Annals of Forest Science (2013) 70:461–470
DOI 10.1007/s13595-013-0277-9

ORIGINAL PAPER

Assessing genetic variation to improve stem straightness in *Eucalyptus globulus*

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Received: 14 August 2012 / Accepted: 21 February 2013 / Published online: 26 April 2013

Abstract
• ***Context*** Stem straightness is an important trait for growers and processors of *Eucalyptus globulus* logs for solid-wood products.
• ***Aims*** The aims of the study were to determine the extent of genetic variation in stem deviation from straightness in *E. globulus* and assess the utility of a six-point subjective scoring method as a selection criterion for stem straightness.
• ***Methods*** Two *E. globulus* progeny trials, grown under solid-wood product regimes, were studied. At age 9 years (post-thinning), stem straightness was measured using both image analysis and a six-point subjective scale. Diameter at breast height (DBH; 1.3 m) was measured at both age 5 (pre-thinning) and age 9 years.
• ***Results*** Significant additive genetic variation was observed. Strong, positive and significant additive genetic correlations were observed between the stem straightness assessment methods and between DBH at ages 5 and 9 years. Significant positive genetic correlations were shown between subjectively scored stem straightness and DBH at both ages 5 and 9 years.
• ***Conclusion*** The six-point subjective scoring method is a cost-effective selection criterion for stem straightness in *E. globulus*. The image measurement technique may be applied where objective estimates of stem straightness are required, for training purposes and to verify subjective scores.

Keywords *Eucalyptus globulus* · Heritability · Correlation · Stem straightness · Image analysis

Handling Editor: Jean-Michel Leban

Contribution of co-authors Dr. Matthew G. Hamilton performed the advanced statistical analyses, offered advice on general data analysis and reviewed and commented on successive drafts of the paper.
Dr. Chris E. Harwood helped coordinate the research project, reviewed and commented on successive drafts of the paper.
Dr. Thomas G. Baker coordinated the research project and assisted in the trial's design and establishment.
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1 Introduction

Eucalyptus globulus is a hardwood species that is widely planted in temperate regions of the world. Over two million ha has been established globally, principally in Australia, Chile, Portugal, Spain and Uruguay (Potts et al. 2004). Most plantations of these plantations are grown for pulpwood production, but there is increasing recognition of the need to produce high-quality plantation-grown timber for solid-wood products (Nolan et al. 2005; Beadle et al. 2007; Washusen 2011). *E. globulus* timber from natural forests has been used for both structural and high-value architectural products in Australia (Bootle 2005). Studies have also shown that, on productive sites, thinned and pruned *E. globulus* plantations can produce high-quality logs for sawn timber and veneer on a rotation of 20–25 years (Washusen et al. 2004; Touza Váquez and Sanz Infante 2002). In Australia alone, over 5,000 ha of plantation *E. globulus* is managed for these products (Wood et al. 2009).

Economic performance in solid-wood production largely depends on the yield of high-grade sawn timber recovered from logs (Washusen 2011), which is partially determined

by stem size and straightness (Ivkovic et al. 2007; Blackburn et al. 2011; Callister et al. 2011). In most sawmills, increasing log diameter and straightness will result in an increased recovery of green sawn timber as a percentage of log volume (Blackburn et al. 2011; Innes et al. 2008; Washusen 2011). Log diameter largely determines the sawing pattern applied, potentially affecting the recovery of dried timber, product quality and product value. Each sawmilling system has a maximum acceptable log sweep (the deviation of the longitudinal axis of a log from a straight line) above which logs are not sawn and are diverted for use in lower-value products (Washusen and Innes 2007). For example, in a modern linear-flow multi-saw system, in which logs are processed in a single pass through a single machine with multiple blades, a maximum stem deviation from straightness of 20 % of small-end diameter over the length of a sawlog is commonly applied (Blackburn et al. 2011). Higher volume recoveries are also achieved from straighter logs in rotary peeled veneer sheet production (Blackburn et al. 2012). If logs are straight, a greater number of veneer billets can potentially be cut from each log and the extent of 'rounding-up' required on each billet before a veneer sheet can be extracted is minimised (Zbonak et al. 2012).

Stem form may also impact on wood properties. For example, *E. globulus* is susceptible to the formation of tension wood, where lignin is mostly absent in the wood cell at localised areas in the tree stem (Washusen 2002). Tension wood develops as a stem re-orients itself, or in response to external bending stresses such as those imposed by prevailing winds (Washusen 2002). While the presence of tension wood in vertically oriented, straight *E. globulus* trees has been demonstrated (Washusen 2002), it was more prevalent in non-vertical *E. globulus* stems in Spanish plantations (Touza Váquez and Sanz Infante 2002). The presence of tension wood in logs can result in distortion defects in sawn boards that have a major impact on the volume of high-grade solid-wood recovered through processing and drying (Washusen 2011).

Subjective visual scoring methods have been widely adopted for the assessment of stem straightness in tree breeding trials (Macdonald et al. 2009). Subjective scoring systems with different numbers of categories have been used to assess stem straightness in *E. globulus* (Lopez et al. 2002; Greaves et al. 2004b; Callister et al. 2011) and other species (Barnes and Gibson 1986; Cooper and Ferguson 1981). Cotterill and Dean (1990) recommended a subjective six-point scoring system from one (least straight) to six (straightest). This type of system is implemented for a trial by visually determining the stem straightness class boundaries in that trial prior to the commencement of assessment that should produce approximately normally distributed frequencies with an approximate mean of 3.5. Therefore, approximately 33 % of trees should be assigned scores 3 and 4, 15 % assigned scores 2 and 5 and 2 % assigned scores of 1 and 6. Validation and communication among assessors prior to and during assessment is important in establishing and maintaining consistency among the assessors when subjectively assessing traits (Macdonald et al. 2009). Cotterill and Dean (1990) demonstrated that the six-point scoring scale produced higher heritabilities and large phenotypic variances, indicating good discrimination of stem straightness, when compared to alternatives such as three-point and nine-point scales.

The six-point subjective scoring method can be performed quickly at low cost, but the relationship between subjective scores and true deviations from straightness is trial- and time-dependent and therefore differences in the mean and variance of true deviations from straightness among trials and within individual trials at different ages are not quantified using the six-point subjective scoring technique. Furthermore, the genetic correlation between the six-point subjective score and the true deviation from straightness has, to date, not been quantified in *E. globulus*, although there have been attempts to quantify subjective scores using direct measurements methods in Sitka spruce (*Picea sitchensis*) (Macdonald et al. 2009) and loblolly pine (*Pinus taeda*) (Williams and Lambeth 1988). Photogrammetric methods using digital cameras to create three-dimensional images of trees have also been used to examine tree stem profiles (Hapca et al. 2007). The methods are precise, but time-consuming, with the fastest individual tree assessment taking 30 min per tree. In a later study in Norway spruce (*Picea abies*) employing these techniques (Hapca et al. 2008), the same researchers concluded that although the photogrammetric method provided superior precision, implementation in forest practices would require a faster methodology.

The primary aim of this study was to examine the genetic architecture of stem straightness in *E. globulus* and to assess the utility of the six-point subjective score as a selection criterion in breeding programmes. To this end, a relatively fast two-dimensional photogrammetric technique to measure true deviation from stem straightness in standing stems was developed. Two progeny trials planted on sites with contrasting rainfall, evaporation and aspect were assessed using this technique to examine additive and non-additive genetic variation and the strength of inter-site correlations. Inter-trait genetic correlations with a six-point subjective straightness score and diameter at breast height over bark (DBH), a standard selection criterion in *E. globulus* breeding programmes, were also estimated.

2 Materials and methods

2.1 Trials

The study was undertaken on two Southern Tree Breeding Association advanced-generation *E. globulus* progeny trials

planted in Victoria, Australia, in mid-2002. The trial sites represented differing climatic conditions. One trial site was near Condah in Western Victoria and the other near Boolarra in South Gippsland (Table 1). The Condah trial was comprised of 124 families and the Boolarra trial 104 families. There were 27 full-sib control-pollinated and 27 open-pollinated families common to both trials (Table 2). The trials were row-column designs (Williams et al. 2002), with five replicates at Boolarra and eight replicates at Condah, and three-tree row-plots of each family in each replicate. Initial spacing at both sites was 4 m between rows and 2.25 m between trees within rows (i.e. 1,111 trees ha^{-1}).

2.2 Establishment of solid-wood silvicultural treatments

The trials were thinned, retaining one tree per plot, based on the following criteria: firstly, stem straightness; secondly, stem size (diameter) and finally uniformity of spacing relative to retained trees in adjacent plots, such that all retained trees were separated by at least 4.5 m along the rows. Trees to be retained were pruned prior to thinning, with both operations completed at Condah at age 4 years and 10 months and at Boolarra at 4 years and 11 months. Pruning was completed in one lift to a height of 6.5 m, with the exception that no more than 50 % by length of the live crown was removed on shorter retained trees. Buffer rows immediately surrounding the trials were similarly thinned to retain one tree in three.

2.3 Trial assessments

Prior to thinning and pruning, DBH was measured with a diameter tape at 1.3 m above ground level, at Condah at age 4 years and 6 months and at Boolarra at 4 years and 7 months (both denoted as DBH5). In May 2011 at an age of 9 years, all remaining trees in both trials were re-measured for DBH (DBH9) and a photographic image of each tree captured for stem straightness assessment. Photographs were taken of all trees using a Nikon coolpix S3000 compact digital camera positioned 5 m from the tree at 1.3 m height and perpendicular to the plane of maximum deviation from straightness (Fig. 1), when observed from a 180° visual examination of the tree. A height stick with precise markings 1,000 mm apart centred on camera height was held vertically next to the tree (Fig. 1) and used as a calibration reference in later image analysis.

Using the photographs, the stems were subjectively assessed according to the commonly used six-point subjective scoring method of Cotterill and Dean (1990). Image analysis software (Bersoft 2012) was then used to measure stem straightness deviation (expressed as millimetres per metre deviation of stem), assessed over a length of 5 m from the base of each stem.

Table 1 Site details

	Boolarra, Victoria	Condah, Victoria
Latitude	38°27′S	37°55′S
Longitude	146°17′E	141°42′E
Altitude above sea level (m)	268	125
Slope (%)	10–20	<5
Aspect	Southeast	–
Mean daily max. temperature—January (°C)	22.6	23.9
Mean daily min. temperature—January (°C)	11.5	10.8
Mean daily max. temperature—July (°C)	10.7	12.4
Mean daily min. temperature—July (°C)	4.6	4.6
Annual rainfall (mm)	1,106	741
Annual pan evaporation (mm)	1,070	1,287
Annual radiation ($MJ\,m^{-2}$)	5,486	5,588

Average climatic data estimated using ESOCLIM (Houlder et al. 2000)

Table 2 Genetic contribution (expressed as a percentage) of genetic groups to full-sib control-pollinated progeny and open-pollinated progeny in the Boolarra and Condah trials at the time of planting

	Boolarra		Condah	
	Control pollinated	Open pollinated	Control pollinated	Open pollinated
Genetic group (% contribution)				
Flinders Island	12.0	2.3	19.6	–
King Island	1.7	–	0.3	–
Otways	10.0	1.4	11.3	–
Southern Furneaux	12.3	1.5	24.3	–
Strzelecki	4.2	1.1	10.3	–
Tasmania	11.4	1.6	4.7	–
Portuguese breeding population	–	32.7	–	28.6
Australian seed orchards	–	7.9	–	–
Unknown	–	–	1.0	
	51.6	48.5	70.5	28.6
Standing progeny (count)				
Age 5, pre-thinning	495	723	1,158	1,019
Age 9, post-thinning	199	260	429	375
Families (count)	47	49	68	54

The total number of control-pollinated and open-pollinated progeny standing in the trials (at age 5 years pre-thinning and at age 9 years post-thinning) and number of families represented are also shown

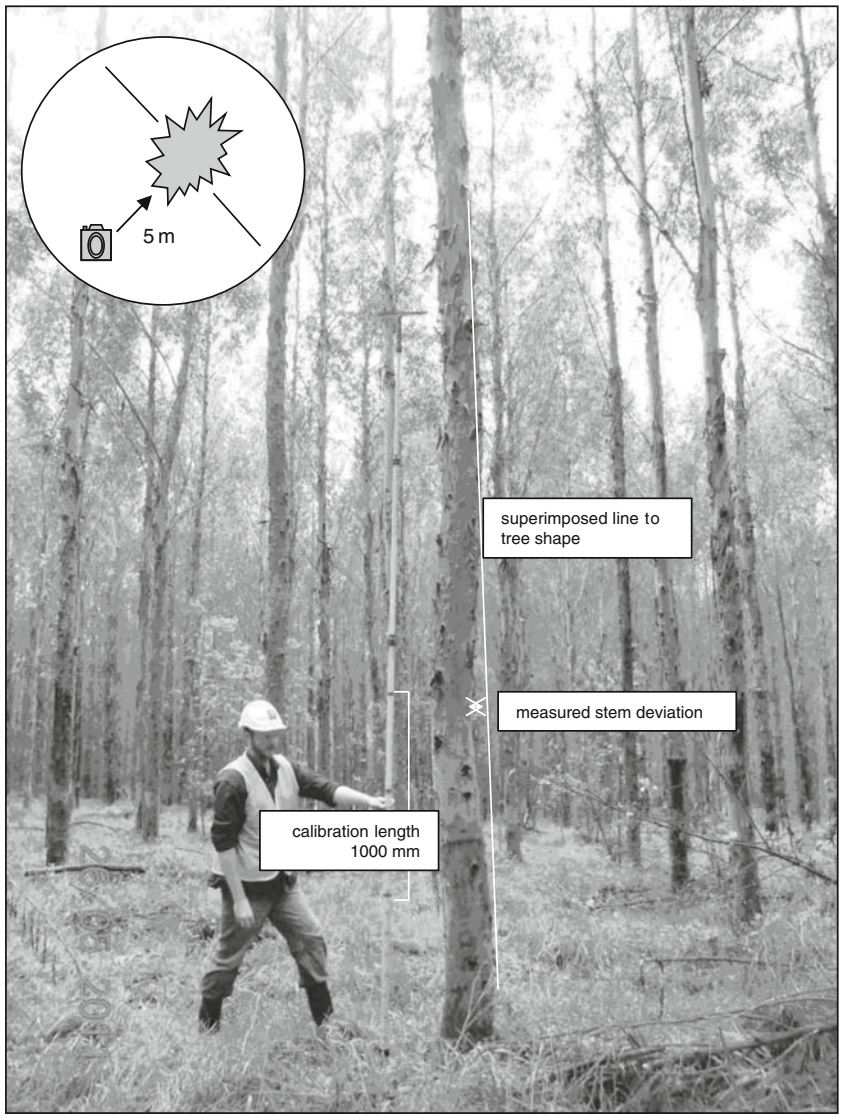

Fig. 1 Measurement of stem deviation from an axially straight line over 5 m using image analysis. The *inset* shows the position of the camera used to capture the image perpendicular to the plane of greatest stem deviation from straightness

2.4 Statistical analyses

Based on the distribution of residuals in preliminary analyses and to achieve an approximately normal distribution of residuals in final analyses, stem deviation measurements were $\log_{10}$-transformed. To estimate variance components, univariate restricted maximum likelihood (REML) analyses were undertaken separately for each trait and trial site using the following linear mixed model:

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \quad (1)$$

where **y** is the vector of trait observations, **b** is a vector of fixed effects with its design matrix **X**, **u** is a vector of random effects with its design matrix **Z**, and **e** is the vector of random residual terms. The models included as fixed effects in **b** the overall mean, replicate and genetic group. The overall mean and replicate effects were fitted as factors, but genetic contributions from each genetic group, expressed as a proportion of the genes in each tree, were fitted as separate covariates by modifying the design matrix **X**. The random effects in **u** were row within replicate, column within replicate, plot within replicate (pre-thinning DBH only), family (control-pollinated families only, to account for specific combining ability effects) and the additive genetic effect. Family and additive genetic effects were estimated within genetic groups to account for past selection in the 'Portuguese breeding population' and 'Australian seed orchards' genetic groups (Table 2) and geographic patterns in genetic variation among native populations (Flinders Island, King Island, Otways, Southern Furneaux, Strzelecki and Tasmania; Table 2) in a manner that is consistent as possible with other studies of *E. globulus* and active breeding programmes.

Individuals of unknown pedigree, which made up 1 % of the Condah trial (Table 2), were excluded from analyses.

Cross type (i.e. open-pollinated c.f. control-pollinated) was not fitted in the model as this effect was confounded with genetic group—all open-pollinated families received either all their genes from the 'Portuguese Breeding Population' genetic group or half of their genes (i.e. the male parent) from the 'Australian Seed Orchards' genetic group and neither of these genetic groups contributed genes to any control-pollinated cross (Table 2).

It was assumed that the joint distribution of the random terms was multivariate normal with the following means and (co)variances:

$$\begin{bmatrix} u \\ e \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix} \right) \tag{2}$$

where **G** is a (co)variance matrix corresponding to **u**, **R** is a (co)variance matrix corresponding to **e** and 0 is a null matrix. The (co)variance matrix **G** was defined as $\mathbf{G_r} \oplus \mathbf{G_c} \oplus \mathbf{G_p} \oplus \mathbf{G_f} \oplus \mathbf{G_a}$, where $\mathbf{G_r} = \sigma^2_{\mathrm{r}} I$, $\mathbf{G_c} = \sigma^2_{\mathrm{c}} I$, $\mathbf{G_p} = \sigma^2_{\mathrm{p}} I$, $\mathbf{G_f} = \sigma^2_{\mathrm{f}} I$, $\mathbf{G_a} = \sigma^2_{\mathrm{a}} A$, and $\oplus$ is the direct sum operation (i.e. model terms in **u** were assumed to be independent). Furthermore, $R = \sigma^2_e I$ and σ^2_r is the row within replicate variance, σ^2_c is the column within replicate variance, σ^2_p is the plot within replicate variance, σ^2_f is the family (i.e. specific combining ability, SCA) variance, σ^2_a is the additive genetic variance, σ^2_e is the residuals variance, **A** is the numerator relationship matrix and **I** is an identity matrix with dimensions equal to the levels of the random term in question. The **A** matrix was modified (Dutkowski and Raymond 2001) to take account of an assumed selfing rate of 30 % in *E. globulus* open-pollinated families (Volker et al. 1994). The significance at the $P<0.05$ level of the family and additive genetic variance for each trait was tested with a one-tailed likelihood ratio test (Gilmour et al. 2009). Due to the different levels of selection among genetic groups and the potential for the confounding of genetic group and cross-type (i.e. open-pollinated and control-pollinated) effects, tests of differences among genetic groups were undertaken excluding open-pollinated data (Table 2) using a Wald *F* test.

For each trait, the narrow-sense heritability (h^2), dominance deviation (d^2) and coefficient of additive genetic variance (%$\mathrm{CV_a}$) were estimated from univariate analyses as follows:

$$\widehat{h}^2 = \frac{\widehat{\sigma}^2_{\mathrm{a}}}{\widehat{\sigma}^2_{\mathrm{p}} + \widehat{\sigma}^2_{\mathrm{f}} + \widehat{\sigma}^2_{\mathrm{a}} + \widehat{\sigma}^2_{\mathrm{e}}} \tag{3}$$

$$\widehat{d}^2 = \frac{4\widehat{\sigma}^2_{\mathrm{f}}}{\widehat{\sigma}^2_{\mathrm{p}} + \widehat{\sigma}^2_{\mathrm{f}} + \widehat{\sigma}^2_{\mathrm{a}} + \widehat{\sigma}^2_{\mathrm{e}}} \tag{4}$$

$$\%\ \widehat{\mathrm{CV}}_{\mathrm{a}} = 100 \times \frac{\sqrt{\widehat{\sigma}^2_{\mathrm{a}}}}{x} \tag{4}$$

Inter-site additive genetic correlations (r_{g}) for each trait were obtained from bivariate analyses. Bivariate models extended Eqs. 1 and 2 with the (co)variance matrices **G** and **R** defined as:

$$G = \begin{bmatrix} \sigma^2_{\mathrm{r_k}} I & 0 \\ 0 & \sigma^2_{\mathrm{r_l}} I \end{bmatrix} \oplus \begin{bmatrix} \sigma^2_{\mathrm{c_k}} I & 0 \\ 0 & \sigma^2_{\mathrm{c_l}} I \end{bmatrix} \oplus \begin{bmatrix} \sigma^2_{\mathrm{p_k}} I & 0 \\ 0 & \sigma^2_{\mathrm{p_l}} I \end{bmatrix} \oplus \begin{bmatrix} \sigma^2_{\mathrm{f_k}} I & \sigma_{\mathrm{f_{k,l}}} I \\ \sigma_{\mathrm{f_{k,l}}} I & \sigma^2_{\mathrm{f_l}} I \end{bmatrix} \oplus \begin{bmatrix} \sigma^2_{\mathrm{a_k}} I & \sigma_{\mathrm{a_{k,l}}} I \\ \sigma_{\mathrm{a_{k,l}}} I & \sigma^2_{\mathrm{a_l}} I \end{bmatrix} \tag{6}$$

$$R = \begin{bmatrix} \sigma^2_{\mathrm{e_k}} I & 0 \\ 0 & \sigma^2_{\mathrm{e_l}} I \end{bmatrix} \tag{7}$$

where k and l refer to the two sites, $\widehat{\sigma}^2_{\mathrm{a_{k,l}}}$ denotes the estimated covariance between the two sites and all other terms are as previously described. Inter-site genetic correlations $\left(r_a = \widehat{r}_{\mathrm{a_{k,l}}}\right)$ were estimated using the following formula:

$$\widehat{r}_{\mathrm{a_{k,l}}} = \frac{\widehat{\sigma}_{\mathrm{a_{k,l}}}}{\sqrt{\widehat{\sigma}^2_{\mathrm{a_k}} \widehat{\sigma}^2_{\mathrm{a_l}}}} \tag{8}$$

Bivariate models were also used to estimate inter-trait intra-site genetic correlations with (co)variance matrices **G** and **R** defined as:

$$G = \begin{bmatrix} \sigma^2_{\mathrm{r_k}} I & \sigma_{\mathrm{r_{k,l}}} I \\ \sigma_{\mathrm{r_{k,l}}} I & \sigma^2_{\mathrm{r_l}} I \end{bmatrix} \oplus \begin{bmatrix} \sigma^2_{\mathrm{c_k}} I & \sigma_{\mathrm{c_{k,l}}} I \\ \sigma_{\mathrm{c_{k,l}}} I & \sigma^2_{\mathrm{c_l}} I \end{bmatrix} \oplus \begin{bmatrix} \sigma^2_{\mathrm{p_k}} I & \sigma_{\mathrm{p_{k,l}}} I \\ \sigma_{\mathrm{p_{k,l}}} I & \sigma^2_{\mathrm{p_l}} I \end{bmatrix} \oplus \begin{bmatrix} \sigma^2_{\mathrm{f_k}} I & \sigma_{\mathrm{f_{k,l}}} I \\ \sigma_{\mathrm{f_{k,l}}} I & \sigma^2_{\mathrm{f_l}} I \end{bmatrix} \oplus \begin{bmatrix} \sigma^2_{\mathrm{a_k}} A & \sigma_{\mathrm{a_{k,l}}} A \\ \sigma_{\mathrm{a_{k,l}}} A & \sigma^2_{\mathrm{a_l}} A \end{bmatrix} \tag{[9]}$$

$$R = \begin{bmatrix} \sigma^2_{\mathrm{e_k}} I & \sigma_{\mathrm{e_{k,l}}} I \\ \sigma_{\mathrm{e_{k,l}}} I & \sigma^2_{\mathrm{e_l}} I \end{bmatrix} \tag{10}$$

where in this case, k and l refer to the two traits, $\sigma_{\mathrm{k,l}}$ denotes the covariance between the two traits and all other terms are as previously described.

Two-tailed likelihood ratio tests were used to test if genetic correlations were significantly different from 0, and one-tailed likelihood ratio tests were used to determine

if these correlations were significantly different from 1 or −1, as appropriate (Gilmour et al. 2009). To determine if inter-trait correlations were significantly different to each other across the two sites, inter-trait bivariate models were run in parallel (i.e. a four-variate model with random terms assumed to be independent across sites) and the difference tested with a likelihood ratio test by fitting a constrained model in which inter-site correlations were forced to be equal across sites. Standard errors of parameters were estimated from the average information matrix, using a standard truncated Taylor series approximation (Gilmour et al. 2009). Analyses were conducted using ASReml (Gilmour et al. 2009). Inter-trait phenotypic Pearson's correlations (r_p) were also estimated, and paired two-tailed *t* tests were used to test if phenotypic correlations were significantly different from zero (Table 4).

3 Results

3.1 Stem straightness

Significant additive genetic variation was evident in measured stem deviation ($\log_{10}$-transformed) at both trials (Table 3), with estimated narrow-sense heritabilities for this trait substantially lower at Boolarra $\left(\widehat{h}^2 = 0.22\right)$ than at Condah $\left(\widehat{h}^2 = 0.49\right)$. The family effect and thus the dominance deviation were not significant at either site. The estimated coefficient of additive genetic variation $(\%C\widehat{V}_{add})$ was 12 % at both Boolarra and Condah, and measured stem straightness means were very similar at the two trials (8.69 mmm^{-1} at Boolarra and 8.65 mmm^{-1} at Condah), when $\log_{10}$ values were back-transformed (Fig. 2). The estimated inter-site genetic correlation was very strong and not significantly different from one $(\widehat{r}_a = 1.10)$.

Subjective stem straightness exhibited a very similar genetic architecture to measured stem deviation. Significant additive genetic variation was observed in this trait at both sites, although estimates of heritability were lower than those for measured stem deviation, and the inter-site correlation was not significantly different from one. No significant family effect was evident at either site. Subjective stem straightness means were very similar across sites. The additive genetic correlations $(\widehat{r}_a = -0.92$ at Boolarra and −0.99 at Condah) and phenotypic correlations (r^p) $(\widehat{r}_p = -0.70$ at Boolarra and −0.69 at Condah) between measured stem deviation and subjective stem straightness were strong and significantly different from zero at both trials (Table 4). No significant differences among native forest genetic groups were identified in either measure of stem straightness.

3.2 Growth

At Condah, but not Boolarra, a significant difference among native forest genetic groups was evident in the case of DBH5 (P=0.041 for all trees and P=0.027 for selected trees), which appeared to be explained in large part by the superior growth of the King Island genetic group (data not shown). No significant differences among genetic groups were detected at either site in DBH9.

Significant additive genetic variation in growth traits was evident at both sites. Furthermore, a significant SCA effect was observed for DBH5 at Boolarra and DBH9 at Condah (Table 3). Narrow-sense heritability estimates for DBH5 based on selected (i.e. retained) trees indicated that selection at the time of thinning introduced substantial bias in parameter estimates—narrow-sense heritability increased substantially with thinning ($\widehat{h}^2 = 0.38$ compared with 0.12 at Boolarra and 0.26 compared with 0.17 at Condah). In both trials, when compared to the mean DBH of all trial trees pre-thinning, the mean DBH of the trees retained after thinning at age 5 years was slightly higher (164 mm compared with 150 mm at Boolarra and 134 mm compared with 127 mm at Condah).

The phenotypic correlation between measured stem deviation and DBH9 was significant at Condah $\left(\widehat{r}_p = -0.09\right)$. Phenotypic correlations between subjective stem straightness and DBH were significant and, although still weak, were consistent in magnitude across trials with larger trees exhibiting straighter stems, for both DBH5 ($\widehat{r}_p = 0.11$ at Boolarra and 0.13 at Condah) and DBH9 ($\widehat{r}_p = 0.20$ at Boolarra and 0.18 at Condah). Additive genetic correlations between stem straightness traits and DBH traits were not significantly different from zero except in the case of subjective stem straightness with DBH9 at Condah $(\widehat{r}_a = 0.44)$.

4 Discussion

4.1 Measured stem deviation

The significant additive genetic variation measured in stem deviation indicates that stem straightness in *E. globulus* could be improved through selective breeding. However, it is likely that post-thinning heritability estimates for stem deviation (Table 3) are inflated, resulting from the phenotypic selection within plots at thinning, where a reduction in the phenotypic variance, rather than in additive genetic variance, would occur (Matheson and Raymond 1984). This is exemplified by the differences in heritability estimates for DBH5 based on trees selected for superior growth and stem straightness only and on estimates based on all trees (Table 3). Genetic parameters for measured deviations

Table. 3 Trial mean, additive variance, narrow-sense heritability $\left(\widehat{h}^2\right)$ and significance of additive variance from zero, dominance ratio $\left(\widehat{d}^2\right)$ and significance of family variance from zero, percentage coefficient of additive variation $(\%C\widehat{V}_{add})$ and inter-site additive genetic correlation $(\widehat{r}_a)$

Trait	Site	Mean	Additive variance	$\widehat{h}^2$	$\widehat{d}^2$	$\%C\widehat{V}_{add}$	$\widehat{r}_a$
Stem deviation (mm, log_{10}-transformed)	Boolarra	0.937 (0.043)	0.013 (0.006)	0.22 (0.11)***	0.36 (0.33) ns	12.2	1.10 (0.25)***
	Condah	0.930 (0.016)	0.026 (0.006)	0.49 (0.10)***	0.01 (0.17) ns	17.3	
Straightness score (1 to 6)	Boolarra	4.63 (0.25)	0.31 (0.18)	0.19 (0.11)**	0.31 (0.31) ns	12.1	1.07 (0.21)***
	Condah	4.38 (0.13)	0.65 (0.19)	0.33 (0.09)***	0.27 (0.23) ns	18.5	
DBH5—all trees (mm)	Boolarra	150 (3)	90 (35)	0.12 (0.05)**	0.25 (0.17)*	6.3	0.67 (0.20)***
	Condah	127 (3)	49 (12)	0.17 (0.04)***	0.08 (0.08) ns	5.5	
DBH5—selected trees (mm)	Boolarra	164 (3)	149 (50)	0.38 (0.12)***	0.31 (0.33) ns	7.4	0.67 (0.20)***
	Condah	134 (3)	46 (14)	0.26 (0.08)***	0.17 (0.18) ns	5.1	
DBH9 (mm)	Boolarra	265 (8)	856 (208)	0.62 (0.12)***	0.00 (0.00) ns	11.1	0.77 (0.15)***
	Condah	223 (7)	257 (60)	0.39 (0.08)**	0.27 (0.19)*	7.2	

Standard errors are shown in parenthesis. Stem deviation and straightness score were assessed at age 9 years and diameter at breast height (DBH) was assessed at age 5 (DBH5) and age 9 (DBH9) years. Trials were selectively thinned for straighter and larger stems at age 5

ns not significant

*$P<0.05$; **$P<0.01$; ***$P<0.001$

from straightness have not previously been published for *E. globulus*, and although post-thinning estimates of heritability in the present study are likely to be biased, the fact that significant additive genetic variation was evident confirms that exploitable genetic variation in this trait is present in the species.

In measured stem straightness, the strong inter-site additive genetic correlation, which is not significantly different from one, indicates that selection of straighter stems at one site would improve stem straightness at environments represented by the other site. Similarly, strong correlations were observed in studies of *E. globulus* by Callister et al. (2011) who found that all but one of seven estimates were greater or equal to 0.67 and by Lopez et al. (2002) who found that six genetic correlation estimates were greater or equal to 0.70.

Despite trees at Boolarra growing more rapidly than those at Condah, the median measured stem deviation (Boolarra=8.0 $mm\,m^{-1}$, Condah=7.6 $mm\,m^{-1}$) and frequency distribution of measured stem deviation after thinning were similar across sites (Fig. 2), indicating that growth rate did not have a large effect on the magnitude of stem deviation or variation in this trait, although a significant weakly negative phenotypic correlation was observed between DBH9 and measured stem deviation at Condah. In addition, at the additive genetic level, the weak and non-significant additive genetic correlations observed between measured stem deviation and DBH indicate that stem deviation is genetically independent of growth. Although the current study suggests that the distribution of stem deviation in thinned *E. globulus* stands was consistent across the environments represented by the two study sites (Fig. 2), examination of this trait across a larger number of sites established with comparable genetic material, as performed by Araújo et al. (2012), is required to determine the extent to which environmental and silvicultural factors affect this important solid-wood trait.

4.2 Subjective straightness score as a selection criterion

The very strong genetic correlation between subjective stem straightness and measured stem deviation indicates that the six-point subjective scoring method is an appropriate

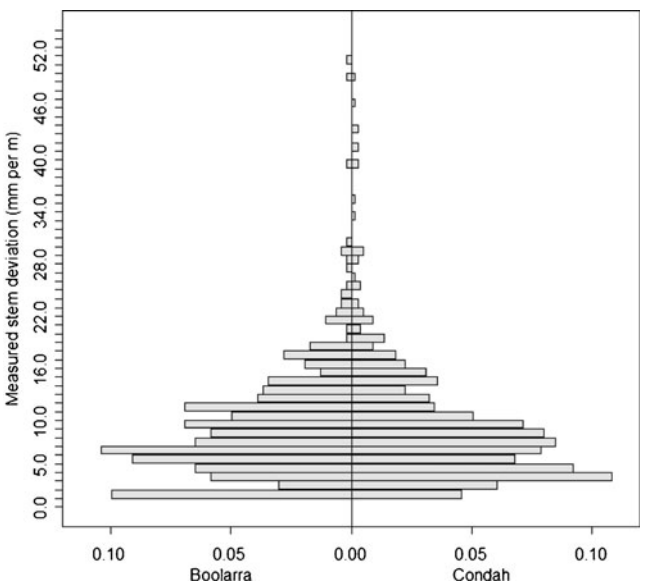

Fig. 2 Frequency distribution histogram of measured stem deviations (in millimetres per metre) at the Boolarra and Condah trials at age 9 years (i.e. post-thinning)

selection criterion for use in breeding programmes aiming to decrease stem deviation. Assuming the inter-age genetic correlation for the six-point scoring method is strong, assessment could be undertaken at a younger age than in the current study. However, Callister et al. (2011) noted that stem straightness narrow-sense heritability was consistently higher in the same *E. globulus* trials at age 5.5 years when compared to heritability at 3.5 years, although they also noted that the effect may have been due to improved scoring rather than biological change.

Estimates of narrow-sense heritabilities for subjective stem straightness were marginally lower than those for stem deviation, most likely reflecting the lower precision of phenotyping using the subjective stem straightness approach. Estimates of narrow-sense heritability for subjective stem straightness were similar to those from studies that used the same six-point scoring method in full-sib control-pollinated *E. globulus* progeny trials: 0.20 (SE 0.06) to 0.34 (SE 0.07) at three sites in southern Western Australia at age 5.5 years (Callister et al. 2011). However, published estimates for subjectively assessed stem straightness using three- or four-point scales in *E. globulus* were generally lower: Lopez et al. (2002) found narrow-sense heritabilities of 0.07 (SE 0.02) and 0.14 (SE 0.03) at 4 years of age in open-pollinated trials, and Greaves et al. (2004b) found narrow-sense heritabilities of 0.10 (SE 0.08) at 6 years of age in a full-sib trial and 0.14 (SE 0.09) at 15 years of age in an open-pollinated trial. Possible contributing factors to the differences between studies include differences in scoring methods, assessor capability, silviculture (including possible inflation of heritability due to selection at thinning in the current study), genetic background and environment.

While phenotypic correlations between measured stem deviation and DBH were generally non-significant in past studies, in present study, a significant, weak and positive correlation was detected. Genetic correlations between subjective stem straightness and DBH were also positive, although significantly different from zero in the case of DBH9 at Condah only (Table 4). This positive relationship suggests that assessors are inclined to assess large-diameter stems more favourably for subjective stem straightness than small-diameter stems. However, in the only other full-sib *E. globulus* study to examine the relationship between DBH and subjective stem straightness using the six-point subjective scoring method, Callister et al. (2011) found highly variable genetic correlations ranging from −0.71 to 0.82 with large standard errors. It is possible that the strength of this relationship is dependent on the assessors, highlighting the need for appropriate assessor training and guidelines that ensure consistent results across studies.

4.3 Assessing stem straightness in breeding programmes

The expense of measuring stem deviation makes it an unsuitable method of assessing large-scale progeny trials. The six-point subjective score method can be applied much more rapidly (~120 stems per assessor per person-hour) than the stem deviation measurement using image analysis (~15 stems per assessor per person-hour to capture and assess images). Prior to subjective assessment, some additional time is required to train new assessors and/or complete pre-assessment validation to establish consistency among individuals involved. The efficiency of either method may be improved if assessment of multiple traits is made (e.g. DBH and branching characteristics) at the same time.

Stem deviation measurement using image analysis could be undertaken in conjunction with the established subjective scoring method. Images could be captured in the field prior to subjective scoring and used for the training of assessor to increase consistency among them. Captured images could also be used to examine changes in stem deviation over time. From a known camera position and lens specification,

Table 4 Inter-trait additive genetic (above diagonal) and phenotypic (below diagonal) correlations with standard errors shown in parenthesis and significance from zero indicated

Trait	Site	Stem deviation	Straightness score	DBH5 (mm)	DBH9 (mm)
Stem deviation (mm, log_{10}-transformed)	Boolarra		−0.92 (0.13)**	−0.17 (0.30) ns	0.08 (0.24) ns
	Condah		−0.99 (0.03)***	−0.19 (0.16) ns	−0.23 (0.15) ns
Straightness score (1 to 6)	Boolarra	−0.70 (0.04)***		0.40 (0.30) ns	0.35 (0.21) ns
	Condah	−0.69 (0.03)***		0.35 (0.18) ns	0.44 (0.16)**
DBH5 (mm)	Boolarra	−0.03 (0.05) ns	0.11 (0.05)**		1.02 (0.04)***
	Condah	−0.02 (0.04) ns	0.13 (0.03)***		0.93 (0.05)***
DBH9 (mm)	Boolarra	−0.06 (0.05) ns	0.20 (0.05)***	0.86 (0.03)***	
	Condah	−0.09 (0.04)**	0.18 (0.03)***	0.80 (0.03)***	

DBH(5 and 9) indicates tree age (years) when diameter was measured

ns not significant

*$P<0.05$; **$P<0.01$; ***$P<0.001$

an image can be taken at a future date, measured and compared to any previous image. However, the most useful application of the technique is likely to be in the quantification of stem deviation across sites. A sample of trees, possibly stratified according to subjective score classes, could be photographed at each site and used to estimate the mean and distribution of deviations from straightness. Such an approach would provide information on inter-site differences in stem deviation, which is not obtained using the six-point subjective scoring method. Quantification of stem deviation from straightness across a range of sites could also be used to refine economic breeding objectives for solid-wood products (Greaves et al. 2004a; Potts et al. 2011).

It was notable in the current study that the distribution of measured deviations from straightness was not normally distributed (Fig. 2) and required log transformation prior to analysis based on the distribution of residuals. A non-normal distribution of true deviations from straightness, together with the standardisation of subjective scores to have an approximately normal distribution and a fixed standard deviation across all sites, will complicate the weighting of subjective scores in multiple trait selection indices.

4.4 Diameter at breast height

Low pre-thinning heritability estimates for DBH5 were comparable to estimates in past studies based on open pollinated and control pollinated seedlots (Potts et al. 2004; Li et al. 2007; Callister et al. 2011). Heritabilities for growth traits in young open-pollinated *E. globulus* trials have been shown to be inflated due to variable levels of inbreeding among families and inbreeding depression in growth (Costa e Silva et al. 2009; Potts et al. 2011). The current trials contained both open-pollinated and control-pollinated families, and it is possible that the higher heritability for pre-thinning DBH5 at the Condah site was due to the presence of a greater percentage of open-pollinated families in that trial (Table 2), although heritability estimates from the two sites were not significantly different to each other.

It has been noted in other studies that estimates of narrow-sense heritability and dominance ratio are approximately equal for growth traits in *E. globulus* (Li et al. 2007; Costa e Silva et al. 2004). This hypothesis could not be rejected in the present study, given the imprecision of dominance ratio estimates (indeed, the expression of dominance variation was significant in the case of DBH5 prior to thinning at Boolarra and DBH9 at Condah only; Table 3). The implications of significant non-additive genetic variation in *E. globulus* growth traits for breeding and deployment programmes are discussed at length in the literature (Li et al. 2007; Costa e Silva et al. 2010; Araújo et al. 2012).

Within-site estimated additive genetic correlations between DBH at ages 5 and 9 (Table 4) were strongly positive and not significantly different from one, indicating that there was no evidence of differences in the growth response to release from competition among genotypes (Matheson and Raymond 1984). These strong and positive and inter-age additive genetic correlations for DBH were consistent with other studies in *E. globulus* stands (Potts et al. 2004; Li et al. 2007; Callister et al. 2011) and support the use of early-age DBH as a selection criterion for increased volume and log diameter at harvest.

5 Conclusion

Results from this study indicate that stem straightness in *E. globulus* could be improved through selective breeding. A strong and favourable genetic correlation between subjective stem straightness and measured stem deviation indicates that the six-point subjective scoring method may be used to decrease stem deviation in tree breeding. Directly measuring stem deviation from photographs provides more precise data than those resulting from the visual scoring albeit at a greater expense. However, the additional expense may be warranted where objective estimates of stem straightness are required, for example for use in training assessors, verifying subjective scores and quantifying stem deviation across sites.

Acknowledgments We thank Gunns Ltd., HVP Plantations and the Southern Tree Breeding Association (STBA) for access to the field trials; David Pilbeam of the STBA for trial design, trial establishment and providing historical trial data and Chris Szota of The University of Melbourne for assistance during trial assessments for this study.

Funding We acknowledge substantial assistance from the Cooperative Research Centre for Forestry.

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