

Article

## Acoustic Wave Velocity as a Selection Trait in *Eucalyptus nitens*

David Blackburn <sup>1,\*</sup>, Matthew Hamilton <sup>1</sup>, Dean Williams <sup>2</sup>, Chris Harwood <sup>3</sup> and Brad Potts <sup>1</sup>

<sup>1</sup> School of Biological Sciences and the National Centre for Future Forest Industries (NCFFI), University of Tasmania, Private Bag 55, Hobart, Tasmania 7000, Australia; E-Mails: Matthew.Hamilton@utas.edu.au (M.H.); B.M.Potts@utas.edu.au (B.P.)

<sup>2</sup> Forestry Tasmania, 79 Melville Street, Hobart, Tasmania 7000, Australia; E-Mail: Dean.Williams@forestrytas.com.au

<sup>3</sup> CSIRO Ecosystem Sciences and Sustainable Agriculture Flagship, Private Bag 12, Hobart, Tasmania 7001, Australia; E-Mail: Chris.Harwood@csiro.au

\* Author to whom correspondence should be addressed; E-Mail: David.Blackburn@utas.edu.au; Tel.: +61-41-016-0221.

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**Abstract:** Previous studies in *Eucalyptus nitens* have revealed favourable genetic correlations exist between acoustic wave velocity (AWV) in standing trees and modulus of elasticity (MOE), which can determine the suitability of trees for structural timber and/or engineered wood products. This study investigates the strength and stability of genetic variation in standing tree AWV across a range of environments in Tasmania, where there are a number of large plantation estates and breeding trials. Trees under study were from open-pollinated progeny trials established in 1993. Across sites, for standing tree AWV the ranking of *E. nitens* races did not change and within-race additive genetic correlations were strong (0.61 to 0.99). Heritabilities (0.16 to 0.74) and coefficients of additive genetic variation (2.6 to 4.8) were moderate for this trait. Correlations between standing tree AWV and both basic density and diameter at breast height (DBH) were favourable. Results indicate that there is potential to improve MOE in *E. nitens* through the exploitation of genetic variation in AWV among and within races, the expression of genetic variation in AWV is relatively stable across different growing environments, and past selection for basic density and growth in pulpwood breeding programs is unlikely to have adversely affected MOE.

**Keywords:** *Eucalyptus nitens*; acoustic wave velocity; wood density; growth; heritability; genotype by environment interaction

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## 1. Introduction

*Eucalyptus nitens* (Dean and Maiden) Maiden is widely-grown in temperate regions of the world for both pulpwood and solid timber products [1]. In Australia, the *E. nitens* plantations estate is 236,000 ha [2], of which approximately 10% has been intensively managed with thinning and pruning [3]. A comparable area of plantation is present in Chile and substantial, albeit smaller, areas are planted in South Africa, China and New Zealand [4]. The species originates from south-eastern Australia and grows naturally in the cool, wet temperate regions of the central highlands of Victoria and nearby mountainous regions of southern NSW, with two other outlying populations occurring at high elevations in New South Wales [4,5]. The species is genetically diverse, and has been separated into five genetically and geographically distinct races, three from central Victoria and two from New South Wales [4]. Meta-analyses of world-wide provenance trials of the species show that at a broad-scale these races are climatically adapted [6]. For example, genotype-by-environment ( $G \times E$ ) interactions in growth were explained by the central Victorian races outperforming the New South Wales races in winter-rainfall zones and *vice versa* in summer-rainfall zones (an effect also observed in South Africa [7]). Accordingly the central Victorian races are deployed in winter rainfall zones such as those found in cool-temperate regions of Chile and Australia.

*Eucalyptus nitens* is susceptible to drought [8,9] and in Tasmania, where most Australian *E. nitens* plantations occur, the species is grown primarily in areas where annual rainfall exceeds 850 mm [10]. *Eucalyptus nitens* is particularly suited to the Tasmanian climate as it is cold hardy [11–13], and it is favoured over *E. globulus* (the more common plantation eucalypt on mainland Australia) on cold sites or those prone to *Mycosphaerella* leaf disease [14,15]. However, within the Tasmanian *E. nitens* planting zone there is considerable variation in climate, topography and geology [16] (Table 1). It is therefore important to understand the extent to which  $G \times E$  affects the growth and wood properties of *E. nitens* at this regional scale, in order to optimise breeding and deployment of the species [17]. If  $G \times E$  is evident, optimisation may be achieved either by breeding for stable performance across diverse environments or targeting different genotypes for different environments [18,19]. Inter-site additive genetic correlations for a trait are often used to quantify the magnitude of  $G \times E$  [20]. Such correlations indicate how well genetic information derived from one site can predict genetic performance at another site and are used to inform tree breeding and deployment strategies [17].

In the present paper, we quantify the importance of  $G \times E$  in Tasmanian-grown *E. nitens* for three key selection criteria: one of which—acoustic wave velocity (AWV)—is increasingly used to assess the value of standing trees for structural timber and engineered wood products (EWPs); while the other two—diameter at breast height (DBH) and wood basic density—are important for the genetic improvement of both pulp- and solid-wood plantations [15,21]. Diameter at breast height and basic density are routinely assessed in *E. nitens* breeding trials [4] and they have been the most studied of

selection criteria [6]. Acoustic wave velocity taken from standing trees has only recently become a selection criterion of interest [22–25].

**Table 1.** Geographic and climatic details of the four *Eucalyptus nitens* progeny trials. Climatic data were estimated using the climatic surfaces in ANUCLIM, module MNTHCLIM (v6.1).

	Tarraleah	Southport	Meunna	Florentine
Latitude	42°16'32"	43°22'41"	41°05'6"	42°39'43"
Longitude	146°27'35"	146°56'3"	145°29'0"	146°28'8"
Elevation	600 m	120 m	270 m	270 m
Annual Rainfall (sum of months)	1130 mm	1139 mm	1526 mm	1433 mm
Annual evaporation (sum of months)	893 mm	970 mm	948 mm	915 mm
Effective annual rainfall	237 mm	169 mm	578 mm	518 mm
Mean Annual Temp	9.8 °C	12.0 °C	12.3 °C	10.7 °C
Mean min temp coolest month	0.1 °C	3.4 °C	4.2 °C	1.2 °C
Geology	Tertiary basalt	Triassic sandstone	Tertiary basalt	Ordovician limestone
Previous land use	Pine plantation	Native forest	Pasture	Native forest
Tasmanian climate zone [26]	Cool-moist	Warm-moist	Warm-moist	Cool-moist

Acoustic wave velocity is correlated with modulus of elasticity (MOE) [25,27], a key structural characteristic which is indicative of end-product stiffness [23,28]. Genetic improvement of MOE could prove particularly beneficial for *E. nitens* veneer products as a study by Farrell *et al.* [29] showed that engineered plywood structural products from this species have MOE values that are on the margins of acceptability for current markets.

Previous studies conducted on a single Tasmanian *E. nitens* progeny trial [24,25] revealed significant genetic variation in AWV, as well as significant and favourable genetic correlations between AWV in standing trees and the commonly-assessed pulpwood selection criteria – DBH, wood basic density and kraft pulp yield. Given the importance of the predictive capacity of standing tree AWV, the paucity of genetic studies of AWV in eucalypts, and the unique opportunity to assemble harvest-age measurements of growth, AWV and basic density from multiple, pedigree-connected trials established in Tasmania, the study aims to directly assist those engaged in *E. nitens* solid-wood breeding by addressing three key questions:

- (i) How strong is the genetic control of AWV?
- (ii) How genetically stable is standing tree AWV across a range of environments in Tasmania?
- (iii) How robust are the reported genetic correlations of AWV with the traditional selection criteria – basic density and DBH?

With an increasing area of plantations managed for solidwood products [3], these questions need to be resolved before AWV can be more generally utilised for the genetic evaluation of *E. nitens* breeding and deployment populations [4,30].

## 2. Experimental Section

### 2.1. *Eucalyptus Nitens* Progeny Trials

*Eucalyptus nitens* open-pollinated progeny trials were planted in August 1993 on four Tasmanian sites—Florentine, Meunna, Southport and Tarraleah (Figure 1, Table 2). These trials tested the progenies of between 408 and 419 native-forest parent trees, sampled from 28 localities extending over most of the natural range of *E. nitens* in the central highlands region of Victoria. Genetically these sampling localities encompassed three distinct races: Southern, Northern and Connor’s Plain [31,32].

Tarraleah and Florentine were established in central Tasmania on sites which experience a “cool-moist” climate [26] (Table 1). In contrast, Meunna and Southport were located in areas that experience a ‘warm-moist’ climate. The majority of Tasmanian *E. nitens* plantations are established within these two climate zones. Tarraleah, the coldest of the four trial sites, had a mean annual temperature of 9.8 °C, 2.5 °C lower than that of Meunna, the warmest site (12.3 °C).

**Figure 1.** Map of Tasmania showing locations of the four *Eucalyptus nitens* base population progeny trials.



The trials used a resolvable incomplete block design (Table 2) and spacing at planting was four metres between rows and two metres between trees within rows. Fertiliser (100 g of superphosphate and 125 g of 20:10:0 N:P:K) was applied at the base of each tree three months after planting. Neither thinning nor pruning was undertaken at Tarraleah, Southport or Florentine prior to the current study.

Meunna was pruned at ages four and eight years as well as selectively thinned at age four years to retain two trees with superior size and stem straightness from each five-tree plot. The Tarraleah trial was harvested in two stages, three replicates at age 13 years and three replicates at age 14 years, to undertake a sawmilling and rotary-peeling study respectively [24,33].

**Table 2.** Design, family and survival details of the four *Eucalyptus nitens* progeny trials assessed for acoustic wave velocity (AWV), basic density (BD) and diameter at breast height (DBH; 1.3 m). Published studies that contributed trait data to this study are indicated.

	Tarraleah	Southport	Meunna	Florentine
Replicates	6	5	5	6
Incomplete blocks (per replicate)	21	21	21	21
Family plots per block	20	20	20	20
Trees per family plot	5	5	5	5
Number of trees planted	12,600	10,500	10,500	12,600
Thinning at year 4/trees per plot remaining	N/A	N/A	2	N/A
Percentage of trees remaining at DBH assessment age	86	90	32	65
Number of families for AWV (age in years) [23,24]	181 (14) <sup>#</sup>	127 (19)	414 (19)	417 (19)
Number of families for core BD (age in years) [34]	104 (9) <sup>#</sup>	N/A	112 (9) <sup>#</sup>	N/A
Number of families for wedge BD (age in years) [23,24]	181 (14) <sup>#</sup>	125 (19)	N/A	N/A
Number of families for DBH (age in years) [23,24,26]	417 (14) <sup>#</sup>	408 (19)	416 (19) <sup>#</sup>	419 (19)

<sup>#</sup> trait data previously published.

Historic and recently-collected AWV, basic density and diameter at breast height (DBH, 1.3 m) data were analysed (Table 4). A Fakopp<sup>TM</sup> microsecond (single pass) timer was used to assess AWV, with probes located in a northerly position at a height of 0.5 m and 1.7 m. The probes were driven into the wood to a depth of approximately 12 mm below the bark, the upper probe pointing down and the lower probe pointing up in a vertical plane at approximately 45 degrees. Assessment of AWV was undertaken on all families at Florentine and Meunna on one healthy tree per family plot at age 19. At Tarraleah, AWV data were collected on a sample of families felled as part of the sawmilling and peeling studies conducted at ages 13 and 14 respectively [24,25,33]. Trees in this trial were selected on the basis of good stem straightness and minimum/maximum size criteria for sawn timber and veneer processing. At Southport, AWV was assessed on a sample of trees selected to maximise the number of families in common with those sampled at Tarraleah (Table 2). Wherever possible, families were represented by a minimum of four trees sampled across multiple replicates and selected at random within plots, excluding trees with a DBH less than 12 cm.

Basic density was assessed using the water displacement method [34]. At Meunna and Tarraleah basic density was assessed on 12 mm radial wood cores extracted from trees at a height of 0.9 m (core basic density) at age nine years [35] (Table 2). At Tarraleah and Southport, disks approximately 50 mm thick were extracted at a height of 5.8 m from the same trees assessed for AWV at ages 13 and 14 (Tarraleah), and 19 years (Southport) respectively. Wedge sectors of approximately 30 degrees extracted from these disks were used to assess wood basic density (wedge basic density).

Diameter at breast height was assessed on all surviving trees at age 19 years except at Tarraleah, where assessment was undertaken prior to felling at ages 13 and 14 years. The numbers of families

assessed in each trial, for each trait under study are shown in Table 2, and the number of families in common across pairs of trial sites is shown in Table 3.

**Table 3.** Number of families in common between the four *Eucalyptus nitens* progeny trials that were assessed for acoustic wave velocity (AWV), basic density (BD) and diameter at breast height (DBH; 1.3 m).

	Southport	Meunna	Florentine
<u>Tarraleah</u>			
AWV	126	177	180
Core BD		102	
Wedge BD	126		
DBH	409	411	416
<u>Southport</u>			
AWV		124	127
DBH		403	408
<u>Meunna</u>			
AWV			414
DBH			416

## 2.2. Statistical Analyses

To gauge the effect of race-by-site interactions the data were analysed in ASReml [36] to perform univariate restricted maximum likelihood analyses fitting an individual additive genetic model (using a pedigree file where the male parent of the open-pollinated families was treated as unknown, as was the parentage of the base parents) across all four trials:

$$Y = \text{MEAN} + \text{TRIAL} + \text{RACE} + \text{RACE} * \text{TRIAL} + \text{REP}(\text{TRIAL}) + \text{IBLOCK}(\text{REP}) + \text{PLOT}(\text{IBLOCK}) + \text{ADD}(\text{RACE}) + \text{ADD}(\text{RACE}) * \text{TRIAL} + \text{RESIDUAL} \quad (1)$$

where; Y is a vector of trait observations, MEAN is the mean value, TRIAL is the fixed trial effect, RACE is the fixed race effect, RACE\*TRIAL is the fixed race by trial interaction, REP(TRIAL) is the random replicate within trial effect, IBLOCK(REP) is the random incomplete block within replicate effect, PLOT(IBLOCK) is the random plot within incomplete block effect, ADD(RACE) is the random within-race additive genetic effect, ADD(RACE)\*TRIAL is the random within-race additive genetic by trial interaction effect and RESIDUAL is a vector of residuals. The additive relationship matrix was modified using the “!SELF” qualifier in ASReml [36] to take account of an assumed selfing rate of 30% in *E. nitens* open-pollinated families [37]. The PLOT(IBLOCK) term was not fitted for the wood quality traits; standing tree AWV, core basic density and wedge basic density, as only one tree per plot was assessed. The significance of the RACE\*TRIAL term for each trait was gauged with a Wald F-test, where ADD(RACE)\*TRIAL was the error term and the approximate denominator degrees of freedom were computed using the numerical derivatives method [36].

To examine the genetic variation present in traits within sites the following individual additive genetic model was fitted to the data in ASReml [36] to perform univariate restricted maximum likelihood analyses:

$$Y = \text{MEAN} + \text{REP} + \text{RACE} + \text{IBLOCK}(\text{REP}) + \text{PLOT}(\text{IBLOCK}) + \text{ADD}(\text{RACE}) + \text{RESIDUAL} \quad (2)$$

where REP is the fixed replicate effect and all other terms are as previously defined.

The phenotypic variance ( $\sigma_{\text{pheno}}^2$ ) [3], open-pollinated narrow-sense heritability ( $h_{\text{op}}^2$ ) [4], percentage coefficient of additive variation ( $\%CV_{\text{add}}$ ) [5], and a dimensionless measure of evolvability [38] were estimated for each trait from univariate site analyses as follows:

$$\hat{\sigma}_{\text{pheno}}^2 = \hat{\sigma}_{\text{add}}^2 + \hat{\sigma}_{\text{plot}}^2 + \hat{\sigma}_{\text{residual}}^2 \quad (3)$$

$$\hat{h}_{\text{op}}^2 = \frac{\hat{\sigma}_{\text{add}}^2}{\hat{\sigma}_{\text{pheno}}^2} \quad (4)$$

$$\%CV_{\text{add}} = 100 * \frac{\sqrt{\hat{\sigma}_{\text{add}}^2}}{\bar{x}} \quad (5)$$

$$\text{Evolvability} = 100 * \frac{\hat{\sigma}_{\text{add}}^2}{\bar{x} \sqrt{\hat{\sigma}_{\text{pheno}}^2}} = \%CV_{\text{add}} * \hat{h}_{\text{op}} \quad (6)$$

where  $\hat{\sigma}_{\text{add}}^2$  and  $\hat{\sigma}_{\text{residual}}^2$  are the variance components for *ADD(RACE)* and *RESIDUAL* respectively.

The significance of the additive variance from zero for each trait was tested using a “one-tailed” likelihood ratio test [39]. Individual race and overall means were calculated using the “predict” statement in ASReml [36].

Bivariate models, which extended the univariate model and included the same explanatory variables as model [2], were used to estimate pair-wise inter-trait and inter-site additive covariances. Bivariate models were used as there were difficulties with convergence when testing the significance of covariances with a full multivariate model. Levels of incomplete block and plot were considered independent across sites, but within-site bivariate models allowed for covariation between all random effects. Additive genetic correlations ( $r_g$ ) were estimated according to the following equation:

$$r_{g_{12}} = \frac{\sigma_{\text{add}_{12}}}{\sqrt{\sigma_{\text{add}_1}^2 \sigma_{\text{add}_2}^2}} \quad (7)$$

where  $r_{g_{12}}$  is the *ADD(RACE)* correlation between traits 1 and 2,  $\hat{\sigma}_{\text{add}_{12}}$  is the *ADD(RACE)* covariance component between traits 1 and 2, and  $\hat{\sigma}_{\text{add}_1}^2$  and  $\hat{\sigma}_{\text{add}_2}^2$  are the *ADD(RACE)* variances for traits 1 and 2 respectively.

To test for the significance of scale-independent  $G \times E$  [38], additive genetic correlations involving the same trait across different sites were tested against one and zero using a “one-tailed” and “two-tailed” likelihood ratio test respectively [36]. The significance of inter-trait additive genetic correlations within sites were similarly tested, but against zero only.

The equality of inter-trait correlations across sites for each trait was tested with a likelihood ratio test by comparing the log likelihood of a model that constrained intra-site correlation estimates to be equal across sites, using the “!VCC” qualifier in ASReml [36], with that of an unconstrained model, which assumed a difference of three degrees of freedom (four trials) in the case of AWV with DBH

and one degree of freedom (two trials) in the cases of AWV with both core and wedge basic density. To conform with previously outlined bivariate analyses, all fixed and random terms were assumed to be independent across sites in both the constrained and unconstrained models. Inter-trait Pearson's correlation coefficients among phenotypic observations were also estimated.

### 3. Results and Discussion

#### 3.1. Results

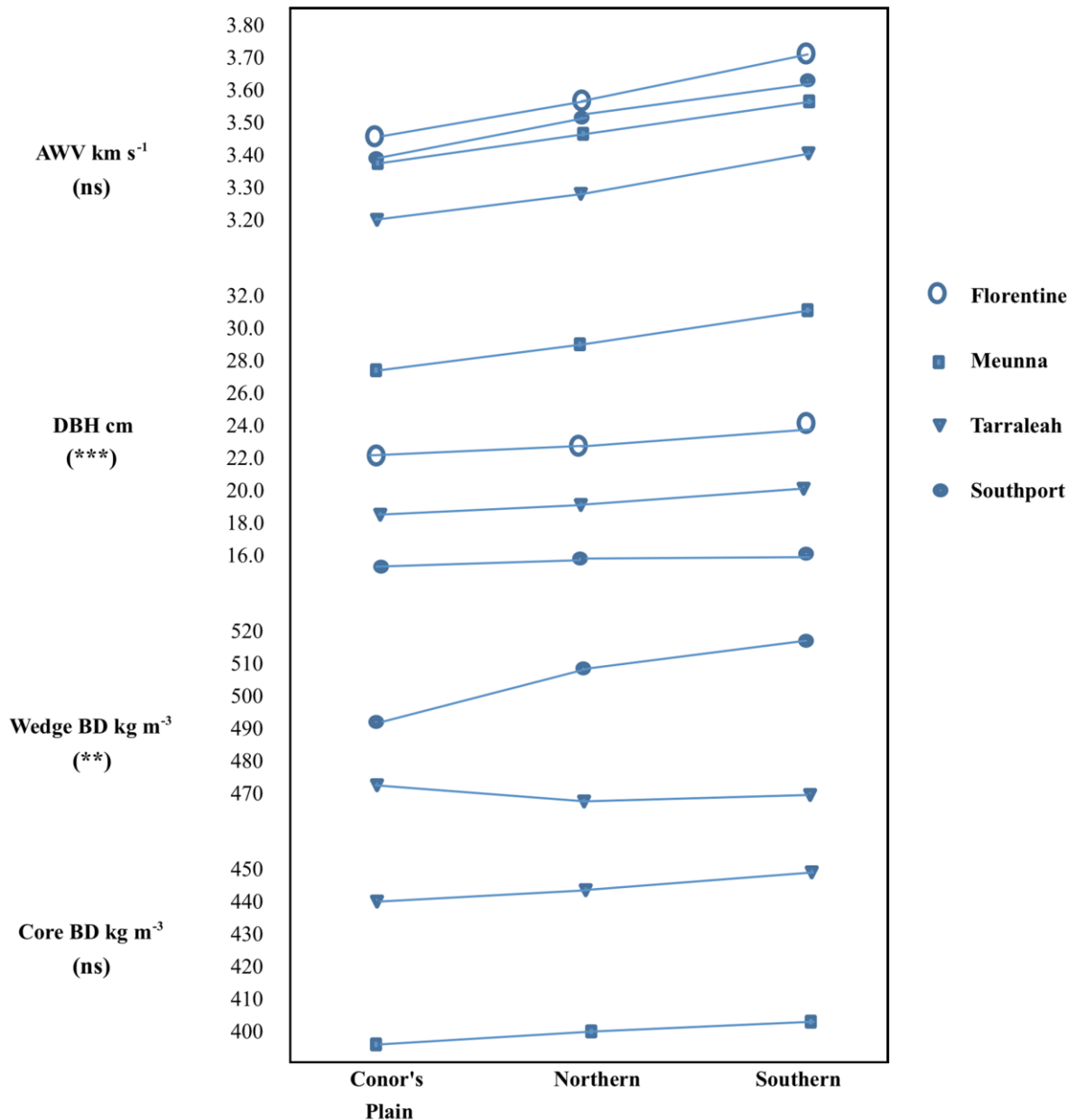
At age 19 there were only minor differences in race means for standing-tree AWV across the Meunna, Southport and Florentine sites (3.43–3.75 km s<sup>-1</sup>; Table 4). Race means at Tarraleah, which was measured at an earlier age (13 and 14 years), were lower (3.25–3.45 km s<sup>-1</sup>). At Tarraleah, the only site where both core and wedge basic density were assessed, basic density in the radial cores was lower than that in the wedge sectors, but this was confounded by age (nine years for cores vs. 13 and 14 for wedge sectors) and by sampling height (0.9 m vs. 5.8 m) differences. The Meunna site, where thinning and pruning had been undertaken, had the largest diameter trees (Table 4). Of the unpruned and unthinned sites, Southport, with a soil developed from a sandstone parent material, was clearly the least productive, although survival at age 19 years was much higher at this site (90%) when compared to Florentine (65%) (Table 2). While survival at Tarraleah at age 14 years (86%) was higher than Florentine (65%) (the other cool moist site) at age 19 years, analysis of earlier measurements showed that at age 14 years the Florentine site had a very similar survival rate (87%) to that of the Tarraleah site.

Significant differences were observed among the races for AWV and DBH at all sites and for wedge basic density at Southport (Table 4). The interaction between site and race was not significant for standing tree AWV or core basic density and, despite a significant interaction ( $p < 0.001$ ), there were no changes in race ranking across sites for DBH (Figure 2). For sites and traits where significant differences were observed among races, the Southern race had the highest values and Connor's Plain the lowest values (Figure 2).

All traits were observed to be under significant within-race additive genetic control (Table 4). Estimated narrow-sense heritabilities were generally moderate to high for standing tree AWV (0.39–0.74), except at Meunna (0.16); low (0.09–0.23) for DBH; and moderate for both core and wedge basic density (0.35–0.43). Estimated coefficients of additive variation (Table 4) were relatively stable across all trials and low for standing tree AWV, core basic density and wedge basic density (2.6%–4.6%), and moderate for DBH (10.0%–14.4%). Similar trends were observed in evolvability: 1.0%–4.1% for AWV, 2.6%–2.9% for basic density and 3.2%–6.1% for DBH.



**Figure 2.** Race means at the four trial sites for acoustic wave velocity (AWV), basic density (BD) and diameter at breast height (DBH; 1.3 m). Some traits were assessed at different ages across sites (see Table 1). The significance of the race by site interaction effect is shown in parenthesis (<sup>ns</sup> not significant, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).



All inter-site additive genetic correlations ( $r_g$ ) involving the same trait were strong (0.61–0.99, Table 5) and positive, and were significantly different from zero ( $p < 0.05$ ). AWV inter-site correlations averaged 0.83, and were not significantly different from one. This compares with an average of 0.80 for DBH, where sample sizes were greater and inter-site correlations were generally significantly different from one. Within sites, estimated additive genetic correlations between standing tree AWV and DBH were significantly different from zero and positive at Florentine and Meunna ( $r_g$  0.71 and 0.51, respectively), but were weak ( $r_g$  0.18 and 0.20, respectively) and not significant at Southport and Tarraleah (Table 6). A two-tailed likelihood ratio test showed the genetic correlations between AWV and DBH were significantly different among sites ( $p = 0.023$ ).

**Table 4.** Estimated race means, significance of the difference among races, within-race additive variance, narrow-sense heritability ( $\hat{h}_{op}^2$ ) and coefficient of additive variance ( $\%C\hat{V}_{add}$ ) and evolvability expressed as a percentage for acoustic wave velocity (AWV), basic density (BD) and diameter at breast height (DBH; 1.3 m) at the four *Eucalyptus nitens* progeny trial sites (standard errors shown in parentheses).

Trait	Site	Age	Southern	Northern	Connor's Plain	Race ( <i>p</i> value)	Additive Variance	$\hat{h}_{op}^2$	$\%C\hat{V}_{add}$	% Evolvability
AWV (km s <sup>-1</sup> )	Florentine	19	3.75 (0.01)	3.60 (0.02)	3.51 (0.03)	***	0.023 (0.005) ***	0.39 (0.09)	4.2	2.6
	Meunna	19	3.62 (0.01)	3.50 (0.01)	3.43 (0.03)	***	0.008 (0.004) *	0.16 (0.08)	2.6	1.0
	Southport	19	3.68 (0.02)	3.57 (0.04)	3.44 (0.06)	***	0.028 (0.008) ***	0.44 (0.13)	4.7	3.1
	Tarraleah	14	3.45 (0.01)	3.31 (0.02)	3.25 (0.04)	***	0.025 (0.004) ***	0.74 (0.11)	4.8	4.1
CoreBD (kg m <sup>-3</sup> )	Meunna	9	407 (2)	404 (3)	400 (5)	ns	352 (110) ***	0.39 (0.12)	4.6	2.9
	Tarraleah	9	454 (2)	450 (3)	446 (5)	ns	382 (113) ***	0.43 (0.12)	4.3	2.8
WedgeBD (kg m <sup>-3</sup> )	Southport	19	521 (3)	513 (5)	496 (9)	*	486 (176) ***	0.35 (0.13)	4.3	2.6
	Tarraleah	14	475 (2)	472 (3)	477 (6)	ns	385 (85) ***	0.40 (0.09)	4.1	2.6
DBH (cm)	Florentine	19	25.6 (0.2)	23.9 (0.2)	22.8 (0.5)	***	6.41 (1.20) ***	0.09 (0.02)	10.5	3.2
	Meunna	19	32.0 (0.2)	29.6 (0.3)	28.3 (0.6)	***	14.72 (2.31) ***	0.23 (0.03)	12.8	6.1
	Southport	19	17.0 (0.2)	16.6 (0.2)	16.4 (0.3)	*	2.78 (0.47) ***	0.11 (0.02)	10.0	3.3
	Tarraleah	14	20.3 (0.2)	19.3 (0.2)	18.8 (0.4)	***	7.89 (0.90) ***	0.18 (0.02)	14.4	6.1

<sup>ns</sup> Not significant, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

**Table 5.** Inter-site additive genetic correlations among the four *Eucalyptus nitens* progeny trial sites for acoustic wave velocity (AWV), basic density (BD) and diameter at breast height (DBH; 1.3 m) (standard errors shown in parentheses). The significance shown is for the test from one. All correlations were highly significantly different from zero ( $p < 0.001$ ) except for the standing tree AWV correlation between Southport and Meunna (0.61), which was not significant at the  $p < 0.05$  level.

Trait	Site	Florentine	Meunna	Southport
AWV (km s <sup>-1</sup> )	Meunna	0.86 (0.26) <sup>ns</sup>		
	Southport	0.87 (0.19) <sup>ns</sup>	0.61 (0.36) <sup>ns</sup>	
	Tarraleah	0.95 (0.13) <sup>ns</sup>	0.68 (0.25) <sup>ns</sup>	0.99 (0.11) <sup>ns</sup>
Core BD (kg m <sup>-3</sup> )	Tarraleah		0.76 (0.18) <sup>ns</sup>	
Wedge BD (kg m <sup>-3</sup> )	Tarraleah			0.70 (0.19) <sup>ns</sup>
DBH (cm)	Meunna	0.79 (0.11) *		
	Southport	0.71 (0.11) **	0.69 (0.10) **	
	Tarraleah	0.93 (0.08) <sup>ns</sup>	0.84 (0.07) **	0.86 (0.08) *

<sup>ns</sup> Not significant, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

As expected, the additive genetic correlation between earlier age core basic density and later age wedge basic density at Tarraleah was strong ( $r_g$  0.99 ± 0.24) and significantly different from zero ( $p < 0.001$ ). Additive genetic correlations between standing tree AWV and basic density were positive ( $r_g$  0.70–0.87) and significantly different from zero ( $p < 0.001$ ), with the exception of Meunna ( $r_g$  0.15) which was not significantly different from zero (Table 6). Furthermore, despite the substantially weaker correlation observed at Meunna, the additive genetic correlations between AWV and basic density were not significantly different across sites. When this correlation was forced to be equal across sites, it was 0.65 (± 0.20) across Meunna and Tarraleah for core basic density and 0.73 (± 0.08) across Tarraleah and Southport for wedge basic density. Additive genetic correlations between DBH and basic density traits were weak and not significantly different from zero ( $r_g$  -0.18–0.15).

### 3.2. Discussion

In this comprehensive study of the genetic control of AWV in eucalypts, we have shown that standing tree AWV in *E. nitens* is under strong genetic control and genetic differences are relatively stable across diverse growing environments at the race and within-race levels. This conclusion is based on the growth of open-pollinated progenies from the Central Victorian races of *E. nitens* grown on sites covering the range of altitudes (120 m to 600 m), over which most plantations of the species are grown on the island of Tasmania [26]. The weakest inter-site additive genetic correlation for AWV was between Southport and Meunna ( $r_g$  0.61). These trials were grown under highly divergent silvicultural regimes, which exacerbated substantial climatic and soil differences between the sites. However, even in this extreme case, the additive genetic correlation across sites was not significantly different from one.

**Table 6.** Inter-trait additive genetic ( $r_g$ ) and phenotypic ( $r_p$ ) correlations among acoustic wave velocity (AWV), basic density (BD) and diameter at breast height (DBH; 1.3 m) within each of the four *Eucalyptus nitens* progeny trial sites (standard errors shown in parentheses). The significance shown is for the test from zero. Trial age in years of each trait assessment is shown as subscripted text.

Site	Trait	AWV (km s <sup>-1</sup> )		DBH (cm)	
		(Meunna <sub>19</sub> Southport <sub>19</sub> Florentine <sub>19</sub> Tarraleah <sub>13,14</sub> )			
		$r_g$	$r_p$	$r_g$	$r_p$
Meunna	Core BD <sub>9</sub> (kg m <sup>-3</sup> )	0.15 (0.35) <sup>ns</sup>	0.24 (0.08) **	-0.18 (0.21) <sup>ns</sup>	-0.02 (0.05) <sup>ns</sup>
	DBH <sub>19</sub> (cm)	0.51 (0.19) **	0.19 (0.03) ***		
Southport	Wedge BD <sub>19</sub> (kg m <sup>-3</sup> )	0.87 (0.17) ***	0.37 (0.04) ***	0.15 (0.23) <sup>ns</sup>	-0.15 (0.05) **
	DBH <sub>19</sub> (cm)	0.18 (0.21) <sup>ns</sup>	0.04 (0.04) <sup>ns</sup>		
Tarraleah	Core BD <sub>9</sub> (kg m <sup>-3</sup> )	0.78 (0.22) **	0.63 (0.23) *	0.12 (0.18) <sup>ns</sup>	0.11 (0.05) *
	Wedge BD <sub>14</sub> (kg m <sup>-3</sup> )	0.70 (0.10) ***	0.23 (0.03) ***	0.24 (0.15) <sup>ns</sup>	-0.04 (0.04) <sup>ns</sup>
	DBH <sub>14</sub> (cm)	0.20 (0.13) <sup>ns</sup>	0.08 (0.03) *		
Florentine	DBH <sub>19</sub> (cm)	0.71 (0.12) ***	0.21 (0.03) ***		

<sup>ns</sup> Not significant, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

For the three sites that were neither pruned nor thinned, the additive genetic correlations for AWW across sites were very strong ( $r_g$  0.87 to 0.99), despite marked differences in site productivity (see DBH in Table 4). Our average additive genetic correlation across sites for standing tree AWW ( $r_g$  0.83) was comparable to that observed for other traits in our study (DBH 0.80 and density 0.73). Our average for DBH was 13% higher than the average of DBH across-site genetic correlation estimates reported in the world-wide literature analyses (106 studies) of Hamilton and Potts [6], which is not surprising given that  $G \times E$  has been tested with a greater diversity of race material across wider environmental ranges in some studies [7].

Where significant  $G \times E$  at the race level was detected it did not usually result in a change in rank order (Figure 2) and in no case was a change in rank observed in a trait where significant differences among races were evident at the aberrant site, suggesting that scale changes are the predominant drivers of  $G \times E$  interaction for the traits studied [17]. Thus rank changes in performance would not be expected if the same genotypes established in these trials were deployed across similar cool-moist and warm-moist climate zones in Tasmania, which represent the majority of the Tasmanian *E. nitens* plantation estate [26]. Notably, the AWW of the Southern race was higher than the other two Central Victorian races across all sites. This is consistent with the Southern race's previously reported superior performance for several traits relevant to veneer [24], as well as solid wood and pulpwood [35] traits.

The genetic stability of AWW rankings across sites (Table 5) bodes well for the use of AWW as a cost effective predictor of MOE in standing trees of *E. nitens*, given that strong genetic correlations between standing tree AWW and static MOE in plywood products has previously been observed at Tarraleah [24,25]. To our knowledge there are no other published studies of  $G \times E$  for AWW in eucalypts, although direct measures of MOE in *Pinus radiata* from two sites in southern NSW; one a cool moist site the other a warmer drier site (mean annual temperatures and rainfall, 10.9 °C, 1270 mm and 12.4 °C, 930 mm respectively) showed no significant  $G \times E$  effect was present [40]. However, the stability of MOE predictions derived from AWW across sites is not well understood [41], and requires further investigation before AWW is more widely adopted as a common selection criterion in *E. nitens* breeding programs.

The lower AWW observed at the Tarraleah site was most likely due to the younger assessment age compared to the other sites, which were of the same age and had similar AWWs. An increase in AWW with age is consistent with previous studies that have found that MOE increases with cambial age [42]. In studies of ten year-old *E. nitens*, Chauhan and Walker [43] found that the MOE of outerwood was significantly greater (about 56%) than the MOE of corewood. This trend was also evident in a study of the closely related species *E. globulus* [44] and other temperate eucalypt species [45], where radial variation in MOE was predicted from studies of micro-fibril angle and density. Basic density has also been shown to increase with cambial age and height in eucalypts [46] and variation in sampling position (5.8 m for the wedges compared with 0.9 m for cores) and sampling age (14 years for wedges and 6 years for cores) is likely to explain the greater density of wedges compared with cores in our study.

The level of genetic control of standing tree AWW (mean  $\hat{h}_{op}^2 = 0.43$ ; Table 4) within races was nearly three-fold higher than that for DBH (0.15). The evolvability of AWW (Table 4) was on average similar to that observed for basic density but slightly lower than that for DBH, indicating that lower

genetic gains would be expected in AWV and basic density than in DBH, assuming a fixed selection intensity applied to a single trait under phenotypic selection. The later-age estimates of narrow-sense heritabilities for standing tree AWV from the Florentine and Southport trial (Table 4) were high and similar to previous estimates for *E. dunnii* (0.42), *E. pilularis* (0.65) [47] and *Pinus radiata* (0.67) [48]. The highest narrow-sense heritability we obtained was from the Tarraleah trial, which was expected because it combined data from two previous studies, which reported high heritabilities, each of which was based on trees from three different replicates of this trial [24,25]. High heritabilities have also been shown in studies of direct and indirect measures of stiffness and strength in *Pinus radiata* [49]. The lower narrow-sense heritability at Meunna, compared to the other three *E. nitens* trials studied is difficult to explain. It is possible that thicker bark on larger stems at Meunna could have increased measurement error and decreased heritability at this site. It is further possible that thinning and pruning at this site reduced the expression of additive genetic variation in AWV [50]. In any case, the very strong inter-site genetic correlations observed for all traits (Table 5) suggests that genetic gains achieved through selection at any one site would, to a large extent, be transferable to environments and silvicultural regimes represented by the other sites [20].

The strong, highly significant and positive additive genetic correlations between standing tree AWV and basic density (assessed using either wedges or cores) observed at the Tarraleah and Southport sites (Table 6), supports the use of standing tree AWV as a selection criterion for the improvement of basic density in *E. nitens*. A strong and positive additive genetic correlation between these traits has also been observed in other species (e.g. 0.57 in *Pinus radiata* [51]). Consistent with the observations for  $G \times E$  and narrow-sense heritability, the main deviant inter-trait additive genetic correlation involving AWV and density in the present study occurred at the thinned and pruned Meunna site where the correlation was close to zero, albeit not significantly different from the strong correlations observed at Tarraleah and Southport. Although positive and significantly different from zero, phenotypic correlations between AWV and basic density in the present study were generally weaker than those observed in *E. dunnii* by Dickson *et al.* [52] (0.67 at age nine years and 0.71 at age 25 years).

The Tarraleah site had the lowest rainfall but was also the coolest site with deep, fertile soil derived from Tertiary basalt, which would contribute to reducing evaporation and improving water holding capacity and therefore the observed good growth. The site of lowest productivity was Southport, with the lowest DBH at age 19 years. This site had the lowest effective rainfall (annual precipitation minus annual evaporation) (Table 1). The soil at Southport, which has poor moisture retention, being derived from Triassic sandstone, may have also contributed to the slower growth there. In studies on *E. nitens* in Chile, the soil type was shown to have a major impact on site productivity [53]. Meunna had the largest diameter trees and had the highest rainfall and temperature on deep, fertile soil derived from Tertiary basalt, although growth would have been substantially increased by thinning at age 4 years. Our study indicates that there is a weak positive additive genetic correlation between AWV and DBH, but suggests that the strength of this favourable relationship is not stable across sites. Other studies in *E. nitens* [24] and *Pinus taeda* [54] have shown no significant genetic correlation between AWV and DBH. The positive genetic correlations of AWV with both basic density and DBH (Table 6) occur despite the absence of a significant correlation between DBH

and density, and indicates that past selection for fast growth and high density in pulpwood breeding programs is unlikely to have adversely affected MOE [24].

#### 4. Conclusions

There is clear potential for the genetic improvement of MOE in *E. nitens* through the exploitation of genetic variation in AWV among and within races. Minimal  $G \times E$  in AWV was evident across four geographically distant and climatically distinct study sites in Tasmania—the ranking of races did not change and within-race additive genetic correlations were strong across sites. Furthermore, heritabilities and coefficients of additive genetic variation were generally high for AWV at these four sites. Of particular note was the higher AWV of the Southern race compared to the other two Central Victorian races, consistent with this race's previously reported superior performance for other veneer, solid-wood and pulpwood traits. Although the strength of the additive genetic relationship between AWV and DBH was not stable across sites, correlations between AWV and both basic density and DBH were favourable at all sites, albeit not significantly different from zero in some cases. This suggests that selection for these traits in pulpwood breeding programs is unlikely to adversely affect MOE.

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#### Author Contributions

David Blackburn coordinated the research project with advice from all co-authors. David Blackburn and Matthew G. Hamilton undertook data collection, performed statistical analyses and wrote the bulk of the text. Dean Williams maintained trials, collected data, and reviewed and commented on successive drafts of the paper. Chris E. Harwood reviewed and commented on successive drafts of the paper. Brad M. Potts provided advice on genetic analyses and assisted in writing.

#### Conflicts of Interest

The authors declare no conflict of interest.

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