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Genetic Parameters and Genotype by Environment Interactions for Green and Basic Density and Stiffness of *Pinus radiata* D. Don Estimated Using Acoustics

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Abstract

Genetic parameters and genotype by environment interactions for wood properties of 13-year-old *Pinus radiata* were determined by sampling two progeny trials on contrasting sites in the southern slopes of New South Wales, Australia. Heritability of green and basic density were determined together with dynamic modulus of elasticity (MOE) measured using TreeTap.

The phenotypic variance in MOE (CV 17–18%) was almost three times that of basic density. MOE and basic density were highly heritable at both sites (h^2 0.57 & 0.79 for MOE & 0.59 and 0.85 for density). There was a

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moderately strong genetic correlation between MOE and basic density (0.64 across-sites). No genotype x environment interaction was detected in MOE or basic density. Basic density and MOE were lower on the warmer, lower rainfall site.

Key words: Pinus radiata, standing tree acoustic tools, dynamic modulus of elasticity, basic density

Introduction

Fifty years of radiata pine (*Pinus radiata* D. Don) breeding has delivered dramatic gains in growth and tree form (JOHNSON, 1991; SHELBOURNE, 1997; MENZIES *et al.,* 2004), but improvements in wood quality have been meagre, partly due to the difficulty of measuring wood properties. The intrinsic properties of radiata pine cause particular problems for timber processors. Whilst radiata pine is a good general purpose softwood (HARRIS, 1991), it has relatively poor stiffness and stability (SORENSSON *et al.,* 1997). Timber stiffness directly influences structural grade recovery and product revenues (TSEHAYE *et al.,* 1995, 2000b; DOWNES *et al.,* 2002) as a certain percentage of logs fail to meet the requirements of machine stress graded timber (WALKER and NAKADA, 1999). For structural timber production, juvenile wood stiffness is now accepted as a key breeding objective (JAYAWICKRAMA *et al.,* 1997; JAYAWICKRAMA, 2001a).

The recent development of acoustic tools has allowed processors to rapidly discern between logs according to stiffness (MATHESON *et al.,* 2002; CARTER *et al.,* 2006). Acoustic tools use sound or stress waves to calculate the dynamic modulus of elasticity (MOE), a measure of stiffness (WANG *et al.,* 2001, 2002; CARTER *et al.,* 2005b; RAYMOND *et al.,* 2007). Resonance tools such as Fibre Gen's (Carter-Holt Harvey) Director HM200 were the first to see routine application in Australia and New Zealand (TSEHAYE *et al.,* 1997; RIDOUTT *et al.,* 1999; DICKSON *et al.,* 2004a). Structural grade recovery can be improved significantly by diverting logs below a certain MOE threshold to other applications (YOUNG, 2002; DICKSON *et al.,* 2004a, b; CARTER *et al.,* 2006), thus avoiding the expense of processing wood that will not meet final specifications (TSEHAYE *et al.,* 2000a; MATHESON *et al.,* 2002). In the near future forest growers may also use acoustic tools to identify high quality wood that will demand a price premium (WU *et al.,* 2004).

Standing tree tools (time of flight, TOF tools) have proven more difficult to develop, and are considered less accurate than resonance tools (ANDREWS, 2002). TOF is typically measured between two accelerometer probes which are hammered into the side of the tree (see WANG *et al.,* 2000). Accuracy problems include variation in the hammer impact, the spacing of probes, signal detection thresholds and unknown density variation (LINDSTRÖM *et al.,* 2002). Standing tree tools only sample a small section of the stem, with the main wavefront passing though the outermost growth rings. Time of flight is sensitive to imperfections such as compression wood (WANG *et al.,* 2002), spiral grain, temperature or moisture content of the wood. Despite these problems, standing tree tools would be of great value for breeding as the potential parent can remain intact (KUMAR *et al.,* 2002). Accuracy problems could also be partly overcome by the development of reliable field procedures, improved tool design and more intensive within-tree sampling.

Dynamic modulus of elasticity (E_d) is calculated from the time of flight using the following equation:

$$E_d = \rho \nu^2 \times 10^{-3} \qquad \text{Equation 1}$$

where ν is the sound velocity (km s^{-1}) and ρ is the density 'as measured' (kg m^{-3}). In practice, for *Pinus radiata* the density of the trees is normally assumed to be a constant at 1000-1100 kg m^{-3} (e.g. GRABIANOWSKI *et al.,* 2004; LASSERRE *et al.,* 2004). Genotypic variation in wood stiffness would be expected but differences may also exist in water use or wood microstructure. These differences would influence green density and could potentially introduce a bias into acoustic measurements on trees. WIELINGA *et al.* (2009) determined that assuming a constant value for green density would introduce a very small error (~3%) into MOE and, given that little variation was found for green density of outer wood (CV of 2.8%), the expense of core sampling and determining actual green density was not warranted.

The potential of standing tree tools as a method of wood quality selection in tree breeding trials has been emphasised (e.g. MATHESON *et al.,* 2002) but there is little published evidence of their success in this application. Standing tree tools have been used for stand level sampling (CARTER *et al.,* 2005a; TOULMIN and RAYMOND, 2007) and in silvicultural trials (CHUANG and WANG, 2001; LASSERRE *et al.,* 2005; WANG *et al.,* 2005). Prior to the current research, only one study has published results for testing on a large number of replicated families (KUMAR *et al.,* 2002; KUMAR, 2004).

In southern New South Wales, radiata pine was typically planted on high altitude ex-native forest sites. However, changing public expectations and reduced land availability have seen a move to ex-pasture and lower rainfall sites (600–800 mm) (WOODS *et al.,* 2001; RAYMOND and ANDERSON, 2005). Growing conditions can affect wood properties both directly (COWN *et al.,* 1991; BEETS *et al.,* 2001) and indirectly through changes in gene expression. This may lead to genotype x environment interaction (G x E) where the relative performance of genotypes changes with growing conditions (FALCONER, 1952). The level of G x E in timber stiffness and many other wood properties has not been tested in Australia (KUMAR, 2004).

This study determines the degree of genetic control for green and basic wood density and G x E for basic density and wood stiffness. The TreeTap, an acoustic tool for standing trees (LASSERRE *et al.,* 2005), was used to sample 37 open-pollinated families in two radiata pine breeding trials with contrasting site characteristics. Fifteen trees per family were sampled at each trial using acoustics and three quarters of these were also cored at 1.3 m to determine outer wood density (outer 5 rings).

Materials and Methods

Study sites

A pair of radiata pine progeny trials in the Tumut region of southern NSW was sampled. The trials were

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planted in June 1993 (COTTERILL, 1993a, b) using a randomised complete block design of 10 replicates with each seedlot represented by a three tree row plot in each replicate. Most of the seedlots were open-pollinated families from second generation selections in three earlier 'International Gene Pool 1973' trials established in NSW at Nundle, Gurnang & Wee Jasper (JOHNSON, 1986). A total of 55 seedlots are represented between the two sites, but not all seedlots were at both sites. A subset of 37 seedlots common to both sites was selected and 15 trees measured with acoustics for each seedlot.

The Green Hills site (35° 28'S 148° 04'E; 830 m above sea level) had previously carried a crop of radiata pine. This site is underlain by granite diorite (Parent Rock Code 9, TURNER *et al.,* 1996), has a mean annual temperature of 10.9 °C and an average rainfall of 1270 mm (Forests NSW, unpublished data). The site is roughly level (0–5° slope) but some soil changes were noticed between replicates. Part of one replicate is underlain by shallow parent rock.

The other site in Carabost State Forest (35° 28'S 147° 51'E, 510 m above sea level) had been rough grazing land. It is underlain by mud/silt stone (Parent Rock Code 5) and as an ex-pasture sites it may have higher levels of available nitrogen due to pasture improvement (MACLAREN, 2002). The site is warmer and drier than Green Hills with a mean annual temperature of 12.4 °C and an average rainfall of 930 mm (Forests NSW, unpublished data). The trial is located on a moderate slope (2–5°) but the landform is relatively constant.

The Carabost site was assessed for growth and form traits in December, 2004, at age 11 years from planting and the Green Hills site was assessed in April-May, 2005, at age 12 years. At that time the survival rate was approximately 90 % at both sites. Wood quality sampling was undertaken in the following summer, during January and February 2006, age 12 years. The diameter at breast height (1.3 m, over bark) (DBH), measured during the 2004/5 assessments, was used in this study.

Standing tree acoustic measurements

TreeTap was designed by Dr. Michael Hayes and Dr. Michael Wang from the School of Engineering, University of Canterbury, in collaboration with Prof. John Walker from the School of Forestry, University of Canterbury. Most standing tree tools have two probes; one that starts the timer when struck, and a second that stops it when the wave is detected. The TreeTap has a third inert starter probe that is struck to initiate the stress-wave. This prevents damage to the sensor probe crystals, and may allow more precise time of flight (TOF) measurements. There are subtle design differences, but measurements are comparable to those found using similar tools (e.g. the FAKOPP®).

The established field methodology for the TreeTap was adopted (HAYES, not dated). The trees were pruned at the time of assessment to height 2.1 m for easy access and the probes were orientated on the northern face of the trees (*Fig. 1*). The top sensor probe (2nd) was set at 2.0 m, the 1st sensor probe was set 1.50 m below the top probe, and the starter probe was set a further 30 cm below the 1st sensor probe. The position of the probes was altered slightly (±100 mm) to avoid knots or other defects, but the distance between the 1st and 2nd sensor probes was measured as accurately as possible (±10 mm). The sensor probes were inserted at 45–55° to the trunk, and the starter probe was inserted at 135–145°. A 'dead blow' hammer was used to insert the sensor probes, and a 200 g steel hammer was used on the starter probe. The steel hammer produces a stress-wave, and the TOF is measured between the 1st and 2nd probes. By striking the starter probe repeatedly eight TOF readings were taken per tree. Readings were stored in the data logger until being downloaded after each day's fieldwork.

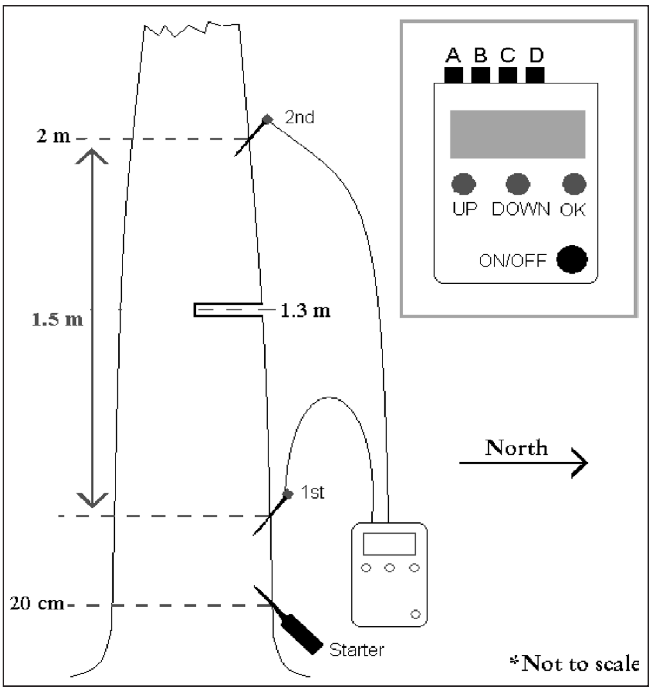

Figure 1. – Positioning of sensor probes and outerwood coring with a close-up of the TreeTap stress-wave timer inset (top-right).

Data were checked after every tree, and again after the data had been downloaded. Dubious readings (greater than 1.5 standard deviations from the mean) were deleted. Mean TOF value for each tree was converted to acoustic velocity and MOE of each tree calculated using a constant green density of 1080 kg m^{-3} which was the mean fresh density measured at the Green Hills trial.

Outerwood cores

Short 12 mm cores were taken at breast height (1.3 m) to determine green and basic density and moisture status of the trees (DOWNES *et al.,* 1997). The majority of the cores were extracted using a motorised corer. However, due to equipment breakdown, 68 cores were extracted using a hand corer. Corer type used for each tree was noted and added as a term in the analyses where applicable. A preliminary experiment demonstrated that, for green density assessment, the samples could be immersed in water and measured reasonably accurately in the laboratory later that day.

Outerwood was defined as the five outside growth rings, not including the earlywood laid down in 2005 (HARRIS and COWN, 1991). Volume for each sample was determined using liquid displacement. Samples were surface dried and weighed green, and then oven-dried at 105 °C until reaching a stable weight (Standards Australia, 1997a; 2000). The cores were removed from the oven in batches of 20–40, and placed into a desiccator to cool before being weighed. Fresh density, basic density, moisture content (MC) and moisture saturation were calculated using equations 2–6 below (HARRIS and COWN, 1991; KININMONTH, 1991).

$$\rho_{fresh} = \frac{Wt_{green}}{V_{green}} \qquad \text{Equation 2}$$

$$\rho_{basic} = \frac{Wt_{oven\ dry}}{V_{green}} \qquad \text{Equation 3}$$

$$MC = \frac{Wt_{green} - Wt_{oven\ dry}}{Wt_{oven-dry}} \times 100 \qquad \text{Equation 4}$$

$$Sat = \frac{MC \times 100}{MC_{\max}} \qquad \text{Equation 5}$$

$$MC_{\max} = \frac{1500 - \rho_{basic}}{1.5 \times \rho_{basic}} \times 100 \qquad \text{Equation 6}$$

where ρ_{fresh} is fresh density, ρ_{basic} is basic density, MC is percent moisture content, Sat is percent moisture saturation, Wt_{green} is sample weight in 'as live' condition, $Wt_{oven\text{-}dry}$ is oven-dried weight, V_{green} is fully swollen volume, MC_{max} is theoretical maximum MC and 1500 kg m^{-3} is density of oven-dry wood cell material

Within trial sampling

On average 15 trees per seedlot were measured with acoustics at each trial. Cores were taken from all the trees tested acoustically at Green Hills. The first 7–8 trees per seedlot tested acoustically at Carabost were cored to obtain independent basic density data. Tree selection rules were used to ensure measurements were representative of final sawlog attributes:

- Only live trees with a DBH greater than 15 cm were measured
- Trees with an excessive lean, sweep, fork or a stem shift below 2 m in height were not measured
- To allow comparisons with DBH, only trees measured during the growth and form assessment were measured (only at Carabost).

A procedure for the sampling of plots was devised to help give a more balanced data set. The first two suitable trees in the plot in the direction of movement up or down the row were measured. If two suitable trees could not be found the plot was skipped. A replacement plot for that seedlot was then measured in the 8th or subsequent replicates where possible. This strategy ensured that plot variances could be estimated, and made sampling within and between seedlots more evenly distributed across the trials.

Data analysis

Preliminary data checking and analyses of variance for each trait were conducted with JMP IN Version 4.0.4 (SAS Institute, 2001). The family analysis employed REML (Residual Maximum Likelihood) mixed linear modelling with GenStat 8th Edition (PAYNE *et al.,* 2005). A within-site genetic model was used to partition genetic (family) and environmental effects (Equation 7).

$$Phenotype = \mu + S(R) + P + F + (\pm corer - type) + error \qquad \text{Equation 7}$$

where μ is the grand mean, S(R) is the replicate effect (fixed), P is the plot effect (random), F is the family effect (random). For some traits corer type was added as a fixed covariate. For some traits the plot term was removed from the model as it contributed little to the analysis (WILLIAMS and MATHESON, 1994).

Narrow-sense heritabilities and genetic correlations at the individual tree level were obtained from equations 8 and 9 respectively. Heritability is simply the estimated resemblance within families (FALCONER and MACKAY, 1996). The narrow-sense heritability includes only additive effects and can be used to predict the response to selection.

$$h^2 = \frac{\sigma_f^2 / \mathrm{r}}{\sigma_f^2 + \sigma_m^2 + \sigma_t^2} \qquad \text{Equation 8}$$

where h^2 is the heritability, r is the coefficient of relationship for half-sib families (i.e. $^1/_4$), σ^2_f is the family variance estimate, σ^2_m is the variance among plots, σ^2_t is the residual variance among trees and the phenotypic variance = $\sigma^2_f + \sigma^2_m + \sigma^2_t$.

$$\mathrm{r}_{Axy} = \frac{\sigma_{xy}^2}{\sqrt{\sigma_x^2 \times \sigma_y^2}} \qquad \text{Equation 9}$$

where r_{Axy} is the genetic correlation between traits (type a), σ^2_x is the family variance of the first trait, σ^2_y is the family variance of the second trait and σ^2_{xy} is the family covariance between the first and second traits.

Approximate standard errors for the heritabilities were obtained following WILLIAMS and MATHESON (1994) using the 'Vfunction' command in GenStat (a Taylor expansion). Approximate standard error estimates for genetic correlations were obtained from equation 10. This equation gives a general indication of the estimate's reliability. The calculation of actual sampling errors was avoided because it is notoriously difficult (FALCONER and MACKAY, 1996).

$$s.e.|\mathrm{r}_{Axy}| = (1 - \mathrm{r}_{Axy}^2)\sqrt{\left(\frac{s.e.|h_x^2| \times s.e.|h_y^2|}{h_x^2 \times h_y^2}\right)} \qquad \text{Equation 10}$$

where: s.e.|r_{Axy}| is the approximate standard error, r_{Axy} is the type a genetic correlation, h^2 is the heritability of traits x and y and s.e.|h^2| is the standard error estimate for the heritability of traits x and y (FALCONER and MACKAY, 1996).

Data from the two sites was then combined using an across-site genetic model (equation 11). This was similar

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to the within-site model except site and family x site interaction terms were added. This allowed a previously ignored source of variation, the G x E interaction, to be estimated. The separation of family x site variance from the family variance improves the accuracy of genetic parameter estimates (WRIGHT, 1976).

$$Phenotype = \mu + S + S(R) + P + F + F \times S + error \qquad \text{Equation 11}$$

where S is the site effect (fixed) and F x S is the family x site interaction (random) (other terms are as for Equation 7). For some traits the family x site term was removed from the model.

If only two sites are involved, G x E can be expressed as a type b genetic correlation (i.e. the same trait at different sites) (FALCONER, 1952). Type b genetic correlations can be used to predict the response that selection at one site will have on the performance at another (FALCONER, 1952). Across-site narrow-sense heritabilities and type b genetic correlations at the individual tree level were obtained from equations 12 and 13 respectively. YAMADA (1962) devised a simpler formula for type b genetic correlations, but equation 13 was chosen as it does not assume equal residual variances between sites.

$$h^2 = \frac{\sigma_f^2 / r}{\sigma_f^2 + \sigma_{fe}^2 + \sigma_m^2 + \sigma_t^2} \qquad \text{Equation 12}$$

where σ^2_{fe} is the estimated family x site variance and the phenotypic variance = $\sigma^2_f + \sigma^2_{fe} + \sigma^2_m + \sigma^2_t$ (other terms are as for Equation 8).

$$r_{Bxy} = \frac{r_{Pxy}}{\sqrt{h^2_{Fx} \times h^2_{Fy}}} \qquad \text{Equation 13}$$

where r_{Bxy} is the type b genetic correlation, r_{Pxy} is the phenotypic correlation between treatment means, h_{Fx}^2 is the family heritability (WRIGHT, 1976) at the first site and h_{Fy}^2 is the family heritability at the second site (BURDON, 1977).

The 'C factor', devised by MATHESON and RAYMOND (1984) as a simple means of gauging the practical implications of G x E interaction, was calculated based on the family, environmental and family x site variance estimates as (Equation 14):

$$C_f = 1 - \frac{\sqrt{\sigma_f^2 + \sigma_e^2 / ns}}{\sqrt{\sigma_f^2 + \sigma_{fs}^2 / s + \sigma_e^2 / ns}} \times 100 \qquad \text{Equation 14}$$

where C_f is the percentage of gain lost between sites (the 'C factor'), σ^2_e is the environmental variance (i.e. $\sigma^2_m + \sigma^2_t$), n is the number of trees per family at each site and s is the number of sites (other terms are as for Equation 12).

Results

After checking the data for potential errors and inconsistencies the distribution of each trait was checked. All traits except fresh density and moisture saturation were approximately normally distributed. Due to a mechanical failure, a hand corer was used on 68 trees in the first 2 replicates at Green Hills. The mean fresh density, MC and moisture saturation of the hand cores were lower than the grand mean so corer type was included as a factor in analysis for these traits.

Overall means and coefficients of variation (*Table 1*) indicated that the mean DBH of the trees sampled for wood quality was higher than the mean of all the trees (DBH(all)). Further, the coefficient of variation was lower for DBH (sampled). This bias was probably due to the tree selection rules used (e.g. DBH > 15 cm). Where possible, DBH (all) was used in further analysis due to the larger sample size.

Means for fresh density, MC and moisture saturation were typically lower than those normally found with destructive sampling of similar age trees (Moreno Chan J. pers. com. 12/1/2006[1]). For example a mean fresh density of 1150 kg m^{-3} or more is expected for outerwood disc sections. This suggests that more moisture was lost

Table 1. – Means and variability in measured traits at Green Hills and Carabost.

	Green Hills				Carabost			
Trait	Mean	N	Std. error	CV	Mean	N	Std. error	CV
DBH (cm) all	19.0	1454	0.103	21.5	19.2	1296	0.077	14.5
DBH (cm) sampled	19.8	549	0.143	16.9	19.9	552	0.093	10.9
Basic density (kg m^{-3})	395	554	1.13	6.76	359	267	1.31	5.96
Fresh density (kg m^{-3}) ²	1080	486	1.37	2.81	—	—	—	—
MC (%) ²	174	486	0.758	9.63	—	—	—	—
Moisture saturation (%) ²	92.5	486	0.171	4.07	—	—	—	—
Acoustic velocity (km s^{-1})	2.72	554	0.011	9.05	2.65	552	0.010	8.64
MOE (GPa)	7.96	554	0.061	18.0	7.63	552	0.056	17.2

² Hand corer trees were excluded to avoid biasing the means and variability of these traits.

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during coring than was replaced by soaking the samples for 2–8 hrs.

Mean DBH was similar at both sites, but the means for basic density and MOE traits were lower at Carabost. DBH and, to a lesser extent, basic density and MOE traits were less variable at Carabost. MOE is effectively the acoustic velocity squared, and therefore has twice the variance of acoustic velocity.

Family based analysis

Corer type was included as a fixed covariate in the within-site models for fresh density, MC, moisture saturation and MOE. Wald tests confirmed that core type effects were significant for these traits ($p < 0.05$). Negative variance estimates were predicted for some traits including: plot variance (σ^2_m) for MC at Green Hills and DBH at Carabost, and family x site variance (σ^2_{fs}) for basic density and MOE in the across-site model. The presence of negative variance estimates is an embarrassment for statisticians (SEARLE *et al.,* 1992) but not entirely surprising given the likely deficiencies in the data. Negative values were generally less than their standard error. Method 4 from SEARLE *et al.* (1992) was chosen as a pragmatic solution to this problem and the relevant term was removed from the model where there was a negative estimate. This approach recognizes a problem with the model, and prevents the other estimates from being distorted (SEARLE *et al.,* 1992).

The heritability of DBH was calculated using only the trees sampled for wood properties, and then including all the trees in the trials. The heritability estimates for DBH (sampled) and DBH (all) were similar at both Green Hills and Carabost (*Table 2*). However, the across-site estimates for DBH differed by $1^1/_2$ standard errors. Further, the across-site estimate for DBH (sampled) sites was less than its standard error. The heritability estimates for DBH (all) are more reliable due to the larger sample size (15 → 27 trees per family), and the diameter bias in the trees that were sampled. The family variance (σ^2_f) estimates for DBH (sampled) had to be used when calculating genetic correlations.

The heritability of all the traits measured at Carabost was higher than at Green Hills. MOE was highly heritable at both sites and across-sites. Fresh density and moisture saturation were not significantly heritable. Basic density was highly heritable at Green Hills and very highly heritable at Carabost. MC was also moderately heritable, and had a very strong genetic correlation with basic density (*Tables 2* and *4*). The across-site heritability of DBH (all) was lower than at either site.

Table 2. – Narrow sense heritabilities at the individual tree level with std. error estimates [in brackets].

	Green Hills		Carabost		Across-sites	
DBH (all)	0.19	[0.06]	0.28[2]	[0.08]	0.14	[0.05]
DBH (sampled)	0.12	[0.10]	0.28[2]	[0.12]	0.02	[0.07]
Basic density	0.59	[0.17]	0.85	[0.29]	0.67[3]	[0.17]
Fresh density	0.11[1]	[0.11]	—	—	—	—
MC	0.53[1][2]	[0.16]	—	—	—	—
Moisture saturation	0.03[1]	[0.09]	—	—	—	—
MOE	0.57	[0.17]	0.79	[0.20]	0.60[3]	[0.15]

[1] Corer type was included as a fixed covariate in the genetic model for these traits.
[2] The plot term was removed from the genetic model for these traits.
[3] The family by site term was removed from the genetic model for the these traits.

Table 3. – Phenotypic pairwise correlation coefficients. Correlations for Green Hills are below the diagonal and those for Carabost are above. Trees sampled with the hand corer were excluded. At Green Hills N = 486 except for correlations with DBH where N = 481. At Carabost N = 552 except for correlations with basic density where N = 267. Probability that correlations are greater than 0: * $p < 0.05$, ** $p < 0.0001$.

	DBH	Basic density	Fresh density	MC	Moisture saturation	MOE
DBH		0.071	—	—	—	- 0.204**
Basic density	0.005		—	—	—	0.272**
Fresh density	0.068	0.409**		—	—	—
MC	0.027	- 0.906**	0.005		—	—
Moisture saturation	0.073	0.075	0.940**	0.342**		—
MOE	- 0.457**	0.268**	0.089*	- 0.261**	- 0.002	

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Table 4. – Genetic correlations between traits with std. error estimates [in brackets]. Correlations for Green Hills are below the diagonal and those for Carabost are above.

	DBH	Basic density	Fresh density	MC	Moisture saturation	MOE
DBH		- 0.52 [1] [0.28]	—	—	—	- 0.56 [1] [0.23]
Basic density	- 0.89 [0.10]		—	—	—	0.71 [0.15]
Fresh density	- 1.05 [bound]	0.78 [0.21]		—	—	—
MC	0.63 [1] [0.30]	- 0.98 [1] [0.01]	- 0.49 [1] [0.41]		—	—
Moisture saturation	- 0.86 [0.39]	0.18 [0.87]	0.75 [0.72]	0.06 [0.92]		—
MOE	- 0.79 [0.19]	0.69 [0.16]	0.25 [0.51]	- 0.73 [0.14]	- 0.31 [0.83]	

[1] The plot term was removed from the genetic model for these traits.

Table 5. – Across-site variance components with std. errors [in brackets], type b genetic correlations (r_{Bxy}) and the 'C factor'.

	σ_p^2	σ_f^2	σ_{fs}^2	r_{Bxy}	C_f (%)
DBH (all)	12.3	0.423 [0.17]	0.224 [0.14]	0.61	8.32
Basic density	651	118 [32.2]	- 16.0 [10.8]	0.95	—
MOE	1.87	0.283 [0.082]	- 0.0041 [0.028]	1.12	—

Across-site heritability estimates for other traits were about halfway between the within-site values.

Genetic and phenotypic correlations between acoustics and other traits

Since fresh density or moisture saturation was not significantly heritable, genetic correlations between these and other traits have no practical meaning. Similarly, the family variance (σ^2_f) estimate for DBH (sampled) at Green Hills was close to zero, and genetic correlations should be interpreted with care. There was no phenotypic correlation between basic density and DBH (*Table 3*), but the genetic correlations were strongly negative (–0.89 and –0.52).

The across-site model was used to obtain more robust estimates of genetic correlations. For this purpose the family x site interaction term was removed from the model. Correlations with DBH (sampled) were not presented because its heritability was effectively zero. The genetic correlation between basic density and MOE was only moderately high (0.64 ± 0.15), indicating a suboptimal correlated response.

The original negative estimates for family x site variance are presented in *Table 5*. Subsequently, the interaction term was dropped from the model for all traits except DBH, effectively making the family x site variance zero. The family x site variance for DBH (all) was around twice its standard error. The level of G x E interaction was interpreted as the deviation from a type b genetic correlation of one. Type b genetic correlations for basic density and MOE were close to or exceeded the theoretical maximum. In contrast, the 'C factor' for DBH (all) was over 8% which represents a considerable loss in genetic gains.

Discussion

No G x E interaction was detected in basic density or MOE. This conforms to the trend that highly heritable traits have low G x E. There have been very few reports of G x E for wood quality traits. Basic density ranked consistently across three sites with 56 families in common from the '268 series' of New Zealand crosses (JAYAWICKRAMA, 2001b). Almost perfect type b correlations were found for basic density and stiffness traits between 2 New Zealand sites (KUMAR, 2004). However, the type b correlation for MOE (Director HM200) was relatively low between an Australian and a New Zealand site (KUMAR, 2004). The two trials in this study are fairly typical of sites where radiata pine is grown in the Tumut region. The genetic gains predicted in MOE should be readily repeatable at least within the area.

The level of G x E in DBH was both statistically and practically significant. The point at which G x E should influence breeding strategies is a matter of individual judgement. MATHESON and RAYMOND (1984) suggested that a C factor above 5% may be cause for concern. The two trials in the study were less than 50 km apart, but

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the interaction was considerable with a type b genetic correlation of 0.61, and an 8% predicted loss in gains. However, from only two sites, any trends in G x E can not be predicted.

Potentially high level of G x E in DBH has been well established elsewhere (e.g. JOHNSON and BURDON, 1990; PEDERICK, 1990; JOHNSON, 1992; ADES and GÉRÉ, 1997; BURDON *et al.,* 1997; JAYAWICKRAMA, 2001b). Within NSW, the potential for soil type to cause G x E was recognised in the breeding strategy written by Johnson in 1989. From the mid 1980's onwards, a policy was implemented of planting progeny and clonal trials across a range of sites to further investigate the potential for site by genotype interactions caused by geology (JOHNSON *et al.,* 2008).

Breeding separate lines for different planting zones can be complex and expensive. So radiata pine breeders have tended to favour 'all round' performers. Genotypes with a high average ranking may not be stable performers. MATHESON and RAYMOND (1984) demonstrated how the level of G x E can be reduced by excluding a few of the most interactive genotypes. However, this strategy will considerably reduce the selection intensity and overall genetic gains (WU and MATHESON, 2005).

Both the accuracy and cost of selection methods need to be considered when evaluating their usefulness (KNOWLES *et al.,* 2004). The objective of this study was not to test the accuracy of the TreeTap, but rather its application to tree breeding. Breeders have been reluctant to use basic density in selection because of the tenuous link to end-product values (MATHESON *et al.,* 1997). Additional traits not only increase the cost of assessment, but there is also a reduction in the gains in each trait (ELDRIDGE *et al.,* 1993). Acoustic testing has been rapidly adopted because of the practical advantages, and the direct link to structural timber recovery rates. The TreeTap measurements took less than half the time per tree (~3 minutes) needed to obtain outerwood basic density (including sample processing). The alternative methods of measuring stiffness are either destructive or much more expensive (e.g. SilviScan-2®) (KNOWLES *et al.,* 2004). A reduction in accuracy when using acoustics will generally be compensated by the lower cost of making measurements (JACQUES *et al.,* 2004). A lower cost allows more genotypes to be screened and better sampling of those genotypes. Ten to 15 trees per family were sufficient to obtain reliable mean estimates.

Fresh density and moisture saturation were not significantly heritable, but the method used may not have detected weak genetic effects. Small errors may have been introduced due to the time of day that the core was taken. Furthermore, plot variance was around a third of the total. Even if fresh density is weakly heritable, any bias in MOE measurements would be small because of the overwhelming importance of acoustic velocity (squared) in the calculation (WIELINGA *et al.,* 2009). SHELBOURNE (1997) had previously reported a high heritability for MC. The high heritability of MC is not surprising given its dependence on basic density.

The other heritability estimates are relativity reliable. The estimate for standing tree MOE (0.60 across-sites) is the most reliable figure available to date. Only 37 families were assessed but replication at two sites makes the estimate more robust. The families tested have diverse genetic backgrounds. A combination of these conditions, plus the recent advances in standing tree methods may explain why the heritability of MOE was 50% higher than in KUMAR (2004).

Across-site heritability estimates for DBH and basic density were close to that normally expected (e.g. JAYAWICKRAMA, 2001b). The across-site estimate for DBH was lower than either of the within-sites values due to the presence of G x E. The heritability of DBH at Green Hills was also close to that normally expected. Heritability estimates for Carabost were relatively high (e.g. DBH 0.28, basic density 0.85). This may be attributed to the lower phenotypic variance particularly in DBH. At Carabost the spacing was more consistent, and there was no interference from pine regeneration or blackberry infestation. The soil type also appeared to change less across the site.

The genetic correlation between DBH and MOE was high (–0.56 ± 0.23 to –0.79 ± 0.19), but needs to be interpreted with care. The number of trees sampled for wood quality was insufficient to obtain reliable family variance estimates for DBH, with the estimate for Green Hills being close to zero. Genetic correlations are notoriously prone to sampling errors and seldom very precise (FALCONER and MACKAY, 1996). Although the estimates for Green Hills are questionable, independent data from Carabost supports the presence of an adverse correlation (WILLIAMS and MATHESON, 1994). A regression analysis involving family means also reinforced this finding ($R^2 = 0.30$). It should be noted that the estimate may differ considerably depending on the genotypes sampled. The genetic correlation may not be as strong within advanced populations where the diameter range has been narrowed (JAYAWICKRAMA, 2001b). KUMAR (2004) reported moderate inverse genetic correlations between DBH and stiffness. A number of independent trials are needed to obtain a reliable value.

Interestingly, basic density was not correlated with DBH at the phenotypic level, but the genetic correlations were strongly negative (–0.52 and –0.89). In addition, the correlation between basic density and MOE was also much stronger at the genetic level. While processing the cores, it was noted that trees with a large diameter often did not have a wide growth increment from 8–12 yrs. At this age, dominant trees would have begun to fully occupy the available growing space. As a result the increment of the outer rings may not be indicative of average growth rate. It is also possible that some trees were in the transition stage between juvenile and mature wood. Mature wood density is more strongly influenced by growing conditions than the juvenile wood (HARRIS and COWN, 1991).

One final interesting result from this study is, although the tree diameters were similar at the two sites, the lower altitude, warmer and drier site produced wood with lower basic density and MOE. This supports other recent results from PORADA *et al.* (2007) and MORENO CHAN (2007) who also found a reduction in den-

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sity and stiffness at Carabost when compared to matched higher altitude, wetter sites. These results differ from those of COWN *et al.* (1991) who found a strong positive relationship between wood density and mean annual temperature in New Zealand. However, within NSW, WILKES (1989) found that higher winter rainfall lead to lower density.

Conclusions

TreeTap acoustic measurements proved to be sufficiently precise for reliable family selection. MOE was highly heritable (0.60 across-sites) and variable (CV ~17%). The high heritability and relatively low cost of assessment would also make the TreeTap well suited to plus-tree selection. However, there was an adverse genetic correlation between MOE and DBH. Fresh density was not significantly heritable or highly variable which validates the use of a constant value. No G x E interaction was detected in MOE, indicating that genetic improvement would be repeatable across a range of conditions. The low the type b genetic correlation for DBH is generally consistent with previous studies on radiata pine.

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