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Document Version:

Author accepted manuscript (postprint)

Citation for published version:

Hamilton, Matthew, Acuna, M, Wiedemann, John, Mitchell, R, Pilbean, David J, Brown, M W, Potts, B M (2015) Genetic control of Eucalyptus globulus harvest traits. *Canadian Journal of Forest Research*, Vol. 45, No. 6, pp.615-624.

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1 **Genetic control of *Eucalyptus globulus* harvest traits**

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1 **Abstract**

2 The cost of harvesting short-rotation plantation eucalypts can be in excess of AU\$2500 ha⁻¹.
3 Despite this high cost, the extent to which harvesting productivity is affected by tree genetics
4 is not well understood. We address this issue in a study of two ten-year-old genetics field
5 trials of *Eucalyptus globulus* in Australia. Standing-tree traits analysed were survival,
6 diameter at breast height, basal area, stem straightness and forking. Harvest traits were
7 volume, harvest time and harvest productivity (m³ min⁻¹). Genetic group and within-group
8 genetic variation (additive and dominance), stand-level family variation, phenotypic and
9 genetic correlations, and the effects of inbreeding were estimated for these traits. The
10 different scenarios studied showed that plantation harvest productivity was affected by tree
11 genetics to some degree, but mainly through positive co-variation with stem diameter.
12 Harvest productivity is thus unlikely to have been adversely affected by past selection. While
13 no significant additive or dominance genetic variation in forking or stem straightness was
14 detected, weak phenotypic correlations were consistent with harvest productivity being
15 higher in straighter trees with no forking. High inbreeding depression was evident for growth
16 and survival, but in open-pollinated progeny this resulted in only a slight reduction in harvest
17 productivity (5.5%) compared with out-crossed progeny.

18
19 **Keywords:** harvest productivity, additive genetic variation, dominance genetic variation,
20 inbreeding depression, standing tree traits

21
22

1 **Introduction**

2

3 In recent decades, mechanised forest harvesting systems have been widely adopted, primarily
4 to reduce harvest costs and improve worker safety. Time-and-motion studies of mechanical
5 harvesting operations have been undertaken to better understand the effect of harvesting
6 systems (Visser and Spinelli 2012), machine type and configuration (Ghaffariyan et al. 2012),
7 machine-operator training, behaviour and experience (Ovaskainen et al. 2004), terrain (Visser
8 and Spinelli 2012; Visser et al. 2009), and stand and tree characteristics (Acuna et al. 2009;
9 Ramantswana et al. 2012; Ramantswana et al. 2013; Spinelli et al. 2002) on harvest
10 productivity. In the short term, knowledge gained from such studies can be used to optimise
11 machines, operator behaviour and harvesting systems but, in the longer term, may be used
12 guide decisions relating to the procurement and sale of land, silvicultural practices, rotation
13 length and tree breeding (Schäfer and Ponce 2007; Whittock et al. 2004)

14

15 Many stand and individual-tree characteristics that potentially affect harvest productivity are
16 known to be under genetic control in commercially-grown tree species (Hamilton and Potts
17 2008; Potts et al. 2004). For example, harvest productivity is influenced by tree survival
18 through its effect on stocking density and stand volume at harvest, growth rate through its
19 effect on piece size at harvest, and branching characteristics and stem form through their
20 effect on stem processing time (Evanson and McConchie 1996; Nurminen et al. 2006;
21 Spinelli et al. 2002; van Wyk 1978; Visser and Spinelli 2012; Wang and Haarlaa 2002).

22 However, the genetics of harvest productivity have not been extensively researched and
23 neither direct estimates of genetic variation in harvest productivity, nor estimates of genetic
24 correlations with standing tree traits, have been published. Estimates of these parameters are

1 required before the impact of past and/or future breeding activities on harvest productivity
2 can be assessed.

3

4 *Eucalyptus globulus* is one of the most widely planted hardwood species in temperate regions
5 of the world, including Australia, Chile, Uruguay, Spain and Portugal (Potts et al. 2011; Potts
6 et al. 2004). The species is principally grown for the production of pulpwood under short-
7 rotation (10-15 years) regimes. Under such regimes harvest costs are a particularly important
8 driver of plantation profitability (Whittock et al. 2007) and can be well in excess of
9 AU\$2500 ha⁻¹ (Acuna et al. 2009). While traits likely to influence harvest productivity such
10 as stem diameter, forking and stem straightness have been reported to be under some degree
11 of genetic control in the species (Blackburn et al. 2013; Callister et al. 2011; Costa e Silva et
12 al. 2009; Lopez et al. 2002), it is unclear how such variation in these cheaply and easily
13 assessed tree characteristics may flow through to impact harvesting productivity in uniform-
14 age plantations.

15

16 While there are extensive clonal plantations of *E. globulus* in some countries (e.g. Spain,
17 Chile and Portugal), most plantations are established with seedlings due to lower propagule
18 costs (Griffin 2014). In Australia, all *E. globulus* plantations are established with seedlings
19 (Potts et al. 2011; Griffin 2014). Until low cost means of deploying control pollinated out
20 crossed seedlots were developed (Patterson et al. 2004), *E. globulus* seedling plantations
21 world-wide were predominantly established with open pollinated seed, initially from either
22 native stands or landraces, and later from genetic improved seed orchard sources (Potts et al.
23 2011; Potts et al. 2004). Although preferentially out-crossing, *E. globulus* open-pollinated
24 families generally contain a sizeable proportion of selfed progeny (Potts et al. 2004). In the
25 case of seed sourced from native forest, open-pollinated progeny may also include crosses of

1 related parents (Jones 2005). Slower growth rates, higher levels of mortality and greater
2 heterogeneity, all of which may affect harvest productivity, have been documented in open-
3 pollinated compared with out-crossed seedlots (Costa e Silva et al. 2010b). While manifest
4 most in open-pollinated seedlots of *E. globulus* from the native stands, due to a combination
5 of both selfing and neighbourhood inbreeding (Hardner et al. 1998), inbreeding depression
6 may also be present in open-pollinated seedlots derived from seed orchards (Hodge et al.
7 1996; Volker 2002).

8
9 The present study aimed to (i) quantify additive and non-additive genetic variation in
10 standing tree growth, survival, forking and straightness, and harvest volume, time and
11 productivity; (ii) quantify differences in standing tree and harvest traits among nine out-
12 crossed families at the stand level; (iii) examine the genetic and phenotypic relationships
13 between cheaply and easily accessed standing tree and harvest traits at both the individual
14 tree and stand level; and (iv) quantify the effect of inbreeding depression on standing tree and
15 harvest traits at the stand level through the comparison of different cross-types (out -crossed,
16 open-pollinated and selfed progeny).

17 18 **Materials and Methods**

19 20 *Trials*

21 Two adjoining unthinned and unpruned *E. globulus* genetic trials were studied – herein
22 referred to as Trial 1 and Trial 2. These trials were established on an ex-pasture site with a
23 slight west-north-westerly aspect (~4.5°) by the Southern Tree Breeding Association (STBA)
24 on a Western Australian Plantation Resources (WAPRES) property near Manjimup, Western
25 Australia (34° 14' 52" S, 116° 3' 32" E) in 1991. Manjimup experiences a Mediterranean

1 climate with an average annual rainfall of 1007 mm and the soil at the site was a deep gravely
2 loam over laterite from granite parent rock. The site was mounded prior to chemical weed
3 control and planting. Trees were spaced 5 m between rows and 1.9 m between trees. Post
4 planting chemical weed control was undertaken one month as well as two years after planting.

5
6 Trial 1 was comprised of 11 replicates, each with six four-by-six-tree blocks of ‘cross-type’
7 treatments with different levels of inbreeding: self-pollinated (one block per replicate), open-
8 pollinated seed-orchard (one block per replicate) and full-sib out-crossed families (four
9 blocks per replicate). Within replicates cross-type treatments were randomly allocated to
10 blocks and, within blocks, families were planted as single-tree plots. In the case of full-sib
11 out-crossed families, an incomplete-block trial design was imposed (i.e. ‘blocks’ were treated
12 as ‘incomplete-blocks’ within replicates). Insufficient seedlings of some families were
13 available at the time of planting and their plantation positions were filled with families with
14 excess individuals, some of which were different to the notional cross type of the block.
15 Filler trees were most common in the plots of selfed progeny and were generally planted in a
16 row along plot boundaries. Trial 1 was used to estimate genetic parameters and inbreeding
17 depression.

18
19 Trial 2 was comprised of nine full-sib out-crossed families, arranged in five-by-five-tree plots
20 (Table 1). The trial was designed as a modified row column design at the plot level
21 (Williams et al. 2002), where plots of over-represented families were randomly assigned to
22 plot positions of under-represented families. It was established as a genetic mapping trial to
23 detect quantitative trait loci (QTL) affecting traits of economic significance (Freeman et al.
24 2013). However, in the current study, it was used to study the effect of family on standing-
25 tree and harvest traits at the stand (i.e. plot) scale.

1

2

Insert Table 1 near here

3

4 *Time and motion study*

5 Trees were harvested using a Caterpillar 511TM Track Harvester with a Waratah

6 HTH616CTM single-grip harvesting and processing head. The machine operator had

7 extensive (11 years) experience. Standard industry harvesting practices were modified for

8 the trial to i) ensure that observers had direct line of sight from a safe distance to the trees as

9 they were felled, ii) to allow for even debris dispersal across the site so as not to bias future

10 research into coppice development and growth, and iii) to avoid harvesting trees from

11 multiple blocks/plots in any given harvesting pass. These modifications meant that, instead

12 of each pass being followed by a pass back along adjacent rows, the machine moved to the

13 other side of the trial/s before making a return pass (i.e. the machine moved in a circular, anti-

14 clockwise, fashion on the site containing the two trials). Accordingly, all trees were felled

15 into open areas to the right of the machine, albeit sometimes against the prevailing wind.

16 Furthermore, in Trial 1 all trees were felled in two-row passes, as incomplete blocks

17 consisted of four trees per row and six trees within rows. In Trial 2, two-row and then three-

18 row passes were felled sequentially to ensure that trees were not harvested across multiple

19 plots (five-by-five trees) in any given harvesting pass. After felling, the machine delimbed,

20 debarked and cut logs to length. Logs were then stacked to the left of the machine and next

21 to standing trees. Stems were cut into 5.2 m logs with no minimum small end diameter.

22

23 All trees, including dead trees, in the trials were felled and, with the exception of extremely

24 suppressed trees (i.e. runts), an attempt was made to process all trees into logs. Harvested

25 dead trees were small in number and size and represented a very small component of total

1 volume. For example, only 13 logs were recovered from dead trees in Trial 1. The harvested
2 volume of dead trees was excluded from analyses. Harvesting of the trials was undertaken
3 over a period of nine days. Work elements recorded for the purposes of the time and motion
4 study are outlined in Table 2. All work elements were manually recorded, with a personal
5 digital assistant (PDA) using TimerPro® software, from a safe distance at the time of felling.
6 To enable post-harvest data validation, the harvesting operation was recorded by a second
7 person using a handheld video recorder as well as by a second camera mounted in the cabin
8 of the harvester.

9

10 *Individual tree traits*

11 In the months leading up to harvest at ten years of age, trees in the trials were assessed for
12 survival, diameter of the most dominant stem at breast height over bark (DBH; 1.3 m), tree
13 height, and the presence/absence of forks below two thirds of tree height. Stem straightness
14 was also assessed in Trial 1 on a one (least straight) to six (most straight) scale (Cotterill and
15 Dean 1990).

16

17 Although, herein described as a harvest trait, stem volume was estimated prior to harvest.
18 Total under-bark volume of all stems was estimated for each tree from over-bark diameter
19 and height measurements using a taper function developed for plantation *E. globulus* by the
20 owner of the trial site, Western Australian Plantation Resources (WAPRES). Under-bark
21 volume estimated according to this taper function is an accurate predictor of recovered
22 volume in operational plantations of similar site quality and tree size. Historic height (age one
23 year) and diameter (age two and four years) were also used. For the estimation of genetic
24 parameters (Trial 1), individual tree harvest times were estimated as the sum of felling and

1 processing work elements (Table 2) and individual tree harvest productivity was estimated as
2 pre-harvest stem volume divided by harvest time.

3

4 *Stand traits*

5 To examine inbreeding depression (four-by-six-tree blocks; Trial 1) and the effect of family
6 on standing tree and harvest traits (i.e. five-by-five-tree plots; Trial 2) at the stand scale, data
7 were analysed at the block/plot level. Average tree height (age one and ten years), basal area
8 (age two, five and ten), average diameter (age ten), proportion of trees with a fork below two
9 thirds of tree height (age ten) and average stem straightness score (age ten) were calculated
10 from pre-harvest individual-tree assessment data. Harvest time was estimated as the sum of
11 felling, processing, brushing/clearing, moving/positioning and stacking/bunching work
12 elements (Table 2). Delay and travel work elements were excluded. Block/Plot level wood
13 volume was estimated as the sum of all pre-harvest stem volumes and harvest productivity
14 was estimated as pre-harvest volume divided by harvest time.

15

16 Insert Table 2 near here

17

18 *Statistical analyses*

19 Genetic parameters from tree level data (Trial 1)

20 To estimate genetic parameters unbiased by variable levels of inbreeding and inbreeding
21 depression (Costa e Silva et al. 2010b), only data from full-sib out-crossed families in Trial 1
22 were used. Two filler trees were excluded from these analyses, as they were not from full-sib
23 out-crossed families. In total, 166 full-sib out-crossed families from 178 parents were
24 represented. The parents were from 12 subraces (Dutkowski and Potts 1999) which were

1 consolidated into five genetic groups due to the low genetic contribution of some subraces
 2 (Table 3). These groups corresponded to the five genetically distinct groups defined by Yeoh
 3 *et al.* (2012) based on the spatial structuring of microsatellite variation (see also Steane *et al.*
 4 2006). Crosses between parents were made both within (33 families) and between genetic
 5 groups (133 families). Survival at the time of felling was 91%.

6

7 Insert Table 3 near here

8

9 To estimate variance components, univariate restricted maximum likelihood (REML)
 10 analyses were undertaken separately for each trait using the following linear mixed model:

11

$$12 \quad (1) \quad \mathbf{Y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

13

14 where \mathbf{y} is the vector of trait observations, \mathbf{b} is a vector of fixed effects with its design matrix
 15 \mathbf{X} , \mathbf{u} is a vector of random effects with its design matrix \mathbf{Z} , and \mathbf{e} is the vector of random
 16 residual terms. The models included as fixed effects in \mathbf{b} the overall mean and replicate. The
 17 random effects in \mathbf{u} were incomplete block within replicate, genetic group general combining
 18 ability (GCA), genetic group specific combining ability (SCA), the additive genetic
 19 component within genetic groups and the full-sib family specific component within genetic
 20 groups.

21

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

24

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

2

3 where \mathbf{G} is a (co)variance matrix corresponding to \mathbf{u} , \mathbf{R} is a (co)variance matrix

4 corresponding to \mathbf{e} and $\mathbf{0}$ is a null matrix. The (co)variance matrix \mathbf{G} was defined as $\mathbf{G}_i \oplus$

5 $\mathbf{G}_{gg} \oplus \mathbf{G}_{gs} \oplus \mathbf{G}_a \oplus \mathbf{G}_f$, where $\mathbf{G}_i = \sigma_i^2 \mathbf{I}$, $\mathbf{G}_{gg} = \sigma_{gg}^2 \mathbf{I}$, $\mathbf{G}_{gs} = \sigma_{gs}^2 \mathbf{I}$, $\mathbf{G}_a = \sigma_a^2 \mathbf{A}$, $\mathbf{G}_f = \sigma_f^2 \mathbf{I}$, and \oplus is

6 the direct sum operation (i.e. model terms in \mathbf{u} were assumed to be independent).

7 Furthermore, $\mathbf{R} = \sigma_e^2 \mathbf{I}$ and σ_i^2 is the incomplete block within replicate variance, σ_{gg}^2 is the

8 genetic group GCA variance, σ_{gs}^2 is the genetic group SCA variance, σ_a^2 is the additive

9 genetic variance, σ_f^2 is the non-additive full-sib family-specific variance, σ_e^2 is the residual

10 variance, \mathbf{A} is the numerator relationship matrix and \mathbf{I} is an identity matrix with dimensions

11 equal to the levels of the random term in question. The significance of the family and

12 additive genetic variance for each trait was tested with a one-tailed likelihood ratio test

13 (Gilmour et al. 2009). For each trait the narrow-sense heritability (h^2), coefficient of additive

14 genetic variance (CV_a), dominance variance σ_d^2 and dominance ratio (d^2) were estimated from

15 univariate analyses as follows:

$$(3) \quad \hat{h}^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_a^2 + \hat{\sigma}_f^2 + \hat{\sigma}_e^2}$$

$$(4) \quad \widehat{CV}_a = \frac{\sqrt{\hat{\sigma}_a^2}}{\bar{x}}$$

$$(5) \quad \hat{\sigma}_d^2 = 4\hat{\sigma}_f^2$$

$$(6) \quad \hat{d}^2 = \frac{4\hat{\sigma}_f^2}{\hat{\sigma}_a^2 + \hat{\sigma}_f^2 + \hat{\sigma}_e^2}$$

20 where \bar{x} is the trait mean and all other parameters are as previously defined. A bivariate

21 model was used to estimate inter-trait genetic correlations with (co) variance matrices \mathbf{G} and

22 \mathbf{R} defined as:

1

$$(7) \quad \mathbf{G} = \begin{bmatrix} \sigma_{i_k}^2 \mathbf{I} & \sigma_{i_{k,l}} \mathbf{I} \\ \sigma_{i_{k,l}} \mathbf{I} & \sigma_{i_l}^2 \mathbf{I} \end{bmatrix} \oplus \begin{bmatrix} \sigma_{g_k}^2 \mathbf{I} & \sigma_{g_{k,l}} \mathbf{I} \\ \sigma_{g_{k,l}} \mathbf{I} & \sigma_{g_l}^2 \mathbf{I} \end{bmatrix} \oplus \begin{bmatrix} \sigma_{g_{c_k}}^2 \mathbf{I} & \sigma_{g_{c_{k,l}}} \mathbf{I} \\ \sigma_{g_{c_{k,l}}} \mathbf{I} & \sigma_{g_{c_l}}^2 \mathbf{I} \end{bmatrix} \oplus \begin{bmatrix} \sigma_{a_k}^2 \mathbf{A} & \sigma_{a_{k,l}} \mathbf{A} \\ \sigma_{a_{k,l}} \mathbf{A} & \sigma_{a_l}^2 \mathbf{A} \end{bmatrix} \oplus$$

$$\begin{bmatrix} \sigma_{f_k}^2 \mathbf{I} & \sigma_{f_{k,l}} \mathbf{I} \\ \sigma_{f_{k,l}} \mathbf{I} & \sigma_{f_l}^2 \mathbf{I} \end{bmatrix}$$

4

$$(8) \quad \mathbf{R} = \begin{bmatrix} \sigma_{e_k}^2 \mathbf{I} & \sigma_{e_{k,l}} \mathbf{I} \\ \sigma_{e_{k,l}} \mathbf{I} & \sigma_{e_l}^2 \mathbf{I} \end{bmatrix}$$

6

where the k and l subscripts refer to the two traits, $\sigma_{k,l}$ denotes the covariance between the

7

two traits and all other terms are as previously described. Inter-trait genetic correlations (r_a)

8

were estimated as:

9

$$(9) \quad \hat{r}_{a_{k,l}} = \frac{\hat{\sigma}_{a_{k,l}}}{\sqrt{\hat{\sigma}_{a_k}^2 \hat{\sigma}_{a_l}^2}}$$

11

Variances for random effects that were not significantly different from zero at the $P=0.10$

level in univariate analyses were fixed to zero in bivariate analyses. Two-tailed likelihood

ratio tests were used to test if genetic correlations were significantly different from zero and

one-tailed likelihood ratio tests were used to determine if these correlations were significantly

different from one (Gilmour et al. 2009). Standard errors of parameters were estimated from

the average information matrix, using a standard truncated Taylor series approximation

(Gilmour et al. 2009). For the presence/absence traits of survival and forking, a binomial

model was fitted with a logit link function.

20

1 Pearson correlation-coefficients among individual-tree phenotypic values, herein referred to
 2 as phenotypic correlations, were also estimated. Two-tailed t-tests were used to test if
 3 phenotypic correlations were significantly different from zero. Analyses were conducted
 4 using ASRemlTM Version 3.0 (Gilmour et al. 2009) and SASTM (version 9.1).

6 Stand-level inbreeding depression (Trial 1)

7
 8 Analyses of stand-level differences among cross-types and inbreeding depression were
 9 undertaken separately for each trait using the model given by Equation 1 where y is the
 10 vector of trait stand-level (i.e. four-by-six-tree block-level) observations and \mathbf{b} , \mathbf{X} , \mathbf{u} , \mathbf{Z} and \mathbf{e}
 11 are as previously defined. The models included in \mathbf{b} the overall mean as a fixed factor, and
 12 the proportion of out-crossed progeny, proportion of open-pollinated progeny and proportion
 13 of selfed progeny in each block as covariates. The random effects in \mathbf{u} were replicate and
 14 replicate by cross-type interaction. Cross-type treatment means were estimated separately for
 15 each cross-type (i.e. the proportion of the cross-type in question was specified as one and the
 16 proportions of the other two cross-types were specified as zero using the predict function of
 17 ASReml; Gilmour et al. 2009). The significance of differences among cross-types were
 18 tested with Wald F tests in separate, but equivalent, analyses using the '!G' function of
 19 ASReml. Replicate by cross-type interaction was fitted as a random term to estimate the
 20 appropriate error term to test the significance of cross-type. Percentage inbreeding
 21 depression for the open-pollinated (ID_{op}) and selfed (ID_{self}) cross-types were estimated for
 22 each trait following Hardner and Potts (1995) as:

$$24 \quad (10) \quad ID_{op} = \frac{\bar{x}_{outcross} - \bar{x}_{op}}{\bar{x}_{outcross}} \times 100$$

$$(11) \quad ID_{\text{self}} = \frac{\bar{x}_{\text{outcross}} - \bar{x}_{\text{self}}}{\bar{x}_{\text{outcross}}} \times 100$$

where $\bar{x}_{\text{outcross}}$, \bar{x}_{op} and \bar{x}_{self} are the estimated trait means for the out-crossed, open-pollinated and selfed treatments respectively.

Stand-level family differences (Trial 2)

Analyses of stand-level family effects in Trial 2 were undertaken separately for each trait using Model 1, where \mathbf{y} is the vector of trait stand-level (i.e. five-by-five-tree plot-level) observations and \mathbf{b} , \mathbf{X} , \mathbf{u} , \mathbf{Z} and \mathbf{e} are as previously defined. The models included as fixed effects in \mathbf{b} were the overall mean and family. The random effects in \mathbf{u} were plot-level row and plot-level column. Family pedigree was not accounted for in the model.

Results

Genetic variation

No significant ($P < 0.05$) genetic group GCA or SCA effects were detected for any trait but significant within-group additive genetic variation was detected in harvest age DBH ($h^2 = 0.16$; $CV_a = 12.6\%$; Table 4), stem straightness ($h^2 = 0.20$; $CV_a = 12.0\%$), stem volume ($h^2 = 0.14$; $CV_a = 21.11\%$) and harvest time ($h^2 = 0.12$; $CV_a = 11.3\%$). The additive genetic variance for harvest productivity was on the margins of being significantly different from zero ($P = 0.064$) and the estimate of narrow-sense heritability was low (0.09). Pre-harvest assessments of growth revealed significant additive genetic variation for DBH at ages two ($h^2 = 0.10$; $CV_a = 6.8\%$) and five years ($h^2 = 0.09$; $CV_a = 6.4\%$) but not for height at age one year ($h^2 = 0.04$; $CV_a = 4.6\%$). No significant additive genetic variation was evident for survival or the presence/absence of forks.

1
2 Significant full-sib family specific (i.e. dominance variance) effects were observed in all pre-
3 harvest assessments of growth traits ($d^2 = 0.18\text{--}0.31$), as well as harvest age DBH ($d^2 = 0.18$;
4 $CV_d = 13.4\%$), stem volume ($d^2 = 0.24$; $CV_d = 28.3\%$) and harvest productivity ($d^2 = 0.31$;
5 $CV_d = 29.1\%$; Table 4). The dominance:additive ratio was close to one for harvest-age DBH
6 and there was a trend towards decreasing dominance ratio and increasing narrow-sense
7 heritability over time (Figure 1). No significant dominance variation was evident for survival,
8 the presence/absence of forks, stem straightness or harvest time. Significant differences
9 among families planted in large plots were present for all traits examined in Trial 2
10 ($P < 0.010$; Figure 2), which may be due to a combination of additive and non-additive
11 genetic effects.

12
13 Insert Table 4 near here

14
15 Insert Figure 1 near here

16
17 Insert Figure 2 near here

18
19 *Correlations*

20
21 In Trial 1, positive additive and dominance genetic correlations were observed between
22 standing tree growth traits and harvest traits. However, genetic correlations between harvest
23 traits and the pre-harvest traits of survival, forking and stem straightness were not
24 significantly different from zero.

1

2 All measures of standing tree growth, including height at age one year, had significant and
 3 positive phenotypic correlations with harvest traits (Table 5). In general, large stems took
 4 longer to harvest than small stems but there was a positive correlation between stem size and
 5 harvest productivity (i.e. as DBH increased the rate of increase in stem volume was greater
 6 than the rate of increase in harvest time; Acuna and Kellogg 2009). Forking tended to
 7 increase harvest time ($r_p = 0.31$) and decrease harvest productivity ($r_p = -0.13$) and straighter
 8 stems tended to exhibit greater harvest volume ($r_p = 0.31$), harvest time ($r_p = 0.12$) and
 9 harvest productivity ($r_p = 0.32$).

10

11 In Trial 2, the direction of plot-level correlations were consistent with phenotypic correlations
 12 in Trial 1 – harvest productivity was positively correlated with average DBH and negatively
 13 correlated with the proportion of trees with forks (Table 6). The plot-level correlation
 14 between survival and harvest productivity was not significantly different from zero.

15

 16 Insert Table 5 near here

17

 18 Insert Table 6 near here

19

20 *Inbreeding depression*

21 Significant differences among cross-type treatments were evident for all standing-tree and
 22 harvest traits except forking (Table 7). Survival in open-pollinated progeny was comparable
 23 with that in out-crossed progeny up to age 5 years (Figure 3) and even at age ten years
 24 inbreeding depression for survival in seed-orchard open-pollinated progeny was low (7.0%)

1 and less than previously reported at age ten years for open-pollinated progeny from native
2 stands (Costa e Silva et al. 2010b; 35.8%). Inbreeding depression for DBH in surviving open
3 pollinated progeny was also negligible (1.5%) at age 10 years, which was reflected in low
4 inbreeding depression in open pollinated progeny for both basal area (7.2%) and harvest
5 volume (6.6%). In keeping with past observations in *E. globulus* (Costa e Silva et al. 2010b;
6 Hardner and Potts 1995), phenotypic variation in DBH at age ten years was greater within
7 open-pollinated than out-crossed plots. Within-plot phenotypic coefficients of variation were
8 0.39 and 0.33 respectively and within-plot phenotypic variances were significantly different,
9 based on a variance ratio test ($F_{221,958} = 1.41, P < 0.001$). Survival and DBH were poorer in the
10 selfed progeny at age two, five and ten years (Figure 3). At age ten years, inbreeding
11 depression for survival (34.7%), DBH (24.2%) and basal area (61.9%) was severe in selfed
12 progeny, in keeping with past findings at a similar age (10–73.6% for survival, 9.5–32.3% for
13 DBH and 48–77.0 for basal area; Costa e Silva et al. 2010b; Costa e Silva et al. 2011; Lopez
14 et al. 2000). Although a significant differences among cross-types was evident for stem
15 straightness, inbreeding depression was minimal (-5.2% for open-pollinated progeny and 4.2%
16 for selfed progeny).

17

18 Insert Table 7 near here

19

20 Insert Figure 3 near here

21

22 Discussion

23 Recurrent selection for more rapid growth, increased survival, decreased forking or increased
24 stem straightness is unlikely to adversely affect harvest productivity, given that additive

1 genetic correlations between harvest productivity and standing tree traits were either
2 favourable or not significantly different from zero. Furthermore, our study indicates that
3 dominance variation in harvest productivity could be exploited through family or clone
4 selection on the basis of DBH at age five years onward, given the strong dominance genetic
5 correlation between these traits. Diameter at breast height is a key selection criterion in most,
6 if not all, *E. globulus* breeding and deployment programs, and tested mass supplementary
7 pollinated families are currently commercially deployed by some *E. globulus* growers to
8 avoid inbreeding depression and exploit non-additive genetic variation (Patterson et al. 2004).
9 The extent of differences among specific families was exemplified by differences among
10 families planted in large-plots in Trial 2, in which harvest productivity for Family 8 was 30%
11 greater than that of Family 6 (Table 1; Figure 2). This equates to a AU\$1.57 m⁻³ difference in
12 the cost of harvesting these families, assuming a harvesting cost of AU\$220 hour⁻¹ (Acuna et
13 al. 2009).

14
15 The observed increase in narrow-sense heritability for DBH is consistent with an increase in
16 the expression of additive genetic variation over time (Stackpole et al. 2010). This is likely
17 due to the dissipation of nursery, establishment and micro-environmental effects and increase
18 in competition effects (Costa e Silva et al. 2013; Lopez et al. 2003). Although the narrow-
19 sense heritability for DBH (0.16 at age ten years) is comparable to past estimates from
20 control-pollinated *E. globulus* trials (Callister et al. 2011; Costa e Silva et al. 2004; Volker et
21 al. 2008), it was low compared with past estimates from open-pollinated trials (e.g. average
22 of 0.28 from 22 reported in Potts et al. 2004). Estimates of heritability from open-pollinated
23 trials for DBH in *E. globulus* are commonly upwardly biased due to variable levels of
24 inbreeding and inbreeding depression among families (Costa e Silva et al. 2010a).

25

1 The additive:dominance ratio of approximately one, as observed for DBH at age ten years,
2 was consistent with Li *et al.* (2007). However, estimates of this parameter were variable over
3 time in the current study and in the literature are highly variable, and often not significantly
4 different from zero (Callister *et al.* 2011; Costa e Silva *et al.* 2004; Costa e Silva *et al.* 2011;
5 Volker *et al.* 2008).

6
7 The lack of additive and dominance variation in survival was likely due to the low level of
8 mortality in out-crossed families in Trial 1 and consequent lack of statistical power. The
9 corresponding lack of significant genetic variation in forking is in keeping with past studies
10 in which genetic control of forking, within populations at least, is generally not significant
11 and/or weak (Callister *et al.* 2011; Ipinza *et al.* 1994; Lopez *et al.* 2002). It is possible that
12 differences in forking among families in Trial 2 reflected differences among subraces
13 represented in the families. Although not significant in our analysis of data from Trial 1,
14 differences among genetic groups in forking were noted by Lopez *et al.* (2002).

15
16 The magnitude of the narrow-sense heritability and lack of significant dominance variation
17 were generally consistent with past findings for stem straightness in *E. globulus* (refer to
18 Blackburn *et al.* 2013), although Callister *et al.* (2011) did note a weak, but highly significant,
19 dominance ratio (0.06 – 0.15) at three sites at 5.5 years of age for this trait. Stem straightness
20 has not been extensively studied in *E. globulus*, ostensibly because it has historically not been
21 deemed of economic importance in pulpwood production (Greaves *et al.* 1997). However,
22 with growing interest in the production sawn timber and veneer it is likely to gain greater
23 attention in tree breeding programs (Blackburn *et al.* 2013; Hamilton *et al.* in press).

24

1 Phenotypic correlations in Trial 1 were consistent with large-diameter trees being associated
2 with increased harvest productivity, forked trees being associated with reduced harvest
3 productivity, and straight trees being associated with increased productivity. However, the
4 relationship between stem straightness and harvest traits could partly confound a small effect
5 of diameter, as there was a weak positive correlation between diameter and stem straightness
6 score (0.30; SE=0.03). Phenotypic correlations between diameter and harvest traits were
7 consistent with large diameter trees taking longer to harvest but overall resulting in greater
8 harvest productivity due to the larger volume. This is in keeping with past studies
9 highlighting the strength of the relationship between piece size and harvest productivity
10 (Acuna and Kellogg 2009), and suggests that harvest productivity can be increased by
11 increasing growth rates and/or delaying harvest. However, to optimise breeding objectives
12 (Whitlock et al. 2007), the timing and type of silvicultural interventions, and harvest age; the
13 size limitations of harvesters, cash flow considerations and profitability across the entire
14 production system must be considered.

15
16 Differences in basal area per hectare and harvest traits among cross-type treatments in Trial 1
17 reflected differences in growth and survival – out-crossed treatments had the greatest average
18 DBH and greatest survival, whereas the selfed treatment had the lowest. The difference in
19 average basal area between out crossed and open-pollinated progeny from seed orchard trees
20 at harvest age was not substantial (i.e. inbreeding depression was low), possibly due to the
21 compensating effect of the death of smaller highly-inbred individuals (Costa e Silva et al.
22 2010b) and increase in resources available to surviving trees between the ages of 5 and 10
23 years (Figure 3). However, greater levels of inbreeding depression have previously been
24 observed in other trials of open-pollinated progeny from seed-orchard trees planted in large
25 plots (32.2% for basal area; Costa e Silva et al. 2010b). Differences in stem straightness

1 among out-crossing treatments most likely reflected the positive correlation between DBH
2 and straightness scores.

3

4 **Conclusion**

5 Tree genetics affects harvest productivity in ten-year-old *E. globulus*. Harvest productivity
6 was 30% greater in the best of nine out-crossed families planted as large blocks than in the
7 worst. This difference primarily reflected genetic variation in stem volume and piece size
8 among these families. Recurrent selection for more rapid growth, increased survival,
9 decreased forking or increased stem straightness is unlikely to adversely affect harvest
10 productivity, assuming harvest age is unchanged. Levels of inbreeding depression in seed-
11 orchard open-pollinated progeny were low for harvest productivity and pre-harvest stand
12 characteristics – survival, DBH, basal area, number of stems and stem straightness.

13

14 **Acknowledgments**

15 We thank the Cooperative Research Centre for Forestry and National Centre for Future
16 Forest Industries for funding, WAPRES for their substantial long term commitment to
17 provision of site, growing of seedlings, trial establishment, stand maintenance & tree
18 measurement, the Southern Tree Breeding Association (STBA) for trial establishment and the
19 provision of trial data, Norizah Kamarudin (University Putra Malaysia) for her technical
20 assistance and Daniel Nock (Planation Logging Company) for harvesting the trials.

21

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9 0457-4.
- 10
- 11

- 1 Table 1. Pedigree of the nine full-sib out-crossed families represented in Trial 2 and the
 2 number of plots each family was represented in the trial.

| ID | Mother | Father | Maternal native-forest grandmother (subrace) | Paternal native-forest grandmother (subrace) | Number of plots in trial |
|-------|----------|----------|---|---|--------------------------------|
| 1 | Glob7479 | Glob5507 | Eastern Otways | South-eastern Tasmania | 17 |
| 2 | Glob7479 | Glob5474 | Eastern Otways | Strzelecki Ranges | 20 |
| 3 | Glob4845 | Glob5617 | Western Otways | Flinders Island | 4 |
| 4 | Glob5797 | Glob5617 | Southern Tasmania | Flinders Island | 23 |
| 5 | Glob4845 | Glob5474 | Western Otways | Strzelecki Ranges | 16 |
| 6 | Glob7479 | Glob5617 | Eastern Otways | Flinders Island | 29 |
| 7 | Glob4845 | Glob5507 | Western Otways | South-eastern Tasmania | 6 |
| 8 | Glob7560 | Glob5474 | Cape Patton | Strzelecki Ranges | 6 |
| 9 | Glob7560 | Glob5507 | Cape Patton | South-eastern Tasmania | 5 |
| Total | | | | | 126 |

3

- 1 Table 2. Description of work elements included in the harvesting time and motion
 2 study.

| Time element | Description |
|--------------------|--|
| Brushing/Clearing | Removal/movement of slash, undergrowth or unmerchantable trees. |
| Delay | Harvester idle due to mechanical, operational, personal or study-induced problems. |
| Felling | Begins when crane begins to engage the tree and ends when processing commences. |
| Moving/Positioning | Not associated with felling and processing. Harvester moving within a pass. |
| Processing | Debarking, delimiting and bucking (i.e. cross-cutting) of logs. |
| Stacking/Bunching | Stacking logs that require repositioning in log piles. |
| Travel | Movement between passes or bays. |

3

- 1 Table 3. Genetic contributions from genetic groups and subraces to full-sib out-crossed
- 2 families and planted progeny in Trial 1.

| Genetic group | Families | Genetic contribution to planted progeny (%) | Subrace ^a | Families | Genetic contribution to planted trees (%) |
|---------------|----------|---|------------------------|----------|---|
| Furneaux | 117 | 41.6 | Flinders Island | 93 | 33.1 |
| | | | Southern Furneaux | 31 | 8.5 |
| King Island | 16 | 5.6 | King Island | 16 | 5.6 |
| Otways | 81 | 25.5 | Cape Patton | 14 | 3.6 |
| | | | Eastern Otways | 2 | 0.3 |
| | | | Western Otways | 67 | 21.7 |
| Strzelecki | 28 | 7.0 | Strzelecki Foothills | 1 | 0.1 |
| | | | Strzelecki Ranges | 27 | 6.9 |
| Tasmania | 57 | 20.2 | North-eastern Tasmania | 12 | 4.4 |
| | | | South-eastern Tasmania | 25 | 7.4 |
| | | | Southern Tasmania | 10 | 3.3 |
| | | | Tasman Peninsula | 15 | 5.1 |

- 3 ^a Follows Dutkowski and Potts (1999)

Table 4. Mean, narrow sense heritability (h^2), dominance ratio (d^2), coefficient of additive genetic variance (CV_a) and coefficient of dominance genetic variance (CV_d) for standing-tree and harvest traits at age ten years. Standard errors are presented in parentheses.

| Trait | Mean | h^2 | d^2 | CV_a (%) | CV_d (%) |
|---|--------------------------|------------------------|------------------------|---------------|----------------|
| Standing tree traits | | | | | |
| DBH (mm) | 210.2 (8.4) | 0.16 (0.07) P=0.003 | 0.18 (0.13) P=0.043 | 12.61 | 13.37 |
| Survival (p/a) ^a | 0.93 (0.02) ^c | 0.38 (0.19) P=0.051 | 0.57 (0.63) P=0.181 | ns | ns |
| Fork (p/a) ^a | 0.32 (0.02) ^c | 0.00 (0.11) P=0.484 | 0.06 (0.43) P=0.440 | ns | ns |
| Stem straightness (score) ^b | 3.39 (0.07) | 0.20 (0.06) P<0.001 | 0.04 (0.1) P=0.337 | 11.97 | 5.40 |
| Harvest traits | | | | | |
| Stem volume ($\log_{10}[x+1]$; m ³) | 0.1470 (0.0102) | 0.14 (0.07) P=0.014 | 0.24 (0.13) P=0.018 | 21.11 | 28.26 |
| Harvest time (min) ^d | 0.2281 (0.0066) | 0.13 (0.05) P=0.003 | 0 ^d | 11.25 | 0 ^d |
| Harvest productivity (m ³ min ⁻¹) ^d | 0.5599 (0.0295) | 0.09 (0.06) P=0.064 | 0.31 (0.14) P=0.004 | 15.33 | 29.12 |

^a significance gauged with a z-test in the case of binary traits; ^b 1 to 6 score, 6 = most straight; ^c backtransformed estimate; ^d Estimate at parameter boundary; ^d harvest time includes felling and processing time elements only, excluding time taken to travel or undertake other tasks between trees.

Table 5. Additive genetic, dominance genetic, and phenotypic correlations between standing-tree traits and harvest traits. Standard errors are in parentheses.

| Standing-tree trait | Age (years) | Correlation type | Harvest traits (aged ten years) | | |
|--------------------------------|-------------|------------------|---|---------------------------------|---|
| | | | Stem volume ($\log_{10}[x+1]$; m ³) | Harvest time (min) ^b | Harvest productivity (m ³ min ⁻¹) ^b |
| Height (m) | 1 | Additive | 0.40 (0.39) P=0.417 | 0.02 (0.02) P=0.506 | 0.04 (0.53) P=0.938 |
| | | Dominance | 0.02 (0.01) P=0.233 | <i>na</i> | 0.02 (0.01) P=0.439 |
| | | Phenotypic | 0.36 (0.03) P<0.001 | 0.36 (0.02) P<0.001 | 0.30 (0.03) P<0.001 |
| DBH (mm) | 2 | Additive | 0.60 (0.23) P=0.136 | 0.65 (0.21) P=0.042 | 0.43 (0.32) P=0.348 |
| | | Dominance | 0.79 (0.22) P=0.107 | <i>na</i> | 0.72 (0.25) P=0.114 |
| | | Phenotypic | 0.55 (0.02) P<0.001 | 0.50 (0.02) P<0.001 | 0.49 (0.02) P<0.001 |
| DBH (mm) | 5 | Additive | 0.76 (0.15) P=0.093 | 0.94 (0.13) P=0.005 | 0.58 (0.26) P=0.269 |
| | | Dominance | 1.03 (0.09) P=0.028 | <i>na</i> | 1.03 (0.10) P=0.017 |
| | | Phenotypic | 0.79 (0.02) P<0.001 | 0.65 (0.02) P<0.001 | 0.71 (0.02) P<0.001 |
| DBH (mm) | 10 | Additive | 0.99 (0.01) P<0.001 | 0.85 (0.12) P=0.003 | 0.92 (0.05) P=0.027 |
| | | Dominance | 1.01 (0.01) P=0.117 | <i>na</i> | 1.06 (0.06) P=0.037 |
| | | Phenotypic | 0.98 (0.01) P<0.001 | 0.71 (0.02) P<0.001 | 0.90 (0.01) P<0.001 |
| Survival | 10 | Additive | 0.26 (0.32) P=0.517 | 0.06 (0.31) P=0.888 | 0.01 (0.01) P=0.752 |
| | | Dominance | 0.56 (0.42) P=0.317 | <i>na</i> | 0.00 (0.00) P=0.203 |
| | | Phenotypic | <i>na</i> | <i>na</i> | <i>na</i> |
| Fork (p/a) | 10 | Additive | <i>na</i> | <i>na</i> | <i>na</i> |
| | | Dominance | <i>na</i> | <i>na</i> | <i>na</i> |
| | | Phenotypic | 0.03 (0.03) P=0.326 | 0.31 (0.03) P<0.001 | -0.13 (0.03) P<0.001 |
| Stem straightness ^a | 10 | Additive | 0.17 (0.27) P=0.56 | 0.34 (0.22) P=0.162 | 0.04 (0.32) P=0.893 |
| | | Dominance | <i>na</i> | <i>na</i> | <i>na</i> |
| | | Phenotypic | 0.31 (0.03) P<0.001 | 0.12 (0.03) P<0.001 | 0.32 (0.03) P<0.001 |

^{na} Parameters were not estimated if one or more of variance components were not significant from zero at the P=0.200 level; ^a1 to 6 score, 6 = most straight; ^b harvest time includes felling and processing time elements only, excluding time taken to travel or undertake other tasks between trees.

Table 6 Family (N=9) and plot-level (N=126) Pearsons correlation coefficients in Trial 2 between standing tree and harvest traits at age ten years.

| Trait | Type | Volume (m ³) | Harvest time (min) ^a | Harvest productivity (m ³ min ⁻¹) ^a |
|---|--------|--------------------------|---------------------------------|---|
| Survival (proportion) | Family | 0.21 (0.37) P=0.585 | 0.47 (0.33) P=0.203 | -0.23 (0.37) P=0.558 |
| | Plot | 0.32 (0.09) P<0.001 | 0.48 (0.08) P<0.001 | -0.05 (0.09) P=0.611 |
| Average DBH (mm) | Family | 0.87 (0.19) P=0.002 | 0.57 (0.31) P=0.110 | 0.93 (0.14) P<0.001 |
| | Plot | 0.83 (0.05) P<0.001 | 0.45 (0.08) P<0.001 | 0.78 (0.06) P<0.001 |
| Basal area (m ² ha ⁻¹) | Family | 0.99 (0.05) P<0.001 | 0.91 (0.16) P<0.001 | 0.70 (0.27) P=0.036 |
| | Plot | 0.98 (0.02) P<0.001 | 0.74 (0.06) P<0.001 | 0.67 (0.07) P<0.001 |
| Forking (proportion) | Family | 0.07 (0.38) P=0.864 | 0.30 (0.36) P=0.433 | -0.21 (0.37) P=0.585 |
| | Plot | 0.01 (0.09) P=0.948 | 0.21 (0.09) P=0.016 | -0.19 (0.09) P=0.030 |

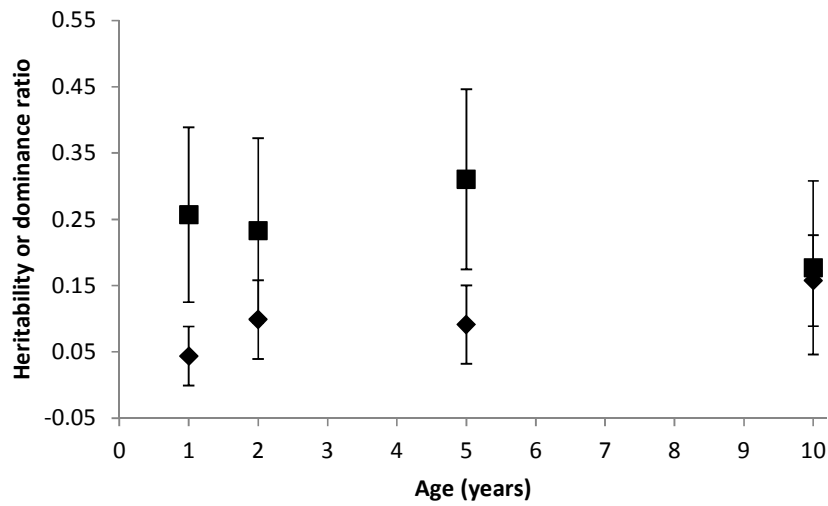
^a Harvest time includes time taken to complete all work elements within plots but excludes travel time between plots.

Table 7: The effects of cross-type on standing tree and harvest traits in Trial 1 at age ten years.

| Trait | Cross type difference (P-value) | Cross type mean (standard error) [inbreeding depression] | | |
|---|---------------------------------|--|------------------------|------------------------|
| | | Out-crossed | Open-pollinated | Selfed |
| Standing tree traits | | | | |
| Survival (%) | <0.001 | 91.4 (1.1) | 85.0 (2.0) [7.0%] | 59.7 (2.7) [34.7%] |
| Average DBH (mm) | <0.001 ^a | 208.2 (4.1) | 205.2 (5.6) [1.5%] | 157.9 (7.1) [24.2%] |
| Basal area (m ² ha ⁻¹) | <0.001 ^a | 36.8 (1.1) | 34.1 (1.7) [7.2%] | 14.0 (2.2) [61.9%] |
| Trees with multiple stems (proportion) | 0.733 | 0.17 (0.01) | 0.15 (0.03) [na] | 0.18 (0.04) [na] |
| Average stem straightness ^b | 0.006 ^a | 3.33 (0.05) | 3.56 (0.08) [-6.9%] | 3.19 (0.11) [4.2%] |
| Harvest traits | | | | |
| Harvest volume (m ³ ha ⁻¹) | <0.001 ^a | 405 (15) | 378 (22) [6.6%] | 130 (29) [67.9%] |
| Harvest time (min ha ⁻¹) ^c | <0.001 | 705 (15) | 630 (23) [10.6%] | 326 (31) [53.8%] |
| Harvest productivity (m ³ min ⁻¹) ^c | <0.001 ^a | 0.57 (0.02) | 0.60 (0.02) [-5.2%] | 0.42 (0.03) [25.9%] |

^{na} no significant difference among cross types; ^a Cross-type by replicate interaction hit the boundary (0) of the parameter space and the residual was used as the error term in the significance test; ^b individual trees scored on a subjective 1 to 6 scale, 6 = most straight; ^c harvest time includes time taken to complete all work elements within plots but excludes travel time between plots.

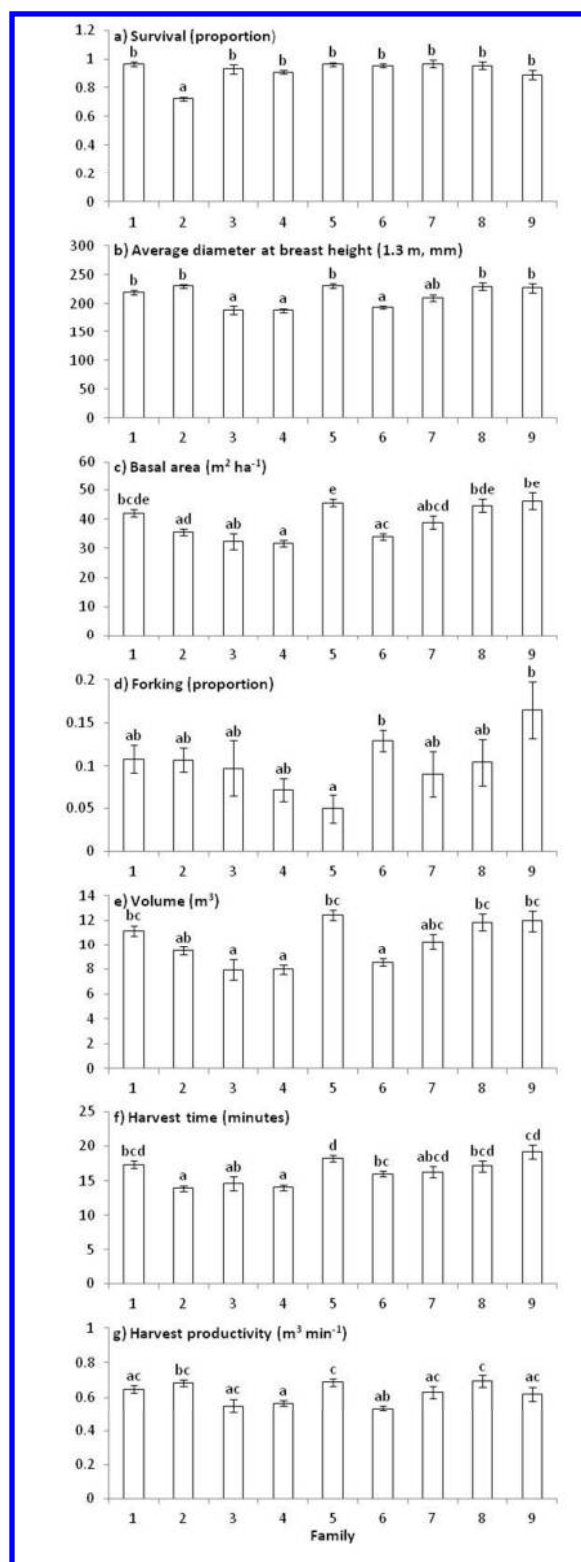
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2

3 Figure 1. Narrow-sense heritabilities (diamonds), dominance ratios (squares) and standard
4 errors estimated from out-crossed progeny in Trial 1 for height at age one year and diameter
5 at breast height (1.3 m) at age two, five and ten years.

6



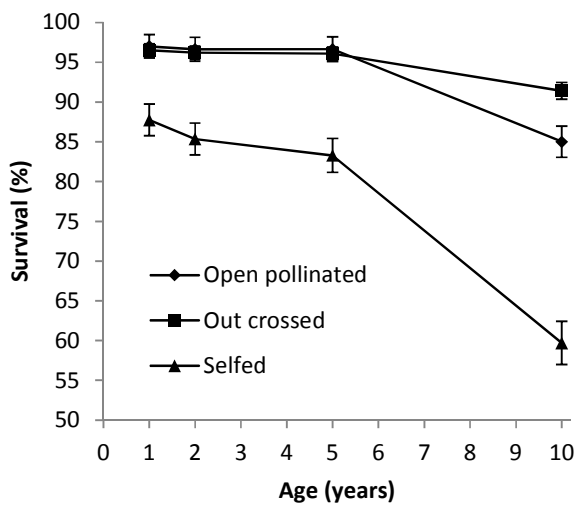
1

2 Figure 2. Family means and standard errors for standing tree (a-d) and harvest traits (e-g)

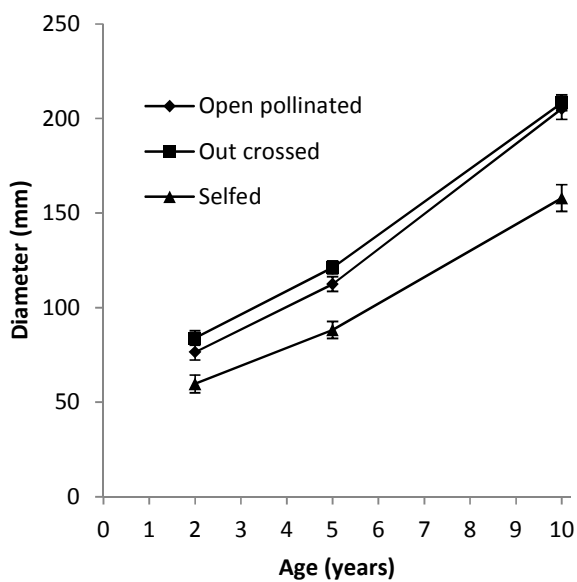
3 based on plot-level data from Trial 2. Families with common letters were not significantly

- 1 different at $P < 0.05$ following a Tukey-Kramer adjustment for multiple comparisons. Harvest
- 2 time includes time taken to complete all work elements within plots but excludes travel time
- 3 between plots.
- 4

1



2



3

4 Figure 3. Mean and standard error of block-level survival and diameter at breast height (1.3
5 m) for out-crossed (squares), open-pollinated (diamonds) and selfed (triangle) treatments in
6 Trial 1.

7