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The Effects of Drying Temperature and Method of Assessment on the Expression of Genetic Variation in Gross Shrinkage of *Eucalyptus globulus* Wood Samples

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Abstract

Genetic variation in wood-sample gross shrinkage and basic density was examined in a *Eucalyptus globulus* base population trial growing in Tasmania, Australia. Gross shrinkage, which includes all components of shrinkage including collapse, was assessed in four ways (calliper- and visually-assessed tangential shrinkage, volumetric shrinkage and radial shrinkage) on samples dried at three temperatures (22 °C, 60 °C and 105 °C). Significant differences between subraces were observed using all measures of gross shrinkage for two or more of the three drying treatments. Furthermore, significant additive genetic variation within subraces was observed in calliper- and visually-assessed gross shrinkage under two or more of the drying treatments, with narrow-sense heritabilities greater than or equal to 0.35. There was no obvious trend in heritabilities or coefficients of additive genetic variation with drying temperature. Under the 105 °C drying treatment, subrace correlations among calliper-, visually- and volume-assessed gross shrinkage were positive and very strong (≥ 0.97), while these measures were less strongly correlated with radial gross shrinkage at the subrace level (≤ 0.77). Within-subrace genetic correlations among the first three measures were also strongly positive (≥ 0.95). These high genetic correlations suggest that different drying regimes and the calliper, visual and volume methods of assessment could be used interchangeably to select for reduced tangential gross shrinkage. Estimated subrace and genetic correlations between basic density and measures of gross shrinkage were universally negative (i.e. favourable), although not all were significantly different to zero.

Key words: Heritability, genetic correlation, genotype-by-drying-regime interaction, drying defect, shrinkage, collapse, basic density.

Introduction

There are large areas of *E. globulus* plantation in Australia (c. 454000 ha in 2005; Parsons *et al.,* 2006), Chile (c. 232,000 ha in 2003), Portugal (c. 700,000 ha in 2002) and Spain (c. 500,000 ha in 2002) (Potts *et al.,* 2004). Although pulpwood production is the principal focus of most *E. globulus* growers, there is increasing interest in producing plantation-grown solid-wood products, such as appearance-grade sawn timber (Raymond, 2000; Greaves *et al.,* 2004a; Nolan *et al.,* 2005). Breeding, along with improved silviculture and the adoption of appropriate processing practices, is a possible means of improving the profitability of such plantations.

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Although sawmilling studies have shown that adequate recoveries of dried appearance-grade products are possible from *E. globulus* grown in appropriately managed plantations (WAUGH and YANG, 1994; MOORE *et al.,* 1996; BRENNAN *et al.,* 2004; NUTTO and VAZQUEZ, 2004; WASHUSEN, 2004; WAUGH, 2004), increasing product recovery and value by reducing drying degrade is likely to be an objective of appearance-grade sawn-timber breeders (RAYMOND, 2000; GREAVES *et al.,* 2004a). The presence of drying defects such as cupping, face checking (i.e. exposed cracks) and internal checking can cause degrade in, and reduce the value of, appearance-grade sawn timber (WASHUSEN *et al.,* 2000; NUTTO and VAZQUEZ, 2004; WAUGH, 2004; NOLAN *et al.,* 2005). Such drying defects are caused by within-board variation in shrinkage (CHAFE, 1992; SVENSSON and MARTENSSON, 1999; NOLAN *et al.,* 2005).

Upon drying, wood shrinks as a result of a number of fundamentally different processes. Collapse occurs early in the drying process if tensile forces, generated as free water is removed from highly impermeable wood fibres, exceed the strength of cell walls, causing them to become distorted (CHAFE, 1992; ILIC, 1999). Treatment with steam (i.e. reconditioning; NOLAN *et al.,* 2003) is commonly undertaken by sawmillers to recover collapse after preliminary drying, but non-recoverable collapse or 'abnormal shrinkage' sometimes remains in boards. Abnormally high levels of shrinkage in *E. globulus* wood are often attributed to the presence of tension wood (CHAFE, 1992; WASHUSEN and ILIC, 2001; WALKER, 2006). Normal shrinkage refers to a reduction in the thickness of cell walls that occurs as bound water is removed from them. It generally occurs late in the drying process after most, or all, free water has been removed from cell cavities (i.e. below the fibre saturation point; CHAFE, 1992; WALKER, 2006). The expression of normal shrinkage varies with moisture content below the fibre saturation point because cell walls swell if they regain moisture after drying.

Gross shrinkage incorporates all components of shrinkage including recoverable collapse, non-recoverable collapse, and 'abnormal' and 'normal' shrinkage. However, gross shrinkage is simply referred to as collapse by some authors, based on the assumption that collapse is the principal cause of the gross shrinkage observed in their studies (KUBE and RAYMOND, 2005). Furthermore, gross shrinkage has been shown to be strongly genetically correlated with recoverable collapse in 12-mm wood cores of *E. nitens* (HAMILTON *et al.,* 2009).

The measurement of gross shrinkage in wood samples, such as 12 mm cores, has been proposed as a means of identifying genotypes that are less prone to expressing drying defects (KUBE and RAYMOND, 2005). Wood cores are routinely extracted from trees in pulpwood breeding programs to assess physical and chemical wood properties (DOWNES *et al.,* 1997; RAYMOND and APIOLAZA, 2004) and gross shrinkage in cores can be measured at minimal additional cost.

The improvement of pulpwood traits, such as rotation-age volume, basic density and pulp yield (BORRALHO *et al.,* 1993; GREAVES and BORRALHO, 1996; GREAVES *et al.,* 1997), has historically been the focus of most *E. globulus* breeding programs. Improvement of these traits may also have favourable implications for sawn-timber producers. Increased growth is desirable for sawn-timber production and increased basic density has been shown to have a favourable relationship with sawn-timber hardness, stiffness and strength properties (DICKSON *et al.,* 2003; MCKENZIE *et al.,* 2003). Furthermore, pulpwood is likely to be a valuable by-product in most sawn-timber production systems. However, the extent to which concurrent genetic gains can be made in a single breeding population in both appearance-grade traits (e.g. drying defects) and pulpwood traits will depend on the strength and direction of genetic correlations among these traits.

The principal aims of this study were to (1) determine if three drying treatments and four methods of assessment revealed genetic variation in sample gross shrinkage, (2) examine if genetic variation in gross shrinkage was stable across drying treatments and methods of assessment, and (3) examine the relationship between gross shrinkage and basic density, a common pulpwood selection trait.

Materials and Methods

Trial

This study was undertaken on trees planted in a Gunns Ltd. *E. globulus* base population progeny trial at West Ridgley in north-western Tasmania (for details, see MACDONALD *et al.,* 1997; and APIOLAZA *et al.,* 2005). It contained the open-pollinated progeny of 451 native forest mothers sampled by the CSIRO Tree Seed Centre in 1987 and 1988 (GARDINER and CRAWFORD, 1987; GARDINER and CRAWFORD, 1988). The mothers were sampled from 13 races and 22 subraces (refer to DUTKOWSKI and POTTS (1999) and http://members.forestry.crc.org.au/globulus).

The trial was divided into two blocks approximately 150 m apart containing two and three replicates respectively. Replicates were comprised of 17 incomplete blocks and families were planted in two-tree plots. Seedlings were established at a spacing of 2 by 4.5 m and the trial was managed as a pulpwood stand without thinning or pruning. At the time of sampling, 15 years after establishment, 46% of the original trees and 91% of the original families were still surviving.

This study examined wood property traits in 250 trees, from 116 families (generally two, but up to three, trees per family) and 10 subraces, felled as part of a sawmilling trial. These were the same trees detailed in HAMILTON *et al.* (2007) with one additional tree from each of the King Island and Southern Furneaux subraces. To enable extraction of a sawlog from each tree, only trees of sufficiently good form and with a diameter at breast height (1.3 m) greater than 21 cm were selected for felling. A single 1.5 m long sawlog was cut from the straightest part of the lower stem in each tree (GREAVES *et al.,* 2004b; HAMILTON *et al.,* 2007).

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Traits

From each felled tree, one disc approximately 100 mm thick was cut from directly below the sawlog. Discs were extracted from the base of sawlogs rather than breast height to avoid decay induced from previous sampling for wood property assessment (HAMILTON *et al.,* 2007). The mean height of disc extraction was 12% of tree height (3.0 m). Discs were wrapped in plastic bags and stored at 4°C as soon as possible after felling to avoid desiccation.

From each disc, three 12 x 12 mm north-south oriented bark-to-bark samples were sawn to include the stem pith using a bench-mounted circular saw. After extraction, the samples were placed in water. These samples were sized to approximate 12 mm cylindrical cores that are routinely extracted from standing trees by *E. globulus* pulpwood breeders for the assessment of physical and or chemical wood properties (DOWNES *et al.,* 1997; RAYMOND and APIOLAZA, 2004).

Each bark-to-bark sample was broken into two pith-to-bark 'half samples' for ease of handling. Decay was observed near the pith of samples from 51% of trees and was removed prior to the measurement of green volume using the water displacement method (TAPPI, 1989). The three matching pairs of half samples from each tree were randomly allocated to three drying treatments: (1) 22°C for 60 days in a controlled temperature room with a relative humidity of approximately 36%, a drying regime suitable for drying cores for chemical analysis and the assessment of air-dry density (HAMILTON *et al.,* 2008) (2) 60°C for 48 hours in an oven and (3) 105°C for 24 hours in an oven, a treatment commonly adopted in breeding programs to assess basic density (DOWNES *et al.,* 1997; RAYMOND and APIOLAZA, 2004). The green radial length of one half sample selected at random from each tree and drying treatment was measured prior to drying. The mean green radial length of half samples in all drying treatments was 104 mm (SD = 23 or 24 mm). Under each drying treatment samples were dried to equilibrium moisture content.

During drying, samples were restrained within aluminium channel of 13 mm internal width (BANDARA, 2006). Samples were aligned within the aluminium channel to ensure that one of their transverse faces was exposed to the air. Samples that were oven dried at 105°C were weighed immediately after drying and their basic densities calculated (TAPPI, 1989). After drying, all samples were stored in an air-conditioned laboratory and allowed to stabilise to equilibrium moisture content (approximately 8%) before sample dimensions were measured. Gross shrinkage was calculated for each tree and drying treatment using four methods:

(1) Calliper-assessed tangential gross shrinkage was calculated as the difference between the mean of two measures of minimum tangential width (one from each of the half samples from each tree and drying treatment) and green sample width (i.e. 12 mm). KUBE and RAYMOND (2005) outlined a similar procedure.

(2) Visually-assessed tangential gross shrinkage. Trees were ranked from best to worst based on subjective visual assessment of gross shrinkage within each drying treatment. High rankings were accorded to trees with obvious tangential gross shrinkage and or washboarding in half samples. These data were then 'normalised' for analysis (i.e. ranks were expressed as proportions of the number of trees plus one, and these proportions were, in turn, expressed as normal deviates, assuming an underlying standard normal distribution).

(3) Volume-assessed gross shrinkage was calculated as the difference between the sum of the two dry half-sample volumes from each tree and drying treatment and the sum of the corresponding green half-sample volumes. Volumes were assessed using the water displacement method (TAPPI, 1989). Volume-assessed gross shrinkage was a composite measure of tangential, radial and longitudinal gross shrinkage.

(4) Radial gross shrinkage was calculated as the differences between the dried and green lengths of each half sample.

Calliper-assessed, volume-assessed and radial gross shrinkage were expressed as percentages of green sample dimensions.

Statistical Analyses

Univariate restricted maximum likelihood (REML) mixed model analyses of basic density and all measures of gross shrinkage under each drying treatment were undertaken by fitting the following linear model:

$$Y = MEAN + BLOCK + HEIGHT + DECAY + SUBRACE + FAM(SUBRACE) + RESIDUAL \quad (1)$$

where Y is a vector of observations for the trait, MEAN is the mean of the trait, BLOCK are the block effects fitted as a fixed factor, HEIGHT are the height of disc extraction effects (expressed as a percentage of tree height) fitted as a covariate, DECAY are the decay effects (i.e. two levels: decay removed and decay not removed) fitted as a fixed factor, SUBRACE are the subrace effects fitted as a fixed factor, *FAM(SUBRACE)* are the family within subrace effects fitted as a random factor and *RESIDUAL* is a vector of residuals.

Initially, replicate within block was fitted as a random factor but this term was not included in the model used for final analyses, as it was not significant in any trait. Furthermore, analysis of DECAY as a dependent binary variable using a probit link function did not reveal a significant subrace or family within subrace effect, indicating that DECAY could be fitted as an explanatory variable in the analysis of basic density and gross shrinkage without introducing significant bias according to a genotype's propensity to exhibit decay.

Overall and subrace least-squares means were estimated for each trait. These were estimated for 12% of tree height assuming no decay was removed from samples, using the PREDICT statement in ASReml (GILMOUR *et al.,* 2006). The significance of the SUBRACE term in each analysis was gauged with an F-test using the degrees of freedom associated with the *FAM(SUBRACE)* term as the denominator degrees of

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freedom. For traits in which the SUBRACE term was significant, Tukey-Kramer honest significant difference tests were undertaken to elucidate which subraces were significantly different to each other.

Additive variance (σ^2_a), phenotypic variance (σ^2_p), narrow-sense open-pollinated heritability (h^2_{op}) and coefficient of additive genetic variance (CV_a) were estimated as follows:

$$\sigma^2_a = \frac{\sigma^2_f}{r} \quad (2)$$

$$\sigma^2_p = (\sigma^2_f + \sigma^2_e) \quad (3)$$

$$h^2_{op} = \frac{\sigma^2_a}{\sigma^2_p} \quad (4)$$

$$CV_a = 100 \times \frac{\sqrt{\sigma^2_a}}{\bar{x}} \quad (5)$$

where σ^2_f is the family within subrace variance, σ^2_e is the residual variance, r is the coefficient of relationship which was fixed to 0.4 to account for an assumed selfing rate of 30% (GRIFFIN and COTTERILL, 1988), and $\bar{x}$ is the trait least-squares mean estimated for 12% of tree height with no decay. The significance of the family within subrace variance and, by implication, additive variance for each trait was tested with a one-tailed likelihood ratio test (GILMOUR *et al.,* 2006).

Intertrait Pearson's correlation coefficients among subrace least square means, herein referred to as 'subrace correlations', were calculated using the PROC CORR procedure in SAS™ (Version 9.1). Intertrait Pearson's correlation coefficients among phenotypic observations were calculated in the same manner. Two-tailed t-tests were used to test subrace and phenotypic correlations against zero.

A bivariate model, which extended the univariate model and estimated covariation between family and residual effects, was used to estimate pairwise within-subrace family correlations between traits and drying treatments (GILMOUR *et al.,* 2006). As families in the trial were open pollinated, estimates of 'family correlations' were considered equivalent to estimates of within-subrace additive 'genetic correlations' (FALCONER and MACKAY, 1996). One-tailed likelihood ratio tests were used to determine if genetic correlations were significantly different to one or minus one (GILMOUR *et al.,* 2006). Two-tailed t-tests were undertaken to test if genetic correlations were significantly different to zero, because difficulties with convergence precluded the use of likelihood ratio tests. Analyses were conducted using ASReml (GILMOUR *et al.,* 2006) and SAS™ (Version 9.1).

Results

Mean gross shrinkage increased with drying temperature. Mean radial gross shrinkage was less than calliper- and volume-assessed gross shrinkage under all drying treatments (*Table 1*).

Significant ($P < 0.05$) differences between subraces were observed using all measures of gross shrinkage for two or more of the three drying treatments (*Table 1*). When dried at 105 °C, Strzelecki Ranges exhibited the least, and King Island and Cape Patton the most, gross shrinkage regardless of assessment method (*Table 2*). Between these extremes, subraces were not significantly different to each other in radial gross shrinkage and the ranking of subraces for calliper-, visually- and volume-assessed gross shrinkage were broadly consistent. Dif-

Table 1. – Trait least-squares mean, F-ratio and significance level of differences among subraces, within-subrace additive variance and level of significance, phenotypic variance, narrow sense heritability, and coefficient of additive genetic variation (CV_a) for each trait and drying treatment. Least-squares means are estimates for 12% of tree height and no decay.

Trait	Drying treatment. (°C)	Least-squares mean (s.e.)	F-ratio and significance level of differences among subraces	Additive variance (s.e.)	Phenotypic variance (s.e.)	h^2_{op} (s.e)	CV_a (%)
Calliper-assessed (%)	22	15.5 (0.4)	1.5 ^{ns}	5.4 (3.5) ns	15.4 (1.4)	0.35 (0.22)	15.0
tangential gross shrinkage	60	23.5 (0.4)	2.2 *	10.3 (4.1) **	17.5 (1.7)	0.59 (0.21)	13.6
	105	28.4 (0.4)	3.4 ***	6.9 (4.2) *	19.0 (1.8)	0.36 (0.21)	9.2
Visually-assessed	22	NA	1.1 ^{ns}	0.32 (0.17) *	0.75 (0.07)	0.43 (0.21)	NA
tangential gross shrinkage	60	NA	3.8 ***	0.33 (0.17) *	0.71 (0.07)	0.47 (0.22)	NA
	105	NA	4.5 ***	0.29 (0.15) *	0.66 (0.06)	0.44 (0.21)	NA
Volume-assessed (%)	22	17.4 (0.2)	2.0 *	0.9 (0.7) ns	3.3 (0.3)	0.28 (0.22)	5.5
gross shrinkage	60	23.5 (0.3)	2.8 **	2.5 (1.8) ns	8.0 (0.7)	0.31 (0.22)	6.7
	105	27.6 (0.3)	3.1 **	2.9 (2.0) ns	8.7 (0.8)	0.33 (0.22)	6.2
Radial (%) gross shrinkage	22	5.0 (0.1)	2.3 *	0.1 (0.2) ns	1.1 (0.1)	0.11 (0.23)	6.8
	60	6.9 (0.1)	1.9 ^{ns}	0.0 (0.0) ns	2.0 (0.2)	0.00 (0.00)	0.0
	105	8.0 (0.2)	2.5 *	0.1 (0.6) ns	2.6 (0.2)	0.05 (0.22)	4.6
Basic density (kg m^{-3})		513 (3)	2.3 *	749 (305) **	1288 (124)	0.58 (0.21)	5.3

^{NA} Not applicable as data was normalised to have mean of zero.
^{ns} Not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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ferences between subraces in basic density were also found to be significant. Strzelecki Ranges and Flinders Island had the highest basic density and King Island and Southeast Tasmania the lowest (*Table 2*).

Significant additive variation within subraces was observed in calliper- and visually-assessed gross shrinkage under all drying treatments, except 22 °C for calliper-assessment (*Table 1*). Estimates of heritability for

Table 2. – Subrace means (and standard errors) for measurements of gross shrinkage in samples dried at 105 °C and basic density. Subraces with common letters for the same trait are not significantly different at $P < 0.05$ following Tukey-Kramer adjustment for multiple comparisons.

Subrace	Gross shrinkage				Basic density
	Calliper-assessed tangential (%)	Visually-assessed tangential	Volume-assessed (%)	Radial (%)	(kg m^{-3})
Cape Patton	31.3 (1.1) e	0.49 (0.22) cd	29.2 (0.8) c	9.0 (0.4) b	516 (10) abc
Eastern Otways	26.8 (1.1) ab	-0.17 (0.20) ab	26.4 (0.7) a	7.9 (0.4) a	518 (9) bc
Flinders Island	28.3 (0.9) abcd	-0.03 (0.18) bc	27.5 (0.6) abc	7.5 (0.3) a	520 (8) c
King Island	30.2 (0.9) de	0.58 (0.17) d	29.1 (0.6) c	8.8 (0.3) b	493 (8) a
Southern Furneaux	26.6 (1.1) a	-0.29 (0.21) ab	26.6 (0.7) ab	8.0 (0.4) ab	517 (9) bc
Southern Tasmania	27.9 (1.1) abcd	-0.01 (0.20) bc	26.9 (0.7) ab	7.8 (0.4) a	517 (9) bc
South-eastern Tasmania	29.5 (1) bcde	0.38 (0.19) cd	28.4 (0.7) bc	8.1 (0.4) ab	495 (9) ab
Strzelecki Ranges	26.0 (0.8) a	-0.48 (0.15) a	26.2 (0.5) a	7.4 (0.3) a	531 (7) c
Western Otways	27.3 (0.9) abc	-0.17 (0.18) ab	26.9 (0.6) ab	8.0 (0.3) a	513 (8) abc
Western Tasmania	29.8 (1.1) cde	0.43 (0.2) cd	28.4 (0.7) bc	7.8 (0.4) a	511 (9) abc

Table 3. – Subrace, genetic and phenotypic correlations (and standard errors) between temperature treatments for each measure of gross shrinkage.

Drying treat. 1	Drying treat. 2	Trait	Correlation		
			Subrace	Genetic	Phenotypic
22°C	60°C	Calliper-assessed (%)	0.83 (0.20)**	1.10 (0.16)*** §	0.74 (0.04)***
		Visually-assessed	NA	0.89 (0.14)***	0.74 (0.04)***
		Volume-assessed (%)	0.92 (0.14)***	0.90 (0.14)***	0.85 (0.03)***
		Radial (%)	0.98 (0.07)***	NA	0.80 (0.04)***
22°C	105°C	Calliper-assessed (%)	0.73 (0.24)*	1.15 (0.31)*** §	0.53 (0.05)***
		Visually-assessed	NA	0.75 (0.20)***	0.61 (0.05)***
		Volume-assessed (%)	0.86 (0.18)**	0.93 (0.21)***	0.73 (0.04)***
		Radial (%)	0.95 (0.11)***	NA	0.72 (0.05)***
60°C	105°C	Calliper-assessed (%)	0.96 (0.10)***	0.97 (0.09)***	0.84 (0.03)***
		Visually-assessed	0.98 (0.07)***	0.89 (0.09)***	0.86 (0.03)***
		Volume-assessed (%)	0.97 (0.09)***	1.01 (0.06)*** §	0.92 (0.03)***
		Radial (%)	0.95 (0.11)***	NA	0.83 (0.04)***

NA Correlations were not calculated if one or more of the traits being compared did not reveal significant genetic variation among subraces or families within subraces at the $P = 0.200$ level.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

§ Correlation estimate is outside the parameter space.

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Table 4. – Subrace, genetic and phenotypic correlations (and standard errors) among measures of gross shrinkage under the 105 °C drying treatment.

Gross shrinkage measurement 1	Gross shrinkage measurement 2	Subrace	Genetic	Phenotypic
Calliper-assessed (%)	Visually-assessed	0.97 (0.09)***	0.95 (0.09)***	0.86 (0.03)***
Calliper-assessed (%)	Volume-assessed (%)	0.98 (0.07)***	1.36 (0.33)*** §	0.67 (0.05)***
Calliper-assessed (%)	Radial (%)	0.75 (0.23)*	NA	0.22 (0.06)***
Visually-assessed	Volume-assessed (%)	0.97 (0.09)***	1.12 (0.19)*** §	0.74 (0.04)***
Visually-assessed	Radial (%)	0.73 (0.24)*	NA	0.34 (0.06)***
Volume-assessed (%)	Radial (%)	0.77 (0.23)**	NA	0.50 (0.06)***

NA Correlations were not calculated if one or more of the traits being compared did not reveal significant genetic variation among families within subraces at the P = 0.200 level.
* P < 0.05, ** P < 0.01, *** P < 0.001.
§ Correlation estimate is outside the parameter space.

these traits were all greater than or equal to 0.35. Coefficients of additive genetic variation were greatest for the calliper assessment method. There was no obvious trend in heritabilities or coefficients of additive genetic variation with drying temperature. No significant additive genetic variation within subrace was observed in volume-assessed (P = 0.108, 0.082 and 0.066 under the 22 °C, 60 °C and 105 °C drying treatments respectively) or radial gross shrinkage (P = 0.320, 0.500 and 0.405 respectively). However, significant additive genetic variation within subrace was observed in basic density.

All calculated subrace, genetic and phenotypic correlations for gross shrinkage among drying treatments were positive and significantly different to zero (*Table 3*). Excluding radial gross shrinkage measurements, no genetic correlations between drying treatments were significantly different to one (P ≥ 0.076). Some of these estimated genetic correlations were outside the parameter space (i.e. they were greater than one), probably due to the relatively small sample size. However, the hypothesis that genetic correlations between drying treatments were positive and strong was further supported by strong and positive (≥ 0.60) Pearson correlations between family within-subrace best linear unbiased predictions (BLUPs) derived from univariate analyses (data not shown).

Although moderate to strong using all methods of gross-shrinkage assessment, phenotypic correlations were lowest (0.53–0.72) between the least similar drying treatments (i.e. 22 °C and 105 °C). Phenotypic correlations between the oven-dried treatments (i.e. 60 °C and 105 °C) were greater than or equal to 0.83.

Correlations among measurement techniques were examined under the 105 °C drying treatment, the treatment most commonly adopted in breeding programs as it is used to assess basic density (Downes *et al.,* 1997; Raymond and Apiolaza, 2004). Subrace correlations between measures of gross shrinkage were positive and significantly different to zero (*Table 4*). However, correlations with radial gross shrinkage were not as strongly positive (≤ 0.77) as those among other measurement techniques, which were all very close to one (≥ 0.97).

Genetic correlations between measures of calliper-, visually- and volume-assessed gross shrinkage were all greater than or equal to 0.95 and significantly different to zero but not significantly different to one (P ≥ 0.065; *Table 4*). Although some estimated genetic correlations were outside the parameter space, Pearson correlations between family within subrace BLUPs were 0.72 or greater, supporting the hypothesis that additive genetic relationships among these traits were strong (*Figure 1*).

All phenotypic correlations among measurement techniques were positive and significantly different to zero (*Table 4*). However, correlations with radial gross shrinkage were weaker than those among other measurement techniques.

All subrace correlations between basic density and measures of gross shrinkage assessed on samples dried

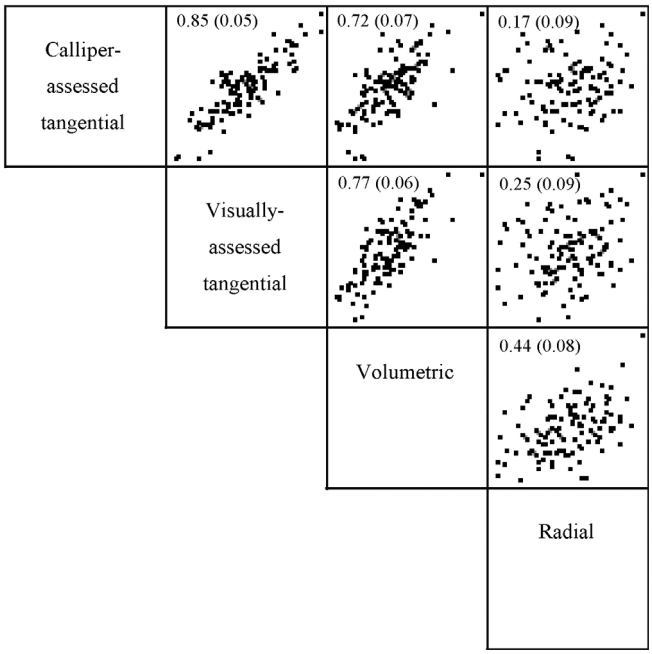

Figure 1. – Scatter matrix of family within subrace best linear unbiased predictions (BLUPs) for measurements of gross shrinkage under the 105 °C drying treatment derived from univariate analyses. Pearson correlations (and standard errors) between family BLUPs are shown.

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Table 5. – Correlations (and standard errors) between sample basic density and measures of gross shrinkage in samples dried at 105 °C.

Trait	Correlation		
	Subrace	Genetic	Phenotypic
Calliper-assessed (%)	-0.60 (0.28)^{ns}	-0.88 (0.27)**	-0.50 (0.05)***
Visually-assessed	-0.75 (0.23)*	-0.63 (0.24)**	-0.51 (0.05)***
Volume-assessed (%)	-0.68 (0.26)*	-0.49 (0.35)^{ns}	-0.35 (0.06)***
Radial (%)	-0.59 (0.29)^{ns}	NA	-0.27 (0.06)***

^{NA} Correlations were not calculated if one or more of the traits being compared did not reveal significant genetic variation among families within subraces at the P=0.200 level.
^{ns} Not significantly different to zero, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

at 105 °C were negative (*Table 5*) but only correlations with visually- and volume-assessed gross shrinkage were significantly different to zero. The genetic correlations of basic density with calliper- and visually-assessed gross shrinkage were strongly negative and significantly different to zero and neither was significantly different to minus one ($P \geq 0.083$). Phenotypic correlations between basic density and all gross shrinkage traits were negative and significantly different to zero.

Discussion

Drying treatments

Although normal shrinkage was confounded with collapse in this study of gross shrinkage, it is likely that only small differences in normal shrinkage were present among drying treatments, because samples were allowed to stabilise to equilibrium moisture content in a common environment prior to gross shrinkage measurement. The observed increase in gross shrinkage at higher drying temperatures was consistent with there being greater collapse in wood dried under more harsh conditions (CHAFE, 1992). However, even under the mildest drying treatment (i.e. 22 °C), gross shrinkage was substantially greater than previous estimates of normal shrinkage in *E. globulus* 12-mm wood cores (RAYMOND *et al.,* 2004), indicating the presence of collapse and or tension wood. Accordingly, the findings of this study may not be applicable to very mild drying treatments, under which little or no collapse might be expressed.

Although the 105 °C drying treatment was the only drying treatment to reveal significant subrace difference for all measures of gross shrinkage, the strongly positive subrace and genetic correlations among drying treatments indicated that the relative performances of genotypes were similar across treatments. From a practical perspective, this indicates that different drying treatments could be used interchangeably in breeding programs with little reduction in selection efficiency and that breeders could adopt drying treatments according to the requirements of other selection traits. For example, the 105 °C drying treatment would be appropriate if basic density was to be assessed but inappropriate if near infrared spectroscopy (NIR) was to be undertaken on samples after drying (DOWNES *et al.,* 1997).

In a study of *E. nitens* shrinkage properties, additive genetic variation in volume-assessed gross shrinkage was principally explained by additive genetic variation in recoverable collapse (HAMILTON *et al.,* 2009). It is likely that this is also the case in *E. globulus*. However, a study designed to examine genetic variation in the separate components of gross shrinkage is required to definitively determine the underlying reasons for the strong genetic correlations observed in gross shrinkage among drying treatments.

Genetic variation in gross shrinkage

The significant differences between subraces in all measures of gross shrinkage indicated that gross shrinkage could be reduced through subrace selection. Furthermore, significant additive variances and moderate to very high heritabilities in calliper- and visually-assessed gross shrinkage indicated that tangential gross shrinkage was under strong additive genetic control and could be reduced through selection within subraces. In addition, the very strong subrace, genetic and phenotypic correlations between these two methods of assessment indicated that these measurement techniques could be used interchangeably in breeding programs with little reduction in selection efficiency. However, both calliper- and visual assessment of gross shrinkage were time consuming in samples that did not exhibit visually obvious shrinkage (e.g. in samples dried under the 22 °C drying treatment), as it was difficult to rank samples or identify points of maximum shrinkage. Furthermore, the visual-assessment technique would not allow comparison of gross shrinkage levels across generations, sites or ages as it is based on a ranking of samples rather than a quantified measure of the magnitude of gross shrinkage.

The very strong subrace, genetic and phenotypic correlations of volume-assessed gross shrinkage with calliper- and visually-assessed gross shrinkage implied that volume-assessment could also be used to select against tangential gross shrinkage. However, additive genetic variance within subraces in volume-assessed gross shrinkage was not significant in this study, although a significant difference between subraces was observed. This method has revealed significant additive genetic variation in *E. nitens* (HAMILTON *et al.,* 2004; HAMILTON *et al.,* 2009) and a larger-scale study is

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required to definitively determine the extent to which volume-assessed gross shrinkage is under additive genetic control in *E. globulus*, particularly given that volume assessment has practical advantages over other measurement techniques. Volume-assessment is rapid, particularly if green-sample volumes are already assessed for the purpose of density measurement, and does not require the visual identification of points of maximum shrinkage.

The lack of significant additive genetic variation in radial gross shrinkage indicated that selection within subraces for reduced radial gross shrinkage would not result in significant genetic gains and, by implication, that selection within subraces for reduced tangential gross shrinkage would reduce the difference between tangential and radial gross shrinkage (i.e. shrinkage anisotropy). Shrinkage anisotropy is the principal cause of cupping in backsawn boards and can result in face checking if boards are restrained from cupping (Svensson and Martensson, 1999). However, it is possible that additive genetic variation was present in radial gross shrinkage but not detected in this study due to the relatively small sample size.

Relationship between gross shrinkage and basic density

The relative performances of subraces in terms of basic density were broadly consistent with previously published results (Dutkowski and Potts, 1999; Muneri and Raymond, 2000; Lopez *et al.,* 2001). Estimates of heritability for basic density were also similar to previous estimates (Volker *et al.,* 1990; MacDonald *et al.,* 1997; Muneri and Raymond, 2000; Raymond *et al.,* 2001; Lopez *et al.,* 2002).

The negative subrace, genetic and phenotypic correlations between basic density and measures of gross shrinkage were consistent with the hypothesis that much of the gross shrinkage observed in this study was due to collapse. In other eucalypt species, trees of relatively low basic density have generally been observed to exhibit relatively high levels of collapse and low levels of normal shrinkage (Chafe, 1992; Ilic, 1999; Hamilton *et al.,* 2009). The strongly negative genetic correlations between basic density and calliper- and visually-assessed gross shrinkage indicated that selection for increased basic density, as currently takes place in pulpwood breeding programs (Raymond and Apiolaza, 2004), would result in a favourable correlated response in tangential gross shrinkage. Significant and negative genetic correlations between core gross shrinkage and basic density have also been observed in *E. nitens* (Hamilton *et al.,* 2004; Kube and Raymond, 2005). Although these findings indicate that indirect genetic gains could be achieved in both tangential gross shrinkage and basic density by selecting trees according to either trait, direct assessment for both traits may be justified in breeding programs given the low cost of the laboratory-based component of their assessment.

In conclusion, subrace and within subrace selection against tangential gross shrinkage is likely to result in significant genetic gains in *E. globulus*. Although a larger-scale study is required to definitively determine the extent of within-subrace genetic variation in volume-assessed gross shrinkage, the very strong genetic correlations observed among calliper-, visually and volume-assessed gross shrinkage indicated that practical considerations should determine which of these methods of assessment is adopted for breeding purposes. None of the measurement techniques examined required specialised skills or equipment but the assessment of volumetric shrinkage was the most rapid of those examined for samples lacking visually-obvious gross shrinkage, such as those dried under the 22°C drying treatment. Although there was significant variation at the subrace level in radial gross shrinkage, there was no evidence of exploitable within subrace genetic variation in this trait, suggesting that selection against tangential shrinkage is also likely to reduce shrinkage anisotropy. Strong subrace and genetic correlations among drying treatments indicated that they could be adopted interchangeably in breeding programs with little reduction in selection efficiency. There was evidence that selection for increased basic density would result in a correlated reduction in gross shrinkage which has favourable implications for genetic improvement programs with concurrent pulpwood and solid-wood breeding objectives.

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