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RESEARCH ARTICLE

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Modelling the effects of genetic improvement on radiata pine wood density

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Abstract

Background: Density is a key wood quality trait, which is moderately to highly heritable, and has been the focus of selective breeding efforts in radiata pine (*Pinus radiata* D.Don) in New Zealand. Forest managers require information on realised gain in wood density in order to help them make decisions about which tree stocks to plant, how to manage stands and when to harvest in order to achieve certain wood quality outcomes. The aim of this study was to quantify realised genetic gain in radiata pine wood density and to incorporate it into existing modelling systems for predicting growth and wood quality.

Methods: A national model of radiata pine wood density, which predicts wood density at breast height as a function of ring number from the pith and a "local parameter", was modified to account for the effects of genetic improvement. The value of this local parameter was estimated for 679 radiata pine families with differing levels of genetic improvement (as quantified by their GF Plus rating for wood density) that were growing in 18 trials established by the Radiata Pine Breeding Company. The value of Wood Density Index (defined as the breast height outerwood density at age 20 years) was calculated from the estimate of the local parameter. Simulations were performed to show the impact of genetic improvement on whole-log average density and the variation in density within a log.

Results: There was a strong positive relationship between GF Plus rating for wood density and Wood Density Index ($R^2 = 0.73$), with a one-unit increase in GF Plus corresponding to a 2.16 kg m^{-3} increase in wood density. An increase in GF Plus density rating from 18 to 27 would result in an increase in breast height outerwood density at age 20 years of 18.5 kg m^{-3}. Over the same range of genetic improvement, average whole-log density is predicted to increase by 14–16 kg m^{-3}. Validation of the model using independent data from older trees showed that it was able to correctly predict the effect of genetic improvement. It also indicated that the assumption that the expression of genetic gain is constant across sites with different wood density potentials is valid, although data from additional trials located across a wider range of sites is required to confirm this.

Conclusions: The effect of genetic improvement on wood density has been quantified and included in growth and yield modelling systems. This enables forest managers to estimate wood density in radiata pine plantations for any site and management regime established using tree stocks with a specific wood density rating.

Background

In New Zealand, management of radiata pine (*Pinus radiata* D.Don) forests has shifted dramatically over the last 90 years. Un-thinned stands that were established in the 1930s were typically grown at high stand densities and on rotations of 45 years or more. However, economic analyses undertaken during the 1960s showed that alternative silvicultural regimes comprising early pruning coupled with pre-commercial thinning could provide very good economic returns (Fenton and Sutton 1968). This resulted in stands being grown at wider spacing, with heavy thinning to concentrate growth on a smaller number of trees. Rotation lengths were shortened considerably from 45 down to 30 years and, in some cases, 25 years (James 1990). It was recognised at least as early as the 1970s that these changes in silvicultural practices would give rise to trees with a higher proportion of corewood, larger branches in the upper un-pruned logs and a reduction in wood density (Burdon et al. 2004; Cown 1992; Harris et al. 1976). Selective breeding to improve wood density was

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recommended as one means to compensate for the reduction in wood quality associated with changing silvicultural practices (Harris et al. 1976).

New Zealand's radiata pine tree breeding programme started in the 1950s when the first plus tree selections were made (Burdon 2008; Carson 1996; Jayawickrama and Carson 2000). The long-standing goal of this programme has been the production of large, fast-grown and well-formed logs, which gave rise to the growth and form (GF) breed (Jayawickrama and Carson 2000). Early radiata pine tree breeding efforts did not focus on wood density or other wood quality traits even though wood density was highlighted as being an important property due to its relationship with a number of other solid wood properties such as stiffness, strength and hardness, as well as with pulp yield and several paper properties (Panshin and de Zeeuw 1980), and it was known that density is a moderately heritable trait (Jayawickrama 2001; Wu et al. 2008; Zobel and Jett 1995). The focus was primarily on growth and form traits until the 1970s (Jayawickrama and Carson 2000), and the adverse genetic correlation that exists between wood density and growth (Jayawickrama 2001) would have contributed to a reduction in wood density. Only since the 1970s has the importance of wood density been recognised and selective breeding been undertaken for this trait (Burdon 2010; Dungey et al. 2009; Jayawickrama and Carson 2000; Wu et al. 2008). Density is now a key trait in New Zealand's radiata pine breeding programme and is included in the GF Plus rating system, which was developed in 1998 by the Radiata Pine Breeding Company (RPBC), Rotorua, New Zealand.

The GF Plus rating for wood density is derived directly from breeding values (an explanation of the system can be found at http://rpbc.co.nz). Ratings are given to seedlots based on the contribution and breeding values of parents represented (Scion, unpublished data). Breeding values are derived from phenotyping individual trees in progeny trials in New Zealand and southeast Australia. An example of methods and types of analyses undertaken for breeding value estimation can be found in Cullis et al. (2014). Under the GF Plus rating system, higher GF Plus ratings indicate greater genetic merit for wood density. However, the relationship between GF Plus rating for wood density and the realised values of this trait for a tree of a given age, growing on a particular site and under specific silvicultural regime has not been quantified. Such information is of use for forest managers in determining the level of genetic improvement needed to produce logs that meet certain wood density thresholds. This may enable structural quality logs to be produced on sites that are currently considered marginal for producing such material. In this paper, we modify an existing model of intra-stem variation in radiata pine wood density (Kimberley et al. 2015a) to include the effect of genetic improvement and show how it can be incorporated into a decision support tool that can be used by forest managers to evaluate different options around planting stock.

Methods

A dataset containing wood density values from families with known GF Plus wood density ratings was supplied by the Radiata Pine Breeding Company. This dataset included information from 18 separate genetics trials that were mainly single-tree plot designs (Table 1). All but one of the trials were located in the North Island of New Zealand, with the remaining trial (FR203_2) located in New South Wales (NSW), Australia. These trials included 679 unique families with many of the families established at more than one trial site. Mean values of wood density for each family were calculated from measurements made on at least 30 trees per family (25,091 individual trees in total). Wood basic density was generally determined for each tree based on a 5-ring core sample taken at breast height (7- or 8-ring core samples were taken at three sites). These cores were mostly collected from rings 1–5 or 6–10 from the pith (Table 1), and this information was used to estimate breeding values and GF Plus density rating for each family (Radiata Pine Breeding Company, unpublished data).

In order to compare values of wood density measured at different ages and to make future predictions at later ages, the Wood Density Index for each family was estimated. The Wood Density Index is conceptually similar to site productivity indices, such as Site Index or 300 Index (Kimberley et al. 2005), and for radiata pine, it is defined as the breast height outerwood density (density of the outermost five annual rings) at age 20 years (Palmer et al. 2013). It is estimated using a national model for the radial variation in radiata pine wood density at breast height (D_{BH}, kg m^{-3}), which was fitted to a comprehensive national dataset that included studies of density measured radially at breast height in 5-ring groups at 340 locations throughout New Zealand (Kimberley et al. 2015a). This model has the following form:

$$D_{\mathrm{BH}} = a + fL + (b - a + L)\left(1 - e^{-c\mathrm{Ring}}\right)^{d} \quad (1)$$

where a, b, c, d and f are model parameters that were estimated from the data (Table 2), L is a local parameter that can be derived either from a national wood density surface (Palmer et al. 2013) or from density measurements made on a sample of trees, and Ring is the ring number from the pith. When Ring = 16 (the mean ring number of a 5-ring outerwood core collected from a 20-year-old tree after allowing 1.5 years for the stem to

Table 1 Details of the trials where wood density was assessed

Trial	Forest	No. of families	No. of trees	Rings from pith assessed for density
AK1061_1	Poutu	68	1224	6–10
FR124_4	Takitoa	15	315	6–10
FR203_1	Ohurakura	193	1676	1–5
FR203_2	NSW	170	2803	1–8
FR260_1	Kaingaroa	31	702	1–7
FR260_3	Tarawera	30	823	1–7
FR38_1	Poutu	58	1132	6–10
FR38_2	Kinleith	59	817	6–10
FR38_3	Paengaroa	27	334	1–10
FR399_3	Tarawera	57	2086	1–5
FR69_1	Poutu	36	719	6–10
RO1836_0	Rotoehu	56	975	6–10
RO2051_1	Mamaku	154	1833	6–10
RO2051_2	Mamaku	150	1393	6–10
RO2111_1	Kaingaroa	89	1834	6–10
RO944_98	Kaingaroa	121	3000	1–5
RO944_99	Kaingaroa	50	425	6–10
RO947_99	Kaingaroa	120	3000	1–5
Total		679	25,091	

attain breast height), the model estimates the Wood Density Index.

The effect of genetic improvement was incorporated into the modelling framework described above by including it as an adjustment to the local parameter (L) in Eq. (1). The local parameter was calculated for different families based on the measured wood density at a specific ring number by re-arranging Eq. (1) such that

$$L = \frac{D_{BH} - a - (b-a)\left(1-e^{-c\mathrm{Ring}}\right)^{d}}{f + \left(1-e^{-c\mathrm{Ring}}\right)^{d}} \qquad (2)$$

where the values of a, b, c, d and f are given in Table 2. The ring number from the pith used in Eq. (2) was taken as the midpoint of the group of rings assessed for density. For example, if density was assessed on rings 6–10 from the pith, then Ring = 8. Using the estimates of L obtained using Eq. (2), a two-way analysis of variance (ANOVA) model, using a fixed effect for family and a random effect for trial, was fitted using the MIXED procedure in SAS software (SAS Institute Inc. 2004–2009). This analysis produced least squares means of L for each family adjusted for the effects of site. Values of the local parameter, L, for each family were then substituted back into Eq. (1) in order to calculate Wood Density Index (i.e. D_{BH} for a 20-year-old tree). A linear regression equation was then fitted using the Wood Density Index of each family as the dependent variable and the previously estimated GF Plus density rating as the independent variable.

Table 2 Parameter estimates and their standard errors for the wood density models given by Eqs. (1) and (2)

Parameter	Estimate	s.e.
a	339.9	2.5
b	459.2	2.5
c	0.1447	0.0092
d	2.44	0.29
f	0.657	0.088

This regression equation was then incorporated into the wood density model in the Forecaster growth and wood property modelling system (West et al. 2013). The impact of genetic improvement in wood density is calculated in this system as the ratio of the mean L value for a specific seedlot or genotype of interest relative to the mean L value for a "standard" seedlot with a GF Plus density rating of 22.

This implementation of the model using Forecaster was then validated against independent data obtained from six genetics trials, all with similar individual-tree plot design, located in different forests across the North Island of New Zealand. Four of the trials contained 10–18 families mostly with low-density wood and with GF Plus density ratings ranging between 7 and 19. The other two trials were larger with one containing 44 families with GF Plus density ratings ranging from 2 to 23 and the other 41 families with GF Plus density ratings between 0 and 33. Approximately 15–30 trees per family were assessed for outerwood density in each trial between ages 15 and 18 years, with a total of about 3000 trees assessed across all trials.

The Forecaster growth and yield model was used to predict tree diameter and wood density at breast height annually up to the assessment age for the trees in each trial. For each trial, the influence of site factors such as temperature and soil on wood density was accounted for using the wood density surface for New Zealand (Palmer et al. 2013) which represents the Wood Density Index for a GF Plus density rating of 22. The wood density model in Forecaster (Kimberley et al. 2015a) uses this Density Index to predict wood density of logs cut from each stem, taking into account factors such as felling age and management regime (e.g. stocking), with genetic adjustments using GF Plus density rating as described in this paper. Forecaster runs require a starting stem list consisting of heights and breast height diameters. These were obtained from early diameter and height measurements. In some trials where heights were not measured, they were generated using Forecaster height-diameter models initialised with information on Site Index for the trial site.

The predictions of wood density and diameter at breast height obtained from Forecaster were used to calculate outerwood density at the assessment age for each family in each trial. Linear regressions of actual vs. predicted density were then fitted for each trial using family means, with the slope parameter of these regressions providing a test of the model performance. A slope coefficient close to 1 would indicate good model performance, while slopes less than or greater than 1 would indicate that the model either over- or under-predicts, respectively, the increase in wood density with GF Plus rating.

Finally, the Forecaster implementation of the model was used to demonstrate the effect of genetic improvement in wood density over a range of conditions. A standard framing regime was simulated on four contrasting sites and with three levels of genetic improvement for wood density. The simulated stand was planted at an initial density of 1000 stems ha^{-1}, thinned to 450 stems ha^{-1} at mean top height 14 m and felled at age 30 years. The four contrasting sites had values of Wood Density Index of 380, 400, 420 and 440 kg m^{-3}. The three values of GF Plus density rating used in the analyses were 18 (broadly equivalent to what is currently growing), 22 (an approximate rating for a typical seedlot or clone planted now) and 27 (a high density seedlot or clone). Using the wood density model within Forecaster, the whole-log values of wood density were estimated for approximately 1300 simulated logs for each site and GF Plus combination. These logs were 5 m in length, and up to five logs were cut from each tree. The mean density of these logs and the proportion of logs above a threshold value of 400 kg m^{-3} were then calculated for each site and GF Plus combination.

Results

GF Plus ratings for wood density for the families in the dataset supplied by the Radiata Pine Breeding Company ranged from −11.3 up to 47.9. This indicated that there was some very good, high-density material (GF Plus over 40), but also some material of low density (−11.3), compared with the average (18.0). From the 5-ring core samples, the corresponding estimates of the local parameter, L, ranged from −50.7 up to 58.2 kg m^{-3}, with a mean of −7.1 kg m^{-3}. Substituting these values into Eq. (1) yielded Wood Density Index values ranging from 366 up to 533 kg m^{-3}, although their distribution was somewhat positively skewed (Fig. 1). There was a strong positive linear relationship between GF Plus wood density rating and Wood Density Index ($R^2 = 0.73$), with a one unit increase in GF Plus rating corresponding to a 2.16 kg m^{-3} increase in Wood Density Index (Fig. 2). For example, those families with the highest level of genetic improvement for wood density have a GF Plus rating of 48, compared with the mean rating of 18 for families used in this analysis. This corresponds to an increase in Wood Density Index of 65 kg m^{-3} (i.e. (48–18) × 2.16). For families with a GF Plus wood density rating of 27, which is more typical of the highest rated material currently being planted, the increase in Wood Density Index is closer to 19 kg m^{-3}. This difference is constant with increasing cambial age after approximately age 20 years (Fig. 3). While the actual level of wood density will vary by site, the change in wood density for a given level of genetic improvement is assumed to be constant across all sites.

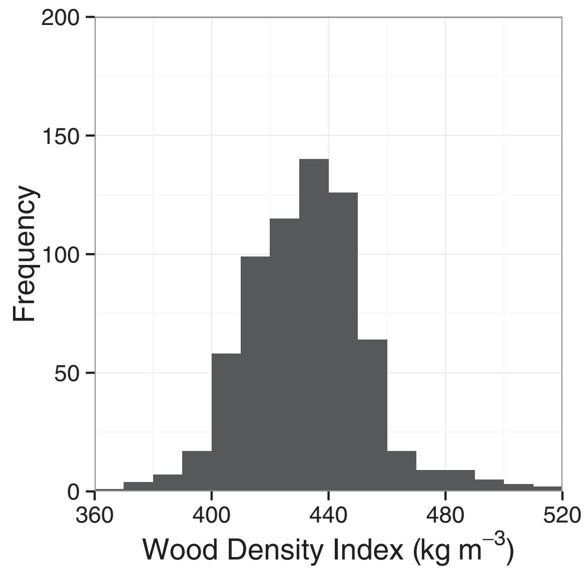

Fig. 1 Histogram showing the range in Wood Density Index values for the 679 improved families

The results of the model validation against density measurements from six independent trials are summarised in Table 3. Averaged across the six trials, predictions were very close to actual densities, differing by only 4 kg m^{-3}. Some individual trials showed significant bias, especially FR123/5 where density was under-predicted by 34 kg m^{-3}, although all other trials had mean prediction biases of not more than 12 kg m^{-3}. Environmental effects on wood density at each trial were accounted for using the Forecaster wood density surface for New Zealand (Palmer et al. 2013). However, this surface cannot be expected to fully account for localised environmental effects, especially the effects of site fertility, and prediction bias in some trials was therefore not unexpected. Because of this, the preferred method of standardising a Forecaster run for a particular site is to use actual wood density measurements from the site from a stand of known GF Plus density rating.

The parameter that best validates the performance of the model is the slope of the linear regression model between actual and predicted wood densities within each

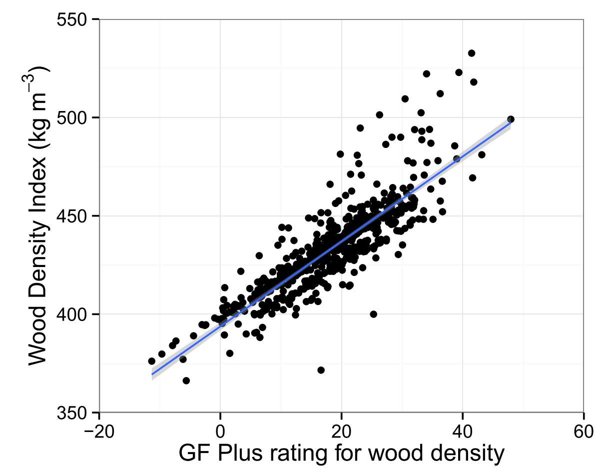

Fig. 2 Relationship between GF Plus wood density rating and the Wood Density Index for 679 radiata pine families. The *solid line* was fitted using ordinary least squares regression

trial. A slope of 1 would indicate that differences in wood density between genotypes are correctly predicted by the model. Slopes of linear regression models of actual vs. predicted density fitted to genotype means within each trial did not differ significantly from 1 in any trial at the 5 % level of significance (Table 3) indicating that the model performs well. A regression model fitted to the combined data with a common slope and separate intercepts for each trial had a slope of 1.09 ± 0.16 (95 % confidence interval) indicating that differences in wood density between families are correctly predicted by the model.

Predictions using the model of wood densities for a range of genetic, site and silvicultural combinations are

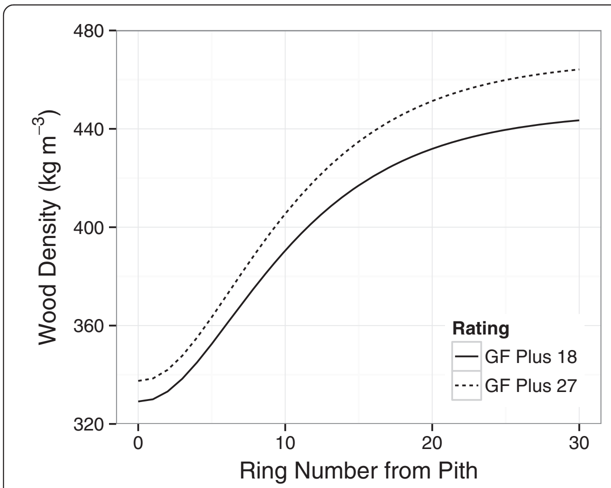

Fig. 3 Example showing the predicted radial profiles of wood density for families with GF Plus ratings for wood density of 18 (typical of material currently growing) and 27 (typical of the maximum value for material currently being planted) growing on a site with a Wood Density Index of 430 kg m^{-3}

shown in Table 4 and Fig. 4. With an increase in GF Plus density rating from 18 to 27, Forecaster predicts that average whole-log density increases by 14–16 kg m^{-3} (Table 4; Fig. 4). The percentage of logs exceeding a threshold of 400 kg m^{-3} depends on the inherent wood density potential of the site. On the site with a Wood Density Index of 380 kg m^{-3}, the proportion of logs exceeding the density threshold of 400 kg m^{-3} increases from 1.9 to 5.0 % with an increase in GF Plus rating for density from 18 up to 27. On the site with a higher wood density potential (Wood Density Index = 440 kg m^{-3}), the proportion exceeding the 400 kg m^{-3} threshold increases from 23.4 to 40.3 % as GF Plus rating increased from 18 up to 27.

Discussion

This analysis represents the first attempt to incorporate the impact of genetic gain for wood density into existing wood density models that themselves are implemented within the Forecaster growth and yield modelling system. Our analysis showed that there is a strong positive relationship between GF Plus rating for wood density and Wood Density Index (defined as the breast height outerwood density at age 20 years for a stand planted between 1990 and 2000). This was to be expected as the data analysed here were used to estimate both the breeding values for wood density and the Wood Density Index. However, the ability to express genetic improvement in terms of actual wood density means that the effects of different levels of genetic improvement on whole-log average density and the proportion of logs that exceed a particular density threshold can be evaluated. This type of analysis, in turn, can be used to support decision making on what seedlot or genotype could be deployed on a particular site in order to meet management goals. If a particular density threshold can be related to structural timber grade recovery, then it should be possible to use the model to estimate what degree of genetic improvement is required in order to be able to produce structural timber at a given site and for a given silvicultural regime.

Wood density varies considerably by site throughout New Zealand, mostly driven by temperature differences (Palmer et al. 2013). On colder sites, it might be possible to partially overcome the inherently lower wood density through deploying planting stock with a higher GF Plus rating for density although deploying genetically improved stock will not completely close the gap in wood density between the highest and lowest sites, which is approximately 75 kg m^{-3} (Cown et al. 1991; Palmer et al. 2013). However, the increase in wood density of a stand with a GF Plus rating of 27 over one with a rating of 18 is almost sufficient to offset the 25 kg m^{-3} reduction in wood density that is predicted to occur in stands

Table 3 Details of trials used for model validation showing actual and predicted mean outerwood density for each trial. The slopes of linear regression models between actual and predicted wood densities within each trial, along with their 95 % confidence intervals. The overall slope is derived from a model fitted to the combined data with separate intercepts for each trial and a common slope parameter

Trial	Forest	No. of families	GF Plus range	Age (years)	Actual mean density (kg m^{-3})	Predicted mean density (kg m^{-3})	Actual vs. predicted (kg m^{-3})	Slope of actual vs. predicted density
FR123/6	Tangoio	14	7–19	17	389	396	−7	1.20 ± 0.83
FR123/5	Takitoa	18	7–19	17	394	360	34	1.14 ± 0.81
FR123/1	Tarawera	18	7–19	17	428	416	12	1.77 ± 0.79
FR170/1	Woodhill	10	7–18	15	437	439	2	0.76 ± 0.83
FR305	Tarawera	44	0–33	18	424	425	−1	0.98 ± 0.19
FR353	Woodhill	41	2–23	16	424	436	−12	1.38 ± 0.36
Overall					416	412	4	1.09 ± 0.16

established on ex-pasture sites compared with more traditional forest sites (Beets et al. 2007).

Several key assumptions have been made in the incorporation of genetic improvement into the wood density model. Firstly, it was assumed that genetic improvement can be modelled in the same manner that site quality is incorporated into a growth model. This means that the difference in density between seedlots increases with ring number from the pith, rather than just being a constant. This is probably a reasonable assumption, on average, but for individual genotypes, it might not be the case (e.g. Ivković et al. 2013). This also assumes that GF Plus density ratings based on young tree data are a robust predictor of outerwood density at harvest age (i.e. 25–30 years). Previous research in radiata pine has shown that the genetic correlation between early-age assessments of wood density and those made at harvest age are moderate to high, generally exceeding 0.7–0.8 after a cambial age of 3 years (Dungey et al. 2006; Kumar and Lee 2002; Li and Wu 2005; Wu et al. 2007). This provides a degree of confidence that families that are assessed as having a higher GF Plus rating for density will indeed have higher outerwood density at rotation age. Importantly, the validation of the model against independent data confirms that it reliably predicts differences in wood density between families of varying GF Plus density ratings at mid-rotation ages of 15–18 years.

Table 4 Summary results from Forecaster simulations with three levels of "GF Plus" genetic improvement across sites with four levels of Wood Density Index

Site-level Wood Density Index (kg m^{-3})	GF Plus wood density rating	Log average density (kg m^{-3})	Percentage of logs exceeding 400 kg m^{-3}
380	18	341	1.9
380	22	349	2.8
380	27	356	5.0
400	18	362	7.8
400	22	370	12.8
400	27	378	19.8
420	18	366	10.3
420	22	373	16.2
420	27	380	22.5
440	18	381	23.4
440	22	388	31.3
440	27	395	40.3

In implementing the model, it has been assumed that the magnitude of the expression of genetic gain is the same on all sites. Studies in radiata pine have shown that there is little evidence of a genotype x environment interaction for wood density (Burdon and Low 1992; Gapare et al. 2009; Wu et al. 2008). This indicates that rank changes are unlikely between families with different levels of genetic improvement across different sites. However, it is not known whether a change in GF Plus density rating of one unit will produce a change in Wood Density Index of 2.16 kg m^{-3} on all sites. For growth traits, the greatest expression of genetic variation and the largest heritability (hence the greatest gains) come from the most productive sites (Burdon et al. 2008; Kimberley et al. 2015b). It is possible that a similar situation could occur for wood density with the greatest gains occurring on the sites with the highest values of the Wood Density Index. However, the validation study of six sites included in this paper shows no evidence of this, although additional data from a greater number of sites would be required to confirm this.

The final assumption relates to the incorporation of the model into the Forecaster modelling system. At present, users of the model are able to increase the GF Plus rating for density, without it having any impact on growth. While an adverse genetic correlation exists between growth and wood density (Burdon and Low 1992; Jayawickrama 2001; Wu et al. 2008), this is not represented directly in Forecaster. In their analysis of 13 published studies that have estimated the genetic correlation

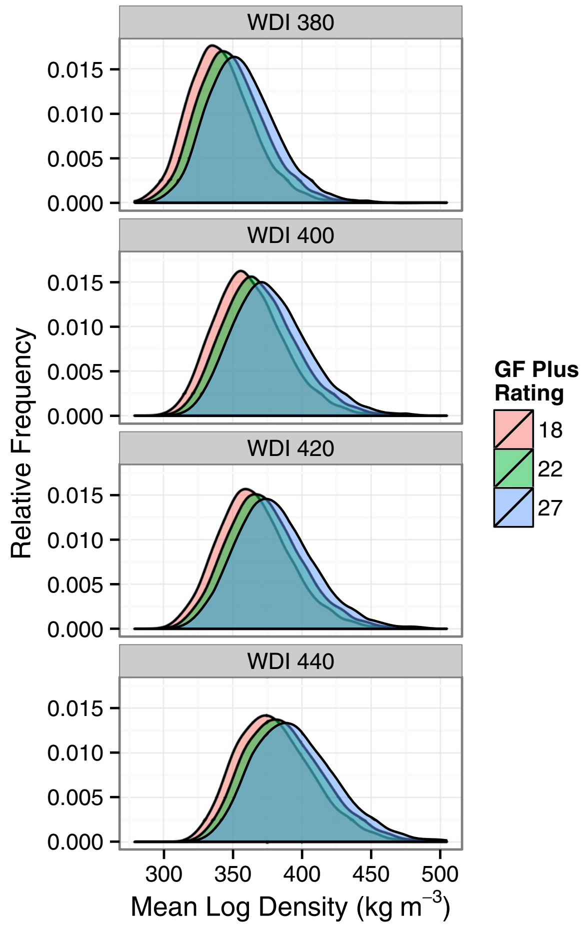

Fig. 4 Distribution of whole-log wood density for stands established using planting stock with different levels of genetic improvement growing on sites with different values of Wood Density Index (WDI)

between diameter growth and wood density for radiata pine, Wu et al. (2008) reported that average values for each individual publication were all negative, ranging from −0.97 to −0.08, with a grand mean of −0.48. However, Burdon and Low (1992) suggested that it is difficult to establish the true trade-off between wood density and per-hectare stem volume production, as the relationship between wood density and stem diameter growth can be modified by competitive influences, particularly as a closed stand gets older.

The Forecaster modelling system also includes a multiplier for growth that is based on the GF Plus rating for growth (Kimberley et al. 2015b). It is presently incumbent upon the user of the model to recognise potential hard trade-offs between volume production and wood density and to select appropriate GF Plus values for growth and wood density. A limitation on the amount of concurrent improvement in both D_{BH} and density is needed in order to ensure that predictions, particularly for future scenarios of trait improvement, are realistic. Further work is recommended to address this issue, so that forest managers can make informed decisions around the growth implications of deploying planting stock with a higher wood density rating.

The Forecaster modelling system also includes models for other wood properties, such as modulus of elasticity and stress wave velocity (West et al. 2013). These models for different wood properties are uncoupled, so, for example, increasing wood density will not increase modulus of elasticity or stress wave velocity (a non-destructive measure of wood stiffness) when it is known that density is a major driver of wood stiffness (Evans and Ilic 2001). Again, further research is needed to couple these models together, so that forest managers can better understand the impacts of genetic improvement on wood stiffness, rather than simply log average density.

Conclusions

The effect of genetic improvement on radiata pine wood density was quantified by developing a linear relationship between GF Plus rating for wood density and Wood Density Index (defined as the breast height outerwood density at age 20 years for a stand planted between 1990 and 2000). Quantifying the effect of genetic improvement in this way enables it to be readily incorporated into existing modelling systems, which in turn enables the effects of different levels of genetic improvement on whole-log average density to be evaluated. Forest managers can use these modelling systems to estimate wood density in radiata pine plantations for any site and management regime established using tree stocks with a specific wood density rating. These analyses can be used to support decision making on what seedlot or genotype could be deployed on a particular site in order to meet management goals.

Competing interests

All authors declare that they have no competing interests.

Authors' contributions

MOK developed the modelling approach, undertook the data analysis and contributed to writing the manuscript. JRM and HSD contributed to writing the manuscript. All authors read and approved the final version of the manuscript.

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