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Genetic variation in wood properties of mid-rotation age *Eucalyptus globoidea*

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Abstract

Background: *Eucalyptus globoidea* Blakely produces ground-durable (Class 2) and stiff wood and has the potential to be grown in New Zealand to supply high-value environmentally-friendly timber for use as posts in the agricultural sector and stiff veneers for the LVL industry. The New Zealand Dryland Forests Initiative (NZDFI) has established a breeding programme for this species. The objective of this study was to identify trees with superior wood properties for commercial propagation enabling the establishment of a domestic plantation resource of ground-durable timber.

Methods: The genetic variation in wood properties at mid-rotation age (8-year-old) of 141 *E. globoidea* families was assessed for the following traits: heartwood diameter, diameter under bark at ~0.5 m height, combined sapwood diameter, heartwood collapse, sapwood collapse, standing tree acoustic velocity and extractive content in the heartwood. Families were ranked and genotypes with large heartwood diameter, high extractive content and stiffness as well as low collapse were identified.

Results: Heartwood diameter (h^2 = 0.51) and extractive content (h^2 = 1.16) showed good heritability, which in combination with high variation are promising traits for a breeding programme. The high heritability for extractive content indicated a closer relatedness within the population than the assumption of unrelated families of half-siblings. The unfavourable correlation between the heartwood diameter and extractive content (genetic correlation (r_g) = −0.45) indicated that a compromise is required for simultaneous improvement of both traits. Heritability estimates for heartwood collapse (h^2 = 0.30) and acoustic velocity (h^2 = 0.36) were moderate.

Conclusions: Genetic selection for wood quality traits of *E. globoidea* is practically feasible. Superior individuals with above average performance for multiple traits were present in the breeding populations, however, this was dependent on the intended end use of the timber.

Keywords: Acoustic velocity; collapse; extractives; genetic gain; heartwood; natural durability; tree breeding; white stringybark

Introduction

Eucalyptus globoidea Blakely, commonly known as white stringybark, belongs to the subgenus *Eucalyptus* (Brooker & Kleinig 1983), and is native to south-eastern Australia's gentle undulating hill country near the coast and mountain slopes, extending to escarpments adjacent to tablelands but not inland of the ranges (Boland et al 2006). It is a species that displays several appealing properties such as early heartwood formation, drought, frost and pest-tolerance, and grows well in the New Zealand environment (Millen et al. 2018). Moreover,

it has high stiffness and strength, and its heartwood is rated Class 2 for in-ground durability, i.e. lasting 15 to 25 years in service (AS5604 2005).

The New Zealand Dryland Forests Initiative (NZDFI) is focusing on establishing a sustainable plantation resource of naturally durable eucalyptus timbers (Millen et al. 2018). Five eucalyptus species have been selected for their breeding programme, including *E. globoidea*, for the establishment of a domestic naturally ground-durable hardwood industry. Such a sustainable domestic resource is an environmentally friendly high-

value alternative not only to copper chromium arsenic (CCA) treated radiata pine, which is difficult to dispose of (Love 2007; Townsend & Solo-Gabriele 2006) but also naturally durable timber imports, which often originate from endangered or unsustainably harvested tropical sources (UNEP 2012). Envisaged uses for *E. globoidea* timber are primarily posts for the agricultural sectors (Millen et al. 2018) but it can also be used for producing stiff veneers for laminated veneer lumber (LVL) (Guo & Altaner 2018) and sawn timber (Jones et al. 2010). For the latter, stiffness and drying without collapse are relevant wood properties (Bootle 2005; Poynton 1979; Somerville & Gatenby 1996). Collapse is wood shrinkage caused by the buckling of the cell walls and flattening of the cell lumen during drying due to negative pressure (Chafe et al. 1992). It is different from normal shrinkage, which is caused by removal of bound water from the cell wall below the fibre saturation point (FSP).

Naturally durable timber has less pronounced and more variable durability than treated wood. The durability varies among trees due to a combination of genetic and environmental factors (Zobel & Jett 1995). Genetic variation can be exploited in a breeding programme, while environmental variation can be addressed by appropriate siting, silviculture and timber processing. There is also variability within trees, since sapwood is never regarded as naturally durable, and typically durability of heartwood decreases towards the pith (AS5604 2005). As a consequence, the heartwood of younger trees tends to have lower durability than heartwood from older trees (Amusant et al. 2004). Therefore, to produce ground-durable posts from young trees grown in short rotation plantations, it is necessary to deploy genetically improved tree stocks. Young trees producing durable timber have been reported in breeding trials of *E. cladocalyx* (Bush et al. 2011).

Assessing wood durability is time consuming and expensive. On the other hand, breeding programmes benefit from large sample sizes (Raymond 2002). Consequently, there has been little focus on natural wood durability in tree breeding programmes. Natural durability assessments in breeding trials, including both sampling heartwood from the trees and assessing its durability, need to be rapid and cost effective. Felling trees and sawing wood samples is destructive and too laborious for routine use in a breeding programme. A rapid means to obtain a heartwood sample without damaging the tree is taking increment cores (Estopa et al. 2017; Jones et al. 2008).

Direct assessments of natural durability by mass loss of wood samples when exposed to fungi (AWPC 2007; CEN 1989; EN-350-1 1994) are impractical in a breeding context due to time and cost (Bush & Walker 2011; Harju & Venäläinen 2006; Pâques et al. 2013). Extractive content in the heartwood are responsible for the natural durability of wood (Bush et al. 2011; Hawley et al. 1924) and have been reported to be under genetic control (Bush et al. 2011; Li et al. 2018). Near-infrared (NIR) spectroscopy has been proven effective in predicting the extractive content in wood (Bush et al. 2011; Li et al. 2018; Stackpole et al. 2011). NIR spectra

can be acquired within seconds from a solid wood surface and are an inexpensive method for assessing the chemical components of wood (Estopa et al. 2017; Greaves et al. 1996; Tsuchikawa & Schwanninger 2013). NIR calibrations for the extractive content were reported to have a root mean square error (RMSE) of 0.91% to 1.16% for *E. bosistoana* F.Muell. (Li 2018), 0.62% for *Sweitenia marcrophylla* King (da Silva et al. 2013), and 0.66% for *E. globoidea* (Kuwabara 2017).

This study examined diameter under bark, heartwood diameter, combined sapwood diameter, extractive content (EC), sapwood collapse, heartwood collapse (all at 0.5 m stem height) and acoustic velocity (a proxy for wood stiffness) of *E. globoidea*. Breeding values of these traits were calculated for 141 half-sib families of 8-year-old *E. globoidea*. The phenotypic and genetic correlations between the wood traits were estimated.

Materials and Methods

The Atkinson trial established in November 2011 at Wairarapa, New Zealand (latitude 41° 35' 21" S and longitude 175° 24' 4" E), with 141 *E. globoidea* half-sib families was used in this study. The families in this trial were grown from seed collected from across the natural range of the species in Australia and from three NZ plantation sites with a known seedlot. The unknown demarcation of the seed collected in Australia means that provenance is undeclared. The trial contained 8640 trees and was laid out in an incomplete block design with each family replicated 40 to 80 times. There were 36 trees per block, planted at a spacing of 2.4 m between rows and 1.8 m within rows. Trees in the trial were assessed for diameter at breast height (DBH) and form in 2015 at age 3.4 years, pruned in August 2018 and thinned in April 2019 to remove trees with poorer stem form.

All living trees not marked for removal and with a DBH larger than 30 mm were sampled with a purpose-built corer. A bark-to-bark 14 mm diameter core including the pith was extracted ~0.5 m above the ground from 2160 trees in March 2019.

Heartwood quantity and quality

Stem diameter under bark and heartwood diameter at 0.5 m height were measured on the green cores after highlighting heartwood with an aqueous 0.1% solution of methyl orange. Combined sapwood diameter was calculated as the difference of the two measures. Heartwood quality was assessed by predicting ethanol soluble extractive content (%) of dry cores from NIR spectra (Tensor 37, Bruker, Germany) obtained with a fibre optic probe at wavelengths from 9000 to 4000 cm^{-1} at 4 cm^{-1} intervals as described earlier (Li & Altaner 2019).

Tangential collapse

After the NIR measurements, the cores were equilibrated to a stable moisture content at 60% relative humidity and 25°C. Ten cores were randomly selected, and the widest tangential diameter was measured with a Vernier calliper. These 10 values were averaged and used as

reference (D_1) for the collapse assessment. Collapse was assessed separately for heartwood and sapwood (Equation 1). The narrowest tangential diameter of each core was measured in the sapwood (D_2), as well as the two narrowest tangential diameters for the heartwood. Two diameters were measured in the heartwood as collapse was more prominent in this region and heartwood is the main target product for durable timber production. The latter were subsequently averaged.

$$Tangential\ collapse\ (\%) = ((D_1 - D_2)/D_1) \times 100 \qquad (1)$$

Standing tree acoustic velocity

Ten trees were randomly sampled per family for those families with more than ten living trees. For families containing fewer than 11 standing trees, all trees in the family were sampled. Acoustic velocity was measured on 1,147 trees with the standing tree time-of-flight TreeTap tool (University of Canterbury, Christchurch, New Zealand) (Toulmin & Raymond 2007). A total of eight measurements were averaged per tree, which were acquired by placing the probes at one stem location; probes were spaced 1 m apart centered about breast height.

Statistical analyses

The data were analysed using R statistical software (R Core Team 2019). A linear mixed model was used for the univariate analyses (heritability) using Equation 2.

$$y_{ijk} = \mu + f_i + b_j + e_{ijk} \qquad (2)$$

where y_{ijk} is a phenotypic observation of a single trait, μ is the overall intercept, f_i is the random effect of the ith family, b_j the random effect of the jth block and e_{ijk} the random residual for the kth individual of the ith family in the jth block. The residuals were assumed to be identically and independently normally distributed. The expected value for the phenotype is μ while the variances for each of the random terms are: $V(f) = \sigma^2_f$, $V(b) = \sigma^2_b$ and $V(e) = \sigma^2_e$.

The notation can be expanded to a bivariate scenario using vectors that have two phenotypes for traits 1 and 2 for each individual. The variances are then Kronecker matrix products $V(\boldsymbol{f}) = \boldsymbol{F}_0 \otimes \boldsymbol{Z}_f$, $V(\boldsymbol{b}) = \boldsymbol{B}_0 \otimes \boldsymbol{Z}_b$, and $V(\boldsymbol{e}) = \boldsymbol{R}_0 \otimes \boldsymbol{I}$ where $\boldsymbol{Z}_f$, $\boldsymbol{Z}_b$ and $\boldsymbol{I}$ are incidence matrices, connecting the observations to model terms and $\boldsymbol{F}_0$, $\boldsymbol{B}_0$ and $\boldsymbol{R}_0$ are illustrated below.

$$\boldsymbol{F_0} = \begin{bmatrix} \sigma^2_{f1} & \sigma_{f12} \\ \sigma_{f12} & \sigma^2_{f2} \end{bmatrix} \quad \boldsymbol{B_0} = \begin{bmatrix} \sigma^2_{b1} & \sigma_{b12} \\ \sigma_{b12} & \sigma^2_{b2} \end{bmatrix} \quad \boldsymbol{R_0} = \begin{bmatrix} \sigma^2_{e1} & \sigma_{e12} \\ \sigma_{e12} & \sigma^2_{e2} \end{bmatrix} \quad (3)$$

where σ^2_{f1}, σ^2_{b1}, and σ^2_{e1} are the variances for family, block and residual; σ_{f12}, σ_{b12}, and σ_{e12} represent the covariances for family, block and residual between traits 1 and 2.

The model was fitted with the Asreml-R package (Butler et al. 2009) to estimate variance components and breeding values. The phenotypic and additive genetic variations were estimated to compute the narrow sense half-sib heritability (h^2) of each trait using Equation 4.

$$h^2 = Var(A)/Var(Y) = 4\sigma^2_f/(\sigma^2_f + \sigma^2_b + \sigma^2_e) \qquad (4)$$

The heritability estimated in this study assumed that families were true half-siblings with a relationship coefficient within families of one quarter.

The coefficient genetic of variation (CGV) for each trait was determined using the equation below.

$$CGV = (\sqrt{4\sigma^2_f}/population\ mean) \times 100 \qquad (5)$$

The coefficient of phenotypic variation (CPV) for each trait was determined using the equation below.

$$CPV = (standard\ deviation/population\ mean) \times 100 \qquad (6)$$

The genetic correlation is a measure of the strength of the genetic association between the performance in one trait and performance in another trait (Bourdon 2000).

$$r_{g(m,n)} = \sigma^2_{fm}/\sqrt{\sigma^2_{fm}\sigma^2_{fn}} \qquad (7)$$

is the covariance between traits m and n; σ^2_{fm} is the genetic variance for trait m; σ^2_{fn} is the genetic variance for trait n and $r_{g(m,n)}$ is the genetic correlation. The Pearson correlation coefficient was used to express the phenotypic correlation (r_p) between the traits.

Results and Discussion

Collapse, acoustic velocity, and heartwood properties

The descriptive statistics, heritability estimates, coefficients of phenotypic variation (CPVs) and coefficients of genetic variation (CGVs) for the assessed wood traits are presented in Table 1. High coefficients of variation were observed for extractive content, combined sapwood diameter, heartwood diameter, diameter under bark and sapwood collapse. Combined sapwood diameter exhibited larger variation than diameter under bark and heartwood diameter. The 8-year-old *E. globoidea* trees had produced more heartwood (mean heartwood diameter 91.0 mm) and had a lower coefficient of phenotypic variation (CPV = 28.9%) than has been reported for *E. bosistoana* (31.7 mm to 42.1 mm with a CPV of 51% to 61%) at 7 years of age (Li et al. 2018). In 9-year-old *E. globulus* Labill, heartwood

TABLE 1: Descriptive statistics, heritability (h^2) with the 95% confidence interval in brackets for *E. globoidea* wood properties at age 8 years; coefficient of phenotypic variation (CPV) and coefficient of genetic variation (CGV); r_c: coefficient of relatedness.

Trait	Mean	Standard deviation	Min	Max	CPV (%)	CGV (%)	h^2 (r_c = 0.25)
Diameter under bark (mm)	141.9	33.7	60	255	23.75	19.59	0.67 (0.49, 0.85)
Heartwood diameter (mm)	91.0	26.3	0	190	28.90	20.70	0.51 (0.36, 0.66)
Combined sapwood diameter (mm)	50.9	16.2	6	150	31.83	25.44	0.63 (0.45, 0.80)
Predicted extractive content (%)	9.4	4.5	−4.4	31.7	47.87	51.58	1.16 (0.90, 1.39)
Acoustic velocity (km/s)	2.96	0.31	2.13	4.27	10.47	6.24	0.36 (0.18, 0.54)
Heartwood collapse (%)	18.2	6.9	−2.9	45.5	37.91	19.16	0.30 (0.17, 0.40)
Sapwood collapse (%)	3.2	5.4	−14.1	25.1	168.75	56.52	0.12 (0.03, 0.21)

diameter ranged from 61 to 98 mm with a CPV of 6.8% to 45.1% (Miranda et al. 2014). The mean heartwood diameter reported for 8-year-old *E. cladocalyx* F.Muell ranged from 58 to 82 mm with a CPV of 29% based on samples collected from three different locations (Bush et al. 2011).

The mean combined sapwood diameter was 50.9 mm with a CPV of 31.8% (Table 1). The average value reported in this study was lower than that reported for 7-year-old *E. bosistoana* (60.4 mm and 70.3 mm) (Li et al. 2018). This confirmed the general observation that *E. globoidea* has a narrow sapwood band (Bootle 2005). A narrow sapwood band is beneficial for post processing operations as less material needs to be removed. The CPV for *E. globoidea* (31.8%) was slightly higher than for *E. bosistoana* (26%) (Li et al. 2018). The sapwood diameter reported for 9-year-old *E. globulus* ranged from 16 to 29 mm (Miranda et al. 2014) and was 50 to 74 mm for 8-year-old *E. cladocalyx* (Bush et al. 2011).

The mean predicted extractive content was 9.4% with a CPV of 47.9%. This was comparable to 7-year-old *E. bosistoana* for which 7.7% and 9.6% extractive content was observed at two different sites, with a CPV of 46% (Li et al. 2018). However, the extractive content of *E. globoidea* was lower than the average 12% observed for similarly-aged *E. cladocalyx* (Bush et al. 2011).

Tangential collapse in the heartwood had a mean of 18.2%, similar to the value of 18.6% reported for the collapse prone *E. nitens* (H.Deane & Maiden) Maiden (Kube 2005) and *E. dunnii* Maiden (14.9%) (Arnold et al. 2004). However, care must be taken when comparing the mean values reported for collapse from different studies, as the measurement techniques differed. This study measured the maximum tangential dimensional change, a combination of normal shrinkage and collapse at the worst part of the sample, which should be related to checking. The coefficient of variation in collapse reported in this study was high (37.91%) and corresponded to the observed value (37%) for 6.5-year-old *E. dunnii* (Arnold et al. 2004). Collapse in the sapwood was lower (3.2%) but more variable (CPV 168.75%) compared to collapse

in heartwood (18.2%; CPV 37.91%). It is thought that collapse is caused by negative pressure generated over gas–liquid surfaces with high curvature when water evaporates from the wood. Extractives can reduce pore size/permeability of cell walls and therefore increase the likelihood of collapse in heartwood (Chafe et al. 1992).

The mean standing tree acoustic velocity ranged from 2.13 to 4.27 km/s with a mean of 2.96 km/s and a CPV of 10.47% (Table 1). It is not straightforward to compare standing tree acoustic velocity measurements with other studies, as commonly used acoustic tools appear to provide different absolute values (Dungey et al. 2012). The standing tree acoustic velocity (TreeTap) of 2.96 km/s was similar to the 2.5 km/s (ranging from 2.2 to 2.8 km/s) reported for the species at age 25 years using the IML hammer (Wiesloch, Germany) (Jones et al. 2010). This is comparable with 2.7 km/s in 10-year-old *Pinus radiata* D.Don in Australia measured with TreeTap (Toulmin & Raymond 2007). It should also be acknowledged that age has a significant effect on the acoustic velocity of young trees, as the microfibril angle (MFA) decreases with cambial age (Lachenbruch et al. 2011) and that the mean acoustic velocity is generally lower in softwoods than hardwoods due to their higher MFA (Lindström et al. 2002).

Comparable CPVs for acoustic velocity were reported in the literature; 7.87% for 8-year-old *E. fastigata* H. Deane & Maiden (Suontama et al. 2018), 8.1 to 10.2% for 20-year-old *Pseudotsuga menziesii* (Mirb) Franco (Klápště et al. 2019) and 9.05% for *P. sylvestris* L. (Hong et al. 2015). An even lower CPV of 2.2% was reported for 10-year-old *P. radiata* (Toulmin & Raymond 2007).

Heritability and coefficient of genetic variation of studied wood properties

This study used a coefficient of relatedness (r_c) of half-siblings (r_c = 0.25), i.e. the families were assumed to be perfect half-siblings and unrelated to each other (Table 1).

Heartwood diameter had a heritability estimate of 0.51 and a CGV of 20.7%. Heritability reports for

heartwood diameter ranged from 0.39 to 0.61 for *E. grandis* W.Hill and *E. cladoclayx* (Bush et al. 2011; Santos et al. 2004), comparable with the result obtained in the current study. The observed heritability and variation in *E. globoidea* are suitable for increasing heartwood production through selective breeding; however, the coefficient of variation may decline with tree age (Bush et al. 2011).

The heritability estimates for combined sapwood diameter and diameter under bark were 0.63 and 0.67 with CGVs of 25.44% and 19.59%, respectively. Similar heritability estimates (0.67 to 0.82) were reported for sapwood diameter in 7-year-old *E. bosistoana* (Li et al. 2018) and *Larix kaempferi* (Lamb.) Carrière (Pâques 2001). The heritability of diameter under bark was comparable to the range (0.29 to 0.72) reported for diameter at breast height (DBH) in previous studies (Kube 2005; Whiteman 1992) and the CGV (19.59%) for diameter under bark was at the lower end of the range (15.1% to 87.1%) reported for growth of *Eucalyptus* hybrid clones (Wu et al. 2017).

The heritability estimate for extractive content was 1.16 and had a CGV of 51.58%. The relatedness coefficient (0.25) used in this study pushed the heritability estimate above 1, potentially indicating deviations from half-siblings and inbreeding effects (Eldridge et al. 1994; Elliott & Byrne 2003). In general, heritability estimates reported for extractive content ranged from 0.19 to 0.56 for *E. bosistoana* and *E. globulus* (Li et al. 2018; Poke et al. 2006). The estimates of heritability in this species might be too high because of the unknown relatedness and the fact that the assessments were restricted to one site (White et al. 2007). The high CGV (51.58%) combined with strong genetic control indicated potential to improving natural durability of *E. globoidea* through selective breeding.

Collapse was moderately heritable in the heartwood (h^2 = 0.30) but was not very variable (CGV of 19.16%), while it had low heritability in the sapwood (h^2 = 0.12) where it was more variable (CGV = 56.52%). The narrow sapwood band in *E. globoidea* is unlikely to be converted into solid wood products. The heritability, although low, along with the coefficient of variation estimates indicated potential for improving tangential collapse in *E. globoidea* heartwood through selection. The heritability of collapse in the heartwood was similar to most values reported for other eucalypts; *E. nitens* (0.23 to 0.61) (Hamilton et al. 2004; Kube 2005) and *E. grandis* (0.23 to 0.31) (Bandara 2006). The location where *E. delegatensis* F.Muell. ex R.T.Baker seed was collected was reported to influence the severity of the collapse, indicating some degree of genetic control (King et al. 1993).

The heritability for standing tree acoustic velocity was 0.36 with a CGV of 6.24% for *E. globoidea*, similar to values reported in the literature: 0.26 to 0.75 for 11- to 13-year-old *P. menziesii* (Douglas fir) (Dungey et al. 2012; Klápště et al. 2019) and 0.35 for an *E. fastigata* progeny trial (Suontama et al. 2018). The coefficient of genetic variation reported in this study was low. Even lower values of genetic variability have been reported in the literature, for example 4.8% to 5.13% for *P. menziesii* and *E. nitens,* respectively (Blackburn et al. 2014; Klápště et al. 2019). The low genetic variability of acoustic velocity limits the potential for genetic improvement of stiffness.

Phenotypic and genetic correlations between traits of 8-year-old *E. globoidea*

The phenotypic and genetic correlations between the wood traits are presented in Tables 2 and 3.

There were positive phenotypic correlations between diameter under bark and sapwood diameter (r_p = 0.65) as well as heartwood diameter (r_p = 0.88) (Table 2).

TABLE 2: Phenotypic correlations between traits for 8-year-old *E. globoidea* (95% confidence interval in brackets).

Trait	Diameter under bark	Sapwood collapse	Heartwood diameter	Combined sapwood diameter	Extractive content	Acoustic velocity
Heartwood collapse	−0.03 (−0.07, 0.02)	0.44 (0.41, 0.48)	0.03 (−0.03, 0.06)	−0.09 (−0.13, −0.05)	0.11 (0.06, 0.15)	−0.01 (−0.07, 0.05)
Diameter under bark		−0.10 (−0.14, −0.06)	0.88 (0.87, 0.89)	0.65 (0.62, 0.67)	−0.31 (−0.35, −0.27)	0.15 (0.10, 0.20)
Sapwood collapse			−0.08 (−0.13, −0.05)	−0.07 (−0.11, −0.02)	−0.01 (−0.06, 0.03)	−0.01 (−0.07, 0.05)
Heartwood diameter				0.20 (0.17, 0.25)	−0.14 (−0.18, −0.10)	0.14 (0.09, 0.20)
Combined sapwood diameter					−0.42 (−0.46, −0.39)	0.08 (0.02, 0.13)
Extractive content						−0.07 (−0.13, −0.02)

TABLE 3: Genetic correlations between the traits for 8-year-old *E. globoidea* (95% confidence interval in brackets).

Trait	Diameter under bark	Sapwood collapse	Heartwood diameter	Combined sapwood diameter	Extractive content	Acoustic velocity
Heartwood collapse	−0.05 (−0.30, 0.22)	0.64 (0.36, 0.90)	−0.09 (−0.36, 0.19)	−0.02 (−0.25, 0.30)	0.23 (−0.01, 0.45)	0.05 (−0.39, 0.48)
Diameter under bark		0.18 (−0.15, 0.50)	0.91 (0.87, 0.95)	0.82 (0.75, 0.89)	−0.67 (−0.81, −0.54)	0.18 (−0.09, 0.45)
Sapwood collapse			0.16 (−0.17, 0.51)	0.16 (−0.17, 0.52)	−0.05 (−0.36, 0.29)	0.05 (−0.55, 0.62)
Heartwood diameter				0.53 (0.35, 0.71)	−0.45 (−0.62, −0.28)	0.10 (−0.19, 0.43)
Combined sapwood diameter					−0.79 (−0.89, −0.69)	0.24 (−0.01, 0.54)
Extractive content						−0.15 (−0.41, 0.12)

The strong positive correlations indicated that larger trees have wider heartwood as well as sapwood. Similar phenotypic correlations were reported between DBH and heartwood diameter for 7-year-old *E. bosistoana* (r_p = 0.59) (Li et al. 2018), 22.5-year-old *E. tereticornis* Sm. (r_p = 0.79) (Kumar & Dhillon 2014)*, Acacia melanoxylon* R.Br. (r_p = 0.88) (Knapic et al. 2006) and 30- to 37-year-old plantation-grown *Pinus radiata* D.Don (r_p = 0.71) (Wilkes 1991). The genetic correlation between heartwood diameter and diameter under bark was stronger than the phenotypic correlation (r_g = 0.91, $CI_{95\%}$ 0.87, 0.95, Table 3). Strong positive genetic correlations between these traits were also reported for 9-year-old *E. globulus* (r_g = 0.99) (Miranda et al. 2014)*,* 7-year-old *E. bosistoana* (r_g = 0.89 to 0.98) (Li et al. 2018), *E. cladocalyx* (r_g = 0.44) (Bush et al. 2011), *L. kaempferi* (r_g = 0.87 to 0.92) (Pâques 2001) and 35-year-old *Juglans nigra* L. (r_g = 0.98) (Woeste 2002). No genetic correlation (r_g = 0.022) was reported between the two traits for 25-year-old *P. sylvestris* (Fries & Ericsson 1998). The growth traits were favourably correlated with heartwood diameter being the most relevant measure when aiming to produce naturally durable timber.

A negative phenotypic correlation was observed between heartwood diameter and extractive content at both the phenotypic (r_p = −0.14, Table 2) and genetic (r_g = −0.45, Table 3) level. A strong negative genetic correlation (r_g = −0.86) was also reported between these traits for 7-year-old *E. bosistoana* (Li et al. 2018). However, a positive genetic correlation between heartwood diameter and extractive content (r_g = 0.32) was found for *L. eurolepis* (Pâques & Charpentier 2015). With the negative correlation observed for *E. globoidea*, trees with more heartwood tend to have lower amounts of extractives in the heartwood, resulting in lower decay resistance (Li et al. 2020). Selection for high durability will compromise heartwood quantity; however, as the correlation applies at the population level, individual trees that excel in both traits (i.e., so-called "correlation breakers") may exist.

The relationship between collapse in the sapwood and heartwood was positive at the phenotypic level (r_p = 0.44, Table 2) and the genetic level (r_g = 0.64, Table 3), suggesting that collapse is related to wood anatomy and amplified by heartwood extractives. No previously published results on the correlations between the two traits in other species were found for comparison. Heartwood collapse was positively correlated with extractive content at both the phenotypic and genetic level (r_p = 0.11; r_g = 0.23). A positive phenotypic correlation was reported between the two traits for *E. regnans* F.Muell. (Chafe 1987). The positive correlation between the traits is in line with current understanding of the causes of drying collapse, as heartwood extractives reduce the permeability of the cell walls and consequently increase the negative pressure during evaporation of water. However, as these correlations were not strong other factors, e.g. density, contribute to collapse.

There were only weak correlations between diameter under bark and acoustic velocity at both the phenotypic and genotypic level (r_p = 0.15; r_g = 0.18, Table 2 and Table 3). Weak phenotypic relationships between these traits have also been reported for 8- to 25-year-old *P. radiata* (0.04 to 0.18) (Chauhan & Walker 2006; Toulmin & Raymond 2007) and 25-year-old *E. dunnii* (0.14) (Joe et al. 2004). In the current study, acoustic velocity was weakly correlated with heartwood diameter at the phenotypic level (r_p = 0.14, $CI_{95\%}$ 0.09, 0.20) but independent at the genetic level (r_g = 0.10, Table 3). Therefore, our results indicate that the two traits need to be improved independently. Furthermore, the weak unfavourable correlations between acoustic velocity and extractive content at the genetic level (r_g = −0.15) and phenotypic level (r_p = −0.07) (Table 2) imply the need for compromise in selecting for the two traits simultaneously.

Selection of superior genetics

Breeding programmes typically aim to improve multiple traits simultaneously, either by selecting the best or culling the poorest performing families. In the absence of economic weights for the traits, superior genotypes can be selected by choosing families with above average breeding values in several traits. Approximately 15% of the 141 *E. globoidea* families showed both above average heartwood diameter and extractive content values (Figure 1). However, in a situation where heartwood collapse as a third trait is considered, only four families met the criteria (highlighted in red in the top right quadrant). If the interest is in using wood for laminated veneer lumber (LVL), stiffness, growth (stem diameter) and collapse are important traits that need to be considered (Figure 2). A total of 18 families highlighted in red in the top right corner of the quadrant met these criteria.

Heritability estimates and breeding values are dependent on the relatedness of the individuals and families. Neither between family nor within family relatedness for the *E. globoidea* trees was known. The presented absolute values are likely overpredictions as no provenance effect was considered and families were not true half-siblings but a mixture of full-siblings and selfed individuals. Nevertheless, the ranking of the families by their breeding values is independent of their relatedness and therefore better performing genotypes can be selected by the industry.

Conclusions

The traits of *E. globoidea* investigated in this study were under varying degrees of genetic control and showed different degrees of variability. Extractive content, an indicator of natural durability, and heartwood diameter, are the two key traits determining the value of the species for the intended use as ground-durable timber, and showed the highest coefficient of phenotypic and genetic variation (CPV = 47.87% and 28.90%). Combined with the narrow sense heritability for heartwood diameter and extractive content of 0.51 and 1.16, respectively, significant genetic gain should be possible for these traits.
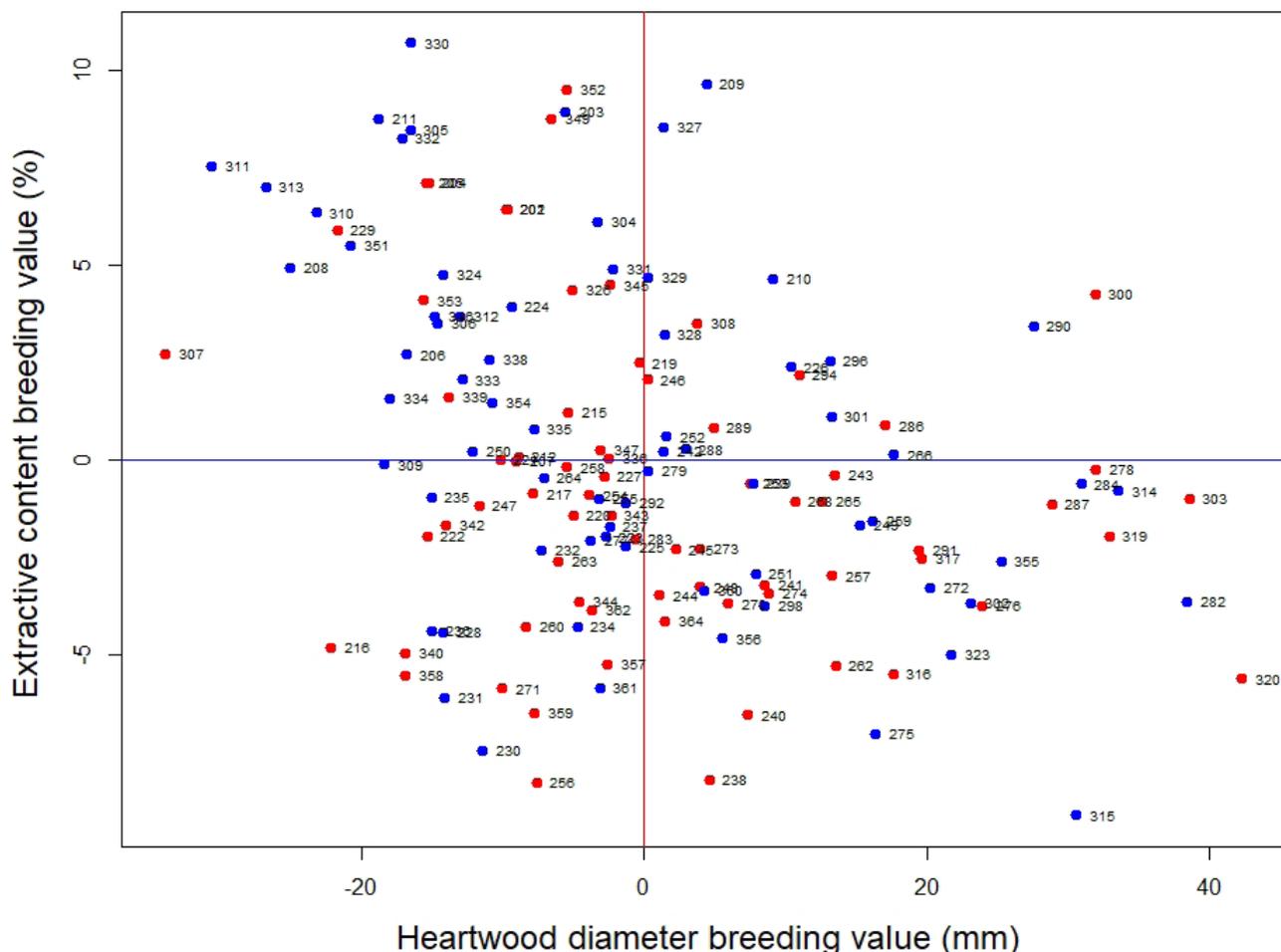

FIGURE 1: Relationship between family breeding values of heartwood diameter and EC for 141 *E. globoidea* families at age ~8 years. Families performing above average are located in the top right quadrant. Families with superior (red) and inferior (blue) average performance for heartwood collapse are highlighted.
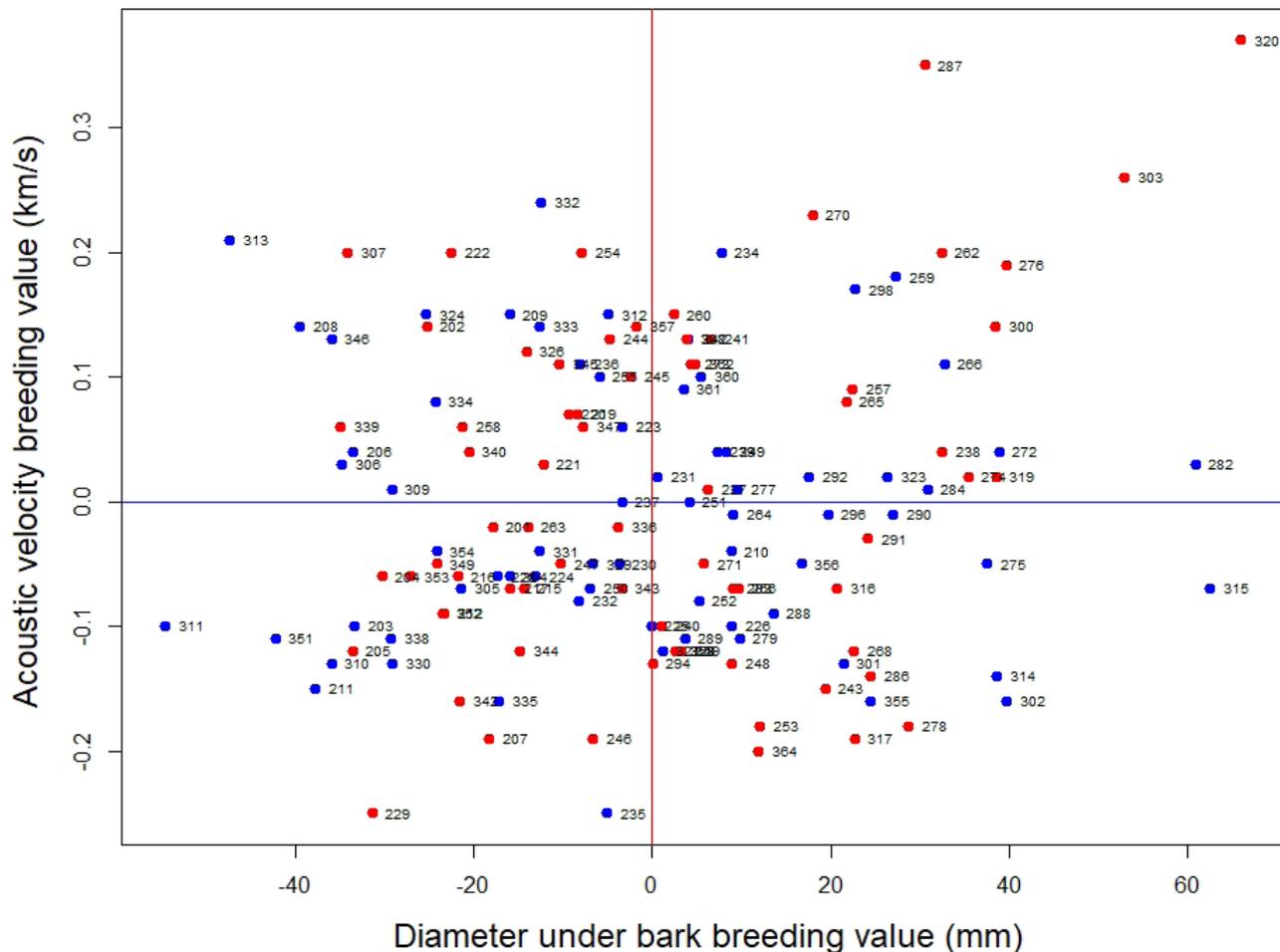
FIGURE 2: Relationship between breeding values of diameter under bark and acoustic velocity for 141 *E. globoidea* families at age ~8 years with the families superior for tangential collapse highlighted in red.

In accordance with the literature and the general understanding of the physical causes of collapse, heartwood was more prone to collapse than sapwood. Collapse in the heartwood was under moderate genetic control and this study showed that maximal tangential collapse can be included at reasonable cost into a breeding programme if core samples are available. Selection of superior genetics among the families would be practically feasible and could be used to increase utilisation of *E. globoidea* for solid timber products. Acoustic velocity was under moderate genetic control (0.36) with low variability, implying improvement of this trait through breeding would be challenging.

Competing interests
The authors declare no competing interests.

Authors' contributions
EI carried out experimental work, data analysis and drafted the manuscript. CA developed the measurement methods and conceived the study. LA designed the trials and data analysis. All authors revised the manuscript.

Abbreviations
CGV: coefficient of genetic variation
CPV: coefficient of phenotypic variation
DBH: diameter at breast height
EC: extractive content
LVL: laminated veneer lumber
MFA: microfibril angle
NIR: Near infrared spectroscopy
NZDFI: New Zealand Dryland Forests Initiative

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