the former having considerably higher density at Latrobe than at Woolnorth, while the latter showed a relatively high density at Woolnorth and a very low density at Latrobe (data not shown). KUBE *et al.* (1995) had previously identified Otway Ranges and some eastern Tasmanian provenances (*e.g.* Seymour) as particularly interactive for growth. NE Tasmania provenances are also known to be well adapted to drought conditions (DUTKOWSKI, 1995), a major factor differentiating the sites at Woolnorth and Latrobe.

Correlation between diameter and Pilodyn

The race and genetic correlations between Pilodyn and diameter (*Table 7*) are of particular importance since efficient selection for pulp production relies strongly on both traits (GREAVES *et al.*, 1997a). The genetic correlations between the 2 traits were generally unfavourable (slightly positive), except at Exeter where race correlation between the 2 traits was –0.50. The combined analysis gave a favourable race correlation of $r_{race} = -0.19$ and an unfavourable genetic (within race) correlation of $r_G = 0.25$.

Such favourable correlations between growth and wood density at the race level suggest that substantial progress can be made with both traits if appropriate race selection is done during the initial stages of a breeding program.

Nevertheless, it was apparent that genetic correlation within a race, between growth and wood density, might be worse than previously assumed. Earlier estimates were inconsistent and unreliable (*e.g.* $r_G = -0.42 \pm 0.46$ and 0.32 ± 0.54 in 2 independent trials in Portugal (BORRALHO *et al.*, 1992b), and $r_G = -0.22$ in the DEAN *et al.* (1990) study. The current combined estimate of $r_G = 0.25 \pm 0.06$ for Pilodyn and diameter (or around –0.25 if expressed in terms of density and growth) is considerably more accurate than previous estimates.

Table 7. – Race (r_{race}) and within race genetic correlation (r_G) between diameter and Pilodyn penetration on each site and across the 5 sites in Tasmania.

Trial	r_{race}	r_G
WN	0.333	0.339 (0.18)
WR	0.277	0.324 (0.13)
MG	-0.001	0.270 (0.12)
LA	-0.037	0.339 (0.16)
EX	-0.499	0.053 (0.17)
Combined	-0.191	0.246 (0.06)

An interesting trend observed was the drop in race correlations between traits, from a high positive value in the western-most site (WN), to a near zero correlation in the eastern-most site (EX). Changes in correlation may be associated with a reduction in genetic and race variances in eastern sites (hence a greater sampling error associated with the estimates). From a climatic point of view, the only W-E trend is rainfall, from 1273 mm in the NW to 953 mm in the NE and a temperature gradient, albeit small, with western sites being somewhat colder than eastern sites, although effects are likely to be masked by large differences in soil characteristics.

Table 8. – Site details.

	Altitude (m)	Mean Temp. (°C)	Rainfall (mm)	Soil Type	Lat	Long
WN	60	16.9	1163	yellow podzol	40 49 S	144 53 E
WR	180	13.5	1273	krasnozem	41 08 S	145 48 E
MG	120	16.7	1130	krasnozem	41 05 S	145 54 E
LA	100	17.1	953	yellow podzol	41 17 S	146 27 E
EX	120	17.2	974	sandy duplex, acid	41 17 S	146 51 E

Implications for breeding programs

Previous work by VOLKER and ORME (1988), KUBE *et al.* (1995) and POTTS and JORDAN (1994b) in Australia, ALMEIDA *et al.* (1995) in Portugal, and DAOQUN *et al.* (1995) in China, found provenance differences for growth to be small and often not statistically significant. The present study, which included a broad collection, covering most of the natural distribution of *E. globulus* in Australia, confirmed that result. For growth alone, VOLKER and RAYMOND's (1988) suggestion of "a single breeding population containing families from many or all provenances" seems therefore an appropriate strategy for *E. globulus*. However, for breeding objectives including both growth and wood density, appropriate account of race effects may be required, both for the estimation of genetic parameters and genetic evaluation. When wood density dominates the breeding objective, it seems that testing and selection of families from high density specific races seems preferable.

Conclusion

The importance of race effects was very different for growth and wood density. Race effects for growth were moderate and in some trials, statistically not significant. On the other hand, for wood density, measured here using Pilodyn, race effects were very large. Once race effects were accounted for, the genetic variance left within a race was moderate for both diameter ($h^2 = 0.20$) and Pilodyn ($h^2 = 0.33$). The genetic correlation between traits was moderately unfavourable ($r_G = 0.25$ between diameter and Pilodyn).

For both growth and wood density in Tasmania, there seem to be relatively low genotype by environment interactions. Overall, additive genetic correlations across trials were high, but growth and wood density at the driest and most marginal site was, nevertheless, less well correlated with the wetter sites. Considering the large differences in growth rate and wood density observed in the 5 sites in Tasmania, results suggest that race effects and breeding values for growth and density in *E. globulus* are stable across a wide range of environments.

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