

# Genetic control of very early compression and opposite wood in *Pinus radiata* and its implications for selection

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Received: 27 July 2010 / Revised: 22 November 2010 / Accepted: 1 December 2010  
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**Abstract** The long time frame for evaluating selection candidates is a major barrier to the deployment of genetic gain from tree breeding programs. This situation is compounded in wood quality studies by constraints on the number of sampled individuals when trees are older and larger. This paper documents the degree of genetic control and genetic association for wood quality traits in 18-month-old leaning *Pinus radiata* seedlings. Trees were separately assessed for basic density, green and dry acoustic velocity, and longitudinal and volumetric shrinkage in opposite and compression wood. Heritability estimates were low to moderate for both compression and opposite wood (ranging from 0.15 to 0.38). Estimated genetic correlations were very high in opposite wood, where green velocity displayed the highest correlations with both longitudinal (−0.89) and volumetric (−0.64) shrinkage, closely followed by dry velocity. These correlations were substantially lower for compression wood. The estimated correlations between compression and opposite wood characteristics were high for most traits except for longitudinal shrinkage. We suggest how these results could be used for very early screening for wood stiffness and dimensional stability. We propose that information on early genetic control of wood quality and the methodologies used to elicit it should be integrated in breeding and deployment programs.

**Keywords** Wood quality · Early selection · Compression wood · Radiata pine · Bayesian models

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Communicated by R. Burdon

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## Introduction

Generation interval is the time needed to produce a new generation in a breeding program. One of the most important contributors to the length of that interval is genetic evaluation, which often extends from one quarter to one third of the rotation (see, for example, White et al. 2007 p. 519). The rationale behind using juvenile selection criteria is to shorten the length of progeny testing necessary to maximize genetic gain per unit of time.

Breeding programs rely on different forms of indirect selection, ranging from simple mass selection to more complex systems like multivariate best linear unbiased prediction (BLUP). As an illustration, genetic gain from juvenile mass selection could be estimated using Searle's equation (1965), which uses the heritabilities at early age and rotation age, together with the genetic correlations between assessments. Provided good estimates of genetic parameters were available, breeders could calculate the response to selection at any time and divide it by the time required to achieve it. The optimal testing time corresponds to the maximum response per year or, better, to the time that maximizes net present value for the breeding program (Newman and Williams 1991). A similar procedure can be followed with other early selection techniques.

Targeting correlated response at rotation age makes sense, and it has been successfully applied, for traits that relate to wood *quantity* (production volume). However, with wood *quality* breeders may not need to target rotation age, potentially reducing testing time. Solid-wood recovery and value are heavily influenced by wood stiffness and dimensional stability, and both characteristics have been included in breeding objectives (e.g., Shelbourne et al. 1997; Greaves 1999; Ivković et al. 2006). Wood stiffness and stability are governed by microfibril angle, basic

density, and spiral grain, all traits that display radial and longitudinal within-tree variation with mostly monotonic trends (e.g., Burdon et al. 2004). Some of these properties (e.g., high microfibril angle) are the least desirable and most variable in corewood—arbitrarily defined as the ten growth rings next to the pith—inducing negative effects on mechanical properties and dimensional stability. Traditionally, corewood properties have been either targeted through the improvement of basic density (Harris et al. 1976) or neglected (Walker and Nakada 1999) on the grounds that wood quality will gradually improve from pith to bark, eventually achieving acceptable wood quality in the outerwood (Watt et al. 2010).

Tree breeding programs dealing with wood quality still focus on traditional selection ages, around 7 or 8 years of age for radiata pine (*Pinus radiata* D. Don) in Australia, Chile, and New Zealand. In contrast, Apiolaza (2009a) suggested exploiting the time trends of wood properties when breeding for wood stiffness and dimensional stability, by targeting the time needed to achieve a wood quality threshold in corewood instead of rotation-age quality. The main assumptions behind this proposal were that

- once trees reached a wood-stiffness threshold they would at least maintain that value and
- additional improvements in quality (over the threshold) were worth less than reaching the threshold.

Once we work under those assumptions, the need for knowing age–age correlations with rotation-age performance all but disappears.

Before breeders opt for reduced testing times, there are two questions to address.

- How early can one observe variation in wood quality traits?
- What is the genetic architecture at that early age?

One of the barriers to characterizing wood in very young stems is that nominally vertical trees accumulate random amounts of compression wood due to crown asymmetries (Apiolaza et al. 2008; Lachenbruch et al. 2010; Apiolaza et al. 2011) and to the fact that trees are rarely truly vertical and straight. This clouds the differences between genotypes. Apiolaza et al. (2011) recommended leaning trees for screening purposes thereby reducing the “noise” introduced in genetic evaluation by intermixing of compression wood and “normal” wood. Leaning trees develop “pure” compression wood on the underside and “pure” opposite (“normal”) wood on the upper side. These two distinct wood types can then be evaluated independently, although our main interest is on the quality of opposite wood.

This paper estimates the degree of genetic control and genetic association between wood quality traits in 18-month-old leaning radiata pine seedlings, with the

purpose of targeting corewood improvement. The assessments include acoustic velocity, dimensional stability, and basic density in both compression and opposite wood. In addition, we discuss breeding and deployment implications of these results. This paper focuses on radiata pine, but this strategy applies to other short-rotation species.

## Materials and methods

A progeny trial comprising 49 radiata pine control-pollinated families was established at Amberley, Canterbury, New Zealand (43°9'20"LS 172°43'50"LE) in September 2007. These families are a subset of the genetic entities available to forest growers in New Zealand's deployment population and derived from the Radiata Pine Breeding Company program (Jayawickrama and Carson 2000). The mating design involved 45 parents with between 1 and 13 crosses each (mean=2.1), following an “opportunistic” approach (i.e., no formal mating design), ex ante randomly chosen with respect to the wood properties under study.

The trial followed a randomized complete block design with single-tree plots and 48 replicates of 7×7 trees. The design allowed for destructive sampling of 12 replicates per year for 4 years, aiming to study the ontogeny of early wood quality. Trees were leaned approximately 25° from their vertical axis in September 2008 to induce the expression of compression wood and isolate the random noise otherwise produced by the uncertain and variable presence throughout the nominally vertical stem in very young trees (Fig. 1a). Stakes were used to tie the stems at several points, ensuring that the bottom 500 mm of the tree was leaning at the required angle; the stakes did not move significantly from their original position. Trees were not assessed for traditional growth traits (e.g., stem diameter and height) as leaning affects growth patterns, generating eccentric stems and shorter trees (Apiolaza et al. 2011). In addition, parents included in this trial already present superior growth as they are part of the production population.

Within-site variability was greater than expected for a trial in agricultural land, with the magnitude of block variance similar to additive variance for most traits. This variability was exacerbated by an unusually wet winter that resulted in patches within the trial being waterlogged for several weeks, with higher mortality, stunted growth, and stem toppling than in the rest of the trial. Dead, stunted, or toppled trees were eliminated from the analysis.

The first 12 blocks of the trial were processed in May and June 2009 with 492 trees destructively sampled taking from each tree a stem bolt 200 mm long (see example in Fig. 1b). Samples were sawn lengthwise and trimmed to segments 100 mm long, and wood traits were assessed

**Fig. 1 a** Staked trees leaning approximately 25° from their vertical axis (*left*) and **b** 200 mm stem bolt displaying characteristic opposite (*light colored*) and compression (*dark colored*) wood before being sawn lengthwise for separate analyses



separately for “opposite” (upper side) and “compression” (lower side of sample) wood for green and dry acoustic velocity ( $\text{km s}^{-1}$ ), longitudinal shrinkage (%), volumetric shrinkage (%), and basic density ( $\text{kg m}^{-3}$ ).

Immediately after sawing, the samples were weighed to an accuracy of 0.001 g and measured for volume by the water displacement method to an accuracy of 0.01  $\text{cm}^3$ . Thereafter, all the samples were assessed for longitudinal dimensions and acoustic velocity. The longitudinal dimension was measured using a specially designed jig attached with a micrometer. Two spherical-headed map pins were inserted in line on the opposite end faces of each specimen. The pinheads formed the reference points for length measurements. The spherical heads of the pins rest precisely on the tubular ends of the jig, one of which corresponds to the hollow cylindrical end of the stem of the micrometer. The displacement of the micrometer was recorded.

Acoustic velocity was measured using WoodSpec, a resonance-based acoustic tool. A piezo speaker was used to sweep the audio frequency range from 500 to 20,000 Hz in 1 s, and a microphone was used to capture the vibrations. The fast Fourier transform analyzer in the tool extracted the fundamental frequency of the longitudinal vibration and acoustic velocity ( $v$ ) was determined from the following formula:

$$v = 2lf$$

where  $l$  is the sample length and  $f$  is the fundamental frequency. Thereafter, all the samples were dried in an oven set at 35°C until they achieved a constant weight.

Longitudinal dimension, weight, and volume of the samples were determined in the oven-dried condition, which corresponded to 4.5% moisture content. The purpose of drying samples at 35°C was to avoid any thermal degradation of chemical constituents of wood as further chemical characterization studies are to be carried out on the samples.

Basic density (BD), longitudinal shrinkage (LS), and volumetric shrinkage (VS) were calculated using standard formulas (Walker 2006):

$$\text{BD} = \frac{W_{\text{od}}}{V_{\text{g}}}$$

$$\text{LS} = 100 \frac{L_{\text{g}} - L_{\text{od}}}{L_{\text{g}}}$$

$$\text{VS} = 100 \frac{V_{\text{g}} - V_{\text{od}}}{V_{\text{g}}}$$

where  $W$ ,  $L$ , and  $V$  represent weight, length, and volume, respectively, and subscripts g and od denote green and oven dry conditions, respectively.

The statistical analyses followed a Bayesian tree (animal) model BLUP approach. In a Bayesian analysis, all effects are random and parameters must have prior distributions. In practice, *fixed* effects are modeled with a default prior of 0 mean and very large ( $10^8$ ) variance. Analyses were conducted separately for opposite and compression wood.

Data for each trait ( $y_i$ ) can be formulated as a univariate tree model:

$$y_i = \mathbf{1}_i m_i + \mathbf{Z}_{1i} \mathbf{b}_i + \mathbf{Z}_{2i} \mathbf{a}_i + \mathbf{e}_i$$

where  $m_i$  is the overall mean, and  $\mathbf{b}_i$ ,  $\mathbf{a}_i$ , and  $\mathbf{e}_i$  correspond to vectors for block, additive genetic effects, and residuals, respectively. The incidence matrices  $\mathbf{1}_i$ ,  $\mathbf{Z}_{1i}$ , and  $\mathbf{Z}_{2i}$  relate the phenotypic observations to the previous vectors. This model was then extended to a multivariate tree model by stacking up the vectors for five traits ( $y_1, y_2, \dots, y_5$ ) within each wood type:

$$\begin{bmatrix} y_1 \\ y_2 \\ \vdots \\ y_5 \end{bmatrix} = \begin{bmatrix} \mathbf{1}_1 m_1 \\ \mathbf{1}_2 m_2 \\ \vdots \\ \mathbf{1}_5 m_5 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{11} & \mathbf{0} & \cdots & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{12} & \cdots & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{Z}_{15} \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \vdots \\ \mathbf{b}_5 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{21} & \mathbf{0} & \cdots & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{22} & \cdots & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{Z}_{25} \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \vdots \\ \mathbf{a}_5 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \vdots \\ \mathbf{e}_5 \end{bmatrix}$$

which considered the following hypercovariance matrices:

$$\mathbf{V} = \begin{bmatrix} c\mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{B}_0 \otimes \mathbf{I}_b & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{G}_0 \otimes \mathbf{A} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R}_0 \otimes \mathbf{I}_r \end{bmatrix} \quad (\text{with})$$

$$\mathbf{B}_0 = \begin{bmatrix} \sigma_{b1}^2 & \sigma_{b12}^2 & \cdots & \sigma_{b15}^2 \\ \sigma_{b12}^2 & \sigma_{b2}^2 & \cdots & \sigma_{b25}^2 \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{b15}^2 & \sigma_{b25}^2 & \cdots & \sigma_{b5}^2 \end{bmatrix}, \mathbf{G}_0 = \begin{bmatrix} \sigma_{a1}^2 & \sigma_{a12}^2 & \cdots & \sigma_{a15}^2 \\ \sigma_{a12}^2 & \sigma_{a2}^2 & \cdots & \sigma_{a25}^2 \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{a15}^2 & \sigma_{a25}^2 & \cdots & \sigma_{a5}^2 \end{bmatrix},$$

$$\mathbf{R}_0 = \begin{bmatrix} \sigma_{e1}^2 & \sigma_{e12}^2 & \cdots & \sigma_{e15}^2 \\ \sigma_{e12}^2 & \sigma_{e2}^2 & \cdots & \sigma_{e25}^2 \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{e15}^2 & \sigma_{e25}^2 & \cdots & \sigma_{e5}^2 \end{bmatrix}, \mathbf{A} \text{ is the numerator relation-}$$

ship matrix,  $\mathbf{I}$  are identity matrices, and  $\mathbf{0}$  are null matrices.  $\mathbf{B}_0$ ,  $\mathbf{G}_0$ , and  $\mathbf{R}_0$  are covariance matrices for

block, additive, and residual effects, respectively. Posterior distributions of heritability ( $h^2$ ) and genetic correlations between traits ( $r_{12}$ ) were estimated using the standard formulas:  $h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_b^2 + \sigma_e^2}$  and  $r_{12} = \frac{\sigma_{a12}^2}{\sigma_{a1}^2 + \sigma_{a2}^2}$ .

Details on the specifications of prior distributions, likelihood, and joint and conditional posterior densities for these model equations can be found in Sorensen and Gianola (2002 pp. 576–584). All models were fitted using Markov Chain Monte Carlo methods implemented in the R software package MCMCglmm (R Development Core Team 2008; Hadfield 2010) using 200,000 iterations, a burn-in (i.e. initial discarding) of 10,000 samples and storing every 200th sample after burn-in. The fitting process considered weak priors for variance components that followed an inverse Wishart distribution. Posterior distributions of the genetic parameters were summarized using the mode and a 95% credible interval.

### Results

The phenotypic coefficients of variation were higher in opposite wood than in compression wood for all traits but basic density (Table 1). In opposite wood, longitudinal and volumetric shrinkage presented the largest variation, followed by green velocity, basic density, and dry velocity. The variability ranking changed slightly in compression wood, from volumetric shrinkage through longitudinal shrinkage, basic density, and green velocity to dry velocity (Table 1). This change in ranking is attributed to physical and chemical differences in compression wood, including the large increase in basic density.

In opposite wood, there was a sixfold difference for longitudinal shrinkage between the best and worst trees, followed by a fourfold difference for volumetric shrinkage. Differences for other traits were more modest (between 1.6 and 1.7 times difference), although they become larger

**Table 1** Phenotypic descriptive statistics for green velocity, dry velocity, longitudinal shrinkage, volumetric shrinkage, and basic density

Trait	Wood type	n	Minimum	Maximum	Mean	Standard deviation	Coefficient of variation (%)
Green velocity (km s <sup>-1</sup> )	O	492	0.81	1.41	1.05	0.10	9.71
	C	481	0.93	1.58	1.23	0.09	7.28
Dry velocity (km s <sup>-1</sup> )	O	479	1.63	2.62	2.13	0.15	6.86
	C	480	1.89	2.52	2.17	0.10	4.46
Longitudinal shrinkage (%)	O	478	0.57	3.62	1.57	0.43	27.53
	C	478	0.89	3.44	2.17	0.39	17.96
Volumetric shrinkage (%)	O	492	8.59	36.41	20.67	4.98	24.07
	C	478	6.14	23.36	13.28	2.79	20.99
Basic density (kg m <sup>-3</sup> )	O	492	240.50	415.40	305.50	28.02	9.17
	C	490	270.60	514.70	380.30	43.94	11.55

O opposite wood, C compression wood

when converting velocity traits to modulus of elasticity estimates using a green density of  $1,100 \text{ kg m}^{-3}$  (Chauhan and Walker 2006). For example, there was a threefold difference for green modulus of elasticity between the best and worst trees ( $2.19=1.1 \times 1.41^2$  versus  $0.72=1.1 \times 0.81^2$ ).

Heritability estimates of wood traits were low to moderate for both compression and opposite wood (Tables 2 and 3). All reported point estimates in the tables are followed by 95% credible intervals between square brackets. In opposite wood, the most heritable trait was longitudinal shrinkage (0.38), followed by dry velocity (0.26) and green velocity (0.25). In compression wood, the highest heritabilities were for basic density (0.34) and green velocity (0.34), followed by dry velocity (0.29). Volumetric shrinkage displayed the lowest heritability for opposite (0.15) and the second lowest for compression wood (0.26).

Estimated genetic correlations between traits were, in general, very high in opposite wood (Table 2). Green velocity displayed the highest correlations with both longitudinal ( $-0.89$ ) and volumetric ( $-0.64$ ) shrinkage, closely followed by dry velocity. These correlations reduced dramatically for compression wood (Table 3), in which high basic density seemed to be involved. In comparison to opposite wood, for compression wood the correlation between green velocity and longitudinal shrinkage disappears (changes from  $-0.89$  to  $0.21$ ), while the correlation with volumetric shrinkage increases (changes from  $-0.64$  to  $-0.79$ ).

The estimated genetic correlations between compression and opposite wood characteristics were high for most traits ( $\sim 0.7$  for green and dry velocity,  $\sim 1.0$  for volumetric shrinkage and basic density, see Table 4), except for longitudinal shrinkage (0.36). There were chain convergence issues for the volumetric shrinkage and basic density correlations, most likely due to very strong correlations between parameters of the model. This meant that successive iterations of the Monte Carlo algorithm were highly correlated and the rate of convergence was slow. Using a tree model (instead of a parental model) to take into account the relatedness between parents was more realistic, but it

may have also exacerbated the convergence problems in obtaining Table 4.

## Discussion

### Bayesian analysis

An interesting feature of Bayesian approaches is that they generate a posterior distribution not only for variance components, but also for calculated parameters such as heritabilities and genetic correlations that do not have a closed expression. This permits obtaining asymmetric credible intervals. These intervals are more realistic than symmetric ones, particularly when considering estimates near the bounds of the parametric space (e.g., heritabilities near 0 or 1, genetic correlations near  $-1$  or  $1$ ). The usual assumption of symmetric confidence intervals used in ML and REML analyses is, sometimes, a very poor approximation to the realized distribution of the genetic parameters (see Tables 2 and 3). One alternative for breeders relying on likelihood methods will be the use of parametric bootstrapping to derive confidence intervals.

Bayesian methodologies have struggled to gain popularity in tree breeding, on one hand because of the additional requirement for statistical sophistication and—maybe more importantly—due to the large effort involved on building ad hoc software (e.g., Soria et al. 1998; Cappa and Cantet 2006, 2008) or the difficulties for using general-purpose Bayesian inference software with pedigreed information (e.g., when applying Winbugs to animal breeding problems, Damgaard 2007). The package MCMCglmm tackles both problems directly.

MCMCglmm makes available statistical functionality inside the R software with a notation not unlike asreml-r. Consequently, problem specification requires little additional understanding. One disadvantage of these methods is that they still are very computationally intensive, particularly when using individual-tree models that require longer chains. In addition, model fitting did not work well for volumetric shrinkage and basic density expressed

**Table 2** Posterior modes for heritability (diagonal) and additive genetic correlations (below diagonal) for opposite wood green velocity, dry velocity, longitudinal shrinkage, volume shrinkage, and basic density obtained from a full multivariate analysis

	Green velocity	Dry velocity	Longitudinal shrinkage	Volumetric shrinkage	Basic density
Green velocity ( $\text{km s}^{-1}$ )	0.25 [0.10 0.54]				
Dry velocity ( $\text{km s}^{-1}$ )	0.82 [0.58 0.94]	0.26 [0.11 0.58]			
Longitudinal shrinkage (%)	$-0.89$ [ $-0.94$ $-0.60$ ]	$-0.83$ [ $-0.93$ $-0.52$ ]	0.38 [0.17 0.68]		
Volumetric shrinkage (%)	$-0.64$ [ $-0.91$ $-0.22$ ]	$-0.59$ [ $-0.83$ 0.02]	0.84 [0.37 0.94]	0.15 [0.05 0.42]	
Basic density ( $\text{kg m}^{-3}$ )	0.58 [0.13 0.85]	0.44 [ $-0.25$ 0.73]	$-0.61$ [ $-0.82$ 0.03]	$-0.57$ [ $-0.88$ $-0.13$ ]	0.20 [0.06 0.42]

Values between brackets indicate 95% credible interval for the genetic parameter

**Table 3** Posterior modes for heritability (diagonal) and additive genetic correlations (below diagonal) for compression wood green velocity, dry velocity, longitudinal shrinkage, volume shrinkage, and basic density obtained from a full multivariate analysis

	Green velocity	Dry velocity	Longitudinal shrinkage	Volumetric shrinkage	Basic density
Green velocity (km s <sup>-1</sup> )	0.34 [0.19 0.62]				
Dry velocity (km s <sup>-1</sup> )	0.62 [0.24 0.82]	0.29 [0.11 0.45]			
Longitudinal shrinkage (%)	0.21 [-0.24 0.70]	-0.32 [-0.70 0.07]	0.25 [0.09 0.46]		
Volumetric shrinkage (%)	-0.79 [-0.89 -0.42]	-0.25 [-0.64 0.23]	-0.38 [-0.81 0.07]	0.26 [0.13 0.51]	
Basic density (kg m <sup>-3</sup> )	0.74 [0.51 0.90]	0.06 [-0.32 0.55]	0.73 [0.31 0.92]	-0.81 [-0.93 -0.52]	0.34 [0.21 0.70]

Values between brackets indicate 95% credible interval for the genetic parameter

in opposite and compression wood, which are highly correlated bivariate analyses. However, REML software like ASReml struggles in the same type of situations (J. Hadfield, personal communication).

### Variability

The estimated phenotypic coefficient of variation for the green velocity of opposite wood was consistent with published values for normal wood in older “straight” radiata pine trees (Chauhan and Walker 2006). However, estimates of variation for both opposite and compression wood basic density were 50% higher than for normal wood in older trees.

There are several potential sources for these differences in variability. The genetic material for this trial was a mix of genotypes from the production population, which has some level of selection for basic density but no selection for wood stiffness. A mix like this (with 45 parents) may be genetically more variable than a plantation stand or it could be phenotypic instability in the material contributing the greater variation. In addition, trees in the trial were only tilted 8–9 months prior to harvesting—thereby developing less volume of “pure” compression and opposite wood than desired—and there were practical difficulties in maintaining the trees at the desired 25° lean. Moreover, microsite variations were greater than expected for an agricultural site, being intensified by an extremely wet winter that resulted in waterlogged patches for several weeks. The combination of these issues generated some commingling of compression and opposite wood rather than the intended “pure” expression. Nearly 20% of the samples from

compression wood side had basic density of less than 350 kg m<sup>-3</sup> and longitudinal shrinkage of less than 2% suggesting a significant proportion of normal wood in compression wood samples. A subsequent genetic trial has been established to address such limitations.

### Genetic parameters

There is scarce information on the early genetic architecture of wood traits for the first quarter of rotation age, particularly for the first 3 years. One exception would be the fast-growth species in the tropics grown for pulpwood, e.g., the *Eucalyptus urophylla* × *Eucalyptus grandis* hybrid in Brazil (Gomide 2009). The heritabilities reported in this study were relatively low, as often estimates for wood properties are greater than 0.4 in older trees (e.g., Shelbourne 1997; Apiolaza and Garrick 2001; Kumar and Lee 2002; Kumar 2004; Dungey et al. 2006; Gapare et al. 2009). Low to moderate heritability suggests plenty of within-family variation; therefore, the best (or worst) trees for a trait will come from several families.

It is important to remember that in genetic evaluation heritability acts as a shrinkage factor towards the trial mean. This means that the breeding value differences between trees are scaled to around 1/5 (for  $h^2=0.2$ ) to 1/3 (for  $h^2=0.3$ ) of the phenotypic differences reported in Table 1.

As far as we know, this paper presents the first example of deliberately creating leaning trees to understand the genetic architecture of opposite and compression wood, as well as for wood-quality screening purposes. However, there are recent published examples of leaning trees to understand provenance differences to improve stem form

**Table 4** Posterior modes for additive genetic correlations ( $r_g$ ) between opposite and compression wood for green velocity, dry velocity, longitudinal shrinkage, volume shrinkage, and basic density

	Green velocity	Dry velocity	Longitudinal shrinkage	Volumetric shrinkage	Basic density
$r_g$	0.74 [0.40 0.88]	0.65 [0.22 0.89]	0.36 [-0.31 0.85]	1.00 [0.88 1.00]	1.00 [0.95 1.00]

Values between brackets indicate 95% credible interval for the genetic parameter

(Sierra de Grado et al. 2008), study compression wood development (Yamashita et al. 2007), and evaluate clones for superior wood quality (Apiolaza et al. 2011).

There were important differences in genetic correlations between those within opposite and those within compression wood, for example, the correlations between green velocity and longitudinal shrinkage ( $-0.89$  versus  $0.21$ ), and dry velocity with longitudinal shrinkage ( $-0.83$  versus  $-0.32$ ) had smaller magnitude. In opposite wood, longitudinal shrinkage and acoustic velocity seems to be mainly associated with the microfibril angle in the S2 layer wherein shrinkage increases and velocity decreases with increasing microfibril angle. In compression wood, however, basic density appears to be the dominant property influencing longitudinal shrinkage. It has been reported that the microfibril angle in the compression wood of stems leaning by more than  $20^\circ$  from the vertical axis does not vary significantly (Yamashita et al. 2007, Siripatanadilok and Leney 1985). In this study, relatively poor correlations in compression wood may also be attributed to the fact that some nominally compression wood samples were partially contaminated by normal wood because trees on waterlogged microsites had varying degrees of lean. Nevertheless, genotypes can also vary in their propensity to develop compression wood (e.g., Shelbourne et al. 1969), an effect that is difficult to separate in the current experiment. We have already established another experiment to explore this issue.

#### Application options

As already mentioned in the “Introduction” section, most wood quality studies focused on performance at 1/4 to 1/3 of rotation age. Nevertheless, others have presented longitudinal data series, mostly studying the changes of genetic control and association between different assessments (e.g., Apiolaza and Garrick 2001, Dungey et al. 2006, Lenz et al. 2010). An additional complication is that most longitudinal data series do not properly take into account the ordered nature of the data, which induces serial correlation, during the analyses. Furthermore, many studies do not report genetic parameters for the first few rings, e.g., due to damaged samples or to the increment core being off center and entirely missing the pith of the tree. Thus, Dungey et al. (2006) reported data from ring 3, while Bouffier et al. (2008) reported from year 6 onwards, which are not directly comparable to our results.

There are several potential approaches to breeding for wood quality. For a given trait, breeders could:

1. Measure the average expression of the trait and select trees displaying the best average value—e.g., highest basic density, lowest shrinkage, etc.—and relating it to rotation-age performance.
2. Obtain a profile of the variation of the property for each tree, properly analyze the longitudinal data series, e.g., using random regressions or modeling covariance structures in a multivariate setting, and select the trees with the best profile.
3. Assess trees only at a very early age and select those trees that have reached a predefined quality threshold.

The first option is the most common, and it has been often applied for breeding basic density, e.g., Loo et al. (1984), Vargas-Hernandez and Adams (1992), Shelbourne (1997), Hannrup and Ekberg (1998), and Lenz et al. (2010).

The second approach is both costly and analytically intensive: it requires methodologies that produce a pith-to-bark profile and sophisticated statistical methodology to make the most of the expensive data collected (e.g., Apiolaza and Garrick 2001; Isik et al. 2008 and Apiolaza 2009b using Silviscan data; Eckard et al. 2010 for resistograph data). This approach involves sampling a small number of large trees that are difficult and slow to handle, so it tends to be for research purposes rather than for operational purposes. For example, in a recent study, Watt et al. (2010) analyzed a 13-year-old clonal trial taking two ramets of 13 clones. These authors suggested that modulus of elasticity (MoE) assessments from age 5 onwards could be used to identify clones with high MoE. However, their Fig. 2c showed that the bottom one third of the clones for MoE could be identified as early as age 3. That article has no data for earlier assessments <3 years. Even so, their data show that a change of philosophy—screening out rather than selecting for—could further reduce selection age. In addition, small sample numbers targeted at the best-growing material will bias the estimates of genetic parameters and any derived estimation of genetic gain (Apiolaza et al. 1999).

The last approach, supported in this paper, deals with a single assessment age for large numbers of very small trees (Apiolaza 2009a) emphasizing speed and consistency over accuracy. Young stems are easy to handle, analyses take days to weeks rather than months to years, and large numbers of trees can be processed, increasing selection intensity. On the other hand, very early screening means that some good trees are bound to be discarded that would, if retained, express good characteristics later in life.

Experience gained in other trials (see, for example, Apiolaza et al. 2011) suggests that

- It is possible to further improve the quality of very early screening by better controlling environmental variation by growing trees in planter bags that are irrigated and fertilized so providing homogeneous growing conditions. This would increase heritability and therefore the accuracy of prediction of genetic values.

- An important limitation to all methodologies is specimen size. Here, experience at Amberley suggests that for radiata pine the desired piece size should be achievable within 2 years of planting.

These two constraints could be relaxed if using highly homogeneous agricultural land for testing or dealing with very high growth rates (as in tropical forestry). This new approach will involve greater expenses for site preparation (or using planter bags). However, they would require less land (at 10,000 stems per hectare) and for a shorter time than traditional experiments, as trees would be harvested after only 2 years. We are already testing this new approach in a deployment population.

Adopting this approach requires rethinking both the breeding objective and the strategy required to achieve it. The objective changes from breeding the best average wood quality to early expression of wood that meets one or more minimum quality thresholds. It also assumes that improvements in outerwood properties are less relevant than in corewood (Apiolaza 2009a). Several tree breeding programs are entering their third generation, having substantially improved growth rate and tree form. Taking superior growth and form for granted and working with such improved material our alternative approach can emphasize very early screening for wood traits both at the breeding and deployment level.

## Conclusions

Bayesian analyses provided a more realistic description of the uncertainty surrounding the estimation of genetic parameters, particularly of values near the boundaries of the parametric space.

There was significant phenotypic and genetic variability for basic density, modulus of elasticity, and longitudinal and volumetric shrinkage. This variability, coupled with moderate heritabilities, would permit effective wood quality screening at a very early age.

Both opposite green and dry acoustic velocities were highly negatively correlated with longitudinal and volumetric dimensional shrinkage. These values support the use of acoustic tools for very early screening of dimensional stability.

Systematically leaning all trees dramatically reduced the noise introduced by the random commingling of opposite and compression wood. This reduction would be further improved by better control of environmental variation, for example using irrigated planter bags with potting mix and slow-release fertilizer.

**Acknowledgments** This project was funded by the New Zealand FRST Compromised Wood (P2080) Programme with participation of Forests New South Wales, Forest and Wood Products Australia, New Zealand Radiata Pine Breeding Company and Weyerhaeuser (USA). Genetic material and land for the trial was provided by Proseed Ltd. Many thanks to Dr Rowland Burdon and two anonymous reviewers for comments that contributed to greatly improving this article.

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