Original article

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# Genetic variation of microfibril angle and its relationship with solid wood and pulpwood traits in two progeny trials of *Eucalyptus nitens* in Tasmania

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**Abstract:** Microfibril angle (MFA) is a key biological trait contributing to wood stiffness, which is a common breeding objective for solid wood products in many tree species. To explore its genetic architecture, area-weighted MFA was measured in two *Eucalyptus nitens* progeny trials in Tasmania, Australia, with common open-pollinated families. Radial strips were extracted from 823 trees in 131 families and MFA assessed using SilviScan-2®. Heritability, genotype-by-environment interaction and inter-trait genetic correlations were evaluated to examine the genetic variability and stability of MFA and its relationships with other solid wood and pulpwood selection traits. Significant family variation was found for MFA in both trials. There was no significant genotype-by-environment interaction and the across-site narrow-sense heritability was 0.27. MFA was genetically independent of basic density, growth, and tree form. However, MFA was strongly and favourable genetically correlated to acoustic wave velocity in standing trees, modulus of elasticity and kraft pulp yield (KPY). The present study has shown that genetic improvement of *E. nitens* for pulpwood selection traits is unlikely to have adversely affected MFA, and thus timber stiffness. Rather these results suggest the possibility that selection for increased KPY may have indirectly improved MFA favourably for solid wood products.

**Keywords:** acoustic wave velocity; cellulose microfibril angle; *Eucalyptus nitens*; kraft pulp yield; modulus of elasticity; wood basic density.

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## 1 Introduction

Microfibril angle (MFA) is an important biological trait affecting many wood properties of trees (Donaldson 2008). MFA is the angle that the cellulose microfibrils in the $S_2$ layer of the secondary cell wall of wood xylem cells make with the fibre axis, and this may vary longitudinally and radially within the tree (Evans et al. 2000). MFA is inversely related to wood stiffness, measured as modulus of elasticity (MOE), with lower angles causing stiffer wood (Barnett and Bonham 2004). MFA alone can account for more than 80% of the variation in MOE in eucalypts (Evans and Ilic 2001; Yang and Evans 2003). Wood stiffness is a key mechanical property for solid wood products and is a measure of the force per unit area required to stretch a sample elastically (without breaking) with a given amount of strain (Walker 2006). Due to its impact on graded product recovery, wood stiffness has been identified as a key breeding objective in solid wood production-systems in several eucalypt species of economic importance (Hamilton et al. 2008; Ivković et al. 2006; Raymond and Apiolaza 2004). While MFA is mainly related to wood stiffness (e.g. MOE), it has also been associated with growth stress and the dimensional stability of timber – also major issues in hardwood species (Donaldson 2008; Donaldson and Turner 2001). It can influence wood shrinkage and collapse (Yang and Fife 2003), which can cause checking which is a serious drying defect that degrades timber (Blakemore 2011).

In addition to its association with key solid wood properties, there is the possibility that MFA is associated with kraft pulp yield in eucalypts. This is because a non-destructive indirect measure of MOE (Dickson et al. 2003) – standing tree acoustic wave velocity (AWV) – has been positively related to kraft pulp yield in *Eucalyptus nitens* (Blackburn et al. 2012; Hamilton and Potts 2008) and *Eucalyptus globulus* (Hamilton et al. 2017; Nickolas et al. 2020). Kraft pulp yield, along with growth and basic density, is an important breeding objective trait for the genetic improvement of eucalypt pulpwood plantations (Borralho et al. 1993; Greaves et al. 1997). Despite the importance of MFA as a key biological characteristic underlying traits that affect profit in both solid wood and pulpwood production systems, there have been few studies of the quantitative genetic control of MFA in forest trees. This is partly due to the high cost and time-consuming measurement process (Lagana et al. 2006). However, the development of technologies such as SilviScan® and Near infra-red (NIR) spectroscopy have now made the measurement of MFA feasible at a sufficiently large scale for genetic studies (Schimleck et al. 2019).

SilviScan® derived-data were used to examine genetic variation in MFA in *E. nitens* (Deane et Maiden) Maiden, a major plantation eucalypt grown in several countries, including Chile, South Africa, New Zealand and Australia (Hamilton et al. 2008; INFOR 2017; Satchell 2015; Swain et al. 2013). *E. nitens* is the second most important hardwood plantation in Australia with around 234,000 ha (Downham and Gavran 2020). The majority of plantations are on the island of Tasmania (89%), where they are grown under a pulpwood silvicultural system (Downham and Gavran 2020). There are several breeding programs in Australia which are mainly pulpwood focused (Hamilton et al. 2008). However, there is increasing interest in growing *E. nitens* under solid wood silvicultural regimes for supplying logs for the production of timber, veneer, and engineered wood products (Blackburn et al. 2018; Hamilton et al. 2008; Potts 2004). This has meant that other traits related to structural uses are of potential importance, including those influenced by MFA such as stiffness (Blackburn et al. 2010).

*Eucalyptus nitens* is an Australian native species that occurs in a number of scattered small populations in areas of high altitude from central and eastern Victoria to northern New South Wales (Hamilton et al. 2011). It is the populations from the central ranges in Victoria which form the basis of most Australian breeding programs (Hamilton et al. 2008), and within this region the populations have been grouped into three races (Hamilton et al. 2011; INFOR 2001). In this species, MFA declines radially across the stem in an asymptotic manner and stabilizes at angles of between 6.4 and 8.2° dependent on site (Vega et al. 2020). At the ring level, *E. nitens* MFA is decreased by water stress (Wimmer et al. 2002) and temporarily increased by early-age tree thinning (Medhurst et al. 2012). Studies on the genetic control of the phenotypic variation in MFA among trees integrate such intra-tree variation using either the average (Hein et al. 2012) or area-weighted (Gräns et al. 2009) values of MFA taken from radial profiles. The genetic architecture of MFA has been studied in several eucalypt species, including *Eucalyptus urophylla* (Hein et al. 2012) and *E. globulus* (Apiolaza et al. 2005; Poke et al. 2006; Thamarus et al. 2004) which suggest it can be under significant genetic control. While association studies have identified SNPs within the CCR gene which explain 4.6% of the variation in MFA within *E. nitens* (Thumma et al. 2005), at the time of this study there have been no quantitative genetic studies of MFA published to date in *E. nitens*.

The present study explores the quantitative genetic architecture of MFA in *E. nitens*, including its genetic and phenotypic correlation with key pulpwood and solid wood selection traits, and the importance of the genotype by environment interactions.

In the case of *E. nitens* it is hypothesises that:

(i) MFA is under significant genetic control and exhibits low genotype-by-environment interaction, as demonstrated for most wood property traits in eucalypts (Hamilton and Potts 2008; Nickolas et al. 2020);
(ii) There is a significant negative genetic correlation of MFA with traits reflecting wood stiffness, including standing tree AWV (Blackburn et al. 2014) and sawnboard MOE (Blackburn et al. 2010); and
(iii) Given the favourable phenotypic and genetic correlations previously reported between kraft pulp yield and wood stiffness traits (MOE and AWV), there is a significant negative genetic correlation between MFA and kraft pulp yield.

# 2 Materials and methods

## 2.1 Trial description

The present study focuses on two trial sites established at Tarraleah and Southport in central and southern Tasmania, respectively. Tarraleah was established on a cool-moist site, whereas Southport was planted in warm-moist climate site as defined by (Wardlaw 2011). The majority of Tasmanian *E. nitens* plantations occur in these climate zones. The trials were planted in 1993 using 420 open-pollinated single-tree seed lots (hereafter 'family') collected from wild populations of *E. nitens* in the Central Highlands region of Victoria (Pederick 1979), which encompassed three races – Northern, Southern and Connor's

Plain (Hamilton et al. 2011). The trial design comprised five (Southport) or six (Tarraleah) replicates of 21 incomplete blocks of 20 five-row plots of each family. Trees at both trials were spaced 4 by 2 m apart and managed as a pulpwood stand with no thinning or pruning. Additional details of the two trials are described in Blackburn et al. (2014).

## 2.2 MFA and associated disc and board measurements

The present study reports novel data for MFA and tree form from these two trials and integrates these data with previously published data taken from standing trees and logs (Figure 1). The area-weighted microfibril angle ($MFA_{ss}$) and dynamic modulus of elasticity ($MOE_{ss}$) were assessed from a subset of 131 families (129 at Southport and 126 at Tarraleah), with 126 families in common between trials. Most families were represented by one tree per plot from each replicate of the field trials. In total, 498 trees were assessed in Southport and 325 in Tarraleah. The trees were felled at age 18 and 14 years of age respectively, and those from Tarraleah used in a processing study (Blackburn et al. 2010). Disc were cut from felled trees at 5.6 m to produce 2 wedges. One wedge was oven dried for wood basic density determination using the water displacement method (TAPPI Standards 2016). The other wedge was air-dried at 30 °C and then stabilized to equilibrium moisture content (approximately 12%) in a controlled-humidity environment. The air-dried wedge was evaluated for wood internal checking using a visual score of one (infrequent or not visible) to six (frequent and highly visible) as defined in Blackburn et al. (2010). One 10 mm square pith to bark strip was extracted from the air-dried wedge and both $MFA_{ss}$ and $MOE_{ss}$ were obtained using SilviScan-2® at 1 mm resolution. Additionally, another 10 mm wide, bark to pith strip was extracted from the disc for NIR spectroscopy. This strip was air dried to approximately 12% moisture content and the outer 5–6 rings ground to woodmeal. NIR spectra were collected only from the wood meal using a Bruker MPA FT-NIR as detailed in Blackburn et al. (2012). Existing calibrations were used to predict kraft pulp yield (KPY) at Kappa 18 (Downes et al. 2009). From the 5.6 m bottom log, one 1.8 m board was cut from the upper end, air-dried and then the static modulus of elasticity ($MOE_B$) measured using a static tester loaded in a four-point configuration (Blackburn et al. 2010).

Of these disc and board traits, wood density has been reported previously (Blackburn et al. 2010, 2012, 2014) for both Southport and Tarraleah (Figure 1). Checking at Tarraleah was previously reported in Blackburn et al. (2010) but has not been published for Southport. KPY was reported (Blackburn et al. 2012) for Tarraleah only (not previously published for Southport). $MOE_B$ has been reported in Tarraleah (Blackburn et al. 2010) and was not measured in Southport (Figure 1).

## 2.3 Standing-tree measurements

The MFA data were also integrated with data from standing trees, much of which had been previously published and here reanalysed. Diameter at breast height (DBH, at 1.3 m) was measured at age 13 and 17 years in Tarraleah and Southport, respectively, and previously reported (Blackburn et al. 2012, 2014; Hamilton et al. 2009). Stem straightness was visually measured using a one (maximum stem deviation) to six (no stem deviation) subjective scale. This scale has been previously shown to be highly correlated with time-consuming, quantitative assessments of straightness from photographs (Blackburn et al. 2013). Stem straightness has been reported for Tarraleah (Blackburn et al. 2011) but not Southport. Branch size was assessed on the lower 2.5 m of the stem (at age five years) using a gauge with three slots to classify the biggest branch in four classes: <1.5 cm , <2.5 cm, <3.5 cm and ≥3.5 cm , and given scores from 1 to 4, respectively. Ramicorns and forks were excluded from the assessment. Branch size was only measured in Southport and has not been previously reported. In addition, a Fakopp microsecond timer tool (Fakopp Enterprise, Ágfalva, Hungary) was used to measure the acoustic wave velocity (AWV) between two probes centred around 1.1 m from the base of each tree. AWV has been previously reported (Blackburn et al. 2012, 2014) and here re-analysed for both Southport and Tarraleah.

## 2.4 Statistical analysis

The analysis was undertaken in four steps. First, each trial was analysed separately to estimate univariate genetic parameters for each trait. The phenotypic values were spatially adjusted by subtracting the spatial residuals from the phenotypic values for each measurement in

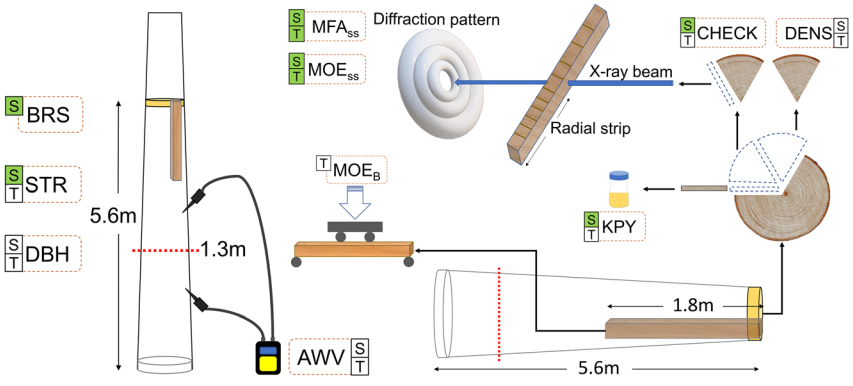


**Figure 1:** Diagram of the measured traits on standing trees, boards, and discs in Southport ('*S*') and Tarraleah ('*T*') *E. nitens* trials in Tasmania.
Green and white labels indicate the novel data analysed and the re-analysed traits from previous publications, respectively. DBH: diameter at breast height, $MFA_{ss}$: Area-weighted microfibril angle, $MOE_{ss}$: Area-weighted modulus of elasticity, AWV: Acoustic wave velocity, DENS: Wood basic density, KPY: kraft pulp yield, CHECK: Internal wood checking, STR: Straightness, BRS: branch size, $MOE_B$: Static modulus of elasticity measured from boards. $MOE_B$ and BRS were not available for the site Southport and Tarraleah, respectively.

each tree (referred to as the 'spatially adjusted data'). This dataset was used in subsequent analyses. Second, a univariate joint analysis was conducted to estimate across-site genetic parameters and examine the race by site and family by site interaction as expressions of genotype-by-environment interaction. Third, a bivariate model, which extended the univariate model and allowed for covariation between random effects was used to estimate genetic correlations between trials, treating the measurement of each trait at different sites as a different variate to explore the two facets of genotype-by-environment (G × E) interaction: *i)* change of rank by examining the strength of Type-B correlations and *ii)* level of expression of genetic variation by testing inter-site variance homogeneity (Burdon and Li 2019). Fourth, a multivariate and multi-site analysis comprising four-variates (two traits and two trials) was conducted to test if intra-site, inter-trait Type-A genetic correlations were homogeneous across sites and to estimate pooled correlations. All genetic analyses were undertaken with ASreml-R package version 4.1 (Butler et al. 2017) within the R environment (R Core Team 2020).

The spatial univariate model (1) fitted for each trial separately followed the mixed linear model:

$$\mathbf{y} = \boldsymbol{\mu} + \mathbf{Xb} + \mathbf{Z}_1\mathbf{f} + \mathbf{Z}_2\mathbf{p} + \mathbf{e} \quad (1)$$

where **y** is the vector of individual-tree observations, and **X** and $\mathbf{Z_{1,2}}$ are the design matrices relating the observations in **y** to the fixed and random effects, respectively. **b** is the vector of fixed effects associated with **y** through **X**. For each trial, the fixed effects were Replicates and Race. Race was the native stand race of origin of the parent trees from which families were derived. Random effects were **f** which is the vector of the family effects, **p** is the vector of plot effects, and **e** is the vector of the residuals, which was decomposed into a spatial dependent ($\xi$) and an independent ($\eta$) error term. **R** is the variance–covariance matrix of the residuals (2) with the structure:

$$\mathbf{R} = \sigma_\xi^2[\mathrm{AR1}(\rho_{\mathrm{col}}) \otimes \mathrm{AR1}(\rho_{\mathrm{row}})] + \mathbf{I}\sigma_\eta^2 \quad (2)$$

where $\sigma_\xi^2$ is the spatially dependant residual variance, $\sigma_\eta^2$ is the independent residual variance, ⊗ is the Kronecker product and AR1($\rho$) represents a first-order autoregressive correlation matrix for rows and columns where $\rho$ is the autocorrelation parameter and **I** is an identity matrix (Dutkowski et al. 2002). The random effects were assumed to be normally distributed. The wood property traits were only measured on one tree per plot and thus the plot term was only fitted for traits which had been assessed across the whole trial (i.e. DBH, stem straightness and branch size). Account was not made of the incomplete block structure of the original design in the statistical model as (i) the trial was subsampled for the wood property traits which disrupted this element of the design but left the replicates well balanced, and (ii) in the case of other traits (i.e. DBH, stem straightness and branch size) this variation is captured by the fitting of the spatial model.

Joint univariate linear mixed models (3) were fitted for the two sites using their spatially adjusted data and the model:

$$\mathbf{y} = \boldsymbol{\mu} + \mathbf{Xb} + \mathbf{Z}_1\mathbf{rs} + \mathbf{Z}_2\mathbf{f} + \mathbf{Z}_3\mathbf{fs} + \mathbf{Z}_4\mathbf{ps} + \mathbf{e} \quad (3)$$

where **y** is the vector of individual-tree spatially adjusted observations, and **X** and $\mathbf{Z_{1,2,3,4}}$ are the design matrices relating the observations in **y** to the fixed and random effects, respectively. **b** includes the Site, Race and their interaction, and the random terms are the replicate within Site (**rs**) the family (**f**), family by Site interaction (**fs**), plot within Site (**ps**) and **e** is the vector of the residuals representing a simple independent error term. The plot term was only fitted for traits where more than one tree was assessed per plot.

The bivariate and four-variate multivariate analyses also used the spatially adjusted data and were multivariate extensions of model 1. The bivariate models treated the same trait at different sites as a different variable and was used to explore G × E in terms of within race variance heterogeneity and rank change (Burdon and Li 2019). Parameterisation of the bivariate model involved a diagonal covariance structure for the error and plot term (DIAG structure) and a general correlation structure for the family term (**f**) that allowed for heterogeneous variances (CORGH structure). The plot term was only fitted for DBH, stem straightness and branch size. Four-variate analyses were used to test for homogeneity of correlations between traits across sites. The parameterisation of the four-variate model used an unstructured variance error model in which between-site covariances were set to zero. The random plot term was fitted as a separate variance whenever one of the traits being compared with the wood properties had multiple trees per plot assessed (i.e. DBH, stem straightness and branch size).

Tests of the fixed effects were undertaken with conditional Wald-type F statistic (e.g. conditional on the effects in **b** to account for the global trend), using the Kenward and Roger (1997) numerical derivatives method to compute approximate denominator degrees of freedom (Butler et al. 2017). Tests of whether specific variance components were greater than zero were undertaken using a one-tailed likelihood ratio test (LRT) comparing the full model to a constrained model with the variance component fixed to zero.

Tests of whether type-B correlation in the bivariate models differed from 1 (i.e. no rank change G × E) used a one-tailed LRT. Homogeneity of family variances was tested by constraining the variances of Southport and Tarraleah trials to be equal (the correlation was unconstrained) and comparing against the unconstrained model using a two-tailed LRT. In the four-variate analyses, traits were standardised by subtracting the phenotypic mean and dividing each trait measurement by the square root of the phenotypic variance for each trial. This was necessary to avoid problems of scale and to facilitate model convergence (Belaber et al. 2019). The homogeneity of the intra-site, inter-trait (Type-A) family-level correlations within Southport and Tarraleah trials was tested using a two-tailed LRT by comparing an unconstrained model to one where the correlations among the different traits within each trial were constrained to be equal. Where these correlations were not significantly different the pooled estimates were presented. Phenotypic (Pearson) correlations were calculated for single-trials as well as across trials. The across trial correlations were calculated by pooling the zero centred, standardised values for each trial. The significance of the phenotypic correlations from zero was tested using the *cor.test* function in R software (R Core Team 2020).

Genetic parameters were calculated after the removal of fixed race differences and t3hus are with-race estimates. Additive variance ($\widehat{\sigma}_a^2$) was estimated as follows:

$$\widehat{\sigma}_a^2 = \frac{\widehat{\sigma}_f^2}{r} \quad (4)$$

where $\widehat{\sigma}_f^2$ was the family variance and $r$ is the coefficient of relationship, assumed to be 0.4 to account for a selfing rate of 30% (Hamilton et al. 2010). Following (Belaber et al. 2019), the single-site, spatially-adjusted

**Table 1:** Grand mean values (Mean) and standard deviation (SD) for various traits of *Eucalyptus nitens* in trials at Tarraleah (TA) and Southport (SP) in Tasmania and the age of measurement (Age).

| Trait | Site | Age | Mean | SD | $F_{Race}$ | $\widehat{h}^2_{op}$ | $\widehat{CV}_a$ |
|---|---|---|---|---|---|---|---|
| $MFA_{ss}$ (°) | SP | 18 | 9.4 | 2.80 | $1.3^{ns}$ | $0.19(0.11)^{*}$ | 10.6 |
| | TA | 14 | 13.2 | 2.74 | $1.1^{ns}$ | $0.45(0.18)^{*}$ | 13.6 |
| $MOE_{ss}$ (GPa) | SP | 18 | 17.2 | 2.70 | $2.8^{ns}$ | $0.47(0.13)^{***}$ | 8.2 |
| | TA | 14 | 13.3 | 1.86 | $1.1^{ns}$ | $0.81(0.18)^{***}$ | 11.7 |
| $MOE_B$ (GPa) | TA | 14 | 10.7 | 1.54 | $6.4^{**}$ | $0.59(0.29)^{**}$ | 9.2 |
| AWV (m $s^{-1}$) | SP | 18 | 4.0 | 0.40 | $9.4^{***}$ | $0.42(0.12)^{***}$ | 5.1 |
| | TA | 15 | 3.7 | 0.31 | $23.8^{***}$ | $0.78(0.10)^{***}$ | 5.5 |
| DENS (kg $m^{-3}$) | SP | 18 | 519.9 | 43.05 | $4.6^{*}$ | $0.32(0.11)^{***}$ | 4.5 |
| | TA | 15 | 474.8 | 31.51 | $0.7^{ns}$ | $0.47(0.10)^{***}$ | 4.1 |
| KPY (%) | SP | 18 | 53.1 | 2.61 | $0.1^{ns}$ | $0.09(0.12)^{ns}$ | 1.2 |
| | TA | 15 | 51.6 | 1.48 | $1.8^{ns}$ | $0.41(0.09)^{***}$ | 1.6 |
| CHECK (1–6) | SP | 18 | 1.5 | 0.96 | $3.3^{*}$ | $0.18(0.12)^{ns}$ | 23.9 |
| | TA | 15 | 2.5 | 1.26 | $0.1^{ns}$ | $0.42(0.11)^{***}$ | 27.0 |
| DBH (cm) | SP | 18 | 16.8 | 5.39 | $5.2^{**}$ | $0.12(0.02)^{***}$ | 10.2 |
| | TA | 13 | 19.8 | 6.52 | $13.1^{***}$ | $0.19(0.02)^{***}$ | 13.9 |
| STR (1–6) | SP | 18 | 3.8 | 1.58 | $35.5^{***}$ | $0.15(0.02)^{***}$ | 13.4 |
| | TA | 13 | 4.3 | 1.39 | $18.8^{***}$ | $0.19(0.02)^{***}$ | 13.3 |
| BRS (1–4) | SP | 5 | 1.6 | 0.62 | $0.1^{ns}$ | $0.11(0.02)^{***}$ | 11.4 |

Also shown are the *F* value comparing the Connor's Plain (CO), Northern (NO) and Southern (SO) races of *E. nitens* ($F_{Race}$), narrow-sense heritability ($\widehat{h}^2_{op}$) and its standard error in parenthesis, and additive genetic coefficient of variation ($\widehat{CV}_a$) followed by their significance. DBH, diameter at breast height; $MFA_{ss}$, area-weighted microfibril angle; $MOE_{ss}$, area-weighted modulus of elasticity; AWV, acoustic wave velocity; DENS, Wood basic density; KPY, kraft pulp yield; CHECK, internal wood checking; STR, straightness; BRS, branch size; $MOE_B$, static modulus of elasticity measured from boards. $MOE_B$ and BRS were not available for the site Southport and Tarraleah, respectively. The significance levels are indicated as $^{ns}P \geq 0.05$; $^{*}0.01 \leq P < 0.05$; $^{**}0.001 \leq P < 0.01$; $^{***}P < 0.001$.

individual narrow-sense heritability ($\widehat{h}^2_{op}$) was estimated for the raw data from each site as:

$$\widehat{h}^2_{op} = \frac{\widehat{\sigma}^2_a}{\widehat{\sigma}^2_{\text{phen}}} = \frac{\widehat{\sigma}^2_a}{\widehat{\sigma}^2_f + \widehat{\sigma}^2_p + \sigma^2_\eta} \quad (5)$$

where $\widehat{\sigma}^2_{\text{phen}}$ was the phenotypic variance estimated as the sum of the family variance, the plot variance ($\widehat{\sigma}^2_p$ – estimated for DBH, stem straightness and branch size only) and the independent error variance ($\sigma^2_\eta$).

The across-site individual narrow-sense heritability ($\widehat{h}^2_{op}$) of the spatially-adjusted data (see above) was estimated as:

$$\widehat{h}^2_{op} = \frac{\widehat{\sigma}^2_a}{\widehat{\sigma}^2_{\text{phen}}} = \frac{\widehat{\sigma}^2_a}{\widehat{\sigma}^2_f + \widehat{\sigma}^2_{fs} + \widehat{\sigma}^2_{ps} + \widehat{\sigma}^2_e} \quad (6)$$

where $\widehat{\sigma}^2_{fs}$ was the family by site interaction variance component, $\widehat{\sigma}^2_{ps}$ was the plot within site variance component and $\widehat{\sigma}^2_e$ was the error variance. In both single- and multi-site heritability estimates, variance components were derived from univariate analyses and the plot variance was only included for DBH, stem straightness and branch size. The additive genetic coefficient of variation ($\widehat{CV}_a$) was calculated as:

$$\widehat{CV}_a = 100 \times \frac{\sqrt{\widehat{\sigma}^2_a}}{\bar{x}} \quad (7)$$

The genetic correlations, whether type-A (intra-site, inter-trait) or type-B (inter-site, single trait), were estimated following Jordan et al. (1999):

$$\widehat{r}_{1,2} = \frac{\widehat{\sigma}_{1,2}}{\sqrt{\widehat{\sigma}^2_1 \times \widehat{\sigma}^2_2}} \quad (8)$$

where $\widehat{r}_{1,2}$ is the correlation between trait 1 and trait 2 at the family level. $\widehat{\sigma}_{1,2}$ is the family covariance between the traits, and $\widehat{\sigma}^2_1$ and $\widehat{\sigma}^2_2$ are the family variance components of the respective traits. Approximate standard errors of the variance components and their functions were calculated from a Taylor series approximation (Butler et al. 2017).

# 3 Results and discussion

## 3.1 Variation range of MFA within and among sites

The mean values of $MFA_{ss}$ and other wood properties, as well as tree growth and form traits at the site level are presented in Table 1. The mean $MFA_{ss}$ values were 9.4 and 13.2° in Southport and Tarraleah, respectively. These means of the area-weighted average values of microfibril angle were approximately 20% lower than the means based on the simple average MFA for the wood strips taken from each tree (not reported). This difference is expected as $MFA_{ss}$ declines radially toward the cambium in *E. nitens* (Vega et al. 2020), and the area weighted estimates give

greater weight to the outerwood values than those close to the pith. These area weighted values thus provide better estimates of the whole disc value (Gräns et al. 2009). The significant site effect ($F_{1,4} = 16.8$, $P < 0.05$, Table 2) could be due to a combination of environment and four-year age difference between the two sites. For example, consistent with a reduction in MFA with age, the older trial (Southport) had the lowest area-weighted mean $MFA_{ss}$. However, other factors may have also contributed to the differences in wood property mean values. For example, the Tarraleah site was cooler and had higher effective rainfall than Southport. The soils at Tarraleah were also more fertile being derived from Tertiary basalt, whereas soils at Southport were derived from nutrient poor Triassic sandstone. Triassic sandstone soils also have poor moisture retention capacity compared with Tertiary basalt, thus the Southport trial is likely to have experienced greater water limitation than Tarraleah (Blackburn et al. 2014). As dry conditions have been shown to reduce MFA by proportionally reducing the amount of earlywood within each ring (Wimmer et al. 2002), it is possible that this, in combination with slower growth (Medhurst et al. 2012) and lower productivity (Vega et al. 2020), could explain the lower MFA observed at Southport.

## 3.2 Genetic control of MFA and stability across sites

$MFA_{ss}$ exhibited no significant difference among races (single trial analyses – Table 1; joint analysis – Table 2) and no significant race by site and family by site interactions, which reflects the absence of genotype-by-environment interaction (joint analysis – Table 2). While the race differences in MFA were not statistically significant, the rank order of the least-square means (Supplementary Table S1) was consistent with their ranking on traits in previous studies. The Southern race (SO) at Southport had the lowest MFA (11.0°) and was also the best in the stiffness related traits (AWV) and pulpwood traits (Blackburn et al. 2012).

Within races, families exhibited significant variation in MFA, indicating MFA is under significant genetic control, with a narrow-sense heritability of 0.19 at Southport and 0.45 at Tarraleah (Table 1). However, the family variances did not differ significantly between sites and the Type-B correlation ($\hat{r}_B = 0.99 \pm 0.34$[SE]) were not significantly different from one (no rank changes) suggesting strong stability in MFA additive genetic variance across sites, regardless of the assessment age and site differences (Table 3). This was confirmed in the joint analysis where the family by site interaction was not significant (LRT, $P > 0.05$) whereas the pooled family term was highly significant (LRT, $P < 0.001$) (Table 2). The absence of G × E for MFA among these trials is noteworthy given the marked difference in growth rates (Table 1 and 2) as well as statistically significant G × E for growth (Table 2). At the time of this study no previous reports of MFA G × E in *E. nitens* were found, but the results presented here are consistent with the two studies of MFA G × E in other forest trees (*Eucalyptus pellita* $\hat{r}_B = 1.0 \pm 0.0$, Hung et al. (2015); *Pinus radiata* $\hat{r}_B = 0.82 \pm 0.13$, Baltunis et al. (2007)). This finding of no significant G × E for MFA is consistent with general trends for wood properties in other eucalypt species (Nickolas et al. 2020), including *E. nitens* (Hamilton and Potts 2008), although the present case did detect statistically significant G × E for wood density (joint analysis family by site $P < 0.05$, Table 2; $\hat{r}_B = 0.64 \pm 0.19$, $P < 0.05$ from 1, Table 4). In the present study the sampling disc for wood density assessment was taken at greater height than in most G × E studies of density in eucalypts which are normally based on breast-height cores (Hamilton et al. 2008). Genetic differences in the pattern of longitudinal variation in density has been reported in eucalypts (Hamilton et al. 2007), and age or environmental effects on such

**Table 2:** Race (*R*), Site (*S*) Race by site ($R \times S$) fixed effects, estimates of family ($\hat{\sigma}_f^2$), family-site ($\hat{\sigma}_{fs}^2$) and residual ($\hat{\sigma}_e^2$) variance components, individual heritability (standard error in parenthesis) and additive genetic coefficient of variation ($\widehat{CV}_a$, %) for the combined analysis of Southport and Tarraleah *E. nitens* trials.

| Trait | *R* | *S* | $R \times S$ | $\hat{\sigma}_f^2$ | $\hat{\sigma}_{fs}^2$ | $\hat{\sigma}_e^2$ | $\hat{h}_{op}^2$ | $\widehat{CV}_a$ |
|---|---|---|---|---|---|---|---|---|
| $MFA_{ss}$ | $1.6^{ns}$ | $16.8^{*}$ | $1.4^{ns}$ | $0.61(0.20)^{***}$ | $0.03(0.22)^{ns}$ | 5.0(0.29) | 0.27(0.01) | 11.6 |
| $MOE_{ss}$ | $3.1^{*}$ | $13.4^{*}$ | $1.6^{ns}$ | $0.71(0.16)^{***}$ | $0.05(0.12)^{ns}$ | 2.7(0.16) | 0.52(0.02) | 8.4 |
| AWV | $27.4^{***}$ | $7.0^{*}$ | $0.32^{ns}$ | $0.01(0.003)^{***}$ | $0.00(0.002)^{ns}$ | 0.05(0.002) | 0.57(0.02) | 5.0 |
| DENS | $4.3^{*}$ | $48.2^{***}$ | $3.3^{*}$ | $104(35.2)^{***}$ | $72.4(36.6)^{*}$ | 894(38.8) | 0.24(0.009) | 3.3 |
| KPY | $1.2^{ns}$ | $6.5^{*}$ | $0.17^{ns}$ | $0.24(0.07)^{***}$ | $0.00\ (0.07)^{ns}$ | 2.2(0.10) | 0.25(0.01) | 1.5 |
| CHECK | $1.8^{ns}$ | $42.2^{***}$ | $2.6^{ns}$ | $0.11(0.03)^{***}$ | $0.01(0.03)^{ns}$ | 0.76(0.04) | 0.31(0.01) | 24.1 |
| DBH | $13.2^{***}$ | $42.6^{***}$ | $5.1^{**}$ | $1.6(0.20)_{***}$ | $0.53(0.15)^{***}$ | 31.0(0.37) | 0.12(0.001) | 10.5 |
| STR | $45.1^{***}$ | $1.9^{ns}$ | $3.1^{*}$ | $0.06(0.01)^{***}$ | $0.04(0.009)^{***}$ | 1.5(0.02) | 0.10(0.001) | 9.8 |

Trait codes are detailed in Table 1. The significance levels are indicated as $^{ns}P \geq 0.05$; $^{*}0.01 \leq P < 0.05$; $^{**}0.001 \leq P < 0.01$; $^{***}P < 0.001$.

**Table 3:** Type B additive (based on family effects) genetic correlations ($\hat{r}_B$), their approximate standard errors (SE) in parenthesis and significance from one, and *P*-values of the LRT test for variance homogeneity between the Southport and Tarraleah *E. nitens* trials.

| Trait | $\hat{r}_B$ (SE) | *P*-values of variance homogeneity test |
|---|---|---|
| $MFA_{ss}$ | $0.99(0.34)^{ns}$ | 0.155 |
| $MOE_{ss}$ | $0.87(0.14)^{ns}$ | 0.042 |
| AWV | $0.97(0.10)^{ns}$ | 0.049 |
| DENS | $0.64(0.19)^{*}$ | 0.262 |
| KPY | $1.00^{(a)ns}$ | 0.088 |
| CHECK | $1.00^{(a)ns}$ | 0.217 |
| DBH | $0.84(0.07)^{*}$ | 0.002 |
| STR | $0.60(0.07)^{***}$ | 0.055 |

Trait codes are detailed in Table 1. $^{(a)}$parameter on the boundary of the parameter space. The significance of the Type-B correlations from one were tested using one-tail LRT. The significance of variance homogeneity was tested using a two-tailed LRT. The significance levels are indicated as $^{ns}P \geq 0.05$; $^{*}0.01 \leq P < 0.05$; $^{**}0.001 \leq P < 0.01$; $^{***}P < 0.001$.

differences could contribute to the observed G × E for density in the present study.

Pooling the results across sites in the joint analysis provided a narrow-sense heritability for $MFA_{ss}$ of 0.27 ± 0.01 (Table 2), which is consistent with the average of the single-site estimates of 0.32. These heritability estimates are similar to that reported for *E. globulus* (0.27 ± 0.24) at age 11 (Apiolaza et al. 2005), but lower than that reported for the tropical eucalypt *E. urophylla* (0.43 ± 0.15) at age 14 (Hein et al. 2012). The heritabilities for MFA are also at the lower end of the values reported in softwoods. For example, Dungey et al. (2006) reported narrow-sense heritabilities of 0.63 ± 0.25 and 0.32 ± 0.14 for area-weighted MFA for 18 year-old *P. radiata*. Ukrainetz et al. (2008) reported a smaller narrow-sense heritability of 0.20 ± 0.08 for average MFA for 26 year-old *Pseudotsuga menziesii*. Another softwood study reported narrow-sense MFA heritabilities of 0.63 ± 0.10 and 0.43 ± 0.11 based on six year-old *P. radiata* trees (Baltunis et al. 2007). Even though the heritability for MFA reported in the present study is low relative to most other studies, it is comparable to three of the five wood properties assessed from the same trees (wood density, KPY and checking – Table 2), and greater than that of DBH and stem straightness in both the single trial (Table 1) and the joint (Table 2) analyses. Lower heritabilities for growth and the other wood traits in Southport compared with Tarraleah was also reported in Blackburn et al. (2012), which they suggested may be related to differences in site conditions. While neither *E. nitens* trial was thinned, Dungey et al. (2006) suggested that in *P. radiata* water availability changes as a result of thinning treatments and may reduce the heritability of MFA.

## 3.3 Inter-trait genetic correlations

Genetic and phenotypic correlations of $MFA_{ss}$ and $MOE_{ss}$ with growth, form and other wood properties are shown in Table 4. All traits studied showed statistically significant levels of family variation in the single or joint analyses variation (Table 1 or 2), justifying the calculation of the pair-wise genetic correlations (Supplementary Table 2). As expected, MFA was highly negatively correlated at the phenotypic and genetic levels with the SilviScan® estimate of MOE ($MOE_{ss}$) taken from the same wood strip.

**Table 4:** Pooled within-site inter-trait genetic (type-A; $\hat{r}_g$) and phenotypic ($\hat{r}_p$) correlations of MFA and MOE with growth and other wood property traits in *E. nitens* with standard errors in parentheses.

| Trait | $MFA_{ss}$ | | $MOE_{ss}$ | |
|---|---|---|---|---|
| | $\hat{r}_g$ | $\hat{r}_p$ | $\hat{r}_g$ | $\hat{r}_p$ |
| $MOE_{ss}$ | $-0.91(0.06)^{***}$ | $-0.82(0.02)^{***}$ | | |
| $MOE_B$[a] | $-0.94(0.25)^{***}$ | $-0.32(0.06)^{***}$ | $0.84(0.15)^{***}$ | $0.42(0.06)^{***}$ |
| AWV | $-0.87(0.13)^{***}$ | $-0.51(0.03)^{***}$ | $0.89(0.06)^{***}$ | $0.63(0.03)^{***}$ |
| DENS | $-0.34(0.18)^{ns}$ | $-0.08(0.04)^{ns}$ | $0.58(0.12)^{***}$ | $0.38(0.03)^{***}$ |
| KPY | $-0.69(0.15)^{***}$ | $-0.46(0.03)^{***}$ | $0.67(0.11)^{***}$ | $0.50(0.03)^{***}$ |
| CHECK | $-0.06(0.22)^{ns}$ | $0.005(0.04)^{ns}$ | $0.01(0.17)^{ns}$ | $-0.05(0.04)^{ns}$ |
| DBH | $-0.07(0.19)^{ns}$ | $0.20(0.03)^{***}$ | $0.13(0.15)^{ns}$ | $-0.24(0.03)^{***}$ |
| STR | $-0.27(0.18)^{ns}$ | $0.03(0.03)^{ns}$ | $0.22(0.14)^{ns}$ | $-0.04(0.03)^{ns}$ |
| BRS[a] | $-0.02(0.28)^{ns}$ | $0.01(0.05)^{ns}$ | $-0.007(0.20)^{ns}$ | $-0.03(0.05)^{ns}$ |

Trait codes are detailed in Table 1. [a]$MOE_B$ and BRS were only measured at Tarraleah and Southport, respectively. The significance levels of the type-A and phenotypic correlations tested from zero are indicated as $^{ns}P \geq 0.05$; $^{*}0.01 \leq P < 0.05$; $^{**}0.001 \leq P < 0.01$; $^{***}P < 0.001$.

### 3.3.1 Genetic correlations with tree growth and form

Despite a weak positive phenotypic correlation of MFA with DBH (0.20 ± 0.03), the genetic correlation (–0.07 ± 0.19) was insignificant, as was also the case for $MOE_{ss}$ (0.13 ± 0.15) (Table 4). This independence of growth and MFA in *E. nitens* accords with results from *E. pellita* (–0.19 ± 0.16; Hung et al. (2015)) and *E. urophylla* (–0.36 ± 0.38; Hein et al. (2012)), but not with the significant negative genetic correlation reported in *E. globulus* (–0.86 ± 0.40; Apiolaza et al. (2005)). The recovery of high value veneer and timber may also be affected by two facets of tree architecture – branch size and stem straightness (Blackburn et al. 2013; McGavin et al. 2015b; Peng et al. 2015). In the present study, there was a low and non-significant genetic and phenotypic correlation of MFA with branch size and stem straightness (Table 4). The genetic correlation between branch size and DBH in this study was not significantly different from zero ($\hat{r}_g$ = –0.11 ± 0.12; Table S2), consistent with previous studies (Hamilton and Potts 2008). Nevertheless, it is recognised that branch size and angle have a significant impact on the recovery of high-grade solid wood products due to degradation of timber value from knots increasing defects in the core and outerwood depending on whether pruning is done (Wood et al. 2009). Stem straightness is under significant genetic control (Table 1), but unlike branch size, it has a strong positive genetic and phenotypic correlations with growth ($\hat{r}_g$ = 0.71 ± 0.04; $\hat{r}_p$ = 0.53 ± 0.01) which is consistent with previous studies in *E. globulus* (Callister et al. 2011) and *E. nitens* (Johnson 1996). Poor stem straightness has a negative effect on volume recovery for solid wood products (Blackburn et al. 2013), and may even increase harvest costs (Hamilton et al. 2015). The genetic independence of MFA from growth, branching and form traits in *E. nitens* has implication for both pulpwood and solid wood production systems as these are key selection traits in one or both systems and their genetic improvement would not be expected to indirectly affect MFA and thus wood stiffness.

### 3.3.2 Genetic correlations with basic density

Wood density or its surrogates are the most frequently genetically studied wood property in eucalypts (Hamilton and Potts 2008). For pulpwood production systems, wood density is important due to its impact on total pulp productivity and transport costs, and its improvement is a key breeding objective (Greaves et al. 1997). It is also an important consideration for producing solid wood products for structural uses where it is negatively associated with wood shrinkage (Hamilton et al. 2009), and positively related to stiffness (Raymond 2002; Walker 2011). However, there is a trade-off between density and stiffness as timber needs to be light for transportation and handling but also stiff (Raymond and Apiolaza 2004). In the present study, both $MFA_{ss}$ and wood density are significantly correlated with MOE (see below), but the genetic correlation between $MFA_{ss}$ and wood density was low and non-significant (–0.34 ± 0.18; Table 4). This independence is in agreement with other studies in eucalypts. For example, Hein et al. (2012) found non-significant genetic correlation between MFA and wood density in *E. urophylla*, as did Apiolaza et al. (2005) find in *E. globulus*. As wood density is often related to cell wall thickness (Salvo et al. 2017), the absence of a significant MFA and wood density genetic correlation suggests that area-weighted MFA is not directly related to cell wall thickness itself. Instead, as suggested by Donaldson (2008), tree-level MFA may be influenced by the proportion of juvenile or earlywood proportions as MFA varies according to these factors.

### 3.3.3 Genetic correlations with KPY

Along with growth per hectare, improvement of wood density and KPY are the main breeding objectives for pulpwood production systems (Hamilton et al. 2008; Raymond 2002). These wood property traits determine the amount of pulp per unit volume of wood that could be obtained (Borralho et al. 1993). $MFA_{ss}$ showed a moderate to strong negative genetic correlation with KPY (–0.69 ± 0.15, Table 4). A few studies have reported genetic correlations between MFA and KPY. For example Hung et al. (2016) similarly reported a moderate to strong negative genetic correlation at the family (–0.77 ± 0.05) and provenance (–0.93 ± 0.04) levels in *Corymbia citriodora*. As MFA is negatively correlated with wood stiffness, the present finding is also consistent with a significant positive genetic correlation between KPY and wood stiffness related traits (i.e. AWV from standing trees and logs) that have been found in *E. nitens* (Blackburn et al. 2012) and *E. globulus* (Hamilton et al. 2017; Nickolas et al. 2020). A similar effect has been found between stiffness related traits (i.e. higher AWV) and increased cellulose content and decreased lignin content corresponding with increased fibre length (Raymond et al. 2010). An explanation for this strong negative correlation between KPY and MFA may partly lie in the synchronous changes in wood properties associated with (i) growth stresses and (ii) changes associated with the age-related transition from core to outerwood. Growth strained wood is less lignified (i.e. higher KPY) and has lower MFA than normal wood (Bailleres et al. 1995). Similarly, the age-related radial changes in wood properties involve MFA decreasing (Vega et al. 2020) and

KPY increasing (Downes et al. 1997) in the outerwood of *E. nitens*. Genetic variation in either susceptibility to growth stresses or the pattern of radial change may thus induce synchronous genetic-based changes in KPY and MFA. Regardless of the mechanism, the present results suggest that, given the low non-significant genetic correlation between MFA and wood density, and moderate favourable genetic correlation with KPY, selection of lower MFA values favoured for wood stiffness would not be expected to have a detrimental impact on pulpwood production objectives.

#### 3.3.4 Genetic correlation with wood stiffness

The estimated genetic correlations between $MFA_{ss}$ and MOE in both trees ($MOE_{ss}$) and boards ($MOE_B$) was significant and strongly negative (Table 4). This genetic relationship is consistent with studies in other species (*C. citriodora* $\hat{r}_g = -0.96 \pm 0.01$, Hung et al. (2016)), confirming MFA as a major contributor to wood stiffness along with wood density. While wood density and MFA appear to be genetically independent (Table 4), both are highly significantly correlated with MOE, consistent with their independent contributions to wood stiffness. SilviScan® strips ($MOE_{ss}$ – dynamic MOE) and board ($MOE_B$ – static MOE) MOE are highly genetic correlated ($\hat{r}_g = 0.84 \pm 0.15$; Table 4), indicating dynamic MOE measurements in standing trees is a good predictor of genotype performance at the product level based on the static bending test. Therefore, in breeding $MFA_{ss}$ and $MOE_{ss}$ could be used to indirectly select for improved stiffness of the final products (i.e. sawn timber and veneer). Further, as MFA and wood density are genetically independent, selection directly on the MFA independent-component of stiffness opens the possibility of increasing stiffness without affecting wood density, which is especially important when there is a requirement for high MOE but minimum structural weight (McGavin et al. 2015a). However, trade-offs between MFA and wood density need to be further investigated in order to understand if they are associated to other desirable/undesirable properties in terms of wood behaviour (i.e. dimensional instability associated with shrinkage) and processing (i.e. drying defects such as collapse) in *E. nitens* (see below).

In standing trees, AWV is generally used as the non-destructive selection trait to indirectly measure wood stiffness in genetic trials due to its relatively easy and fast assessment (Schimleck et al. 2019). This study shows a strong favourable genetic correlation of standing tree AWV with SilviScan® strip assessed MFA ($\hat{r}_g = -0.87 \pm 0.13$; Table 4), whereas that with the disc measured wood density was considerably lower ($\hat{r}_g = 0.66 \pm 0.09$; see Supplementary Table S2 for details). This is the first study to confirm MFA as major contributor to AWV, further validating the use of AWV as a proxy of MOE in *E. nitens*.

#### 3.3.5 Genetic correlation with internal checking

Surface and internal checking can occur within growth rings during the drying of the wood, and these cracks can make eucalypt sawn timber unsuitable for high-value sawn boards, reducing appearance-grade recovery (Blakemore 2011). Checking can be induced by collapse due to abnormal shrinkage arising from the physical collapse of fibre cells, generally in the early stages of the drying process (Chafe et al. 1992). Collapse has shown strong negative genetic correlation with wood density in *E. nitens* (Kube and Raymond 2005) and is a commonly considered cause of internal checking (Ilic and Hillis 1986). Collapse-induced internal checking is a permanent form of degrade that is usually not evident until after the wood is further processed making it a high cost degrade (Ilic 1999).

Increasing wood density and increasing cell wall thickness are parameters expected *a priori* to contribute to resistance to collapse under drying stresses (Ball et al. 2005). In *Eucalyptus regnans*, internal checking was manifest in growth rings of back-sawn boards in which the earlywood air-dry density was below 450 kg $m^{-3}$ (Ilic 1999). The size and number of internal checks also has been shown to increase with a decrease in earlywood density. However, there are few studies on the relationship between MFA and internal checking. At a micro-scale, a study of wood fracture by Stanzl-Tschegg (2006) found that energy absorption increases with MFA, and that cells are more brittle when MFA is low and the cells are more prone to fracture, thus more likely to develop checks. At a macro-scale (tree level), Ilic (2001) found that board MOE was negatively related to the number of internal checks after drying, suggesting increasing stiffness reduces the probability of checking. These apparently contrasting results may be due to the dependence (correlation) of both MOE and AWV on wood density. The wedge level assessment of checking used in the present study was from discs extracted from 5.6 m up the stem of the felled trees, which has been shown to be significantly positively genetically correlated with the internal checking in dried boards from the same tree (Blackburn et al. 2010). However, in the present study, neither MFA, MOE nor wood density exhibited significant genetic or phenotypic correlations with checking as assessed from wedges from the same discs used to assessed the other traits (Table 4; see Supplementary Table S2 for details). While no similar studies have been published in eucalypts, a weak negative non-significant genetic correlation of checking with stiffness

measured indirectly using acoustic instruments has been reported in *P. radiata* (Ball et al. 2005; Kumar 2004). There is similarly some evidence of a weak negative genetic relationship between AWV and checking in the present study ($\hat{r}_g$ = −0.31 ± 0.13), but the phenotypic correlation is non-significant ($\hat{r}_p$ = −0.04 ± 0.03) (Supplementary Table S2). Overall, these results suggest that at least at the disc level, low wood stiffness (high MFA, low MOE and wood density) is unlikely to be genetically associated with check development, although the low negative genetic association with tree level AWV warrants further investigation.

# 4 Conclusions

This study indicates that variation in MFA is under genetic control in *E. nitens* which is consistent with other wood properties (e.g. wood density, pulp yield and MOE) in this and previous studies. MFA is confirmed as a major determinant of MOE in trees and boards and highly genetically correlated with the indirect assessments of these attributes in standing trees using acoustics (AWV). Genetic correlations suggest MFA and wood density independently contribute to MOE. Thus, the genetic improvement of both MFA and wood density could independently improve MOE. This highlights opportunities for solid wood improvement as MFA assessment technologies become more accessible and because of the absence of significant genotype-by-environment interaction which indicates that multiple site/environment deployment of genetic material would be efficient. Genetic correlations suggest that MFA improvement is compatible with the presently pulpwood focused improvement programmes in *E. nitens*, and indeed may have already been indirectly improved through previous selection on pulp yield. However, more studies are needed to confirm these genetic correlations in *E. nitens* as well as the relationship of MFA with other relevant wood properties for pulpwood and solid wood products.

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