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Genetic improvement of stiffness of radiata pine: synthesis of results from acoustic assessments

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Abstract

The main objectives of this study were to: (i) review results from various published and unpublished studies on genetic parameters of stiffness of *Pinus radiata* D.Don (radiata pine); and (ii) evaluate potential for simultaneous genetic improvement of quantity and quality of structural timber. Standing-tree acoustic velocity data were first converted to average butt-log timber stiffness (Log1MOE), and were used for genetic parameter estimation and genetic gain predictions. Results from a number of different-aged seedlings and clonal trials were summarised.

Average Log1MOE varied from 5.4 to 9.1 GPa with phenotypic coefficients of variation ranging from 11 to 16%. On average, the additive genetic control of Log1MOE in the trials aged 9 – 12 years appeared moderate ($\hat{h}^2 \approx 0.35$). Estimated between-sites genetic correlations generally ranged from 0.60 to 0.90, indicating relatively low genotype-by-environment interaction. Results from trials aged 11 – 15 years indicated that Log1MOE could be increased on average by about 11% when the top 5% of families are selected. This level of improvement would only push the average corewood MOE of the production population to about 7.0 GPa. Indications are that simultaneous genetic gains for MOE and timber volume should not be seriously affected by a negative genetic correlation. A mix of tools, namely genetics, siting, silviculture and segregation, would need to be adopted to maximise quality and quantity of structural grade timber from radiata pine plantations in New Zealand.

Keywords: stiffness; corewood; heritability; genetic parameters; genotype-environment interaction; *Pinus radiata.*

Introduction

Genetic improvement for radiata pine (*Pinus radiata* D.Don) in New Zealand started in the 1950s (Jayawickrama et al., 1997; Burdon, 2004; Burdon et al., 2008) with sustained progress since then. This programme has been shown to deliver large gains, important to the industry, in traits such as diameter, volume, straightness, log quality, wood density, disease resistance and branching habit. In one study, realised gains of 34% were observed in age-17 stem volume from a single generation of breeding (Carson et al., 1999). A major product from wood is sawn timber, largely for light structural purposes. Production of rough-sawn timber in New Zealand, derived from radiata pine plantations, increased from 2.28 million m^3 in 1993 to 4.17 million m^3 in 2007 (MAF, 2007). In Australia, intensive breeding of the species began at a similar time, with important linkages between breeding programmes in the two countries (Burdon, 2004; Burdon et al., 2008).

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Since the inception of New Zealand's radiata pine breeding programme, economic considerations have altered management regimes, with flow-on effects on breeding objectives. Reducing the harvest age of pine plantations (which is done largely to reduce the effective cost of producing wood) increases the proportion of lower-quality corewood in the wood supply. Current log grading rules, as defined in terms of small-end diameter, sweep, length and branch index, are not good predictors of intrinsic timber properties. However, adoption of machine stress grading has led to a greater appreciation of the value of timber stiffness and strength. The processing industry has difficulty in producing products to specification. On the other hand, forest owners are experiencing falling log prices and shrinking margins. Better understanding of the current resource and matching it to the best market opportunities are among various options available to improve value recovery from the current resource.

Increased interest in the genetic improvement of wood properties has resulted from several factors. These include: pressures to counter the adverse impacts of harvesting younger crops, often grown to pruned clearwood regimes at wide tree spacing; a realisation that several properties other than density are important, and can affect stiffness, stability, and appearance; and the availability of new technology to assess a greater range of properties (Jayawickrama, 2001). Several recent studies (Kumar et al., 2002; Kumar, 2004; Dungey & Sorensson, 2006; Baltunis et al., 2007; Wu et al., 2007; Kumar et al., 2008a, b) have explored the feasibility of breeding for non-traditional wood properties (viz. stiffness, reduced internal checking, and reduced resin pockets) in radiata pine.

Because the price-quality response on log price for wood-quality traits such as stiffness is not yet clear, forest growers feel exposed to a risk of uncertain returns if they plant germplasm improved for wood properties (Sorensson, 2008). Nonetheless, the New Zealand Radiata Pine Breeding Company (RPBC), and a number of other New Zealand forestry companies (such as ArborGen Australasia, and Forest Genetics CellFor Limited) are actively pursuing development of radiata pine germplasm with improved wood properties, especially stiffness, as well as improved growth and form (GF). Wood stiffness, measured in terms of its modulus of elasticity (MOE), is the most important property of structural timber. Outerwood stiffness is determined largely by basic density (Harris et al., 1976; Cown et al., 1999; Burdon et al., 2001; Kumar et al., 2006), but corewood stiffness is also influenced strongly by microfibril angle (Cave & Walker, 1994; Walker & Nakada, 1999).

Various direct, indirect and surrogate tests can be used to estimate wood stiffness (Bethge & Mattheck, 1998; Xiping et al., 2000; Jayawickrama, 2001; Kumar et al., 2002; Lindstrom et al., 2002; Matheson et al., 2002). Various studies (e.g. Kumar et al., 2002, 2004; Dungey & Sorensson, 2006; Li et al., 2007; Kumar et al., 2008a, b; Matheson et al., 2008) have advocated the use of non-destructive standing-tree tools for measuring acoustic velocity (a surrogate for timber bending MOE) in large progeny/clonal trials. Such assessments can provide reduced costs and/or greater selection intensities, the latter being strongly conducive to greater genetic gain.

In the New Zealand radiata pine breeding programme, a number of seedling progeny trials and clonal trials have been evaluated non-destructively for understanding the genetics of wood properties and the potential for selecting families or clones that combine improved growth, form and wood properties (Kumar, 2004; Dungey & Sorensson, 2006; Kumar et al., 2008a, b). As different trials were assessed using different tools, one of the main objectives of this study was to convert the existing acoustic data into estimates of timber stiffness (MOE), and re-estimating genetic parameters therefrom. These estimates were then used to predict potential genetic gain in MOE, with regard to site conditions and ages of the various trials, to provide a more general picture of achievable genetic gains. Findings from other genetic studies of stiffness in radiata pine are reviewed briefly in relation to ours. Also addressed briefly is the potential for simultaneous genetic improvement of quantity and quality of structural timber.

Material and Methods

Genetic material

A subset of progeny trials established over the last 30 years has recently been measured for acoustic stiffness (Table 1). Based on the mating design structure and the type of genetic materials used, these trials can be grouped into three categories: Open-pollinated (OP) trials; Female-Tester trials; and Clonal trials.

Open-pollinated trials

Open-pollinated trials of first-generation plus trees from three different selection series, namely '880', '885' and '887', have been measured for acoustic stiffness. Background information on these different selection series can be found in Jayawickrama et al. (1997). Although these trials consisted of a large number of OP families planted at a number of sites, the assessment of acoustic stiffness was carried out in a subset of families at a limited number of sites (Table 1), owing to various practical and financial constraints.

Female-Tester trials

A series of Female-Tester trials were established in 1992 and 1993, where the genotypes under test (the

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TABLE 1: Sites and Genetic Material

Trial	Year planted	Site	Age (y)	Assessment tool	Number of families[c] or clones	Number of trees assessed[d]
'887' series OP	1988	Kinleith	13	HITMAN[a]	72 [e,f]	15
		Paengaroa	15	HITMAN	60 [e,f]	15
'880' series OP	1981	Rotoehu	25	TreeTap[b]	50 [e]	15
	1992	Tarawera	12	TreeTap	18	17
'885' series OP	1987	Kaingaroa Cpt 324	17	TreeTap	82	18
1992 Female-Tester	1992	Kaingaroa Cpt 1276	11	HITMAN	62 [e,g]	20
		Woodhill	12	TreeTap	90	16
		Kinleith	13	TreeTap	110	17
1993 Female-Tester	1993	Warrengong	10	HITMAN	29 [g]	20
			11	TreeTap	63	20
		Esk	13	TreeTap	56 [e,h]	17
1997 GF Clone	1997	Tarawera	9	TreeTap	308 [e,i]	3
		Woodhill	9	TreeTap	325 [e,i]	6

[a] Used on butt logs approximately 5 m long.

[b] Used on standing trees (University of Canterbury, 2008).

[c] Represents the number of OP families or pollen-parent families or clones sampled, depending on the trial.

[d] Represents the number of trees per OP family or offspring per pollen-parent family or number of ramets per clone, depending on the trial.

[e] Families or clones also assessed for wood density.

[f] Reported by Kumar (2004) without velocity data converted to MOE, but including stick-specimen determinations of MOE.

[g] Reported by Kumar (2004) without velocity data converted to MOE.

[h] Reported by Kumar et al. (2008a) without velocity data converted to MOE.

[i] Reported by Kumar et al. (2008a, b) without velocity data converted to MOE.

pollen parents) were crossed with each of the five mid-to-high ranked (based on GF traits) female testers. A subset of pollen-parent families at some selected sites have been assessed for acoustic stiffness (Table 1). The families assessed for acoustic stiffness represented a wide range of GF performance. The number of offspring assessed in each pollen-parent family varied from 16 to 20, with approximately equal representation of each of the five Female-Tester parents.

Clonal trial

A group of 33 full-sib families, involving 33 parents of average-to-high performance for DBH (diameter at breast height (1.4 m)) of various selection series, namely '850' (3 parents), '268' (17 parents), '875' (5 parents) and '880' (8 parents), were used for establishing a clonal test. On average, each parent was involved in two crosses, but this number varied from one to five. Ten clones from each of the 33 full-sib families were chosen for trial establishment in July 1997 at two sites, namely Tarawera and Woodhill. Both Tarawera and Woodhill were ex-forest sites, but their soil types were scoria-ash and coastal sand, respectively.

Field layouts and interconnections

In all of these trials, a sets-in-replicates design with single-tree plots was used, with one seedling (or ramet) per family (or clone) planted in each replicate at each site. Open-pollinated trials of different series ('880', '885' and '887') did not have any common families. Between the two sites of the '880' series OP trial, there were 15 common families. Similarly, 60 families in common were assessed at the two sites of the '887' series. Although the 1992 and 1993 Female-Tester trials were planted at different times, these trials were well connected through the number of common families. The number of common pollen-parent families between various pairs of five sites of Female-Tester trials in this study, varied from 35 (between Esk and Kaingaroa) to 89 (between Kinleith and Woodhill).

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Assessment and data conversion

In the progeny trials that were assessed in the late 1990s and earlier this decade, the HITMAN (Harris & Andrews, 1999) resonance tool was used on butt logs (5 m long). A number of standing-tree tools, including FAKOPP (ALNUS Bt Hungary, 2000), IML Hammer (Instrumenta Mechanik Labor, 2001) and TreeTap™ (University of Canterbury, 2008) have been evaluated in the New Zealand radiata pine breeding programme. Based on the knowledge gained from these tool-evaluation studies, and also for various practical reasons, the NZRPBC is now using TreeTap™ for routine assessment of progeny trials (Table 1). The number of families and trees/family assessed at sites varied (Table 1). In the clonal trial, all available ramets of each clone were assessed for acoustic velocity (using TreeTap™) at Woodhill. At Tarawera, only the three out of six replicates that had relatively high survival and the best growth were assessed (Table 1).

As shown in Table 1, two acoustic tools (HITMAN, used on logs; and TreeTap™, used on standing trees) have been used for assessing stiffness of a wide range of genetic material of different ages at different sites. As different tools vary in terms of how and what they measure, it is difficult to draw general inferences on population characteristics. In order to better understand the within-population variation, it is desirable to convert these various measures of stiffness to some 'common scale'. Some of the data, shown in Table 1, had previously been analysed (Kumar, 2004; Kumar et al., 2008a, b) for understanding genetic parameters of acoustic stiffness.

Earlier, unpublished studies contained proprietary equations to convert HITMAN and TreeTap™ data to average dried-lumber stiffness of the butt log (Log1MOE). These equations only required either HITMAN or TreeTap™ values from each tree. Thus, we used these equations to obtain predicted Log1MOE using the following form:

$$LN(Log1MOE) = \beta_0 + \beta_1 LN(VEL) \quad [1]$$

where LN refers to the natural logarithm, and VEL refers to acoustic velocity measured using HITMAN or TreeTap. Different equations, with separate β_0 and β_1 values, were used to convert the HITMAN and TreeTap values respectively to Log1MOE.

Data analysis

Estimation of within-site parameters

Open-pollinated trials

The following linear model was used for estimation of genetic parameters at each site (set effects being negligible):

$$Phenotype = \mu + R + F + error \quad [2]$$

where μ, R and F represent the general mean and replicate- and family effects, respectively. Replicate was considered as a fixed effect, while family- and error effects were treated as random effects. Restricted maximum likelihood (REML) estimates of genetic and phenotypic variances were obtained through an iterative process in ASREML Software (Gilmour et al., 1997). Estimates of individual-tree narrow-sense heritability (h^2) were obtained from:

$$\hat{h}^2 = 4\hat{\sigma}_f^2 / (\hat{\sigma}_f^2 + \hat{\sigma}_e^2) \quad [3]$$

where σ_f^2 and σ_e^2 are the among-family (or general combining ability, i.e. GCA) and residual (in this case, within-family) variance components, respectively. Approximate standard errors of h^2 estimates were obtained using ASREML Software (Gilmour et al., 1997).

Female-Tester trials

As this experiment consisted of crossing between the male (pollen) and the Female-Tester parents, the following mixed linear model was used for estimation of genetic parameters at each site:

$$Phenotype = \mu + R + T + P + T*P + error \quad [4]$$

where μ, R, T, P and $T*P$ represent the general mean, and effects of replicate, tester parent, pollen parent, and interaction between the tester and the pollen parents, respectively. Replicate was considered as a fixed effect while all other effects were random effects. A pooled estimate of the GCA variance component (σ^2_{gca}) was obtained by pooling the estimates for the tester (T) and the pollen (P) effects, weighting according to the respective degrees of freedom. The variance component for the $T*P$ effect represented specific combining ability (SCA) variance (σ^2_{sca}). Restricted maximum likelihood estimates of variance components were obtained through an iterative process in ASREML Software (Gilmour et al., 1997). Estimates of within-site narrow-sense (h^2) and broad-sense heritability (H^2) were obtained from:

$$\hat{h}^2 = 4\hat{\sigma}^2_{gca} / (2\hat{\sigma}^2_{gca} + \hat{\sigma}^2_{sca} + \hat{\sigma}^2_e) \quad [5]$$

$$\hat{H}^2 = (4\hat{\sigma}^2_{gca} + 4\hat{\sigma}^2_{sca}) / (2\hat{\sigma}^2_{gca} + \hat{\sigma}^2_{sca} + \hat{\sigma}^2_e). \quad [6]$$

Clonal trial

The following mixed linear model was used for partitioning of variance components at each site:

$$Phenotype = \mu + R + M + F + M*F + C(M*F) + error \quad [7]$$

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where μ, R, M, F, M*F and C(M*F) represent the general mean, and effects of replicate, male parent, female parent, interaction of male and female parents, and clones-within-family, respectively. Replicate was considered as a fixed effect while all other effects were random effects. Estimates of GCA variance components for the male and the female effects were $\hat{\sigma}_M^2$ and $\hat{\sigma}_F^2$ respectively, σ_{MF}^2 denotes variance due to interaction among male and female parents, and $\sigma_{C(MF)}^2$ denotes clones-within-family variance; and σ_e^2 here denotes ramets-within-clone variance. Estimates of h^2 and H^2 were obtained from:

$$\hat{h}^2 = 2(\hat{\sigma}_M^2 + \hat{\sigma}_F^2) / (\hat{\sigma}_M^2 + \hat{\sigma}_F^2 + \hat{\sigma}_{MF}^2 + \hat{\sigma}_{C(MF)}^2 + \hat{\sigma}_e^2) \quad [8]$$

$$\hat{H}^2 = \hat{\sigma}_C^2 / (\hat{\sigma}_C^2 + \hat{\sigma}_e^2) \quad [9]$$

where $\hat{\sigma}_C^2 = \hat{\sigma}_M^2 + \hat{\sigma}_F^2 + \hat{\sigma}_{MF}^2 + \hat{\sigma}_{C(MF)}^2$.

Estimation of across-sites parameters

Across-sites analysis was performed for a subset of the sites that had some common genetic entries. For this purpose, the Equations [2], [4] and [7] were expanded to include the effects of site, and its interactions with other genetic effects in the model. Across-sites estimates of heritabilities were calculated by incorporating the additional interaction effects in the denominator of the equations explained above. Estimated of between-sites genetic correlations (r_B) were obtained using the following 'general equation' (from Yamada, 1962):

$$r_B = \hat{\sigma}_f^2 / (\hat{\sigma}_f^2 + \hat{\sigma}_{fs}^2) . \quad [10]$$

The estimated variance components for families and family-by-site interaction respectively ($\hat{\sigma}_f^2$ and $\hat{\sigma}_{fs}^2$) shown in the above equation reflect those of the OP trial. These were replaced with the pooled (from pollen- and tester parents) estimates in case of Female-Tester trials. For the Clonal test, $\hat{\sigma}_C^2$ and $\hat{\sigma}_{CS}^2$ were used in place of $\hat{\sigma}_f^2$ and $\hat{\sigma}_{fs}^2$, respectively in Equation [10]. For the Female-Tester trials, Equation [10] was used to obtain an overall (across five sites) estimate of type-B genetic correlation, but to estimate type-B correlations for all pairs of five sites, we used the approach of Burdon (1977):

$$r_B = \hat{\sigma}_{gca12} / \sqrt{\hat{\sigma}^2_{gca1} \times \hat{\sigma}^2_{gca2}} . \quad [11]$$

The covariance (σ_{gca12}) is estimated directly as the mean cross-product between group (pollen-parent families) means at a pair of sites 1 and 2. Estimates of GCA variance components at the two sites were represented by $\hat{\sigma}_{gca1}^2$ and $\hat{\sigma}_{gca2}^2$ respectively. Pooled estimates (from tester and pollen parents) of GCA variances, as explained above, were used in Equation [11]. ASREML Software (Gilmour et al., 1997) was used for implementing the analysis described above and for estimating genetic parameters.

Prediction of genetic gain

Families or parents performing best in the study regions could be considered for making further crosses and deployment in the respective areas. In this study, where assessment age varied widely, information from existing data was derived. Despite these limitations, predicted genetic gain (Δ_g) in Log1MOE, from family selection at each site, was obtained using the following relationship:

$$\hat{\Delta}_g = 2\, i\, \hat{h}_f^2\, \hat{\sigma}_{\bar{f}} . \quad [12]$$

A selection rate of 5% was assumed (i = 2.063), and estimated half-sib-family-mean heritability ($\hat{h}_f^2$) and estimated phenotypic standard deviation of family means ($\hat{\sigma}_{\bar{f}}$) from each site were used for predicting gain. An estimate of h_f^2 was obtained following Falconer & Mackay (1996, page 234). The factor of 2 was used in Equation [12] in order to take account of selection of pollen parents as well as seed parents. Genetic gains from selection on clonal values were predicted from:

$$\hat{\Delta}_g = i\, \hat{H}_C^2\, \hat{\sigma}_{\bar{C}} . \quad [13]$$

A selection rate of 5% was assumed (i = 2.063), and estimated clonal-mean heritability ($\hat{H}_{\bar{C}}^2 = \hat{\sigma}_C^2 / (\hat{\sigma}_C^2 + \hat{\sigma}_e^2 / r)$) where r is the number of ramets per clone, and estimated phenotypic standard deviation of clonal means ($\hat{\sigma}_{\bar{C}}$) from each of the two sites of clonal test, were used for predicting gain.

Best Linear Unbiased Prediction (BLUP) of breeding values (BVs) of seed parents (for OP trials), pollen parents (for Female-Tester trials), and clonal genetic values (GCVs) of clones (in the clonal trial), obtained externally from previous analyses (e.g. RPBC BVs Database; Kumar et al., 2008b), were used to investigate the relationship between MOE and DBH and to evaluate the feasibility of selecting genotypes for both traits.

Results and Discussion

Basic statistics

The site means for Log1MOE, along with coefficients of variation (CVs), are shown in Table 2. The average Log1MOE varied from about 5.4 GPa (at Warrengong) to about 9.1 GPa (at Rotoehu). Since the site-, age-, and genetic effects are confounded, it would be difficult

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TABLE 2: Means and tree-to-tree coefficients of variation (CV) of Log1MOE at different sites.

Trial	Site	Approx. Latitude (S)	Altitude (m)	Age (y)	Log1MOE[a] (GPa)	CV (%)
'887' series OP	Kinleith	38° 30'	370	13	5.55	14.4
	Paengaroa	37° 45'	60	15	6.76	12.3
'880' series OP	Rotoehu	38° 00'	260	25	9.07	6.7
	Tarawera	38° 00'	95	12	7.94	9.2
'885' series OP	Kaingaroa Cpt 324	38° 30'	570	17	7.90	9.9
1992 Female-Tester	Kaingaroa Cpt 1276	38° 15'	450	11	5.72	14.5
	Woodhill	36° 45'	15	12	6.92	11.2
	Kinleith	38° 15'	330	13	6.81	13.0
1993 Female-Tester	Warrengong	33° 21'	900	11	5.39	16.0
	Esk	39° 15'	425	13	6.45	12.8
1997 GF Clone	Tarawera	38° 00'	*ca.* 50	9	5.63	10.8
	Woodhill	36° 45'	15	9	6.41	9.4

[a] Obtained using Equation [1] with separate coefficients for HITMAN and TreeTap™.

to generalise these results. The CVs were generally in the 9 – 14% range. The highest CV was observed at Warrengong. This could partly be due to the fact that different measuring equipment was used on different sets of families and at different ages at this site. If only the sites in a similar age-group (i.e. 9 – 13 years) are compared, the average Log1MOE at Warrengong is the lowest, which could be due to colder climate and consequent slow rate of stand development on this site.

At Rotoehu, based on age-25 assessment, the average MOE of the boards from the butt log would be about 9 GPa. This can be compared with unpublished results from Wood Quality Initiative (WQI) studies, subject to two reservations: (1) that altitudes of stands were not stated in those studies; and (2) that the bases on which the figures obtained were not identical throughout. The reported average butt-log timber MOE values from age-25 trees were 6.29, 7.28 and 8.15 GPa in Mawhera Forest, Cpt 70, near Greymouth (approx. Lat. 42° 30' S), in Golden Downs Forest (approx. Lat. 41° 30' S) and in Kaingaroa Forest (approx. Lat. 38° 30' S), respectively; these values indicate effects of site in line with general expectations. The genetic material at Golden Downs and Kaingaroa was GF14 (Gwavas OP Seed Orchard), but the genetic identity of the material near Greymouth was not known. The relatively higher MOE at Rotoehu in our study could be due to a combination of both genetics ('880'-series parents were selected for both high density and DBH) and site (near-coastal site). The phenotypic CVs for Log1MOE in this study are lower than those reported (about 25%) for small clear specimens (Burdon et al., 2001; Kumar, 2004). However, some unpublished utilisation studies where the actual average MOE of timber from the butt logs was obtained, suggested CVs in the range of 11 – 16%, which is somewhat similar to those observed in this study.

Genetic parameters

Family (OP or pollen-parent) and clonal differences were highly significant ($p < 0.001$) at all sites, except at Kinleith ($p < 0.05$) as suggested by the likelihood ratio test. Estimated narrow-sense (h^2) and broad-sense (H^2) heritabilities are shown in Table 3. A wide range (0.08 – 0.73) of $\hat{h}^2$ was observed for inferred Log1MOE at different sites. Approximate standard errors of $\hat{h}^2$ varied from about 0.04 (for Female-Tester trial at Kinleith) to 0.17 (for '880' series trial at Tarawera). Our results suggested that, on average, the genetic control of butt-log MOE in the trials aged 9 – 12 could be regarded as moderate ($h^2 \approx 0.35$). The information from the Female-Tester trials and the clonal trial provided an opportunity to estimate H^2. The estimated H^2 was higher than estimated h^2 at all sites except Kinleith (Table 3). Overall, heritability estimates from data converted to MOE agreed well but not exactly with those reported previously (Kumar, 2004; Kumar et al., 2008a, b) using unconverted acoustic data from some of these sites.

The ratio (%) of estimated non-additive variance to the additive variance varied from zero (at Kinleith) to about 60% (at Woodhill and Tarawera) with an average of 36%, which is about twice of that reported by Matheson et al. (2008). Dungey and Sorensson (2006) obtained an even higher ratio (compared to our study) for acoustic velocity, which could partly be due to the small number (19) of full-sib families in their

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TABLE 3: Estimates of within-site narrow-sense heritability (h^2) of Log1MOE. Estimates of broad-sense heritability (H^2), if estimable, are also shown along with their approximate standard errors (in parentheses).

Trial	Site	Age (y)	$\hat{h}^2$	$\hat{H}^2$
'887' series OP	Kinleith	13	0.19 (0.07)	-
	Paengaroa	15	0.33 (0.10)	-
'880' series OP	Rotoehu	25	0.55 (0.14)	-
	Tarawera	12	0.29 (0.17)	-
'885' series OP	Kaingaroa Cpt 324	17	0.73 (0.12)	-
1992 Female-Tester	Kaingaroa Cpt 1276	11	0.64 (0.12)	0.85 (0.14)
	Woodhill	12	0.36 (0.08)	0.58 (0.10)
	Kinleith	13	0.08 (0.04)	0.08 (0.04)
1993 Female-Tester	Warrengong	11	0.31 (0.07)	0.43 (0.08)
	Esk	13	0.37 (0.10)	0.42 (0.13)
1997 GF Clone	Tarawera	9	0.33 (0.12)	0.53 (0.04)
	Woodhill	9	0.39 (0.13)	0.57 (0.03)

study. Nonetheless, these results suggested that the non-additive genetic component could also be playing a role in the expression of MOE, and thus different deployment strategies could be used to capture this genetic variation.

Because no families were common to all the trial series, estimated between-sites genetic correlations (r_B) were obtained separately for the '880' series (two sites), '887' series (two sites) and Female-Tester trials (five sites). For inferred Log1MOE, r_B values were 0.43, 0.91, and 0.60 for the '880' series, '887' series, and Female-Tester trials, respectively. A relatively low r_B (0.43) between the two sites of the '880' series could be due to various factors, including very different age of assessment, and a very small number (15) of common families. Estimated across-sites h^2 of Log1MOE was 0.24, 0.20 and 0.19 for the '887' series, '880' series OP trials, and Female-Tester trials, respectively. Poor between-site genetic correlation for the '880' series trial and Female-Tester trials would be the main reason for across-sites estimated h^2 being considerably lower than within-site estimates. Among the Female-Tester trial sites, Kinleith surprisingly showed (Table 4) very imperfect r_B with other sites, but no convincing explanation could be found.

Genetic gain in corewood stiffness

One of the aims of this project was to investigate the potential for making genetic selections to improve corewood stiffness. The results presented in Table 3 regarding the genetic control clearly suggested potential to select families for this trait. The next question is how much improvement could be made in different forest-growing regions? As stiffness and its CV appeared to be influenced by site (Table 2), the level of required genetic improvement could be different for different regions.

Results shown in Table 5 suggested that there is a reasonable potential for increasing corewood stiffness. Using information from trials aged 11 – 15 years indicated that Log1MOE could be increased on average by about 11% when the top 5% of families are selected (Table 5). The average corewood MOE of

TABLE 4: Estimated genetic correlations (r_B) for Log1 MOE between pairs of sites, along with the number of common pollen-parent families and approximate standard errors (in parentheses), of Female-Tester trials.

	Esk	Warrengong	Woodhill	Kinleith
Kaingaroa	0.86 (35; 0.04)	0.92 (51; 0.02)	0.72 (46; 0.07)	0.72 (61; 0.10)
Esk		> 1.0 (53; n/a)	0.86 (51; 0.04)	0.48 (56; 0.20)
Warrengong			0.89 (56; 0.03)	0.71 (74; 0.12)
Woodhill				0.57 (89; 0.16)

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TABLE 5: Predicted genetic gain in Log1MOE at different sites. A selection rate of 5% (i = 2.063) was assumed. Equation [13] was used for the clonal trial, and Equation [12] for all other sites.

Trial	Site	Age (y)	$\hat{h}^2_{\bar{f}}$	Phenotypic SD (σ_f)	Site mean (GPa)	Gain (% of site mean)
'887' series OP	Kinleith	13	0.44	0.25	5.55	8.2
	Paengaroa	15	0.59	0.30	6.76	10.8
'880' series OP	Rotoehu	25	0.70	0.26	9.07	8.3
	Tarawera	12	0.59	0.25	7.94	7.7
'885' series OP	Kaingaroa	17	0.80	0.37	7.90	15.5
1992 Female-Tester	Kaingaroa	11	0.84	0.38	5.72	23.0
	Woodhill	12	0.63	0.28	6.92	10.5
	Kinleith	13	0.28	0.24	6.81	4.1
1993 Female-Tester	Warrengong	11	0.65	0.25	5.39	12.4
	Esk	13	0.66	0.32	6.45	13.5
1997 GF Clone	Tarawera	9	0.78*	0.55	5.63	15.7
	Woodhill	9	0.89*	0.60	6.41	17.2

* Indicates repeatability of clonal mean, $\hat{H}^2_{\bar{c}}$.

the current breeding germplasm appears to be about 6.30 GPa. A predicted improvement of about 11% from family selection would only push the average corewood MOE of the production population to about 7.0 GPa, which is short of the declared target of 8.0 GPa. Clonal selection appears to provide relatively higher genetic gain (about 16%) at the studied sites.

As discussed earlier, the average corewood MOE of New Zealand radiata pine timber appears to be about 6.3 GPa, which increases up to about 8 – 10 GPa in the outerwood. The factors contributing to generally higher outerwood MOE (compared to corewood) include low microfibril angle (MFA) and high wood density. It could be argued that the added cost of increasing MOE through selection might not be worthwhile. However, it is desirable to improve both corewood- and outerwood MOE, particularly for trees planted at farm sites and various sites in the South Island of New Zealand. Selection for corewood MOE for increasing outerwood MOE would require reasonably high age-age genetic correlations.

To maximise gain in corewood, selection for MOE at age 6 – 7 years would be most effective (Dungey & Sorensson, 2006), but selection at this age might not maximise gain in the outerwood MOE (Kumar et al., 2006). Studies on age-age genetic correlations have given mixed results. For instance, estimated genetic correlations of area-weighted MOE of breast-height rings 3 – 5 with rings 6 – 10, 11 – 15, 16 – 20, and 21 – 25 were 0.90, 0.89, 0.80 and 0.26 respectively (Kumar et al., 2006). Using 30 open-pollinated families with six trees per family, an Australian study (Wu et al., 2007) reported a genetic correlation of about 0.36 between rings 1 – 5 and rings 1 – 31 area-weighted-MOE. In some recent unpublished New Zealand studies (S. Kumar et al., Scion, New Zealand), genetic correlation estimates between early age (rings 5 – 7) and later age (20 – 25 years) MOE were found to be about 0.50. Although the sample sizes in all of these studies were small (50 or less families), they all suggest very imperfect corewood-outerwood genetic correlation for MOE.

Acoustic velocity data apply to outerwood at the age and height of assessment. While genetic correlations with outerwood values may be imperfect, assessments on young trees have a two-fold advantage. Firstly, early assessment helps increase genetic gain per generation; secondly, the gain in stiffness from selecting for MOE *per se* is likely to be more critical.

Genetic correlations between corewood- and outerwood- density have been reported to be very high (e.g. Cown et al., 1992; Kumar & Lee, 2002; Li & Wu, 2005), and density is also the major factor influencing MOE in the outerwood (Cown et al., 1999). If there is to be additional emphasis on improving both outerwood MOE as well as corewood MOE, then family selection based on density and acoustic MOE, assessed at age 6 – 7 years, would be a good option (Kumar et al., 2006). However, as discussed earlier, although outerwood gains may be useful, the gain from genetic improvement of corewood alone will not substantially improve the production of high-quality radiata pine corewood for structural uses.

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Simultaneous improvement of volume and stiffness

In order to maximise profit from commercial plantations, forest growers would like to plant 'improved germplasm' aimed at increasing both quality and quantity of wood and timber (Sorensson, 2008). A number of recent studies (Kumar et al., 2002; Kumar, 2004; Baltunis et al., 2007; Kumar et al., 2008a, b; Matheson et al., 2008) have reported a negative genetic correlation (about -0.35) between DBH and MOE, which suggests that simultaneous selection for both DBH and MOE could yield even less gain in MOE compared to that from selection for MOE alone (e.g. Table 5). The RPBC recently conducted a large-scale genetic evaluation for a number of traits including DBH and MOE. Although there are more than 2000 selections for which breeding values have been estimated for growth and form traits, there are only about 500 parents with MOE breeding values available. This is largely due to the higher assessment costs of various wood properties.

The parental BVs extracted from the RPBC breeding-value database, for DBH and MOE are plotted in Figure 1. The assessment age for MOE varied between 11 and 17 years, while DBH was assessed at around age 8. As the parents assessed for MOE were generally superior for growth, their DBH BVs tend to exceed the candidate-population mean (Figure 1). Nonetheless, these results show that there are a number of parents which are top-ranked for MOE and still have above-average BVs for DBH. This indicates that simultaneous improvement of growth and MOE is feasible, although the achievable gain would be lower (especially for DBH) compared to selection for either trait singly.

The across-sites clonal genetic values (CGVs) previously estimated (Kumar et al., 2008b) from age-9 data from the two sites (Tarawera and Woodhill) are shown in Figure 2. Results suggested that clones with very high growth rate largely had lower CGV for MOE. Similarly, clones that were ranked high for MOE appeared to be relatively slow growers (Figure 2). These results follow similar trends observed in progeny trials (Figure 1) and suggest some attractive potential for genetic improvement of MOE. Deployment of the top-ranked clone for MOE would yield 26% gain in MOE and about 2.5% gain in DBH. A mix of five particular clones from those tested here could yield 16% and 4% gain in MOE and DBH, respectively.

It is important to note that the observed correlation between DBH and MOE breeding values are considerably different between Figures 1 and 2. Apart from different age of assessments, the varying precision of predicted BLUP values would also affect the reliability of these correlations. Nonetheless, the possibility of identifying 'correlation breakers' was clearly evident from these results. Cown & Sorensson (2008), using data from an age-12 clonal trial, highlighted the possibility of selecting clones with superior growth and wood density. These authors argued that clones would create more value for forest growers because of higher uniformity compared to seedling seedlots.

Achieving simultaneous improvement for traits involved in adverse genetic correlations is always a challenge for tree breeders. The classic adverse genetic correlation involves wood density and stem diameter/volume. The concept of breed differentiation

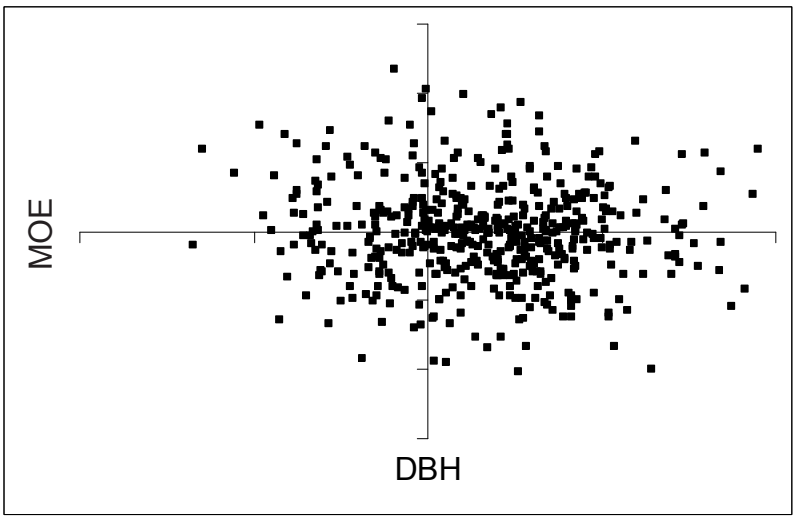

FIGURE 1: Correlation (*r*) between BLUP parental breeding values (BVs)for DBH and predicted MOE. N = 500, *r* = -0.07. DBH was assessed at around age 8 years, while age for MOE assessment varied between 11 and 17 years. Vertical line denotes mean for all candidates assessed for DBH.

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to address adverse genetic correlation between growth and various wood properties has been around for some time. Variables to be taken into account in composing and deploying breeds, seedlots or clonal portfolios will depend not only on site and choice of silvicultural options; they will also depend upon target markets, especially structural versus appearance grades. As part of the New Zealand radiata pine breeding strategy, a High Wood Density (HD) elite population was formed with an aim of selecting genotypes (dubbed as 'correlation breakers') with high wood density and acceptable growth (Jayawickrama & Carson, 2001). Using age-8 DBH and density data from a HD cloned elite population, Kumar et al. (2008b) reported a near-zero estimated genotypic correlation between DBH and density. The latter suggested that a breeding goal involving adversely correlated traits could be achieved by forming an appropriate elite breeding population alongside the underpinning 'Main' breeding population. Modulus of elasticity was not considered as a selection trait in the formation of the HD elite, and the genetic relationship between DBH and MOE in this population was not very different from that in a 'Growth and Form' elite population (Kumar et al., 2008b).

Non-genetic factors

In addition to genetic quality of deployment material, non-genetic factors (e.g. site and silviculture) could have large influences on the quality of the timber. As seen from Table 1, the average MOE could vary by as much as 1.0 GPa between sites for a given age. It suggests that it would be easier at some sites than others to grow forest resources that could meet certain thresholds for stiffness. Silvicultural factors (e.g. stocking and pruning) could have a big influence on the quality of timber. Mason (2008) reported a significant influence of stocking density on acoustic velocity, whereby acoustic velocity tended to be higher with higher stocking densities. Increasing initial stocking density of radiata pine plantings from 833 to 2500 stems/ha raised green dynamic MOE of corewood from 5.0 to 6.7 GPa as measured with a sonic velocity tester (Lasserre et al., 2005), but such practice could compromise overall grade recovery. Another silvicultural variable, extending the rotation length, would certainly have a big impact on MOE but would not be popular with forest owners and managers because of added production cost. However, extending the rotation length could have advantages for carbon sequestration partly because of increased biomass, and thus the added costs may be less important at the forest-estate level than at the stand level.

Some studies (e.g. Cown et al., 1987) suggested that knot size is a major determinant for board degrade in sawmills. Although knot size (or branch index) could be considered as a potential genetic selection trait, unpublished and published data (e.g. Wu et al., 2008) have shown poor genetic control of this trait. Instead, optimisation of silvicultural practices (e.g stocking density and/or pruning regimes) would be better options to deal with knot size. A useful alternative could be indirect genetic selection based on branch cluster frequency. It is important to note that there could be considerable variation in the optimal branch-habit requirement for each of the various timber-grade categories. An ideal approach would be to combine genetics, site characteristics and silviculture practices to maximise wood quality.

For any given combination of genetics, site and silviculture, there would be a large tree-to-tree variation for stiffness in any given stand. As end-users (processors) of logs seek to maintain and improve

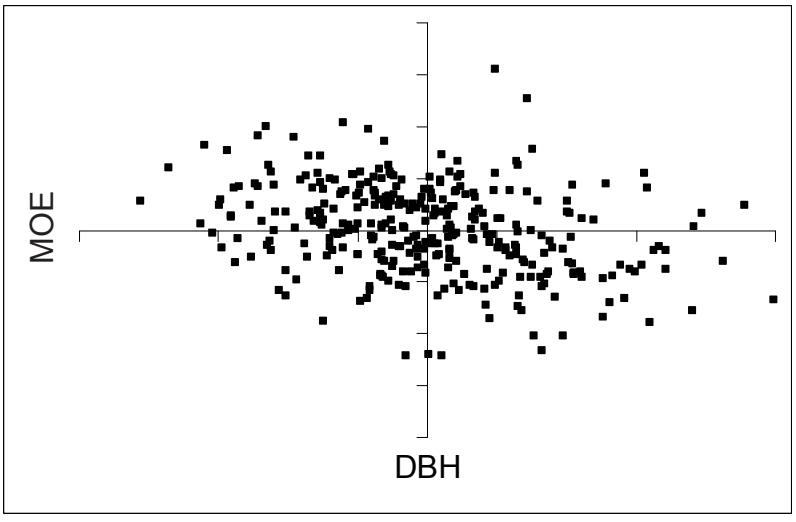

FIGURE 2: Correlation (*r*) between BLUP clonal genetic values (CGVs) for DBH and predicted MOE. N = 325, *r* = -0.32. DBH and MOE were assessed at ages 7 and 9 years respectively. Vertical line denotes mean for all candidates assessed for DBH.

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profitability of domestic processing there is continual pressure on log suppliers to segregate logs according to the external dimensions and characteristics that best align with the products and markets of the end-user. The use of acoustic segregation of radiata pine logs for structural board production has been recommended in New Zealand (Tsehaye et al., 2000) and Australia (Dickson et al., 2004). Acoustic velocity is expected to be also a practical non-destructive method for identifying wood prone to longitudinal shrinkage. Recently published (e.g. Gapare et al., 2009) and unpublished studies (e.g. Kumar et al. Scion New Zealand) showed a moderate favourable genetic correlation between standing-tree acoustic velocity and longitudinal shrinkage predicted using Near Infra-Red Spectroscopy.

Conclusions

Large tree-to-tree variation along with moderate heritability indicated an opportunity for improving corewood stiffness by genetic selection. Since the site and age effects were confounded, it was not feasible to study across-site patterns in order to identify breeding targets for different sites. The average estimated corewood MOE of the current germplasm was 6.30 GPa. A predicted improvement of about 11% from family selection would only increase this to 7.0 GPa in the production population, which is still lower than the declared target of 8.0 GPa. However, formation of a cloned elite population and exploiting large within-family variation could provide a set of forwards selections that could better meet the required threshold for the seed-orchard parents. Alternatively, clonal selection coupled with favourable site selection for deployment appears to be a credible solution as well. A mix of genetics, site, silviculture and segregation tools would need to be adopted to maximise quality and quantity of structural-grade timber from radiata pine plantations in New Zealand.

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