

Genetic variation in drying collapse and heartwood properties at mid-rotation age of *Eucalyptus globoidea*

Vikash Ghildiyal¹, Ebenezer Iyiola², Monika Sharma³, Luis A. Apiolaza⁴, Clemens Altaner^{*,5}

School of Forestry, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

ARTICLE INFO

Keywords:

Breeding values
Drying collapse
Extractives
Natural durability
Tree breeding
White Stringybark

ABSTRACT

Main causes of drying degrade in most plantation-grown eucalypt timber are collapse and checking. Appropriate but costly sawing and drying techniques are employed to alleviate these problems. *Eucalyptus globoidea* is an emerging plantation species. This study investigated the genetic control of collapse and other tree features in an *E. globoidea* breeding population established at three different sites. Using a 14-mm diameter corer, thousands of *E. globoidea* trees representing 163 families were sampled, and genetic parameters for heartwood and sapwood collapse, extractive content, and heartwood diameter were estimated. Heartwood collapse was under genetic control with a narrow sense heritability ranging from 0.22 to 0.44. Considering the coefficient of genetic variability of ~13–23%, heartwood collapse in *E. globoidea* can be reduced through selection. The significant genetic correlation between sites for heartwood collapse ($r_g = 0.73$ – 0.83) suggested low genotype by environment ($G \times E$) interaction. In line with the physical causes of collapse, heartwood collapse was positively correlated with extractive content. Extractive content and heartwood diameter are other traits of interest, as *E. globoidea* is grown for its ground-durable heartwood. The heritability of extractive content ranged from 0.40 to 0.71. Heartwood diameter was shown to be negatively correlated to extractive content. No significant genotype by environment ($G \times E$) interaction was found for extractive content while genotype by environment ($G \times E$) interactions for heartwood and sapwood diameter were small. Finally, 12 families had above-average heartwood diameter, extractive content, and below-average heartwood collapse. In summary, this study has shown that genetic selection for collapse and other wood properties of *E. globoidea* is feasible.

1. Introduction

The genus *Eucalyptus* is one of the most widely cultivated hardwood genera for fibre production (Myburg et al., 2014; Seng Hua et al., 2022). With the increasing demand for climate friendly building materials, the fast-growing *Eucalyptus* crop has immense potential to sustainably supply the solid wood processing industry. However, its susceptibility to collapse and internal checking during drying needs to be remediated (Blakemore and Northway, 2009; Chafe et al., 1992; Jacobs, 1981).

Collapse also occurs in other wood species such as oaks or Western Red Cedar, especially when combining thin cell walls and low permeability (Tiemann, 1941; Thomas and Erickson, 1963).

There are technical solutions to mitigate drying collapse (Ananías et al., 2020; Chafe, 1992; Dawson et al., 2020; Ghildiyal et al., 2022). However, strategies such as appropriate sawing techniques (Campbell and Hartley, 1978; Chafe, 1992; Jacobs, 1979), drying pre-treatments (Ellwood, 1953; Kong et al., 2018; Vermass and Bariska, 1995; Zhang et al., 2011) or reconditioning (Chafe et al., 1992; Jacobs, 1979) are not

Abbreviations: CGV, coefficient of genetic variation; CPV, coefficient of phenotypic variation; DBH, diameter at breast height; EC, extractive content; h^2 , narrow-sense heritability; HWC, heartwood collapse; HWD, heartwood diameter; NIR, near infrared spectroscopy; NZDFI, New Zealand dryland forests innovation; rc, Relatedness coefficient; r_g , genetic correlation; r_p , phenotypic correlation.

* Corresponding author.

E-mail address: clemens.altaner@canterbury.ac.nz (C. Altaner).

¹ ORCID: 0000-0002-5253-6080

² ORCID: 0000-0001-7781-7762

³ ORCID: 0000-0002-3907-1784

⁴ ORCID: 0000-0003-0958-3540

⁵ ORCID: 0000-0003-4542-4432

<https://doi.org/10.1016/j.indcrop.2023.116891>

Received 18 January 2023; Received in revised form 3 May 2023; Accepted 15 May 2023

0926-6690/© 2023 Elsevier B.V. All rights reserved.

Table 1
Description of 2011 *E. globoidea* breeding trials including main site characteristics.

Site	Latitude	Longitude	Annual rainfall (mm)	Tree age (cored)	Families sampled	Trees sampled
Avery	41°43'59" S	174°09'60" E	600–800	9.2	163	2711
Atkinson	41°35'21" S	175°24'04" E	800–1200	8	141	2128
JNL Ngaumu	41°02'17" S	175°52'33" E	900–1200	9.8	115	910

necessarily economical (Blakemore and Northway, 2009; Chafe et al., 1992) and occur ongoing costs. Exploiting the genetic control of within-species variation via tree breeding has the potential to eliminate the checking and collapse problems in the longer term (Blakemore and Northway, 2009; Kube and Raymond, 2005).

Eucalyptus globoidea Blakely, known as White Stringybark, is a medium to large hardwood reaching a height of 24–30 m and a diameter of 60–90 cm (Poynton, 1979) that grows in the gentle undulating hill region of south-eastern Australia along the coast and on mountain slopes (Boland et al., 2006). It also grows well in the drier and warmer regions of New Zealand (Salekin et al., 2021) and has shown good pest tolerance (Lin et al., 2017). *E. globoidea* is one of several eucalyptus species domesticated by the New Zealand Dryland Forests Innovation (NZDFI) to produce a sustainable plantation resource of ground durable high-value timber (Millen et al., 2018) to supply agricultural posts, laminated veneer lumber (LVL) (Guo and Altaner, 2018) and sawn timber products (Jones et al., 2010). After over a decade of development, the first improved *E. globoidea* became available for sale in 2021 from the breeding programme. The NZDFI promotes the establishment of up to ten durable eucalypts catchments of 5000 ha within 40 km of an identified wood processing site between 2020 and 2050 (Millen et al., 2018). Proposed plantation regimes for these plantations are 15–20 years for peeler/pole production and 30–40 years for sawlog production (Millen et al., 2020).

Old-growth *E. globoidea* timber has an air-dry density of 820–900 kg/m³ and good mechanical properties, featuring a stiffness of 17 GPa and a strength of 133 MPa (Bootle, 2005). Its heartwood is categorised as class 2 for in-ground durability, i.e. lasting 15–25 years in service (AS5604, 2005). However, it can experience collapse and checking during drying (Bootle, 2005; Poynton, 1979; Somerville and Gatenby, 1996).

Large variation in wood properties between trees of a species, including collapse, have been reported (Chafe et al., 1992; Purnell, 1988). Some of this variation is genetically controlled (Kube and Raymond, 2005; Purnell, 1988). As for collapse, natural durability varies between trees and within trees (Zobel and Jett, 2012), with heartwood closer to the pith (the first few growth rings) having lower durability than outer heartwood (AS5604, 2005). However, young eucalypt trees that produce durable timber have been reported (Bush et al., 2011; Bush and Walker, 2011; Li et al., 2018). The presence of extractives in heartwood is one of the key factors for natural durability (Rudman, 1964), hence quantifying extractive content could provide an alternative approach to predict natural durability within species (Li et al., 2020; Moya et al., 2014). The chemical constituents of materials are reflected in Near Infrared Reflectance (NIR) spectra, which can be easily obtained (Li et al., 2020). Near infrared (NIR) spectroscopy has been shown to be useful in predicting the extractive content of heartwood (Bush et al., 2011; Li et al., 2018). The main extractive compounds in the heartwood of light-coloured eucalyptus species were reported to be ellagi- and galletannins, also known as hydrolysable tannins (Hillis, 1991). However, these were also reported to be non-toxic to wood-damaging organisms, suggesting that other, unidentified compounds are present in the heartwood of the light-coloured but durable heartwood of *E. globoidea*.

This study tested the hypothesis that collapse and heartwood properties are under genetic control in the NZDFI *E. globoidea* breeding population planted on three sites at mid-rotation age. The objectives of

this study were: 1) estimating genetic parameters and stability across environments for tangential collapse, extractive content, core length and heartwood and sapwood diameters, 2) evaluating the relationships between collapse and other heartwood traits relevant to the NZDFI breeding programme and 3) provide breeding values for the traits to allow the selection of fit-for-purpose planting stock.

2. Material and methods

2.1. Trials

Three open-pollinated *E. globoidea* single-tree plot progeny trials were planted in 2011 by the NZDFI in New Zealand at 2.4 m × 1.8 m spacing. The trials represented 163 families, i.e. offspring of seed collected from one mother tree, with 163 families present at Avery in Marlborough, 141 families present at Atkinson in the Wairarapa and 115 families present at JNL Ngaumu in the Wairarapa. The seed was collected from across the natural range of the species in Australia and from three New Zealand plantation sites established from a known seed lot. Table 1 summarises the features of the three sites.

At the Avery site, 298 incomplete blocks were established, with 36 trees in each block, totalling 10,728 trees. The number of individuals per family ranged from 31 to 81. The trial was assessed for DBH (diameter over bark at breast height, assessed at 1.4 m from the ground), total height and form at the age of 9 years in October 2020 and cored in December 2020.

At the Atkinson site, each family was replicated 40–80 times across the site in 240 incomplete blocks with 36 trees per block, totalling 8640 trees. The trial was assessed for DBH, growth and form, and thinned to 6491 remaining trees in 2015. The trial was cored in April 2019.

At the JNL Ngaumu site, 240 incomplete blocks were established with 30 trees in each block totalling 7200 trees. The number of individuals per family ranged from 39 to 89. The DBH was measured on randomly selected trees for coring in May 2021 and cored in June 2021.

2.2. Coring

Up to 20 trees with a DBH above 50 mm were randomly selected from each family for sampling in the Avery trial, resulting in 2711 trees. From the Atkinson trial, all living trees not marked for removal with a diameter larger than 30 mm were sampled, resulting in 2128 trees. From the JNL Ngaumu trial, up to 12 trees with an estimated diameter of above 50 mm based on their DBH in 2017 were randomly selected from each family for sampling. In total 910 trees were cored.

A bark-to-bark 14 mm diameter core including the pith was extracted at a height of 0.5 m using a purpose-built corer.

2.3. Core length, heartwood diameter

The heartwood diameter and core length (without bark) in the stem were assessed in the green state on the cores. The heartwood was highlighted by immersing cores in an aqueous 0.1% solution of methyl orange that changed heartwood colour to pink while the sapwood remained yellowish.

Table 2

Descriptive statistics and heritability (h^2) (95% confidence interval (CI₉₅) in parentheses) for *E. globoidea* wood properties at Avery aged 9.2 years (n = 2711), at Atkinson aged 8 years (n = 2128) and JNL Ngaumu aged 9.8 years (n = 910); CPV: coefficient of phenotypic variation and CGV: coefficient of genetic variation.

Trait	Sites	Mean	Min	Max	CPV (%)	CGV (%)	h^2 (rc = 0.25) ^b
Tangential collapse HW (%)^a	Avery	21.20	0.56	44.10	32.31	15.15	0.22 (0.13, 0.31)
	Atkinson	26.51	7.55	51.08	23.58	12.89	0.30 (0.18, 0.42)
	JNL	17.12	0.07	38.68	34.05	22.68	0.44 (0.22, 0.65)
Tangential collapse SW (%)^a	Avery	11.67	0	35.57	44.56	16.85	0.14 (0.07, 0.21)
	Atkinson	13.10	-2.45	32.77	36.56	12.96	0.12 (0.04, 0.21)
	JNL	11.82	0	33.12	40.19	18.51	0.21 (0.03, 0.38)
Core length (mm)	Avery	81.89	30	177	26.50	24.19	0.81 (0.63, 0.98)
	Atkinson	141.80	60	255	23.72	20.02	0.71 (0.53, 0.89)
	JNL	121.09	38	230	28.88	33.45	1.34 (1.01, 1.63)
Heartwood diameter (mm)	Avery	47.97	0	145	47.76	33.71	0.49 (0.35, 0.62)
	Atkinson	90.89	0	190	28.85	21.16	0.53 (0.38, 0.69)
	JNL	80.25	0	174	37.63	41.68	1.22 (0.89, 1.50)
Sapwood diameter (mm)	Avery	33.91	0	116	37.48	27.92	0.55 (0.40, 0.69)
	Atkinson	50.90	6	150	31.94	25.66	0.65 (0.47, 0.82)
	JNL	40.84	5	100	33.64	22.83	0.46 (0.25, 0.66)
Extractive content (%)	Avery	3.61	0.54	26.33	59.00	37.26	0.40 (0.28, 0.52)
	Atkinson	3.37	0.5	32.12	62.02	51.67	0.71 (0.53, 0.89)
	JNL	2.67	0.51	25.16	58.80	36.59	0.39 (0.21, 0.57)

^a maximum tangential shrinkage

^b rc = 0.25 i.e the relatedness coefficient for assumed true half-siblings

2.4. Drying and extractive content

Core samples were oven-dried at 60 °C. Extractive content was predicted from Near Infrared (NIR) spectra with a multivariate statistical model developed by Li and Altaner (2019) for three durable eucalypt species. NIR spectra were taken on the sanded transverse (i.e. end-grain) surface of the oven-dried cores using a fibreoptics probe connected to a Bruker Tensor 37 spectrometer. The average heartwood extractive content for the tree was calculated by averaging the radial values per core.

2.5. Maximal tangential shrinkage (tangential collapse)

A reference mean green core diameter (widest tangential diameter) D_{green} of 14.31 mm (SD = 0.51 mm) was obtained by averaging green core diameters of 500 randomly selected cores assessed at three positions along each core. The narrowest tangential diameters (D_{dry}) of each core equilibrated to ~12% moisture content in a climate-controlled room at 65% relative humidity, 25 °C was determined in the sapwood as well as in the heartwood. It was observed that collapse was more prominent in the heartwood as compared with sapwood, therefore the two narrowest tangential diameters were measured in the heartwood region.

The maximal tangential shrinkage in the core was calculated separately for heartwood and sapwood according to the following equation, where D stands for tangential diameter:

$$\text{Maximal tangential shrinkage} = \frac{D_{\text{green}} - D_{\text{dry}}}{D_{\text{green}}} \times 100\% \quad (1)$$

2.6. Statistical analysis

Data were analysed with the R software (R Core Team, 2021). Descriptive statistics including the coefficient of phenotypic variation (CPV) were calculated for each trait. The Pearson correlation coefficient was reported as phenotypic correlation (r_p) between traits. Analyses of variance (ANOVA) were performed to compare the significant difference between the site means.

2.6.1. Genetic analysis

A linear mixed effect model was used for the univariate analyses. Univariate analyses were simplified from a general model including a fixed overall mean, and random incomplete blocks within replicate, and family effects with the following model:

$$y = X\mathbf{m} + \mathbf{Z}_1\mathbf{b} + \mathbf{Z}_2\mathbf{f} + \mathbf{e} \quad (2)$$

Where y is the vector of phenotypic observations for a single site, \mathbf{m} is the vector of the fixed effect of the overall mean, \mathbf{b} is the vector of incomplete-block effects, \mathbf{f} is the vector of family effects (¼ of the additive genetic effects) and \mathbf{e} is the vector of the (assumed to be identically and independently normally distributed) residuals. X , \mathbf{Z}_1 and \mathbf{Z}_2 are incidence matrices linking the phenotypic observations to the overall mean, incomplete-block and family effect vectors, respectively (Apio-laza, 2012).

Subsequently the correlation between the two trials were determined by expanding the above equation by stacking up the vectors, in such a way that \mathbf{m} , \mathbf{b} , \mathbf{f} , and \mathbf{e} contain the values for both trials (Apio-laza, 2012).

Variance components and breeding values were estimated using the fitted model in the ASReml-R 4.0 package (Butler et al., 2017). The phenotypic and additive genetic variation were estimated to calculate the narrow sense half-sibling heritability (h^2) of each trait using Equation 3.

$$h^2 = \frac{\text{Additive variance}}{\text{Phenotypic variance}} = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_b^2 + \sigma_r^2} \quad (3)$$

where σ_f^2 is the variance for the family; σ_b^2 is the variance for the incomplete block and σ_r^2 is the residual variance. The heritability calculated in this study assumed that families were true half-siblings with a relatedness coefficient (rc) among families of one quarter.

The confidence intervals for genetic parameters were estimated using parametric bootstrapping, which involved simulating observations from the distribution for each of the variance components (incomplete blocks, families, and residuals) and computing the heritability for each set of observations. This generated a distribution for the genetic parameter, from which we derived the 0.025 and 0.975 quantiles for the limits of the 95% confidence interval.

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

Table 3

Phenotypic correlations (r_p) between traits for 9.2-year-old *E. globoidea* at Avery (AV), for 8-year-old *E. globoidea* at Atkinson (AT) and for 9.8-year-old *E. globoidea* at JNL Ngaumu (JNL). CI₉₅ in parentheses – values with a CI₉₅ excluding 0 are highlighted in bold.

Traits	Tangential collapse SW			Core length			Heartwood diameter			Sapwood diameter			Extractive content		
	AV	AT	JNL	AV	AT	JNL	AV	AT	JNL	AV	AT	JNL	AV	AT	JNL
Site	AV	AT	JNL	AV	AT	JNL	AV	AT	JNL	AV	AT	JNL	AV	AT	JNL
Tangential collapse	0.45	0.45	0.44	0.22	-0.03	-0.03	0.30	0.02	0.00	-0.15	-0.09	-0.07	0.11	0.13	0.19
	(0.42, 0.48)	(0.41, 0.48)	(0.38, 0.49)	(0.18, 0.25)	(-0.07, 0.02)	(-0.09, 0.04)	(0.26, 0.33)	(-0.02, 0.06)	(-0.06, 0.07)	(-0.19, -0.11)	(-0.13, -0.04)	(-0.14, -0.01)	(0.07, 0.15)	(0.08, 0.17)	(0.13, 0.26)
Tangential collapse HW				0.08	-0.10	-0.01	0.09	-0.08	-0.05	-0.02	-0.07	0.08	-0.05	-0.00	-0.02
				(0.04, 0.12)	(-0.14, -0.06)	(-0.08, 0.06)	(0.05, 0.13)	(-0.12, -0.04)	(-0.11, 0.02)	(-0.06, 0.02)	(-0.11, -0.02)	(0.01, 0.14)	(-0.09, -0.01)	(-0.04, 0.04)	(-0.09, -0.05)
Core length							0.84	0.88	0.92	0.19	0.65	0.52	0.03	-0.17	-0.16
							(0.83, 0.85)	(0.87, 0.89)	(0.91, 0.93)	(0.16, 0.23)	(0.62, 0.67)	(0.47, 0.57)	(0.00, 0.07)	(-0.21, -0.13)	(-0.23, -0.10)
Heartwood diameter										-0.37	0.21	0.15	0.12	-0.06	-0.12
										(-0.40, -0.34)	(0.17, 0.25)	(0.08, 0.21)	(0.08, 0.16)	(-0.11, -0.02)	(-0.19, -0.06)
Sapwood diameter													-0.16	-0.26	-0.15
													(-0.20, -0.12)	(-0.30, -0.22)	(-0.22, -0.09)

$$CGV = \frac{\sqrt{4 \sigma_f^2}}{\text{Population mean}} \quad (4)$$

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

$$CPV = \frac{\text{Standard deviation}}{\text{Population mean}} \times 100 \quad (5)$$

2.6.2. Genetic correlation

The genetic correlation (r_g) is a term used to describe correlated response to selection (Eldridge et al., 1993). It measures the strength of the genetic association or breeding values between the performance in one trait and performance in another trait (Bourdon, 2000). It can be expressed as the ratio of the additive genetic covariance between two traits (i and j) to the square root of the product of their additive genetic variances, as shown in Eq. 6. The family covariance and family variances are divided by the relatedness coefficient, i.e. $\frac{1}{4}$ in this study for the assumed half-sibling families.

$$r_g(ij) = \frac{4 \sigma_{fij}}{\sqrt{(4 \sigma_i^2 \times 4 \sigma_j^2)}} \quad (6)$$

σ_{fij} is the family covariance between the two traits i and j ; σ_i^2 is the family variance for trait i and σ_j^2 is the family variance for trait j .

3. Results and discussion

The summary statistics of the measurements in the NZDFI *E. globoidea* breeding populations at Avery (9.5-year-old), Atkinson (8-year-old) and JNL Ngaumu (9.8-year-old) are given in Table 2.

3.1. Collapse

The heritability estimates and coefficients of genetic variation for tangential collapse in the heartwood ranged from 0.22 to 0.44 and ~13% to ~23%, respectively (Avery: $h^2 = 0.22$; CGV = 15.15%, Atkinson: $h^2 = 0.30$; CGV = 12.89%, JNL Ngaumu: $h^2 = 0.44$; CGV = 22.68%) (Table 2). Comparisons to other studies are not straight forward as the true relatedness within the progeny trials is typically unknown and assumptions differ between studies. In general, the heritability of tangential collapse in the heartwood appeared to be lower than most reported estimates for other eucalypts, such as for *E. nitens*: $h^2 = 0.11 - 0.62$, $rc = 0.4$ (normalised h^2 to rc of $\frac{1}{4} = 0.36 - 0.97$) (Hamilton et al., 2004; Kube, 2005), *E. dunnii*: $h^2 = 0.63$, $rc = 0.4$ (normalised h^2 to rc of $\frac{1}{4} = 1.01$) (Harwood et al., 2005), *E. grandis*: $h^2 = 0.29$, $rc = 0.4$ (normalised h^2 to rc of $\frac{1}{4} = 0.46$) (Bandara, 2006). The

heritability estimates in conjunction with the coefficient of genetic variability indicated that heartwood collapse in *E. globoidea* can be reduced through selection. Family rankings for tangential collapse in heartwood were displayed in Supplementary Figure 1.

Sapwood collapse was not as severe as heartwood collapse and lower heritability was observed (Table 2). During solid wood processing, the target product of *E. globoidea* is heartwood and little sapwood could be recovered. Therefore, collapse in sapwood is of minor concern.

3.1.1. Tree size

Sapwood has no natural durability (AS5604, 2005). As a result, if *E. globoidea* is grown for its durable wood, heartwood diameter is a more meaningful measure than the growth of the whole stem. Heartwood diameter was under genetic control in all trials (Avery: $h^2 = 0.49$, Atkinson: $h^2 = 0.53$, JNL Ngaumu: $h^2 = 1.22$) (Table 2). The CGV for heartwood diameter ranged from ~21 to ~42% (Avery: 33.71%; Atkinson: 21.16%; JNL Ngaumu: 41.68%) (Table 2). This mostly fell into the range of reported heritability estimates and CGV for heartwood diameter of other tree species such as *Sequoia sempervirens* ($h^2 = 0.4 - 0.5$, $rc = 1$; CGV = 39–48%) (Meason et al., 2016), *Tectona grandis* ($h^2 = 0.27$, $rc = 1$) (Naranjo et al., 2012), *Pinus sylvestris* ($h^2 = 0.3 - 0.5$, $rc = 0.5$) (Ericsson and Fries, 1999; Fries and Ericsson, 1998), and *Pinus radiata* ($h^2 = 0.49$) (Cown et al., 1992). The observation that heritability exceeded 1 for this trait at one site suggested a deviation of the true relatedness of the trees from the assumed half-sibling families, but it should be kept in mind that this site also had the smallest sample. Higher CGV were reported for *E. bosistoana* (51–61%) (Li et al., 2018), while lower CGV were reported for heartwood diameter of *T. grandis* (14.5%) (Naranjo et al., 2012) and *P. sylvestris* (17–20%) (Fries and Ericsson, 1998) as well as for heartwood to sapwood ratio in 8-year-old *E. grandis* (7.58%) (Santos et al., 2004).

The sapwood band of *E. globoidea* was narrower (~42 mm) (Table 2) than that of *E. bosistoana* at age ~7-years (~65 mm) (Li et al., 2018). This supported reports of *E. globoidea* having a narrow sapwood band and consequently that the species is suitable for growing heartwood volume (Bootle, 2005; Poynton, 1979).

Heritability estimates for core length were higher than for heartwood or sapwood but with overlapping 95% confidence intervals for all sites: Avery ($h^2 = 0.81$), Atkinson ($h^2 = 0.71$) and JNL Ngaumu ($h^2 = 1.34$) (Table 2).

The estimated heritabilities for heartwood diameter (Avery: $h^2 = 0.49$; Atkinson: $h^2 = 0.53$; JNL Ngaumu: $h^2 = 1.22$) and sapwood diameter (Avery: $h^2 = 0.55$; Atkinson: $h^2 = 0.65$; JNL Ngaumu: $h^2 = 0.46$) were comparable (Table 2). This was similar to what was reported for *E. bosistoana* (Li et al., 2018). Family rankings for heartwood quantity are displayed in Supplementary Figure 2.

Table 4 Estimated genetic correlations (r_g) between traits for 9.2-year-old *E. globoides* at Avery (AV), for 8-year-old *E. globoides* at Atkinson (AT) and for 9.8-year-old *E. globoides* at JNL Ngaumu (JNL). Cl_{95} in parentheses – values with a Cl_{95} excluding 0 are highlighted in bold.

Trait	Tangential collapse SW			Core length			Heartwood diameter			Sapwood diameter			Extractive content		
	AV	AT	JNL	AV	AT	JNL									
Tangential collapse HW	0.57 (0.29, 0.82)	0.64 (0.37, 0.90)	0.72 (0.37, 1.06)	0.06 (-0.22, 0.33)	-0.05 (-0.28, 0.22)	-0.25 (-0.55, 0.02)	0.21 (-0.05, 0.47)	-0.10 (-0.35, 0.17)	-0.24 (-0.50, 0.07)	-0.16 (-0.42, 0.11)	0.03 (-0.25, 0.30)	-0.37 (-0.71, -0.04)	0.35 (0.09, 0.62)	0.32 (0.07, 0.54)	0.38 (0.04, 0.69)
Tangential collapse SW	0.47 (0.21, 0.73)	0.17 (-0.16, 0.52)	0.11 (-0.26, 0.51)	0.52 (0.27, 0.77)	0.17 (-0.16, 0.53)	0.20 (-0.18, 0.58)	0.52 (0.27, 0.77)	0.17 (-0.16, 0.53)	0.20 (-0.18, 0.58)	0.10 (-0.19, 0.39)	0.16 (-0.20, 0.49)	-0.17 (-0.68, 0.29)	-0.19 (-0.51, 0.09)	-0.02 (-0.37, 0.30)	0.04 (-0.41, 0.48)
Core length				0.88 (0.83, 0.93)	0.93 (0.89, 0.96)	0.99 (0.98, 1.00)	0.88 (0.83, 0.93)	0.93 (0.89, 0.96)	0.99 (0.98, 1.00)	0.58 (0.44, 0.74)	0.83 (0.75, 0.91)	0.86 (0.73, 0.99)	-0.56 (-0.71, -0.40)	-0.62 (-0.77, -0.47)	-0.82 (-1.01, -0.64)
Heartwood diameter										0.14 (-0.07, 0.36)	0.55 (0.36, 0.74)	0.78 (0.56, 0.99)	-0.35 (-0.56, -0.14)	-0.50 (-0.68, -0.29)	-0.79 (-0.98, -0.60)
Sapwood diameter													-0.55 (-0.73, -0.38)	-0.64 (-0.77, -0.50)	-0.82 (-1.06, -0.56)

3.1.2. Heartwood quality

Natural durability is a key trait for the intended use of *E. globoides* timber. Like all properties of a natural material, natural durability is variable. A more consistently performing product can be obtained by exploiting genetic control of that variation. Natural durability is resource intensive to measure but related to heartwood extractives (Li et al., 2020) and heartwood extractives can be predicted efficiently by NIR spectroscopy (Li et al., 2018).

The mean predicted extractive contents in *E. globoides* heartwood at age 8- to 9.5-years-old were 3.61% (Avery), 3.37% (Atkinson) and 2.67% (JNL Ngaumu) (Table 2). The mean values were lower compared with those of *E. bosistoana* (7.5–9.6%) at age 7-year-old (Li et al., 2018). Family rankings for heartwood quality were displayed in Supplementary Figure 3.

The heritability estimates for heartwood extractives (Avery: $h^2 = 0.40$; Atkinson: $h^2 = 0.71$; JNL Ngaumu: $h^2 = 0.39$) were comparable to the heritability estimates in the class 1 ground-durable *E. bosistoana* ($h^2 = 0.3–0.6$) at age 7-year-old (Li et al., 2018) and *E. cladocalyx* ($h^2 = 0.4$) at age 8-year-old (Bush et al., 2011).

3.2. Phenotypic and genetic correlations between traits

The phenotypic and genetic correlations between traits were displayed for each site in Table 3 and Table 4.

3.2.1. Collapse (maximum tangential shrinkage)

Heartwood extractives had weak to moderate positive phenotypic and genetic correlations to heartwood collapse (Avery: $r_p = 0.11$, $r_g = 0.35$; Atkinson: $r_p = 0.13$, $r_g = 0.32$; JNL Ngaumu: $r_p = 0.19$, $r_g = 0.38$), while they did not affect sapwood collapse (Table 3 and Table 4). This was in accordance with the argument that extractives reduce cell wall permeability leading to higher negative pressure during drying by increasing the curvature of the liquid-gas interfaces. It is also consistent with reports that the two traits were positively correlated at the phenotypic level in several other eucalypts (Chafe, 1987). However, while significant, these correlations were not strong indicating that other factors, for example density (i.e. cell wall strength), contributed to collapse (Chafe et al., 1992; Kube and Raymond, 2005).

Heartwood collapse was not significantly correlated to tree diameter, i.e. core length, and heartwood diameter (Table 3 and Table 4). In contrast, moderate to strong positive genetic and phenotypic correlations ($r_g = 0.75 \pm 0.10$ s.e., $r_p = 0.47$) were found between the two traits in 12-year-old *E. nitens* (Kube, 2005), implying that faster growing trees were more prone to collapse. Collapse is associated with wood anatomy (Chafe et al., 1992), and variation in the occurrence of collapse prone cells between species could contribute to these differences.

Sapwood and heartwood collapse were positively correlated at the phenotypic (Avery: $r_p = 0.45$; Atkinson: $r_p = 0.45$; JNL Ngaumu: $r_p = 0.44$) (Table 3) and the genetic level (Avery: $r_g = 0.57$; Atkinson: $r_g = 0.64$; JNL Ngaumu: $r_g = 0.72$) (Table 4), indicating that trees selected for low collapse in heartwood will also have low collapse in sapwood. This suggests that wood anatomy, e.g. cell wall thickness of collapse prone cells, is a key factor in collapse, as wood anatomy is independent of heartwood formation.

3.2.2. Tree growth

The strong positive phenotypic correlations between core length and heartwood (Avery: $r_p = 0.84$; Atkinson: $r_p = 0.88$; JNL Ngaumu: $r_p = 0.92$) as well as sapwood diameter (Avery: $r_p = 0.19$; Atkinson: $r_p = 0.65$; JNL Ngaumu: $r_p = 0.52$) indicated that in general larger trees have not only more heartwood but also a wider sapwood band (Table 3). Similar positive phenotypic correlations between core length and heartwood diameter were reported for other species: *E. tereticornis* at age ~22-year-old ($r_p = 0.79$) (Kumar and Dhillon, 2014), plantation-grown *P. radiata* at age 30–37-year-old ($r_p = 0.71$) (Wilkes, 1991), or *Acacia melanoxylon* ($r_p = 0.88$) (Knapic et al., 2006). Likewise, a positive correlation was

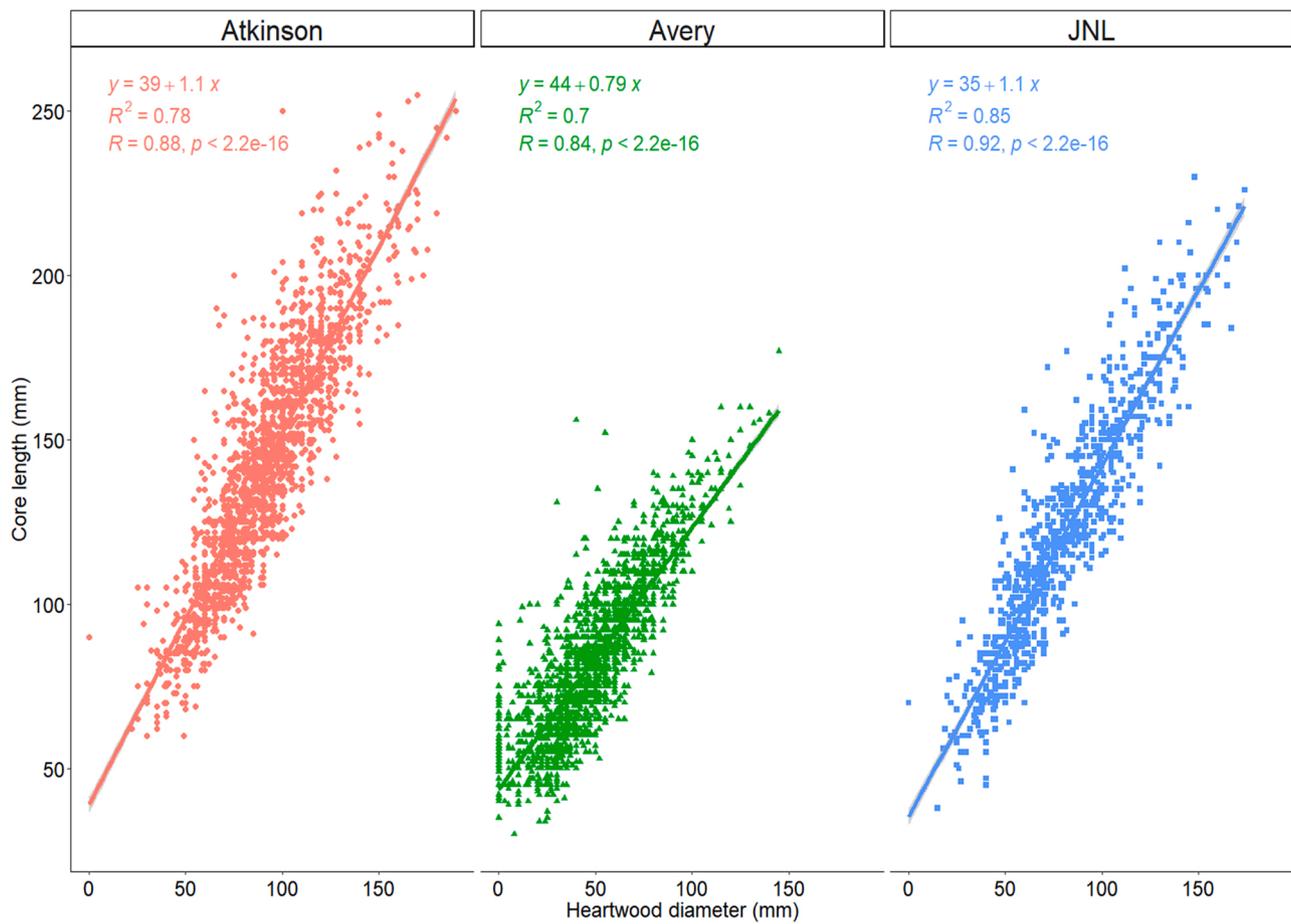


Fig. 1. Relationship between core length and heartwood diameter for *E. globoidea* grown at the Atkinson (red circles), Avery (green triangles) and JNL Ngaumu (blue squares) sites.

recorded between heartwood diameter and DBH for 7-year-old *E. bosistoana* ($r_p = 0.59$) (Li et al., 2018).

The genetic correlations between core length and heartwood diameter in the three trials were also positive (Avery: $r_g = 0.88$; Atkinson: $r_g = 0.93$; JNL Ngaumu: $r_g = 0.99$) (Table 4). This was consistent with the other studies, where strong positive genetic correlations between these traits were reported: $r_g = 0.99$ for 9-year-old *E. globulus* (Miranda et al., 2014), $r_g = 0.89$ – 0.98 for 7-year-old *E. bosistoana* (Li et al., 2018), $r_g = 0.44$ for *E. cladocalyx* (Bush et al., 2011), $r_g = 0.87$ – 0.92 for *Larix kaempferi* (Pâques, 2001), and $r_g = 0.98$ for 35-year-old *Juglans nigra* (Woeste, 2002).

3.2.3. Heartwood

Significant negative genetic correlations were found between heartwood diameter and extractive content: Avery: $r_g = -0.35$; Atkinson: $r_g = -0.50$; JNL Ngaumu: $r_g = -0.79$ (Table 4), matching observations for 7-year-old *E. bosistoana* ($r_g = -0.86 \pm 0.18$ se.) (Li et al., 2018). This unfavourable correlation implies that genotypes with more heartwood tend to have lower amounts of extractives in the heartwood, i.e. durability. However, a positive genetic correlation between heartwood diameter and extractive content has been reported in another genus ($r_g = 0.32$ for *L. eurolepis*) (Pâques and Charpentier, 2015).

3.3. Site effects on wood traits

There were significant differences in the mean values between sites for tangential collapse ($p < 2 \times 10^{-16}$), heartwood ($p < 2 \times 10^{-16}$), and sapwood diameter ($p < 2 \times 10^{-16}$) (Table 2). Site effects on heartwood and sapwood diameters were also observed for ~7-year-old

Table 5

Genetic correlations (r_g) between 9.2-year-old *E. globoidea* at Avery, 8-year-old *E. globoidea* at Atkinson and 9.8-year-old *E. globoidea* at JNL Ngaumu (JNL) for different traits. CI₉₅ in parentheses with values excluding 0 highlighted in bold.

Trait	Avery and Atkinson	Atkinson and JNL	Avery and JNL
Tangential collapse HW	0.73 (0.46, 1.01)	0.78 (0.52, 1.06)	0.83 (0.52, 1.16)
Tangential collapse SW	0.64 (0.22, 1.07)	0.94 (0.49, 1.42)	0.81 (0.38, 1.25)
Core length	0.98 (0.92, 1.04)	0.92 (0.83, 1.01)	0.90 (0.81, 0.99)
Heartwood diameter	0.90 (0.80, 1.01)	0.87 (0.75, 0.99)	0.73 (0.57, 0.88)
Sapwood diameter	0.63 (0.47, 0.80)	0.93 (0.76, 1.11)	0.85 (0.65, 1.05)
Extractive content	0.99 (0.90, 1.07)	0.96 (0.81, 1.11)	0.97 (0.81, 1.14)

E. bosistoana (Li et al., 2018). The nature of the site factors cannot be deduced from this data as only three sites were included, and they are confounded with age of assessment. But investigating site factors contributing to collapse and heartwood properties could inform growers on choosing the correct site for such trees.

The narrowest sapwood band in the Avery site might be a consequence of being the driest site (Table 1). Wider sapwood bands were associated with 'wetter' sites for *T. grandis* of similar sizes and age (Pérez Cordero and Kanninen, 2003). Similarly, *P. radiata* formed 8–14% less sapwood at breast height at a warm-dry site (Moreno Chan et al., 2012). While the trees at Atkinson had a larger heartwood diameter, they deposited less extractives in their heartwood (3.37%) compared with

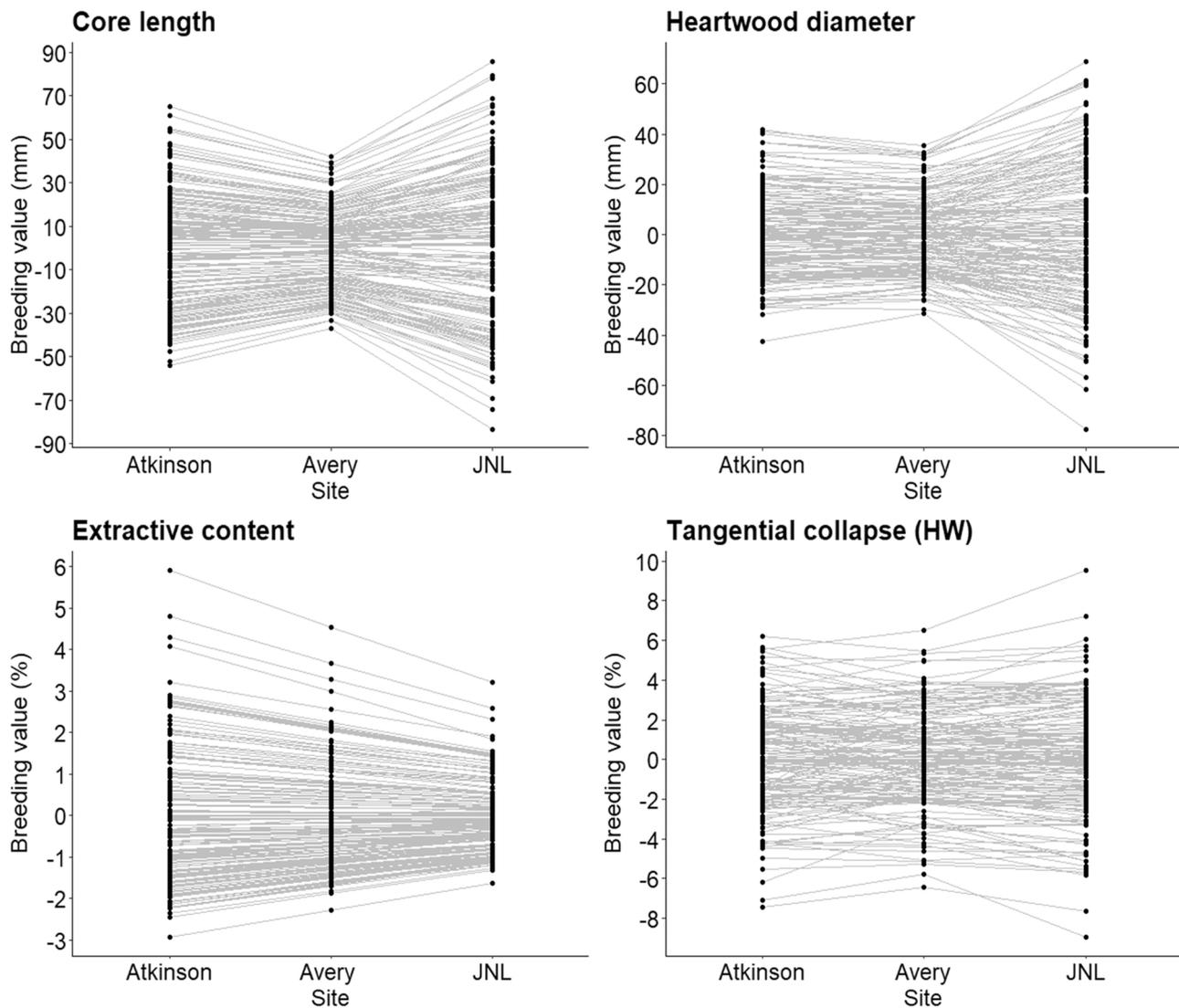


Fig. 2. Ranking correlation between *E. globoidea* family breeding values of three sites (Atkinson, Avery and JNL Ngaumu) for core length, heartwood diameter, extractive content and tangential heartwood collapse (HW).

those at Avery (3.61%) (Table 2). An analogous site effect on heartwood diameter and extractive content was reported for ~7-year-old *E. bosistoana* (Li et al., 2018).

The site with lowest extractives (JNL Ngaumu: 2.67%) had the least heartwood collapse (JNL Ngaumu: 17.12%) (Table 2). This was consistent with the current understanding of the underlying causes of collapse (Chafe et al., 1992; Yang and Liu, 2018), i.e., heartwood extractives reducing wood permeability and consequently increasing the negative pressure during drying. However, the confounding effect of density needs to be considered (Chafe et al., 1992; Kube and Raymond, 2005).

The strong phenotypic relationship between core length and heartwood diameter was displayed in Fig. 1. The core length (i.e. tree size) at which the trees started to form heartwood varied between sites and ranged between of 35–44 mm. Site effects on the heartwood formation should be incorporated into recently developed heartwood taper and volume models for this species (Boczniewicz et al., 2022).

The genetic correlations between the three *E. globoidea* breeding trial sites were displayed in (Table 5). The comparison of the family breeding value rankings between the three sites were visualized for different traits in Fig. 2.

The genetic correlations for heartwood collapse between sites ranged between $r_g = 0.73$ and 0.83 (Table 5). This was consistent with the

reported strong genetic correlation for tangential collapse between three sites in *E. nitens* (Kube and Raymond, 2005). Similar or stronger genetic correlation (Table 5) were observed across the sites for the growth traits core length ($r_g = 0.90$ – 0.98), heartwood diameter ($r_g = 0.73$ – 0.90) and sapwood diameter ($r_g = 0.63$ – 0.93), again similar to what was reported for *E. bosistoana* (Li et al., 2018). Rankings for extractive content were the most consistent across the sites (Avery and Atkinson: $r_g = 0.99$, Atkinson and JNL Ngaumu: $r_g = 0.96$, Avery and JNL Ngaumu: $r_g = 0.97$) (Table 5). The genetic correlation for this trait between two sites reported for *E. bosistoana* was $r_g = 0.6$ (Li et al., 2018).

Stable rankings, in particular for the top and bottom families (Fig. 2) imply little benefit of developing site-specific planting stock optimised to exploit genotype by environment ($G \times E$) interactions (Table 5, Fig. 2). From a breeding perspective, strong genetic correlations between sites suggesting that families selected in one site were also performing well in the other, giving confidence in selections based on a few trials.

Genetic correlations for the combined site analysis across sites were shown in Table 6. Significant positive genetic correlations across sites were observed between the growth traits core length and heartwood diameter. Further significant negative correlations between the growth traits, i.e. core length and heartwood diameter, and extractive content were observed. This implied that the performance of the families in any

Table 6

Genetic cross correlation between traits from 9.2-year-old *E. globoidea* at Avery (AV), 8-year-old *E. globoidea* at Atkinson (AT) and 9.8-year-old *E. globoidea* at JNL Ngaumu (JNL) (95% confidence intervals in parentheses; 95% CI excluding 0 are highlighted in bold).

Traits	Site	Core length	Heartwood diameter	Extractive content
Tangential collapse HW	AV & AT	0.21 (-0.06, 0.48)	0.25 (-0.03, 0.55)	0.26 (-0.02, 0.54)
	AT & AV	-0.11 (-0.37, 0.15)	-0.15 (-0.41, 0.15)	0.40 (0.13, 0.67)
	AT & JNL	-0.26 (-0.54, 0.04)	-0.28 (-0.56, -0.00)	0.34 (0.04, 0.65)
	JNL & AT	-0.08 (-0.39, 0.23)	-0.07 (-0.41, 0.26)	0.38 (0.08, 0.68)
	JNL & AV	0.02 (-0.26, 0.30)	0.13 (-0.18, 0.45)	0.29 (-0.03, 0.59)
	AV & JNL	0.04 (-0.24, 0.34)	0.07 (-0.23, 0.40)	0.33 (-0.02, 0.68)
Core length	AV & AT		0.91 (0.81, 1.00)	-0.64 (-0.78, -0.50)
	AT & AV		0.90 (0.81, 1.00)	-0.51 (-0.69, -0.33)
	AT & JNL		0.89 (0.79, 0.99)	-0.60 (-0.84, -0.36)
	JNL & AT		0.87 (0.75, 0.98)	-0.78 (-0.90, -0.65)
	JNL & AV		0.70 (0.55, 0.85)	-0.76 (-0.91, -0.62)
	AV & JNL		0.91 (0.81, 1.00)	-0.59 (-0.82, -0.37)
Heartwood diameter	AV & AT			-0.51 (-0.70, -0.32)
	AT & AV			-0.43 (-0.66, -0.22)
	AT & JNL			-0.49 (-0.76, -0.49)
	JNL & AT			-0.73 (-0.89, -0.59)
	JNL & AV			-0.75 (-0.91, -0.59)
	AV & JNL			-0.38 (-0.65, -0.11)

of these traits on any of the sites can be predicted with confidence from assessing one trait in any one site.

The observed genetic cross correlations between heartwood collapse and the other traits were mostly statistically insignificant (Table 6). This implied that heartwood collapse is better assessed and selected directly and not inferred from correlated traits on other sites.

3.4. Breeding values and multiple trait selection

As traits are usually not independent (Table 4), selection for one trait influences the genetic gain of others. Hence, selecting for multiple traits requires industry-determined breeding goals, which should ideally be based on economic weights (Candy and Gerrand, 1997; Evison and Apiolaza, 2015; Jansson et al., 2017). In the absence of economic weights, superior genetics can be identified by using independent culling levels. The main wood property traits of interest in NZDFI's *E. globoidea* breeding programme are extractive content (EC), heartwood diameter (HWD) and heartwood collapse (HWC). Families with superior breeding values for these traits were identified in Supplementary Table 1 and visualised in Fig. 3. Tallying above average performance of a family for target traits allowed to identify superior genotypes. The relationship between family breeding values of key traits was visualised separately for the three sites in Fig. 3.

Sixty-seven families produced timber with less than average (superior) heartwood collapse on all three sites (Fig. 3, Supplementary Table 1). However, 81 families met the criteria if selected from Avery and Atkinson sites separately and 79 families met these criteria in the JNL Ngaumu site. If additionally to low collapse also large heartwood diameter is desired, the number of families to be selected from all sites reduced to 31. Forty families in the Avery trial, 46 families in the Atkinson trial and 43 families in the JNL Ngaumu trial met these criteria (Supplementary Table 1).

Nine families met the criteria of good heartwood features i.e., heartwood diameter, extractives, and low collapse on all the three sites. However, 10 families in the Avery trial, 11 families in the Atkinson and JNL Ngaumu trials, if selected separately, met these criteria (Fig. 3, Supplementary Table 1).

The breeder may not want to take collapse into consideration (or weigh the trait less) since eliminating the worst families from the breeding population could avoid most of the processing problems. In that case, to simultaneously improve the durability (i.e. extractive content) and heartwood diameter in the species, 15 families were performing above average at all three sites (Fig. 3, Supplementary Table 1). The small number of families producing larger quantities and good quality heartwood is a consequence of the unfavourable negative

correlation between these traits (Table 4). In a culling scenario for heartwood collapse, where the worst performing 10% (i.e. 16 families) of the families are removed, the number of families selected for good heartwood features (i.e. extractive content and heartwood diameter) would be 12 when all sites are considered and 17 families at the Avery site, 16 families at the Atkinson site and 15 families at the JNL Ngaumu site if selected from each site separately.

E. globoidea is a class 2 ground-durable timber, not as durable as class 1 *E. bosistoana* (AS5604, 2005), hence in a case where the wood users are interested in highly ground-durable products, intense selection for extractive content would be essential. In that situation, 64 families met the criterion of above average extractives in all sites. A similar number of families met this criterion if selected from each site separately (Supplementary Table 1). When intense selection for extractive content would be required, these numbers would reduce.

In these trials, a good number of families were established, which contributed to identifying families with good overall performance. The decision which families to select for further breeding and seed production lies with the durable heartwood industry.

4. Conclusion

Collapse and other tree traits in the NZDFI *E. globoidea* breeding population planted on three sites, estimated for 163 *E. globoidea* families, were under varying degree of genetic control. The narrow sense heritability ranging from 0.12 to 1.22 combined with sufficient genetic variability will allow meaningful improvements through a breeding programme. While traits were affected by site factors, the rankings were stable between sites, giving confidence in the performance of the selected material on deployment sites. Superior genetics within families could be selected and employed to encourage the utilisation of *E. globoidea* for solid wood products.

Funding

This work has been financially supported by the New Zealand Ministry of Business, Innovation and Employment (MBIE) funded Specialty Wood Products Partnership (FFRX1501) and the New Zealand Institute of Forestry (NZIF) Foundation.

CRedit authorship contribution statement

Vikash Ghildiyal: Writing – original draft, review and editing, material collection, investigation, conceptualisation, data analysis. **Ebenezer Iyiola:** Material collection and investigation, data analysis

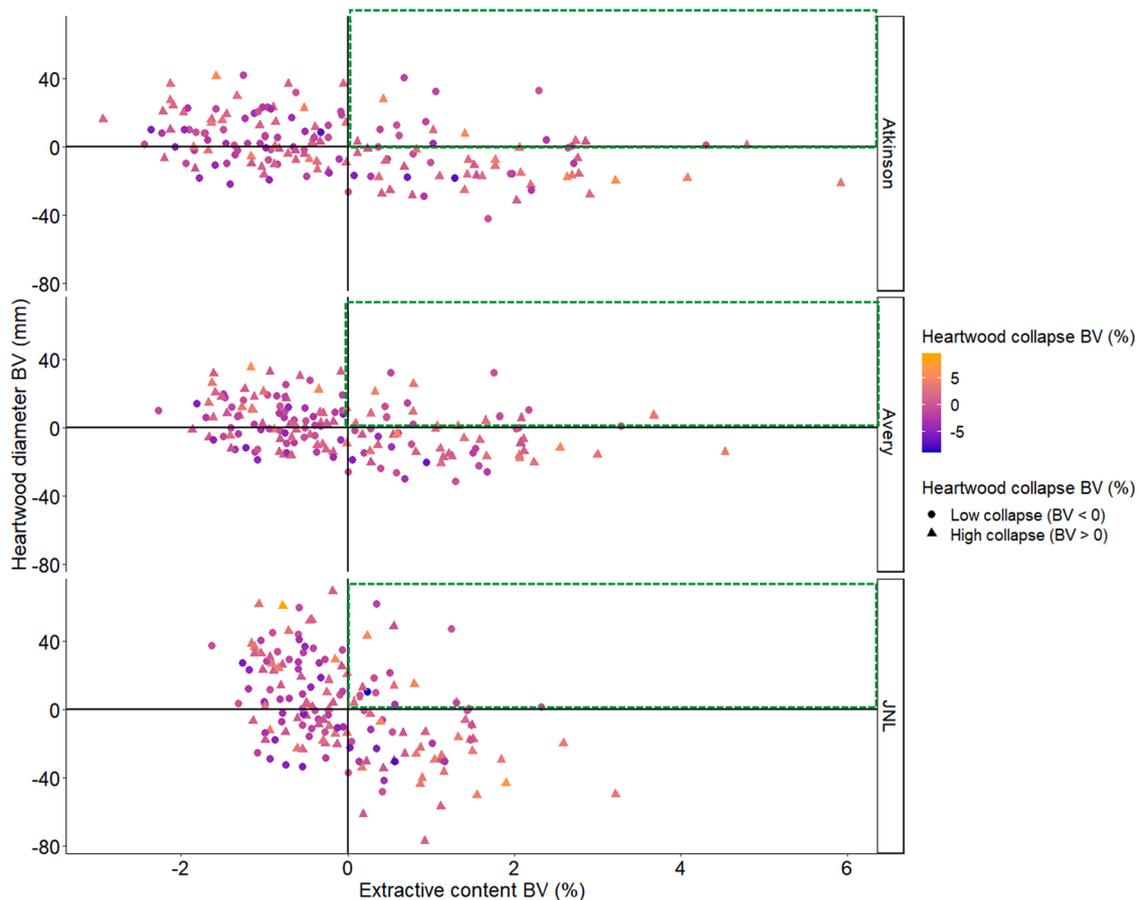


Fig. 3. Relationship between family breeding values of heartwood diameter and extractive content for 162 *E. globoides* families at Atkinson at age ~8-year-old, at Avery at age ~9.2-year-old and at JNL Ngaumu at age ~9.8-year-old. Families performing above average for heartwood quality and quantity are located in the green highlighted upper-right corner of each graph. Families with good (circle - below average) and bad (triangle - above average) performance for collapse (HWC) are indicated; the color gradient encoded the family breeding value for HWC from low (blue) to high (orange).

and editing. **Monika Sharma:** Data curation and analysis, editing. **Luis A. Apiolaza:** Experimental design, methodology, data analysis, review and editing. **Clemens Altaner:** Conceptualization, Methodology, investigation, writing – review and editing, supervision, funding acquisition.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Clemens Altaner reports financial support was provided by the New Zealand Ministry of Business, Innovation and Employment (MBIE) funded Specialty Wood Products Partnership (FFRX1501). Vikash Ghildiyal reports financial support was provided by the New Zealand Institute of Forestry (NZIF) Foundation. Clemens Altaner is Science Team Leader of the New Zealand Dryland Forests Innovation (NZDFI).

Data availability

Data will be made available on request.

Acknowledgements

The authors appreciate the assistance of Meike Holzenkämpfer, Gert Hendriks, Ash Millen, Lisa Nguyen, Hamish Scown and Daniel Boczniewicz in sample collection and processing. The New Zealand Dryland Forests Innovation (NZDFI) established and maintained the breeding trials.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.indcrop.2023.116891](https://doi.org/10.1016/j.indcrop.2023.116891).

References

- Ananías, R.A., Sepúlveda-Villarroel, V., Pérez-Peña, N., Torres-Mella, J., Salvo-Sepúlveda, L., Castillo-Ulloa, D., Salinas-Lira, C., 2020. Radio frequency vacuum drying of *Eucalyptus nitens* juvenile wood. *BioResources* 15, 4886–4897. <https://doi.org/10.15376/biores.15.3.4886-4897>.
- Apiolaza, L.A., 2012. Basic density of radiata pine in New Zealand: genetic and environmental factors. *Tree Genet. Genomes* 8, 87–96. <https://doi.org/10.1007/s11295-011-0423-1>.
- Bandara, K.M.A., 2006. Genetic improvement of solid wood product value of subtropical eucalypts: a case study of *Eucalyptus grandis* and *E. dunnii*. Australia National University, Australia.
- AS5604, 2005. Timber-Natural durability ratings. *Aust. Stand.* 604, 29p.
- Blakemore, P., Northway, R., 2009. Review of, and recommendations for, research into preventing or ameliorating drying related internal and surface checking in commercially important hardwood species in south-eastern Australia. In: Limited, F. W.P.A. (Ed.), Final report received by FWPA in November, Australia.
- Boczniewicz, D., Mason, E.G., Morgenroth, J.A., 2022. Developing fully compatible taper and volume equations for all stem components of *Eucalyptus globoides* Blakely trees in New Zealand. *N. Z. J. For. Sci.* 52. <https://doi.org/10.33494/nzjfs522022x180x>.
- Boland, D.J., Brooker, M.I.H., Chippendale, G., Hall, N., Hyland, B., Johnston, R.D., Kleinig, D., McDonald, M., Turner, J., 2006. Forest trees of Australia. CSIRO publishing.
- Boote, K., 2005. Wood in Australia. Types. Properties and Uses, 2nd edn... McGraw-Hill, Australia, Sydney, Australia, p. 452.
- Bourdon, R.M., 2000. Understanding animal breeding. Prentice Hall, Upper Saddle River, NJ.
- Bush, D., Walker, J., 2011. Selecting and breeding eucalypts for natural durability. In: Walker, J. (Ed.), Developing a eucalypt resource: learning from Australia and

- elsewhere. Wood Technology Research Centre. University of Canterbury, Blenheim New Zealand, pp. 125–136.
- Bush, D., McCarthy, K., Meder, R., 2011. Genetic variation of natural durability traits in *Eucalyptus cladocalyx* (sugar gum). *Ann. For. Sci.* 68, 1057–1066. <https://doi.org/10.1007/s13595-011-0121-z>.
- Butler, D., Cullis, B., Gilmour, A., Gogel, B., Thompson, R., 2017. ASReml-R reference manual version 4. VSN International Ltd, Hemel Hempstead, HP1 1ES, UK.
- Campbell, G., Hartley, J., 1978. Drying and dried wood. In: Hillis, W.E., Brown, A.G. (Eds.), *Eucalypts for wood production*. Academic Press, Australia, pp. 328–336.
- Candy, S., Gerrand, A., 1997. Comparison of financial returns from sawlog regimes for *Eucalyptus nitens* plantations in Tasmania. *Tasforests* 9, 35–50 <https://doi.org/10.5000/12220/8067>.
- Chafe, S., Barnacle, J., Hunter, A., Ilic, J., Northway, R., Rozsa, A., 1992. Collapse: An introduction. CSIRO Division of Forest Products.
- Chafe, S.C., 1987. Collapse, volumetric shrinkage, specific gravity and extractives in *Eucalyptus* and other species - Part 2: The influence of wood extractives. *Wood Sci. Technol.* 21, 27–41. <https://doi.org/10.1007/BF00349715>.
- Chafe, S.C., 1992. Collapse: an introduction. CSIRO Division of Forest Products.
- Core Team, R., 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Published 2018.
- Cown, D., Young, G., Burdon, R., 1992. Variation in wood characteristics of 20-year-old half-sib families of *Pinus radiata*. *NZ J. Sci.* 22, 63–76.
- Dawson, B.S., Pearson, H., Kimberley, M.O., Davy, B., Dickson, A.R., 2020. Effect of supercritical CO₂ treatment and kiln drying on collapse in *Eucalyptus nitens* wood. *Eur. J. Wood Wood Prod.* 78, 209–217. <https://doi.org/10.1007/s00107-020-01500-5>.
- Eldridge, K., Davidson, J., Harwood, C., Wyk, Gv, 1993. *Eucalypt domestication and breeding*. Clarendon Press.
- Ellwood, E.L., 1953. Properties of American beech in tension perpendicular to the grain and their relation to drying. *Forest Product. Journal* 3, 202–209.
- Ericsson, T., Fries, A., 1999. High heritability for heartwood in north Swedish Scots pine. *Theor. Appl. Genet.* 98, 732–735. <https://doi.org/10.1007/s001220051128>.
- Evison, D.C., Apiolaza, L.A., 2015. Incorporating economic weights into radiata pine breeding selection decisions. *Can. J. For. Res.* 45, 135–140. <https://doi.org/10.1139/cjfr-2014-0363>.
- Fries, A., Ericsson, T., 1998. Genetic parameters in diallel-crossed Scots pine favor heartwood formation breeding objectives. *Can. J. For. Res.* 28, 937–941. <https://doi.org/10.1139/x98-061>.
- Ghildiyal, V., Herel, R., Heffernan, B., Altaner, C., 2022. The effect of Joule heating on collapse and water absorption of wood. *Wood Mater. Sci. Eng.* 1–9. <https://doi.org/10.1080/17480272.2022.2121660>.
- Guo, F., Altaner, C.M., 2018. Properties of rotary peeled veneer and laminated veneer lumber (LVL) from New Zealand grown *Eucalyptus globoides*. *N. Z. J. For. Sci.* 48 (3), 10. <https://doi.org/10.1186/s40490-018-0109-7>.
- Hamilton, M., Potts, B., Harwood, C., Apiolaza, L., Gore, P., 2004. Comparison of non-destructive assessment techniques for shrinkage and collapse in *Eucalyptus nitens*, *Eucalyptus* in a Changing World. Proc. of IUFRO Conference, Portugal, p. p. 2.
- Harwood, C., Bandara, K., Washusen, R., Northway, R., Henson, M., Boyton, S., 2005. Variation in wood properties of plantation-grown *Eucalyptus dumii* relevant to solid-wood products. *FWPRDC Rep. PNO 4*, 3003.
- Hillis W.E., 1991. *Eucalypts - Chemistry, Uses* [Editorial Material]. *Appita J.* 44(4), 239–244. English.
- Jacobs, M., 1979. *Eucalypts for planting*. *Fao*.
- Jacobs, M.R., 1981. *Eucalypts for planting*. Food and Agriculture Organization of the United Nations.
- Jansson, G., Hansen, J.K., Haapanen, M., Kvaalen, H., Steffenrem, A., 2017. The genetic and economic gains from forest tree breeding programmes in Scandinavia and Finland. *Scand. J. For. Res.* 32, 273–286. <https://doi.org/10.1080/02827581.2016.1242770>.
- Jones, T.G., McConnochie, R.M., Shelbourne, T., Low, C.B., 2010. Sawing and grade recovery of 25-year-old *Eucalyptus fastigata*, *E. globoides*, *E. muelleriana* and *E. pilularis*. *New Zealand Journal of Forestry Science* 40, 19–31.
- Knapic, S., Tavares, F., Pereira, H., 2006. Heartwood and sapwood variation in *Acacia melanoxylon* R. Br. trees in Portugal. *For.: Int. J. For. Res.* 79, 371–380. <https://doi.org/10.1093/forestry/cpl010>.
- Kong, L., Zhao, Z., He, Z., Yi, S., 2018. Development of schedule to steaming prior to drying and its effects on *Eucalyptus grandis* × *E. urophylla* wood. *Eur. J. Wood Wood Prod.* 76, 591–600. <https://doi.org/10.1007/s00107-017-1199-2>.
- Kube, P.D., 2005. Genetic improvement of the wood properties of *Eucalyptus nitens*: Breeding to improve solid wood and pulp properties. PhD Thesis. University of Tasmania, Australia.
- Kube, P.D., Raymond, C.A., 2005. Breeding to minimise the effects of collapse in *Eucalyptus nitens* sawn timber. *Forest. Genetics* 12, 23–34.
- Kumar, A., Dhillion, G., 2014. Variation of sapwood and heartwood content in half-sib progenies of *Eucalyptus tereticornis* Sm. *Indian J. Nat. Prod. Resour.* 5 (4), 338–344.
- Li, Y., Altaner, C., 2019. Calibration of near infrared spectroscopy (NIRS) data of three *Eucalyptus* species with extractive contents determined by ASE extraction for rapid identification of species and high extractive contents. *Holzforchung* 73, 537–545. <https://doi.org/10.1515/hf-2018-0166>.
- Li, Y., Apiolaza, L.A., Altaner, C., 2018. Genetic variation in heartwood properties and growth traits of *Eucalyptus bosistoana*. *Eur. J. For. Res.* 137, 565–572. <https://doi.org/10.1007/s10342-018-1125-0>.
- Li, Y., Sharma, M., Altaner, C., Cookson, L.J., 2020. An approach to quantify natural durability of *Eucalyptus bosistoana* by near infrared spectroscopy for genetic selection. *Ind. Crops Prod.* 154, 112676 <https://doi.org/10.1016/j.indcrop.2020.112676>.
- Lin, H., Murray, T.J., Mason, E.G., 2017. Incidence of and defoliation by a newly introduced pest, *Paropsisterna variicollis* (Coleoptera: Chrysomelidae), on eleven durable eucalyptus species in Hawke's Bay, New Zealand. *N. Z. Plant Prot.* 70, 45–51. (<https://journal.nzpps.org/index.php/nzpp/article/view/26>).
- Meason, D., Kennedy, S., Dungey, H., 2016. Two New Zealand-based common garden experiments of the range-wide 'Kuser' clonal collection of *Sequoia sempervirens* reveal patterns of provenance variation in growth and wood properties. *N. For.* 47, 635–651. <https://doi.org/10.1007/s11056-016-9535-7>.
- Millen, P., van Ballekom, S., Altaner, C., Apiolaza, L., Mason, E., McConnochie, R., Morgenroth, J., Murray, T., 2018. Durable eucalypt forests—a multi-regional opportunity for investment in New Zealand drylands. *New Zealand. J. For.* 63, 11–23.
- Millen, P., Altaner, C., Palmer, H., 2020. Durable hardwood peeler pole plantations. A new growing regime for eucalypts. *N. Z. Tree Grow.* 41 (2), 8–13.
- Miranda, I., Gominho, J., Araújo, C., Pereira, H., 2014. Family effects in heartwood content of *Eucalyptus globulus* L. *Eur. J. For. Res.* 133, 81–87. <https://doi.org/10.1007/s10342-013-0741-y>.
- Moreno Chan, J., Raymond, C., Walker, J., 2012. Development of heartwood in response to water stress for radiata pine in Southern New South Wales, Australia. *Trees* 27. <https://doi.org/10.1007/s00468-012-0815-3>.
- Moya, R., Bond, B., Quesada, H., 2014. A review of heartwood properties of *Tectona grandis* trees from fast-growth plantations. *Wood Science and Technology* 48 (2), 411–433. <https://doi.org/10.1007/s00226-014-0618-3>.
- Myburg, A.A., Grattapaglia, D., Tuskan, G.A., Hellsten, U., Hayes, R.D., Grimwood, J., Jenkins, J., Lindquist, E., Tice, H., Bauer, D., 2014. The genome of *Eucalyptus grandis*. *Nature* 510, 356–362. <https://doi.org/10.1038/nature13308>.
- Naranjo, S.S., Moya, R., Chauhan, S., 2012. Early genetic evaluation of morphology and some wood properties of *Tectona grandis* L. clones. *Silvae Genet.* 61, 58–65. <https://doi.org/10.1515/sg-2012-0008>.
- Pâques, L., 2001. Genetic control of heartwood content in larch. *Silvae Genet.* 50, 69–74.
- Pâques, L.E., Charpentier, J.-P., 2015. Perspectives for genetic improvement in heartwood size and extractive content in relation to natural durability and aesthetics in interspecific hybrid larch (*Larix* × *eurolapis*). *Eur. J. For. Res.* 134, 857–868. <https://doi.org/10.1007/s10342-015-0895-x>.
- Pérez Cordero, L.D., Kanninen, M., 2003. Heartwood, sapwood and bark content, and wood dry density of young and mature teak (*Tectona grandis*) trees grown in Costa Rica. *Silva Fenn.* 37, 511. <https://doi.org/10.14214/sf.511>.
- Poynton, R., 1979. Tree planting in southern Africa: the eucalypts. Department of Forestry.
- Purnell, R., 1988. Variation in wood properties of *Eucalyptus nitens* in a provenance trial on the eastern Transvaal highveld in South Africa. *South Afr. For. J.* 144, 10–22. <https://doi.org/10.1080/00382167.1988.9630311>.
- Rudman, P., 1964. Durability in the genus *Eucalyptus*. *Aust. For.* 28, 242–257. <https://doi.org/10.1080/00049158.1964.10675949>.
- Salekin, S., Mason, E.G., Morgenroth, J., Bloomberg, M., Meason, D.F., 2021. Hybrid height and survival model for juvenile *Eucalyptus globoides* (Blakely) and *E. bosistoana* (F. Muell) in New Zealand. *For. Ecol. Manag.* 490, 119074 <https://doi.org/10.1016/j.foreco.2021.119074>.
- Santos, P., Geraldi, I.O., Garcia, J.N., 2004. Estimates of genetic parameters of wood traits for sawn timber production in *Eucalyptus grandis*. *Genet. Mol. Biol.* 27, 567–573. <https://doi.org/10.1590/S1415-47522004000400017>.
- Seng Hua, L., Wei Chen, L., Antov, P., Kristak, L., Md Tahir, P., 2022. Engineering wood products from eucalyptus spp. *Adv. Mater. Sci. Eng.* 2022. <https://doi.org/10.1155/2022/8000780>.
- Somerville, A., Gatenby, S., 1996. Evaluation of *Eucalyptus globoides* grown on Matakana Island, Forest and Farm Plantation Management Cooperative Report. *Report No: PM036*.
- Thomas, D.P., Erickson, H.D., 1963. Collapse and honeycomb in Western Red Cedar in relation to green-wood liquid permeability. Western Dry Kiln Clubs. Meeting (15th: 1963: Portland, Or.).
- Tiemann, H.D., 1941. Collapse in Wood as Shown by the Microscope. *Journal of Forestry* 39(3), 271–282. doi:10.1093/jof/39.3.271%J *Journal of Forestry*.
- Vermass, H.F., Bariska, M., 1995. Collapse during low temperature drying of *Eucalyptus grandis* W Hill and *Pinus sylvestris* L. *Holzforchung und Holzverwert.* 47, 35–40.
- Wilkes, J., 1991. Heartwood development and its relationship to growth in *Pinus radiata*. *Wood Sci. Technol.* 25, 85–90. <https://doi.org/10.1007/BF00226808>.
- Woeste, K.E., 2002. Heartwood production in a 35-year-old black walnut progeny test. *Can. J. For. Res.* 32, 177–181. <https://doi.org/10.1139/x01-177>.
- Yang, L., Liu, H., 2018. A review of *Eucalyptus* wood collapse and its control during drying. *BioResources* 13, 2171–2181. <https://doi.org/10.15376/biores.13.1.Yang>.
- Zhang, Y., Miao, P., Zhuang, S., Wang, X., Xia, J., Wu, L., 2011. Improving the dry-ability of *Eucalyptus* by pre-microwave or pre-freezing treatment. *J. Nanjing For. Univ.* 35, 61–64. <https://doi.org/10.3969/j.jssn.1000-2006.2011.02.013>.
- Zobel, B.J., Jett, J.B., 2012. *Genetics of wood production. & Business Media*. Springer Science.