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Modelling microfibril angle variation in New Zealand-grown radiata pine

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Abstract

Background: Microfibril angle (MFA) is a property of wood cell walls that has a strong influence on end-product quality, particularly for solid timber. Forest managers, tree breeders and wood processors require more quantitative information on the inter- and intra-stem variation in MFA in order to understand the impacts of their decisions on wood quality. The aim of this study was to develop parametric models that can be used to predict the intra- and inter-stem variation in MFA in radiata pine (*Pinus radiata* D. Don) trees growing in New Zealand

Methods: Empirical models were developed using a dataset that contained records from 347 trees in which radial profiles of MFA have been measured at different heights up the stem. Radial variation in MFA was modelled as a function of cambial age using both a modified logistic function and a modified Michaelis-Menten equation. Additional terms were added to these models to account for differences in MFA with relative height up the stem.

Results: Values of MFA ranged from more than 40° near the pith to approximately 10-15° in the outerwood. Values greater than 30° were largely confined to the inner rings of the butt logs. A variance components analysis showed that most of the variation in MFA occurred within stems, with less than 15% of the variation due to differences between sites. The final models were able to account for 57-63% of the variation in MFA and inclusion of a relative height term significantly improved the model fit.

Conclusions: Radiata pine has a region of high microfibril angle in the first 10-15 growth rings from the pith, particularly at the base of the tree. Growth rate had a small positive influence on average MFA (wider rings resulting in higher MFA values). Site differences were small, indicating that regional variation in wood stiffness is due more to the known trends in wood density. The models developed here can be coupled to growth models to examine how the combination of site productivity and silvicultural regime affect the size of the central zone containing high MFA wood.

Keywords: Microfibril angle; Wood properties; Radiata pine; Radial variation; Ultrastructure

Background

The mechanical and physio-mechanical properties (mainly stiffness, shrinkage and stability) of wood are determined by the fundamental structure of its cells (Barnett and Bonham 2004; Cave 1969; Harris and Meylan 1965; McLean et al. 2010; Wardrop and Preston 1947). Studies in radiata pine (*Pinus radiata* D. Don) and other softwood species have shown that the two most influential wood properties are basic density and the angle of the cellulose microfibrils (MFA) in the S2 layer of wood cell walls (Cown et al. 1999; Donaldson 1997; Wagner et al. 2012; Walker and Butterfield 1995; Walker 1996; Xu and

Walker 2004). Microfibril angle has been considered so important that several authors have proposed using it as a criterion for differentiating juvenile and mature wood (Clark et al. 2006; Mansfield et al. 2009). Longitudinal shrinkage and stiffness of radiata pine wood (and in wood of other species) are adversely correlated with high MFA (Astley et al. 1998a, b; Evans et al. 2001), which has negative consequences for the utilisation of the wood from parts of a tree where there is high MFA. However, there is only general information describing the variation in MFA within and between trees. Few, if any, empirical models exist that are able to quantify the patterns of variation that are observed in radiata pine MFA. This is partly due to difficulties in collecting large

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datasets on MFA variation using many of the early measurement techniques, which were based on microscopy and were relatively slow (Batchelor et al. 1997; Donaldson 2008; Verbelen and Stickens 1995). However, other methods such as near-infrared spectroscopy (Schimleck and Evans 2002) and X-ray diffraction (Cave 1966, 1997; Evans 1999) enable data on MFA to be more readily collected on large numbers of samples. The latter method is widely used due to automation and the possibility of increased resolution of measurements of within-growth ring variation (Evans et al. 2001).

Previous studies that investigated the within-tree variation in MFA found that very large values of MFA (circa 45°) are common in the innermost growth rings (Donaldson 2008). These values decrease rapidly across the corewood zone, which generally constitutes the first 10 to 15 growth rings from the pith (Cown 1992), before stabilising at values of 10-15° in the outerwood. For a given cambial age, values of MFA decline with increasing distance up the stem and the rate of decline in MFA with increasing cambial age is also generally lower further up the stem. The value of MFA has also been found to stabilise at an earlier cambial age further up the stem (Butterfield 1997; Cave and Walker 1994; Cown et al. 2004; Donaldson 1992, 1993; Evans et al. 2001; Watt et al. 2011). Similar within-tree patterns in MFA have been observed in a number of other conifer species (Auty et al. 2013; Jordan et al. 2005; Mansfield et al. 2009; Megraw 1998) and also in hybrid poplars (Fang et al. 2006). High values of MFA that are observed near the pith have been hypothesised to provide young trees with the flexibility to bend through large angles, in response to wind and snow loading, without breaking (Barnett and Bonham 2004; Booker and Sell 1998; Lichtenegger et al. 1999).

More quantitative information on the variation in MFA within and between trees is required by forest managers and wood processors in order to understand the implications of past and proposed silvicultural practices on the quality of the forest resource. For example, the reduction in rotation length and the move to more widely spaced stands has resulted in trees with a greater proportion of juvenile wood with high MFA, low stiffness and high longitudinal shrinkage (Zobel and Sprague 1998). Wider tree spacing also results in an increase in radial growth rates, which can be further enhanced through treatments such as fertilisation and weed control. Research in other species has shown that treatments which enhance radial growth can affect MFA (Lindström et al. 1998; Lundgren 2004; Sarén et al. 2004). Therefore, it is important to determine whether MFA is simply a function of cambial age or whether it is also affected by rate of growth as expressed through growth ring width. Developing higher resolution wood property models that are ultimately able to be linked

to growth models is a constructive step towards better understanding the effects of factors such as site and silviculture on end product performance (Houllier et al. 1995; Kellomaki et al. 1999; Leban et al. 1996; Seifert 1999).

Models for the radial and vertical trends in MFA have been developed for loblolly pine (*Pinus taeda* L.) (Jordan et al. 2005, 2007), Scots pine (*Pinus sylvestris* L.) (Auty et al. 2013), lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.) (Wang and Stewart 2012) and *Acacia mangium* (Abdullah et al. 2010; Tabet et al. 2012), where cambial age and height in the stem have been identified as the main contributors to variation. An early attempt to describe MFA variation in radiata pine was a model based on data from polarised light studies (Tian and Cown 1995). Since the development of this early model, considerable amounts of data have been collected on radiata pine MFA. Most of these data have been collected using the SilviScan instrument (Evans et al. 2000). Ring-level data are now available from different heights in the stem for trees growing across the range of site types where radiata pine typically grows in New Zealand. Using available data on radiata pine MFA, the overall objectives of this study were to: (1) quantify the extent of variation in MFA within and between trees; (2) develop empirical models that are able to explain the observed intra-stem patterns in MFA; and (3) to determine whether observed radial patterns are affected by growth rate.

Methods

Data sources

A database was assembled from previous studies containing ring-level values of MFA that were obtained from 26 sites across New Zealand spanning the extreme north to the extreme south of New Zealand (Table 1). Data were obtained from 347 radiata pine trees ranging in age from 18 to 33 years. In most cases, at least ten trees per site and four heights per tree are represented, with individual growth ring MFA data from pith to bark. The orientation of the radial strips that were cut from these discs was selected to avoid areas of visually obvious compression wood which is known to exhibit abnormally high values of MFA. The common feature of the data selected for model construction was that data were obtained from several heights within sampled trees (typically 0, 1.4, 5 and 20 m from the base of the stem) and all radial positions were represented. All of the MFA data were obtained using SilviScan (Evans et al. 1999). Ring-width data were also available from SilviScan and were calculated using the ring boundaries identified by SilviScan.

Total tree height measurements were absent in most studies. Because of the different ages in the dataset and the need to be able to predict the intra-stem patterns in

Table 1 Summary of the studies in which microfibril angle data were collected

Site No.	Region	Forest	Age (yrs)	n (trees)	Sample heights (m)
1	Auckland	Aupouri	25	10	0, 1.4, 5, 20
2	Auckland	Mangakahia	23	40	0, 1.4, 5, 20
3	Auckland	Athenree	25	10	0,1.4, 5,10,15,20,25
4	Auckland	Woodhill	33	20	1.4
5	Rotorua	Kaingarua	18	20	1.4
6	Rotorua	Kaingarua	18	20	1.4
7	Rotorua	Kaingarua	25	25	0, 5, 10
8	Rotorua	Kaingarua	25	10	0, 1.4, 5, 20
9	Rotorua	Kaingarua	25	10	0, 1.4, 5, 20
10	East Coast	Ruatoria	25	10	0, 1.4, 5, 20
11	Hawkes Bay	Mohaka	25	10	0, 1.4, 5, 20
12	Wellington	Lismore	25	6	0, 1.4, 5, 20
13	Wellington	Ngaumu	25	10	0, 1.4, 5, 20
14	Nelson	Wyeburn – Marlborough	18	20	1.4
15	Nelson	Lansdowne – Marlborough	18	20	1.4
16	Nelson	Golden Downs	25	25	0, 5, 10
17	Nelson	Rabbit Island	25	10	0, 1.4, 5, 20
18	Nelson	Golden Downs	25	10	0, 1.4, 5, 20
19	Nelson	Waimea	25	10	0, 1.4, 5, 20
20	Nelson	Golden Downs	33	7	1.4
21	Canterbury	Ashley	25	9	0, 1.4, 5, 20
22	Canterbury	Eyrewell	25	10	0, 1.4, 5, 20
23	Canterbury	Waimate	25	10	0, 1.4, 5, 20
24	Southland	Blackmount – Southland	25	2	0, 1.4, 5, 20
25	Southland	Rowallan – Southland	25	7	0, 1.4, 5, 21
26	Southland	Longwood – Southland	25	6	0, 1.4, 5, 22

MFA for a wide range of tree sizes, it is helpful to know the relative height that each sample was taken from as well as the absolute height. To overcome the problem of missing heights, total height was predicted for each tree using a compatible volume and taper function along with data on the diameter and heights of each disc sampled from the tree. For each tree, the estimated value of total height was adjusted incrementally and the difference between the actual and predicted diameters of the discs determined. The predicted height of each tree was selected, such that the difference between actual and predicted disc diameters was minimised (Appendix 1). When tested using a dataset where total tree height was known, this approach was able to predict tree height to within 5% of the measured value. The relative height that each disc was sampled from was estimated by dividing the absolute sampling height by the predicted height of the corresponding tree.

Data analyses

Because the data had a hierarchical structure (i.e. growth rings within discs, within trees, within stands), a mixed-modelling approach was adopted to ensure that appropriate estimates of parameter standard errors were obtained and tests of parameter significance were valid (Pinheiro and Bates 2000). A variance components analysis was undertaken using Restricted Maximum Likelihood to determine how much of the variation in MFA was attributable to each stratum (i.e., site, tree, disc or ring) in the dataset. A number of different model forms were then evaluated for their ability to explain the radial trends in MFA. Once the most suitable model form was identified, the second step was to determine whether the model parameters varied as a function of height within the tree. Model selection was based on visual analysis of plots of the normalised residuals versus fitted and explanatory variables (Pinheiro and Bates 2000) and Akaike's information criterion (AIC, (Akaike 1974)), which measures the

relative adequacy of different nested models. Akaike's information criterion is used when comparing models fitted to the same dataset and the model with the lower AIC is generally preferred. Parameter estimates were obtained using the maximum-likelihood method, and only those parameters that were significant ($p < 0.05$) were retained in the final models. Two sets of fit indices (R^2) were calculated using the equations given in Parresol (Parresol 1999). In the first set, the predicted values were estimated from only the fixed-effects terms of each model, and in the second, they were calculated from both the fixed and random effects. All statistical analyses were carried out using functions contained in the nlme library (Pinheiro et al. 2012) of the R statistical programming environment (R Development Core Team 2013).

Two model forms were used to explain the radial variation in MFA. The first was a modified logistic function, which predicts MFA as a function of ring number from the pith. It has previously been applied to loblolly pine (Jordan et al. 2005) and has the following form:

$$y_{ijkl} = \frac{\alpha_0}{1 + e^{\alpha_1 \cdot CA_{ijkl}}} + \alpha_2 + a_{2,i} + a_{2,ij} + a_{2,ijk} + \varepsilon_{ijkl} \quad (1)$$

where y_{ijkl} is the mean MFA (degree) in each annual growth ring, CA_{ijkl} is the cambial age (years) of the l^{th} annual ring of the k^{th} disc from the j^{th} tree at the i^{th} site, α_0 , α_1 and α_2 are fixed effects parameters to be estimated, representing the initial value near the pith, the rate parameter and the lower asymptote, respectively; ε_{ijkl} is the random error due to the l^{th} annual ring of the k^{th} disc from the j^{th} tree at the i^{th} site. Since α_2 assumes a constant value across all cambial ages, this parameter was allowed to vary randomly in each stratum. Hence, $a_{2,i}$, $a_{2,ij}$ and $a_{2,ijk}$ represent the random effects of the i^{th} site, the j^{th} tree from the i^{th} site, and k^{th} disc from the j^{th} tree from the i^{th} site, respectively.

In order to test whether there is a growth rate (ring width) effect on MFA, an alternative model, in the form of a modified Michaelis-Menten equation, was also fitted as it can accommodate a ring-width term (Auty et al. 2013). In this study, we used a standard Michaelis-Menten equation with an added intercept term:

$$y_{ijkl} = \frac{\beta_0 CA_{ijkl}}{\beta_1 + CA_{ijkl}} + \beta_2 + b_{2,i} + b_{2,ij} + b_{2,ijk} + \varepsilon_{ijkl}$$

with $\beta_0 = \beta_{00} + \beta_{01} RW_{ijkl}$

(2)

where RW_{ijkl} is the width (millimetres) of the l^{th} annual ring of the k^{th} disc from the j^{th} tree at the i^{th} site, β_{00} , β_{01} , β_1 and β_2 are the fixed effects parameters to be estimated. In this equation, β_1 represents the rate parameter

and β_2 the intercept, while the lower asymptote is given by $\beta_1 + \beta_2$. The random effects of the i^{th} site, j^{th} tree in i^{th} site and k^{th} disc from j^{th} tree in i^{th} site are given by $b_{2,i}$, $b_{2,ij}$ and $b_{2,ijk}$, respectively. In order to incorporate the increasing influence of ring width at higher cambial ages, the β_0 parameter was allowed to vary as a function of ring width. This had the effect of changing the asymptotic mature wood value of MFA without altering the initial value near the pith.

In fitting the models to the data, heteroscedasticity was modelled as a power function of the absolute values of cambial age, while a first-order autoregressive correlation structure AR(1) was applied to model correlation among observations at successive cambial ages within each grouping factor. More details about these variance and autocorrelation functions are given in Auty et al. (2013) and Jordan et al. (2005).

For both models, the fixed-effects parameters were also modified to include possible effects of height up the stem. Linear, log-linear and quadratic relative height terms were added to the models given by Eqs. (1) and (2) following the approach described in Jordan et al. (2005). For terms involving the natural logarithm of relative height, a small value (0.1) was added to the relative height term to avoid zero values, which would have resulted in infinite values when the natural logarithm of this term was taken.

In order to visualise the intra-stem pattern in MFA, the models were then applied to a single 29-year-old tree (DBH = 32.8 cm, height = 36.9 m) that had spatial information on ring number from the pith generated at 5 mm resolution in the radial direction and 100 mm resolution in the longitudinal direction. This information was generated using the Forecaster growth and yield modelling system (West et al. 2013).

Results

Microfibril angle was found to consistently decrease from pith to bark at all stem levels (Figure 1). The highest values were observed near the pith in the lower part of the stem, i.e. below 5 m from the base of the stem. Above this height, values of the MFA near the pith appeared to be relatively constant with increasing height up the stem (Figure 1). The variance components analysis performed on the logarithm of MFA, showed that 68% of the total variation in MFA was due to radial variation within trees, 15% was due to vertical variation within stems, 3% was due to differences among trees within a stand and 14% was due to differences between sites.

The modified logistic function (Eq. 1) was able to explain approximately 46% of the variation in MFA based on the fixed effects alone (66% when including the random effects of site, tree and disc) (Table 2). The model based on the modified Michaelis-Menten equation (Eq. 2)

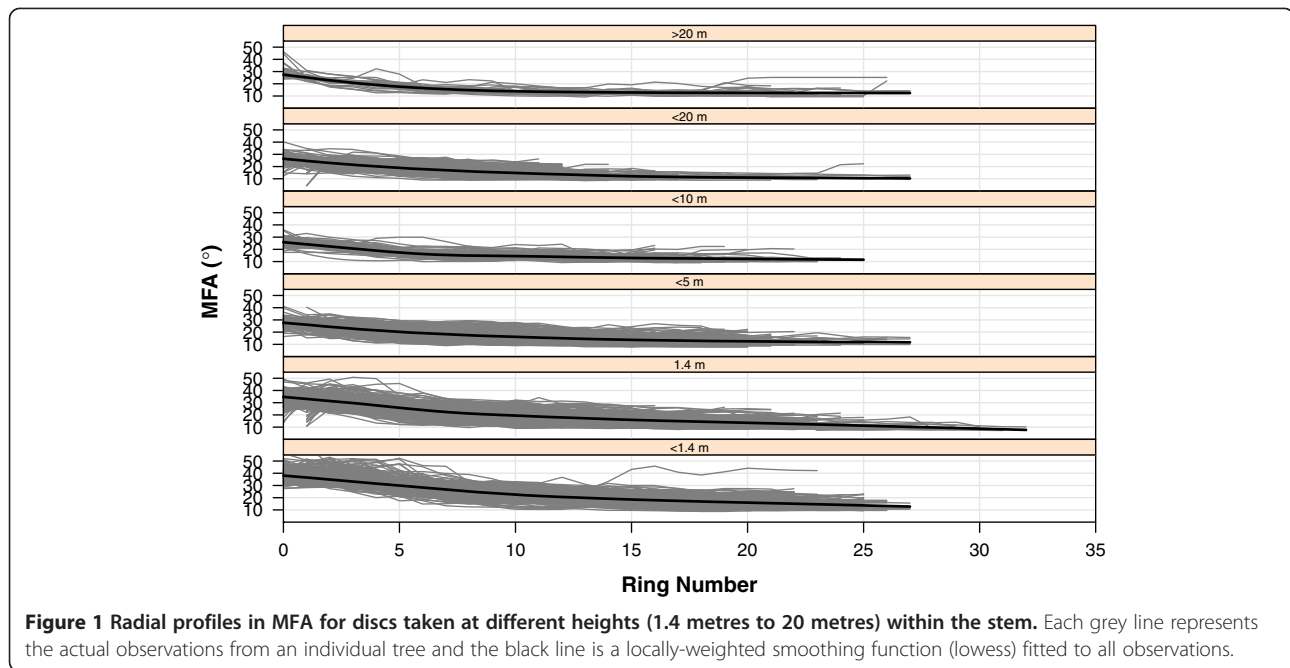


Figure 1 Radial profiles in MFA for discs taken at different heights (1.4 metres to 20 metres) within the stem. Each grey line represents the actual observations from an individual tree and the black line is a locally-weighted smoothing function (lowess) fitted to all observations.

performed better than the modified logistic function and was able to explain 54% of the variation in MFA based on the fixed effects (Table 3). The ring-width term in this model was positive and significant, indicating that there is a small positive effect of growth rate on MFA (Table 3). This is consistent with previous studies in other species (Auty et al. 2013; Downes et al. 2002; Herman et al. 1999; Lindström et al. 1998; Sarén et al. 2004; Wimmer et al. 2002) and indicates that treatments that increase growth rates could have a negative impact on wood stiffness.

Modelling variation with height

Adding linear terms for relative height (HT_{rel}) to each of the parameters in the modified logistic function (see Eq. (3)) resulted in a significant improvement in the model fit and all the height terms were significant. Quadratic terms for HT_{rel} were added to the model (results not shown) and these were found to be significant, but the resulting predictions of MFA were found to be non-plausible, so these terms were dropped. The natural logarithm of $HT_{rel} + 0.1$ was also found to be significant in the model, with the exception of the term added to

the lower asymptote (α_5) (Eq. 4). The model given by Eq. (3) was able to explain 62% of the variation in MFA based on the fixed effects alone (78% when the random effects of site, tree and disc were included) (Table 4). The modified logistic equation with $\log HT_{rel}$ terms added (Eq. 4) performed slightly better and was able to explain 65% of the variation in MFA (81% when the random effects of site, tree and disc were included). The parameter estimates for the two models are given in Table 5.

$$y_{ijkl} = \frac{\alpha_0 + \alpha_3 HT_{rel,ijk}}{1 + e^{(\alpha_1 + \alpha_4 HT_{rel,ijk}) \cdot CA_{ijkl}}} + (\alpha_2 + \alpha_5 HT_{rel,ijk}) + a_{2,i} + a_{2,ij} + a_{2,ijk} + \varepsilon_{ijkl} \quad (3)$$

Table 2 AIC, log-likelihood and fit indices for the models to predict MFA given by Eqs. 1 & 2

Model	AIC	Log-likelihood	Fit indices (R^2)			
			Fixed	Site	Tree	Disc
Eq. (1)	89381	-44681	0.46	0.54	0.57	0.66
Eq. (2)	86235	-43107	0.54	0.59	0.61	0.64

Table 3 Parameter estimates and associated standard errors (s.e.) and tests of significance for the models given by Eq. (1) and Eq (2)

Parameter	Estimate	s.e.	t-value	p-value
Eq. (1)				
α_0	42.897	0.402	106.607	<0.001
α_1	0.163	0.002	79.901	<0.001
α_2	12.413	0.474	26.214	<0.001
Eq. (2)				
β_{00}	-32.350	0.445	-72.659	<0.001
β_1	3.454	0.128	27.020	<0.001
β_2	39.932	0.689	57.999	<0.001
β_{01}	0.524	0.007	70.130	<0.001

Table 4 AIC, log-likelihood and fit indices for the models to predict MFA given by Eqs. 3-6

Model	AIC	Log-likelihood	Fit indices (R ²)			
			Fixed	Site	Tree	Disc
Eq. (3)	85873	-42924	0.62	0.70	0.75	0.78
Eq. (4)	85477	-42726	0.65	0.73	0.78	0.81
Eq. (5)	83964	-41970	0.59	0.65	0.67	0.70
Eq. (6)	83934	-41955	0.62	0.67	0.70	0.70

$$y_{ijkl} = \frac{\alpha_0 + \alpha_3 \log HT_{rel,ijk}}{1 + e^{(\alpha_1 + \alpha_4 \log HT_{rel,ijk}) \cdot CA_{ijkl}}} + \alpha_2 + a_{2,i} + a_{2,ij} + a_{2,ijk} + \varepsilon_{ijkl} \quad (4)$$

Relative height and $\log(HT_{rel})$ terms were also found to be significant when added to the Michaelis-Menten equation (Eqs. 5 & 6). The models given by Eqs. 5 and 6 were able to explain 59 and 62% of the variation in MFA, respectively (Table 4). Parameter estimates for the

Table 5 Parameter estimates and associated standard errors (s.e.) and tests of significance for the models given by Eqs. (6)-(9)

Parameter	Estimate	s.e.	t-value	p-value
Eq. (6)				
α_0	50.510	0.423	119.295	<0.001
α_1	0.148	0.002	69.569	<0.001
α_2	13.209	0.457	28.877	<0.001
α_3	-51.438	2.625	-19.596	<0.001
α_4	0.503	0.027	18.576	<0.001
α_5	2.069	0.510	4.060	<0.001
Eq. (7)				
α_0	15.275	1.117	13.674	<0.001
α_1	0.335	0.010	34.670	<0.001
α_2	13.458	0.451	29.871	<0.001
α_3	-16.783	0.588	-28.566	<0.001
α_4	0.082	0.004	18.410	<0.001
Eq. (8)				
β_0	-32.156	0.418	-76.850	<0.001
β_1	3.663	0.138	26.494	<0.001
β_2	40.178	0.657	61.124	<0.001
β_3	0.518	0.008	67.041	<0.001
β_4	-5.462	0.556	-9.818	<0.001
Eq. (9)				
β_0	-32.109	0.407	-78.874	<0.001
β_1	3.718	0.140	26.509	<0.001
β_2	36.190	0.710	50.987	<0.001
β_3	0.517	0.008	66.477	<0.001
β_4	-1.895	0.154	-12.310	<0.001

two models are given in Table 4. Based on the goodness of fit statistics (Table 5), it appears that the model given by Eq. (4) is able to explain the greatest amount of variation in MFA, although all four models perform similarly.

$$y_{ijkl} = \frac{(\beta_0 + \beta_3 RW_{ijkl}) CA_{ijkl}}{\beta_1 + CA_{ijkl}} + \beta_2 + \beta_4 HT_{rel,ijk} + b_{2,i} + b_{2,ij} + b_{2,ijk} + \varepsilon_{ijkl} \quad (5)$$

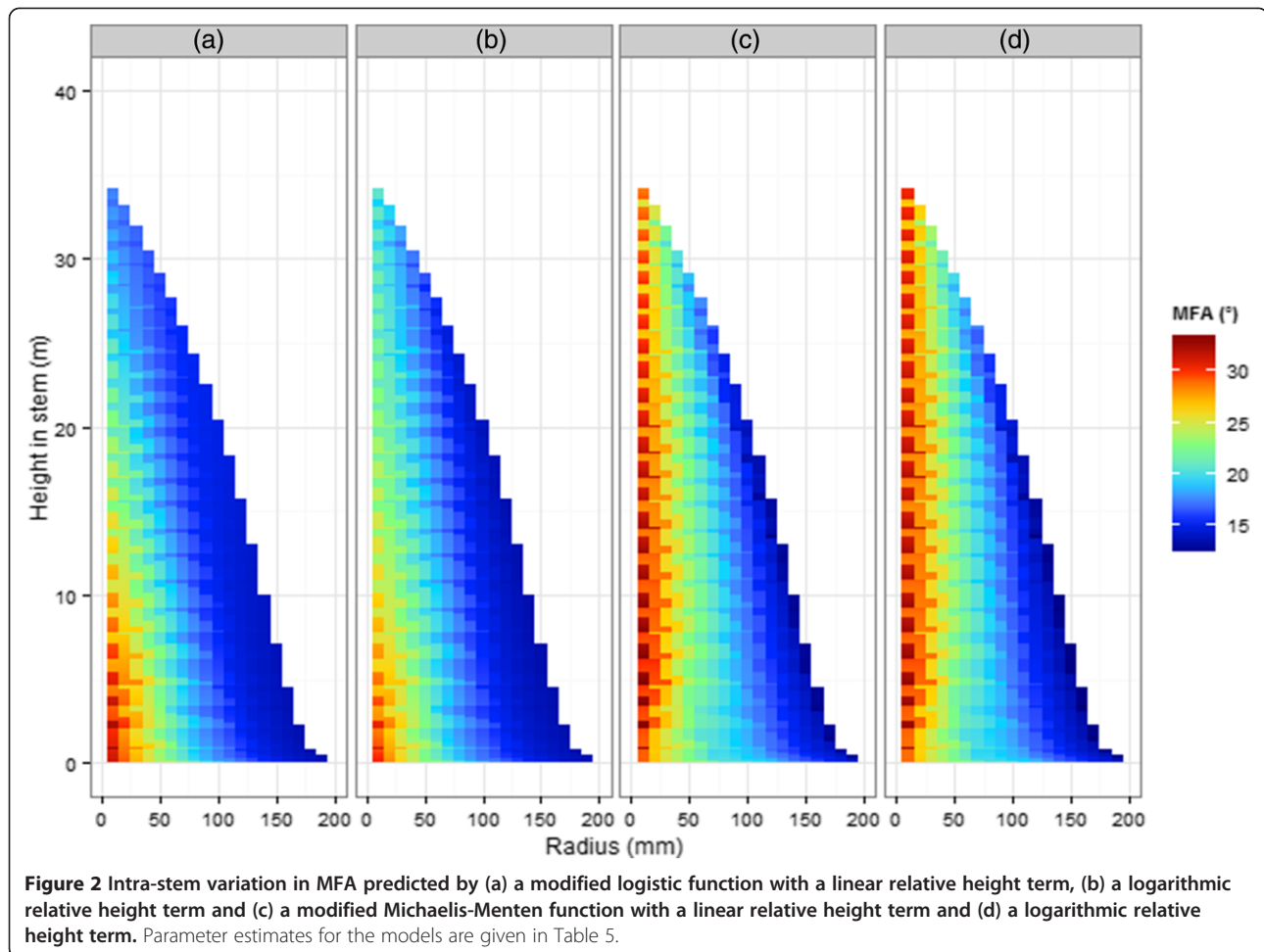
$$y_{ijkl} = \frac{(\beta_0 + \beta_3 RW_{ijkl}) CA_{ijkl}}{\beta_1 + CA_{ijkl}} + \beta_2 + \beta_4 \log HT_{rel,ijk} + b_{2,i} + b_{2,ij} + b_{2,ijk} + \varepsilon_{ijkl} \quad (6)$$

Visualisation of model predictions

The intra-stem variation in MFA predicted by the four models (Eqs. 3-6) is shown in Figure 2. Qualitatively, the model based on $\log(HT_{rel})$ appears to give a more realistic representation of the low stiffness core at all heights in the tree than the model simply based on HT_{rel} , but the predicted low stiffness zone at the base of the tree is not as severe (Figure 2a and b). The predictions from the two Michaelis-Menten equations were very similar to each other (Figure 2c and d), but indicated that the high MFA zone extended much higher in the stem than the modified logistic model.

Discussion

Despite the acknowledged influence of MFA on wood performance, there is relatively little information on the factors influencing its magnitude (apart from cambial age and height in the stem) in comparison to wood properties such as density. This is not altogether surprising as the analyses undertaken in this study showed that approximately 82% of the variation in MFA was in the longitudinal and radial directions within the stem, with less than 15% of the variation occurring among sites. The level of variation between sites was much higher than the 2% found for Scots pine by Auty et al. (2013), but lower than that found in loblolly pine (Jordan et al. 2006). These differences presumably reflected the relative distribution of sites sampled in New Zealand compared with these other two studies. While site-level variation was relatively small, it is still considered worthwhile to investigate this further as previous studies have shown that MFA is affected by exposure to wind (Telewski 1989) and mean temperature during the growing season (Cortini et al. 2014). Other site factors, such as soil type and rainfall distribution, may also be important, particularly when studies have shown that irrigation and fertilisation can increase MFA (Downes et al. 2002; Wimmer et al. 2002). Previous studies have also shown



that there are genetic differences in MFA in radiata pine and other species (Donaldson 1993; Vainio et al. 2002), while it has also been shown to be a moderately heritable trait (Baltunis et al. 2007; Burdon and Low 1992; Dungey et al. 2006; Gapare et al. 2007; Jayawickrama 2001; Wu et al. 2008). The genetic origin of the study trees is very diverse, with many originating from open-pollinated families, and this is likely to have accounted for some of the unexplained variation in the models (Cortini et al. 2014). There are several large-plot trials in New Zealand that contain trees from different, but known, genetic origins (e.g. Carson et al. 1999), which could provide potential future opportunities to investigate genetic differences in radiata pine MFA in more detail.

The models developed here have quantified much previous knowledge about intra-stem variation in MFA. Visualisations of the two-dimensional patterns in MFA highlight the issue of juvenile wood (corewood) in radiata pine, which in addition to having high MFA also has low wood density and high spiral grain angle (Burdon et al. 2004; Cown 1992). Solid timber cut from this part of the tree will inevitably have low stiffness because of low

density and high MFA, and a high propensity to twist because of high spiral grain (Cown et al. 2010), so will be unsuitable for many appearance and structural applications. It is clear from this and other studies that high microfibril angle is a characteristic feature of the juvenile core of radiata pine and many conifers, and it is adversely affected by increased growth rates (Dumbrell and McGrath 2000; Herman et al. 1999; Sarén et al. 2004; Watt et al. 2011). The impact of the presence of juvenile wood is exacerbated by the positive relationship between growth rate and MFA. This presents a challenge since silviculture in New Zealand has traditionally favoured rapid diameter growth – so not only is the core larger, but its properties are poorer. However, if increasing site productivity is the main goal of forest management there are options for increasing overall volume while restraining individual stem growth. Unfortunately, it is very difficult to restrict the size of the juvenile core and the overall proportion of juvenile wood through spacing, except at the extremes (West 1997), but more conservative thinning may give more uniform final crops with better average stem form, smaller branches and less radial

variation in wood properties. Silvicultural influences on the distributions of internal wood properties were not examined in this study, but analysis of data from replicated silvicultural trials has shown that tree spacing does have a significant influence on MFA (Lasserre et al. 2009; Watt et al. 2011). Therefore, while increased stand density may not reduce the size of the juvenile wood zone and the overall proportion of juvenile wood, it may improve the properties of the wood found in the first 10-15 growth rings from the pith.

Stiffness variation is best explained by a combination of MFA and wood density (Cown et al. 1999; Downes et al. 2002; Megraw et al. 1999). Given that site-level variation in MFA is relatively small, we hypothesise that regional differences in modulus of elasticity that are observed across New Zealand (Watt and Zoric 2010) are driven by differences in wood density (Palmer et al. 2013), rather than site-level differences in MFA. This hypothesis will be further tested using data from a subset of 17 sites which contain trees from the same seedlot, grown under the same silvicultural regime, and where data were collected on density, MFA and SilviScan-derived modulus of elasticity. Detailed information of soil properties and climate are also available, which will permit further investigation into possible explanatory variables responsible for site-level variation.

The models developed in this study are intended to be coupled to a growth model which enables the effects of different management practices and site productivity on the microfibril angle distribution and the size of this corewood zone to be examined. There are two important issues to consider here. Firstly, the models need to be tested against data from stands with contrasting growth rates, e.g. stands established at different densities or thinned to different densities. Factors such as crown size and shape also need to be considered as these might help to explain additional variation in MFA. Most of the data used to develop the models came from stands that had received similar silvicultural treatments and, therefore, their ability to accurately predict the effects of treatments such as thinning and pruning is untested. Secondly, forest managers who use such systems require an objective way to compare trees grown under different regimes. One way to do this would be to determine the proportion of the cross-sectional area of a disc or the volume of a log that has values of MFA above a certain threshold (say, 15°). This would also provide a quantitative measure that forest managers could use to compare regimes.

There are several limitations to the data used to develop the models as well as the models themselves. Firstly, some caution should be exercised when interpreting the longitudinal trends in MFA within a stem, particularly in the uppermost part of the stem, as most

of the data were collected from below 60% of relative height. Secondly, total height was not directly measured on the vast majority of sample trees, but was instead predicted from sectional measurements made along the stem. While this has introduced another potential source of error into the data, it is unlikely to have manifestly affected the results obtained from this study. However, the authors strongly recommend that tree height is measured in all future wood quality studies to better enable modelling of the intra-stem distribution of wood properties and to enable the mechanisms by which silvicultural treatments alter these properties to be elucidated. Thirdly, the data were collected from only a single pith-to-bark radial sample from each selected height along the stem. Therefore, potential circumferential variation in MFA is unknown and cannot be included in the model, although one study has suggested that this is not a significant source of error (Hein and Brancheriau 2011). A recently developed automated system (Emms and Hosking 2006) is able to provide information on the three-dimensional MFA variation within a wood disc, and hence within complete stems. The system measures the ultrasonic velocity in the longitudinal direction, which is strongly and negatively correlated with MFA determined by X-ray diffraction (Scion, unpublished data). Finally, the “best” models developed in this study were able to explain about 60% of the variation in MFA. The 40% unexplained variation is important as it is hypothesised that it is this variation, when superimposed on top of the explained variation (explained by the types of models developed in this study) which drives end product performance (Jonathan Harrington, Scion – pers. comm). More detailed analyses are needed to understand this variation and to be able to account for it in wood properties models, possibly through the introduction of random perturbations to the predictions from the models developed in this study.

Conclusions

This study summarises one of the most comprehensive datasets on MFA for a single species anywhere in the world. Approximately 82% of the total variation in MFA was due to differences within the stem of a tree, with less than 15% due to differences among sites. This intra-stem variation could be modelled as a function of cambial age and relative height within the stem, with the “best” models explaining about 60% of the variation in MFA. Like many other conifer species, radiata pine has a region of high microfibril angle in the first 10-15 growth rings from the pith, particularly at the base of the tree. Because of the silvicultural regimes that radiata pine is grown under (i.e. relatively wide initial spacing and short rotation lengths) the volume occupied by this high MFA wood is relatively high. The models developed in this

study are able to be coupled to growth models enabling the impacts of site productivity and silvicultural regimes on the MFA distribution with a tree to be investigated.

Appendix 1 – Derivation of method to estimate tree height from sectional measurements

For many studies contained in the dataset, total height of the trees was not measured during data collection. The total height of a given tree was estimated from the diameters and heights above the ground of the discs from the tree using a taper equation. A compatible polynomial volume-taper equation for radiata pine in New Zealand was used for this purpose, which has the following form:

$$d^2 = \frac{V}{kH} \left(\beta_1 X + \beta_2 X^2 + \beta_3 X^3 + \beta_4 X^4 + \beta_5 X^5 + \beta_6 X^{\beta_7} + \beta_8 X^{\beta_9} \right) \quad (A1)$$

where d is the inside bark diameter (cm) at height h (m) above the ground; V is the volume equation

$$V = D^{\alpha_1} \left(\frac{H^2}{H-1.4} \right)^{\alpha_2} \exp(\alpha_3);$$

k is $\frac{\pi}{4} \times 10^{-4}$, the constant for converting square diameter to basal area; H is total height (m) with 1.4 being breast height; D is outside bark diameter at breast height in cm; X is $\left(\frac{H-h}{H}\right)$; and α_1 to α_3 and β_1 to β_9 are equation coefficients.

Different sets of coefficients for Equation [A1] were available, including local coefficients specific to many of the forests where MFA data were collected. The compatible volume and taper equation for the direct sawlog regime developed by Katz et al. (1984) generally performed better than the local taper and volume functions, and hence was used to estimate the heights of trees in all forests.

The total height H , of a given tree, was numerically estimated from Equation [1] by searching for the value of H that gave a taper curve that minimised the sum of squared residuals given the observed diameters and heights above ground of the discs from the tree. This was achieved by use of a SAS macro that had been programmed to search across a range of total height values (0.5 m above the height above ground of the topmost disc to a distance of 60 m beyond this starting point), at intervals of 0.01 m, and return the value of H corresponding to the minimised sum of squared residuals. An evaluation of this approach showed that the total height estimates were generally reasonable. However, it was possible that total heights of a few of the trees were overestimated as their height estimates were beyond the expected maximum values for radiata pine trees of a

given age. Graphical plots of the taper equations of best fit (not shown), overlain on the disc diameter and height data from select trees across the range of tree dbh in the data, also showed that the total heights of the larger diameter trees were slightly overestimated, especially those trees where diameter at breast height was greater than 50 cm the topmost disc was sampled at only 10 m above the ground.

Competing interests

All authors declare that they have no competing interests.

Authors' contributions

JRM conceived the idea for the overall analysis of available data, undertook the data analysis and writing of the manuscript. DJC and RBMcK planned most of the wood quality assessments and contributed to the interpretation of the results and writing of the manuscript. All authors read and approved the final version of the manuscript.

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