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Modelling the Variation in Spiral Grain Angle and Microfibril Angle in Radiata Pine

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EXECUTIVE SUMMARY

Spiral grain angle (SGA) and microfibril angle (MFA) are two wood properties that have a strong influence on end-product quality, particularly for solid timber. Forest managers, tree breeders and wood processors require information on the inter- and intra-stem variation in these wood properties in order to understand the impacts of their decisions on wood quality.

A meta-analysis was undertaken of all known data on MFA and SGA collected from radiata pine (*Pinus radiata* D. Don) trees growing in New Zealand. A dataset was assembled that contained records from over 400 trees that had MFA measured at different heights up the stem and measurements of spiral grain angle from more than 1400 individual trees. A variance components analysis showed that most of the variation in both MFA and SGA occurred within the stem of a tree (see table below), with less than 15% of the variation in these properties due to differences between sites. Given that the data came from a wide range of sites, the relatively small amount on intra-site variation was unexpected. Similarly, the relatively small amount of tree-to-tree variation within a stand (3.5% for MFA and 14.2% for SGA) was also unexpected.

Wood property	Percentage of variation associated with each stratum					Total % variation accounted for by best performing model
	Radial	Longitudinal	Total intra-stem variation	Tree-to-tree variation within a site	Between site variation	
MFA	67.5	14.5	82.0	3.5	14.5	63%
SGA	55.4	23.1	78.5	14.2	7.3	30%

Different model forms were evaluated for their ability to account for the radial variation in MFA and SGA. A modified Michaelis-Menten equation based on cambial age (i.e. ring number from the pith) and ring width was able to explain approximately 53% of the variation in MFA. Microfibril angle decreased with increasing cambial age and was positively associated with ring width. This indicates that management interventions that accelerate growth may have an adverse effect on MFA. MFA also decreased with increasing height up the stem and hence all of the models to explain radial variation could be successfully modified to include a relative height (i.e. height in the stem relative to the total height of the tree) term. A modified logistic model that included cambial age and relative height terms explained approximately 63% of the variation in MFA. Visual inspection of predictions from this model applied to a simulated tree generated using FFR Forecaster indicated that these results were consistent with knowledge about MFA variation within a stem.

Various linear and nonlinear model forms were evaluated for their ability to predict the radial variation in SGA. The simple linear model based on cambial age performed best, but only explained 26% of the variation in SGA. However, this was better than similar studies in Norway spruce (*Picea abies* Karst.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Including a relative height term in this linear model increased the proportion of variation in SGA that was explained to 30%. Model results showed that SGA decreased from pith to bark and increased with height up the stem, with low values of SGA only found in the lower peripheral part of the stem.

By incorporating these models into a growth and yield simulation system such as FFR Forecaster they can be used by forest managers to estimate the proportion of a stem, disc or log with MFA or SGA values that exceed a certain threshold. This would provide a quantitative basis on which to compare different silvicultural regimes or the effect of increased tree growth. The significance of the ring width term in the Michaelis-Menten equation that was used to model the radial variation in MFA indicates that treatments that increase the radial growth rate of trees would be expected to have a negative effect on this property. While ring width data were not available for the SGA dataset, previous research described in the literature indicates that this property is also negatively associated with radial growth rate.

Further work is required to better understand the variation that was not explained by these models as it is hypothesised that it is this variation, when superimposed on the patterns that can be predicted by the models developed in this study, which really drives end product performance. The models developed here could be used to better understand this variation by applying them to the data collected in the destructive sampling project to remove the “baseline” trends in MFA and SGA. If the residual variation is essentially random and consistent between trees and sites, then it can be added to the models developed here and used to drive product quality simulations.

INTRODUCTION

The performance of many wood products, particularly solid timber, is strongly influenced by two wood properties: microfibril angle (MFA) and spiral grain angle (SGA). Forest managers, tree breeders and wood processors need accurate data on the inter- and intra-stem variation in these properties in order to understand the impacts of their decisions on the quality of the products that will be produced from trees. For example, this information is required in order to correctly determine the heritability of these traits and for assessing the impacts of site factors (e.g. site productivity, wind exposure) and silvicultural treatments such as initial spacing, timing and intensity of thinning and rotation length. Given the desire to increase the growth rates of our forests, it will be increasingly important to be able to quantify the impacts of such decisions on those wood properties that strongly affect utilisation.

In softwoods, microfibril angle is defined as the winding angle of the cellulose microfibrils in the S2 layer of the cell wall relative to the longitudinal axis of the tracheid [1-3]. A low value of MFA indicates that the cellulose fibrils have a small deviation from the vertical, while a large value indicates that they have a much flatter winding angle. MFA has a strong influence on the stiffness, strength, shrinkage properties and dimensional stability of solid timber [4-8]. Many different methods have been developed to measure MFA in individual fibres and solid wood samples. Two of the most common approaches are based on direct observation using polarised light microscopy and indirect observation using X-ray diffraction, which is possible because of the crystalline structure of the wood cell wall [9]. The latter method is widely used due to automation that enables large numbers of tracheids to be rapidly assessed and increased resolution, which allows measurement of within-growth ring variation [10]. The SilviScan instrument developed by CSIRO uses X-ray diffraction to estimate MFA in wood samples. Large numbers of radial samples from radiata pine (*Pinus radiata* D. Don) trees growing throughout New Zealand have been analysed using this instrument in order to quantify the variation in MFA.

Within tree variation in MFA has been studied for a number of species, including radiata pine. Very large values of MFA (circa 45°) are common in the innermost growth rings in conifers. These values fall rapidly across the corewood zone, which generally constitutes the first 10 to 15 growth rings, before stabilising in the outerwood [7, 11-17]. For a given cambial age, values of MFA decline with increasing height [11, 13, 18]. The rate of decline in MFA with increasing cambial age is generally lower as height increases and at greater heights MFA has been found to stabilise at an earlier cambial age [18, 19].

The second property that affects the performance of solid wood is spiral grain angle. Spiral grain angle (SGA) is defined as the orientation of fibres (tracheids) with reference to the longitudinal axis of the tree stem [20]. While the function of spiral grain and the process by which it is formed has created much debate in the scientific literature [21], the fact remains that a spiral grain angle of only a few degrees can cause problems. Lack of dimensional stability caused by spiral grain is one of the factors that has the greatest influence on the utilisation of wood from a wide range of species, including radiata pine [22]. The relatively high values of SGA found in radiata pine [23], particularly in juvenile wood, can cause twist in dry lumber, distortion in plywood sheets, surfacing problems during machining [24, 25] and are a major cause of drying degrade [26-28]. Given that twist accounts for at least 90% of the distortion problems in radiata pine solid timber [29], understanding the variation in SGA within and between trees and developing approaches to reduce SGA would help to reduce the amount of downgraded timber.

Grain orientation in most conifers, including radiata pine, follows a common (but not universal) pattern in which it is almost parallel to the axis of the stem near the pith, increases leftward (as viewed from the bark) with increasing distance from the pith, reaching a maximum angle in a few years, then decreases slowly, passing through zero degrees and then begins its increase as right hand spiral grain [20, 21, 30]. Typically, the maximum left hand spiral is reached between the 4th and 6th growth ring from the pith and the crossing over to a right hand spiral occurs between the 15th and 25th growth ring. The maximum left hand grain angle is often about 5° and the rightward increase after passing through zero may be very slow, or fast or inconsistent [21]. In radiata pine, SGA generally declines from the innermost rings to about the 15th ring from the pith [30], while in the longitudinal direction there is generally an increase in SGA with height in the lower stem [24, 30].

Twist arising from spiral grain is exaggerated by any characteristic that increases the radial shrinkage gradients. Therefore, it is necessary to consider the intra-stem patterns in SGA and MFA together, as the latter affects longitudinal shrinkage [6]. In radiata pine, spiral grain is highest in the corewood zone and it increases in severity up the stem, unlike MFA which is large at the base and decreases up the stem [31]. Thus the worst effects of spiral grain are observed in the smaller top logs, whereas the worst effects of large MFA are found in the corewood of the butt log [31].

Despite the large amount of data that have been collected on MFA and SGA in radiata pine, much of it through the Wood Quality Initiative (WQI), few published studies have attempted to model the radial and vertical trends in these properties coincidently. Models for the radial and vertical trends in MFA have been developed for other species, such as loblolly pine (*Pinus taeda* L.) [32] and Scots pine (*Pinus sylvestris* L.) [33], and similar approaches will be applied to data from radiata pine. Tian et al. [34] analysed the intra-stem variation in SGA and the results were made available through STANDQUA. However, a considerable amount of new data have been collected since STANDQUA was built and the functions developed by Tian et al [34] were for explicit heights in a tree and, therefore, are unlikely to be generalisable to different sized trees. Therefore, the objective of this study was to undertake a meta-analysis of the available data on MFA and SGA in New Zealand-grown radiata pine and to use these data to develop models to explain the general intra-stem trends in these properties.

Objectives

The objectives of this study were to:

1. Develop models that can explain the intra-stem variation (radial and longitudinal) in MFA and SGA for different sized trees; and
2. Investigate the extent to which these intra-stem patterns are affected by site and silvicultural factors and the need for including future adjustments in the models.

This report describes the development of models to predict intra-stem variation in SGA and MFA through undertaking a meta-analysis of historical data on these two properties. These models will be capable of being linked with a growth and yield simulator (i.e. FFR Forecaster) to enable different silvicultural scenarios to be evaluated. Some preliminary work related to Objective 2 is described, but this is covered more fully in the analysis of data from the Shellocks trial and the WQI benchmarking study, which are reported separately.

METHODS

Description of Data Sources

Two databases were assembled, one contained historical data on MFA and the other containing data on SGA that have been collected across numerous studies. Data on MFA were obtained from 441 sample trees from 30 sites geographically distributed across New Zealand, ranging from the extreme north to the extreme south (Table 1). The trees ranged in age from 13 up to 33 years. Most of the observations in the dataset were from various WQI studies, particularly the benchmarking and within-stand variation studies. Another significant source of data was a series of trials undertaken to look at the fibre and pulp properties of radiata pine (Sites 28-31) [35]. Microfibril angle was determined for each individual growth ring from pith to bark using SilviScan and, in most cases, at least four stem heights were sampled on each tree. Ring width data were also available from SilviScan and were calculated using the ring boundaries identified by the X-ray densitometer.

Data on SGA were obtained from 1400 individual trees, ranging in age from 11 years up to 35 years, from 57 different sites located across New Zealand (Table 2). Many of these data came from the same WQI studies in which MFA was also measured. Spiral grain angle was generally measured at multiple heights on each tree. The predominant method used to measure SGA in these studies involved the scribing of specific tangential surfaces of blocks removed from discs, with values averaged for the same annual ring on either side of the pith to eliminate variation due to disc “tilt” (misalignment relative to the stem axis). Because of the time consuming nature of measuring SGA using this approach, measurements were generally made on every second growth ring from the pith and in some cases on every 5th ring after ring 15 from the pith (Table 2). Unfortunately, ring width data were not available for trees in this dataset.

One issue that became apparent was the absence of total tree height measurements in a number of studies, particularly most of the WQI studies. Because of the different sized trees in the dataset and the need to be able to predict the intra-stem patterns in MFA and SGA for a wide range of tree sizes, it is useful to know the relative height that each sample was taken from as well as the absolute height. To overcome this problem, 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 increased incrementally and the difference between the actual and predicted diameters of the discs determined (see Appendix 1 for details). The predicted height of each tree was selected, such that the difference between actual and predicted disc diameters was minimised.

Data Analysis

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[36]. A variance components analysis was undertaken to determine how much of the variation in MFA and SGA 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 and SGA. 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 [36] and Akaike’s information criterion (AIC,[37]), which measures the relative adequacy of different nested models. AIC 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 [38]. 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 [39] of the R [redacted]

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

Site No.	Study	Region	Forest	Cpt/Treatment	Age (yrs)	n trees	Sample heights (m)
1	WQI Benchmarking	Auckland	Aupouri	92	25	10	0, 1.4, 5, 20
2	WQI Benchmarking	Auckland	Mangakahia	200, 350, 500 & 1100sph	23	40	0, 1.4, 5, 20
3	WQI Benchmarking	Auckland	Athenree	14	25	10	0,1.4, 5,10,15,20,25
4	FFR Final crop stocking trial	Auckland	Woodhill	100, 200, 400sph with early & late thinning + control	33	20	1.4
6	WQI Within Stand Variation	Rotorua	Kaingaroa	927 - uniform site	18	20	1.4
7	WQI Within Stand Variation	Rotorua	Kaingaroa	928 & 929 - variable sites	18	20	1.4
8	WQI Utilisation study	Rotorua	Kaingaroa	1218	25	25	0, 5, 10
9	WQI Benchmarking	Rotorua	Kaingaroa	1210	25	10	0, 1.4, 5, 20
10	WQI Benchmarking	Rotorua	Kaingaroa	222	25	10	0, 1.4, 5, 20
11	WQI Benchmarking	East Coast	Ruatoria	303	25	10	0, 1.4, 5, 20
12	WQI Benchmarking	Hawkes Bay	Mohaka	205	25	10	0, 1.4, 5, 20
13	WQI Benchmarking	Wellington	Lismore	204	25	6	0, 1.4, 5, 20
14	WQI Benchmarking	Wellington	Ngaumu	6	25	10	0, 1.4, 5, 20
15	WQI Within Stand Variation	Nelson	Wyeburn – Marlborough	18/2	18	20	1.4
16	WQI Within Stand Variation	Nelson	Lansdowne – Marlborough	31/1	18	20	1.4
17	WQI Utilisation study	Nelson	Golden Downs	26	25	25	0, 5, 10
18	WQI Benchmarking	Nelson	Rabbit Island	NN405	25	10	0, 1.4, 5, 20
19	WQI Benchmarking	Nelson	Golden Downs	66	25	10	0, 1.4, 5, 20
20	WQI Benchmarking	Nelson	Waimea	114	25	10	0, 1.4, 5, 20
21	FFR Final crop stocking trial	Nelson	Golden Downs	100, 200, 400sph with early & late thinning + control	33	7	1.4
22	WQI Benchmarking	Canterbury	Ashley	601	25	9	0, 1.4, 5, 20
23	WQI Benchmarking	Canterbury	Eyrewell	7	25	10	0, 1.4, 5, 20
24	WQI Benchmarking	Canterbury	Waimate	Lobb's Hole	25	10	0, 1.4, 5, 20
25	WQI Benchmarking	Southland	Blackmount – Southland	600	25	2	0, 1.4, 5, 20
26	WQI Benchmarking	Southland	Rowallan – Southland	152	25	7	0, 1.4, 5, 21
27	WQI Benchmarking	Southland	Longwood – Southland	62	25	6	0, 1.4, 5, 22
28	11 Clones	Rotorua	Kaingaroa	327	16	24	0,1.4,5,11,16.5,22
29	25 Family 1	Rotorua	Rotoehu	29	13	25	0,1.4,5.5,10,15,20
30	25 Family 2	Rotorua	Rotoehu	29	15	25	0,1.4,5,11,16.5,22
[redacted]	[redacted]	[redacted]	[redacted]	[redacted]	27	20	0,4,8,13,18,24,28

Table 2. Summary of the studies in which spiral grain angle data were collected.

Site No.	Study	Region	Forest	Cpt/Location/Treatment	Age (yrs)	No. of trees	Heights	Rings
1	Seedlings & 1-5 yr-old cuttings	Auckland	Tairua	Pritchard's Block	11	60	0,1.4,6.4,11.4	2, 4, 6, 8, 10, 11
2	Contract	Auckland	Mangakahia	Opouteke	19	38	5, 10, 15	2, 4, 6, 8, 10, 15
3	WQI Spacing trial - Forsyth Downs	Auckland	Mangakahia	200, 350, 500 &1100sph	23	40	0, 1.4, 5,10,15,20,25	2, 4, 6, 8, 10, 15
4	WQI Benchmarking	Auckland	Aupouri	92	25	10	0, 1.4, 5, 10,15,20, 25	5, 10, 15, 20, 25
5	WQI Benchmarking	Auckland	Athenree	14	25	10	0, 1.4, 5, 10,15, 20, 25	5, 10, 15, 20, 25
6	FFR Final crop stocking trial	Auckland	Woodhill	100, 200, 400spha with early & late thinning + control	33	20	1.4, 5, 10,15,20,25, 30	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30
7	Contract	Auckland	Northland Forests	4 separate forests	-	83 logs	Varies - peeler logs cut in half	2, 4, 6, 8, 10, 15, 20
8	Effect of B	Rotorua	Rerewhakaaitu	273	12	30	0, 1.4, 5, 10	2, 4, 6, 8, 10
9	25 Family 1	Rotorua	Rotoehu	29	13	25	0, 1.4,5.5,10,15, 20	2, 4, 6, 8, 10, 12, 14
11	25 Family 2	Rotorua	Rotoehu	29	15	25	0, 1.4,5.5,10,15,20	2, 4, 6, 8, 10, 12, 14
12	11 Clones	Rotorua	Kaingaroa	327	16	25	0,1.4,6,11,16,21	2, 4, 6, 8, 10, 12, 14
13	WQI G14 v GF19	Rotorua	Tarawera	Cpt 30: GF14 =15 trees GF19= 54trees	17	69	1.4, 5,10	2, 4, 6, 8, 10, 12, 14, 16
14	Tikitere Stocking Trial 1993	Rotorua	Tikitere	100,200&400spha	19	9	0,6,11,15	2, 4, 6, 8, 10, 12, 14, 16, 18
15	Effect of Age	Rotorua	Kaingaroa	905	21	30	0,4.9,9.8,14.7,19.6, 24	2,4,6,8,10,12,14,16,18, 20
16	Clone 55	Rotorua	Kaingaroa	1350	22	14	5.5	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17
17	FRI study Disc v tree study	Rotorua	Kaingaroa	1350	22?	16	0, 1.4, 7, 12.5, 18, 23	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22
18	Saw-Dry-Rip	Rotorua	Tarawera Valley	82/1A	23	11	0, 4.9, 9.8, 14.7, 19.6, 24.5	2, 4, 6, 8, 10, 15, 20
19	Tikitere Stocking Trial 1997	Rotorua	Tikitere	200&400spha	23	20	0, 5, 10, 15, 20, 25, 30	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22
20	Puruki Clones	Rotorua	Puruki Exp Catchment		24	33	0, 5, 10, 15, 20, 25, 30	2, 4, 6, 8, 10, 15, 20, outer ring

Table 2 ctd. Summary of the studies in which spiral grain angle data were collected.

Site No.	Study	Region	Forest	Cpt/Location/Treatment	Age (yrs)	No. of trees	Heights	Rings
21	FRI study Disc v tree study	Rotorua	Kaingaroa	1013	25	7	0, 1.4, 7, 12.5, 17.5, 23	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24
22	Seedlings & 1-5 yr-old cuttings	Rotorua	Kaingaroa	367	11	60	0, 1.4, 6.4, 11.4	2, 4, 6, 8, 10, 11
23	Effect of Age	Rotorua	Kaingaroa	1013	25	50	0, 6, 11, 16, 21, 26	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22
24	Cuttings v seedlings comp	Rotorua	Kaingaroa	1350	25	20	0, 1.4, 6.4, 11.4, 16.4, 21, 26, 31	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24
25	WQI Utilisation study	Rotorua	Kaingaroa	1218	25	25	0, 5, 10	5, 10, 15, 25
26	WQI Benchmarking	Rotorua	Kaingaroa	1210	25	10	0, 1.4, 5, 10, 15, 20, 25	5, 10, 15, 20, 25
27	WQI Benchmarking	Rotorua	Kaingaroa	222	25	10	0, 1.4, 5, 10, 15, 20, 25	5, 10, 15, 20, 25
28	Effect of Age	Rotorua	Kaingaroa	1013	26	30	0, 5, 10, 15, 20, 25	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24
29	Tikitere Stocking Trial 1999	Rotorua	Tikitere	100,200&400spha	26	19+59 2nd log discs	0, 5, 10, 15, 20, 25	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22
30	Value Recovery 1	Rotorua	Kaingaroa	1350	27	20	0, 3.9, 8.8, 13.7, 18.6, 23.4, 28.2	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26
31	875 and 880 Forward Sel	Rotorua	Kaingaroa		27	20	0, 1.4, 5, 10, 15, 20, 25, 30, 35	2, 4, 6, 8, 10, 15, 20, 25, outer ring
32	Value Recovery 2	Rotorua	Kaingaroa	1350	28	22	0, 2.5, 5, 7.5, 10, 12.5, 15, 17.5, 20, 22.5, 25, 30, 35	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26
33	Circumferential variation and comp. with spiralometer	Rotorua	Northern Boundary		28	20	1.4	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 27
34	Effect of Age	Rotorua	Kaingaroa	1302	30	30	0, 5, 10, 15, 20, 25, 30	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30
35	WQI Study	Rotorua	Kaingaroa	1350	33	19	10	2,4,6,8,10,12,15,20,25
36	Tarawera Spacing Trial	Rotorua	Tarawera Valley	54	35	30	0, 5, 10, 15, 20, 25, 30, 35	2, 4, 6, 8, 10, 15, 20, 25
[redacted]						10	0, 1.4, 5, 10, 15, 20,	5, 10, 15, 20, 25

Table 2 ctd. Summary of the studies in which spiral grain angle data were collected.

Site No.	Study	Region	Forest	Cpt/Location/Treatment	Age (yrs)	No. of trees	Heights	Rings
38	Contract	East Coast	Confidential	4 separate regions	17-26	95	1.4	2,4,6,8,10,15,20,25
39	Contract	East Coast	Confidential		-	24	0,5.5,11,16.5,20,24	2,4,6,8,10,15,20,25
40	Contract	East Coast	Confidential		-	22	0,5.5,11,16.5,20,24	2,4, 6,8, 10, 15, 20, 25
41	WQI Benchmarking	Hawkes Bay	Mohaka	205	25	10	0,1.4,5,10,15,20,25	5, 10, 15, 20, 25
42	WQI Benchmarking	Wellington	Lismore	204	25	6	0,1.4,5,10,15,20,25	5, 10, 15, 20, 25
43	WQI Benchmarking	Wellington	Ngaumu	6	25	10	0,1.4,5,10,15,20,25	5, 10, 15, 20, 25
44	Contract	Nelson	Confidential		22	15	0,4.5,10.2,15.9	2, 4, 6, 8, 10, 15, 20
45	Thinning & fertiliser effects	Nelson	Tasman Forest Nelson	N191	25	30	0,6,12	14, 20, 25
46	WQI Utilisation study	Nelson	Golden Downs	26	25	25	0,5,10	5, 10, 15, 25
47	WQI Benchmarking	Nelson	Rabbit Island	NN405	25	10	0,1.4,5,10,15,20,25	5, 10, 15, 20, 25
48	WQI Benchmarking	Nelson	Golden Downs	66	25	10	0,1.4,5,10,15,20,25	5, 10, 15, 20, 25
49	WQI Benchmarking	Nelson	Waimea	114	25	10	0,1.4,5,10,15,20,25	5, 10, 15, 20, 25
50	FFR Final crop stocking trial	Nelson	Golden Downs	100, 200, 400spha with early & late thinning + control	33	9 + 5X1.4m discs	1.4,5,10,15,20,25,30	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30
51	WQI Benchmarking	Canterbury	Ashley	601	25	10	0,1.4,5,10,15,20,25	5, 10, 15, 20, 25
52	WQI Benchmarking	Canterbury	Eyrewell	7	25	10	0, 1.4,5,10,15,20, 25	5, 10, 15, 20, 25
53	WQI Benchmarking	Canterbury	Waimate	Lobb's Hole	25	10	0,1.4,5,10,15,20,25	5, 10, 15, 20, 25
54	Contract	Southland	Confidential		25	10	1.4, 5.7, 11.2, 16.7	2, 4, 6, 8, 10, 15, 20
55	WQI Benchmarking	Southland - Blackmount	Blackmount	600	25	2	0, 1.4, 5, 10, 15, 20, 25	5, 10, 15, 20, 25
56	WQI Benchmarking	Southland – Rowallan	Rowallan	152	25	7	0, 1.4, 5, 10, 15, 20, 25	5, 10, 15, 20, 25
57	WQI Benchmarking	Southland - Longwood	Longwood	62	25	6	0,1.4,5,10,15,20,25	5, 10, 15, 20, 25
58	Contract	Southland	Confidential		26	10	1.4, 5.7, 11.2, 16.7	2, 4, 6, 8, 10, 15, 20, 25

Microfibril Angle

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 [32] and has the following form:

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

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 [33]. In this study, we used a standard Michaelis-Menten equation with an added intercept term:

$$y_{ijkl} = \frac{\beta_0 CA_{ijkl}}{\beta_1 + CA_{ijkl}} + \beta_2 + b_{2,i} + b_{2,ij} + b_{2,ijk} + \varepsilon_{ijkl} \qquad [2]$$
$$\text{with } \beta_0 = \beta_{00} + \beta_{01} RW_{ijkl}$$

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_{01}, β_{02}, 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.

For both models, the fixed effects parameters were also modified to include the possible effect of height. Linear, log-linear and quadratic height terms were added to the model following the approach described by Jordan et al. [32]. 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 modelling system.

Spiral Grain Angle

Three different model forms were used to explain the radial variation in SGA. The first was a simple linear function that is based on the approach taken by Gjerdrum et al [41] to model SGA in Norway spruce (*Picea abies* (L.) Karst.). The difference in the current study is that distance from pith is replaced with ring number from the pith, such that the model has the following form:

$$y_{ijkl} = \gamma_0 + \gamma_1 CA_{ijkl} + c_{0,i} + c_{0,ij} + c_{0,ijk} + \varepsilon_{ijkl} \qquad [3]$$

where, y_{ijkl} is the mean SGA (degree) of the l^{th} annual growth ring in the k^{th} disc of the j^{th} tree from the i^{th} site, γ_0 and γ_1 are the fixed effects parameters and $c_{0,i}$, $c_{0,ij}$ and $c_{0,ijk}$ represent the random [redacted] approach taken by Tian et al.[34], who modelled SGA as a function of the natural logarithm of cambial age:

$$y_{ijkl} = \delta_0 + \delta_1 logCA_{ijkl} + d_{0,i} + d_{0,ij} + d_{0,ijk} + \varepsilon_{ijkl} \quad [4]$$

where, y_{ijkl} is the mean SGA (degree) as defined in Equation 3, δ_0 and δ_1 are the fixed effects parameters and $d_{0,i}$, $d_{0,ij}$ and $d_{0,ijk}$ represent the random effects of the i^{th} site, j^{th} tree in the i^{th} site and k^{th} disc in the j^{th} tree in the i^{th} site, respectively.

The third model form was the nonlinear function used by Fonweban et al. [42] to model the radial variation in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) spiral grain angle. This model has the following form:

$$y_{ijkl} = \left((\omega_0 + o_{0,i} + o_{0,ij} + o_{0,ijk}) + \omega_1 CA_{ijkl}\right) e^{(-\omega_2 CA_{ijkl})} + \varepsilon_{ijkl} \quad [5]$$

where, y_{ijkl} is the mean SGA (degree) as defined in Equation 3, ω_0, ω_1 and ω_2 are the fixed effects parameters and $o_{0,i}$, $o_{0,ij}$ and $o_{0,ijk}$ represent the random effects of the i^{th} site, the j^{th} tree in the i^{th} site and the k^{th} disc in the j^{th} tree in the i^{th} site , respectively.

For all three models, the fixed effects parameters were also modified to include the possible effect of height. As with the MFA models, linear, log-linear and quadratic height terms were added to the model following the approach described by Jordan et al. [32]. Because ring width data were not available for many of the sites, this variable could not be included in the models.

RESULTS AND DISCUSSION

Microfibril Angle

Values of MFA ranged from more than 40° near the pith to approximately 10-15° in the outerwood (Figure 1). Values greater than 30° were largely confined to the inner rings of the butt logs. A small number of values of MFA less than 5° were observed and these were assumed to be erroneous and hence removed from the analysis. 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 a tree, 14% was due to vertical variation within a tree, 4% was due to differences between trees within a stand and 14% was due to differences between sites. The level of variation between sites was much higher than the 2% found for Scots pine by Auty et al. [33], which likely reflects the much wider range of sites and genotypes sampled in New Zealand. It also indicates that site factors such as climate (particularly wind exposure) as well as stand structure could be important in explaining additional variation in MFA. More effort is required to collect data on likely candidate parameters so that they can be included in the model. However, the analysis indicates that approximately 82% of the variation in MFA is intra-stem and, therefore, it is important to develop robust models to predict this intra-stem variation.

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 3). The model based on the modified Michaelis-Menten equation (Eq. 2) performed better than the modified logistic function and was able to explain 53% 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 4). This is consistent with previous studies in other species [33, 43-46] and indicates that treatments that increase growth rates could have a negative impact on wood stiffness.

Table 3. 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)	107288	-53634	0.46	0.54	0.57	0.66
Eq. (2)	103926	-51952	0.53	0.59	0.62	0.66

Table 4. 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	42.088	0.368	114.300	<0.001
α_1	0.167	0.002	84.897	<0.001
α_2	12.382	0.472	26.208	<0.001
Eq. (2)				
β_{00}	-31.641	0.412	-76.640	<0.001
β_1	3.325	0.120	27.678	<0.001
β_2	39.390	0.657	59.927	<0.001
β_{01}	0.495	0.007	72.425	<0.001

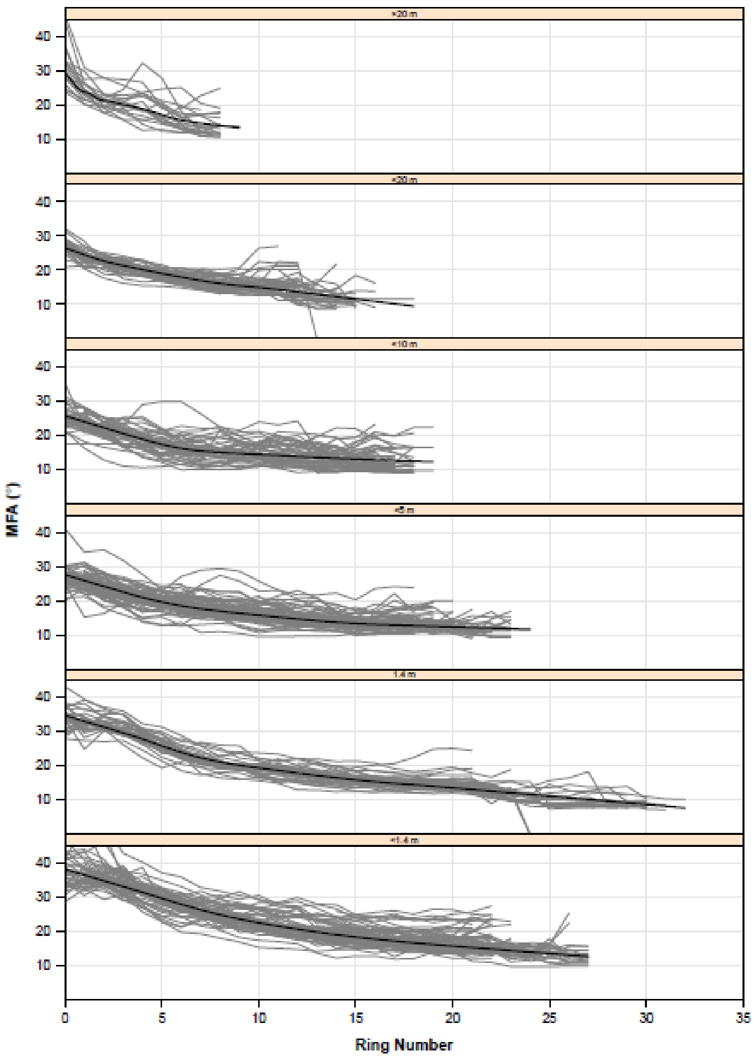

Figure 1. Radial profiles in MFA for discs taken at different heights (1.4 metres to 20 metres) within the stem. Each grey line represents the actual observations from an individual tree and the black line is a locally-weighted smoothing function (lowess) fitted to all observations.

Modelling Variation in MFA with Height

Height terms were added to the models given by Eqs. (1) and (2). There is some debate on whether this is appropriate as some biometricians believe that this is pseudo-replication as there is already a random effect of disc in the model, which effectively accounts for the variation due to sampling height within the stem. However, we believe that it is legitimate to include both terms in the models. Adding linear terms for relative height (HT_{rel}) to each of the parameters in the modified logistic function (see Eq. (6)) 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 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 (to avoid 0 values) was also found to be significant in the model, with the exception of the term added to the lower asymptote (α_5) (Eq. 7). 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).

Relative height and log(HT_{rel}) terms were also found to be significant when added to the Michaelis-Menten equation (Eqs. 8 & 9). The predictions from the two Michaelis-Menten equations were very similar to each other (Figure 2d and c), but indicated that the high MFA zone extended much higher in the stem than the modified logistic model. This is likely to be due to the fact that a nominal ring width of 10 mm was assumed in these simulations, rather than being allowed to vary with position in the stem. Additional simulations are required to compare the different model forms when a more realistic ring width distribution is assumed. However, based on the goodness of fit statistics (Table 5), it appears that the model given by Eq. (7) is able to explain the greatest amount of variation in MFA, although all four models perform similarly. 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. The final parameter estimates for all four models are given in Table 6.

$$y_{ijkl} = \frac{\alpha_0 + \alpha_3 HT_{rel,ijk}}{1 + e^{(\alpha_1 + \alpha_4 HT_{rel,ijk}) \cdot CA_{ijkl}}} + (\alpha_2 + \alpha_5 HT_{rel,ijk}) + a_{2,i} + a_{2,ij} + a_{2,ijk} + \varepsilon_{ijkl} \quad [6]$$

$$y_{ijkl} = \frac{\alpha_0 + \alpha_3 \log HT_{rel,ijk}}{1 + e^{(\alpha_1 + \alpha_4 \log HT_{rel,ijk}) \cdot CA_{ijkl}}} + \alpha_2 + a_{2,i} + a_{2,ij} + a_{2,ijk} + \varepsilon_{ijkl} \quad [7]$$

$$y_{ijkl} = \frac{(\beta_0 + \beta_3 RW_{ijkl}) CA_{ijkl}}{\beta_1 + CA_{ijkl}} + \beta_2 + \beta_4 HT_{rel,ijk} + b_{2,i} + b_{2,ij} + b_{2,ijk} + \varepsilon_{ijkl} \quad [8]$$

$$y_{ijkl} = \frac{(\beta_0 + \beta_3 RW_{ijkl}) CA_{ijkl}}{\beta_1 + CA_{ijkl}} + \beta_2 + \beta_4 \log HT_{rel,ijk} + b_{2,i} + b_{2,ij} + b_{2,ijk} + \varepsilon_{ijkl} \quad [9]$$

Table 5. AIC, log-likelihood and fit indices for the models to predict MFA given by Eqs. 6-9.

Model	AIC	Log-likelihood	Fit indices (R^2)			
			Fixed	Site	Tree	Disc
Eq. (6)	103705	-51840	0.60	0.68	0.72	0.77
Eq. (7)	103328	-51652	0.63	0.70	0.75	0.79
Eq. (8)	101638	-50807	0.57	0.64	0.66	0.69
Eq. (9)	101605	-50790	0.59	0.66	0.69	0.70

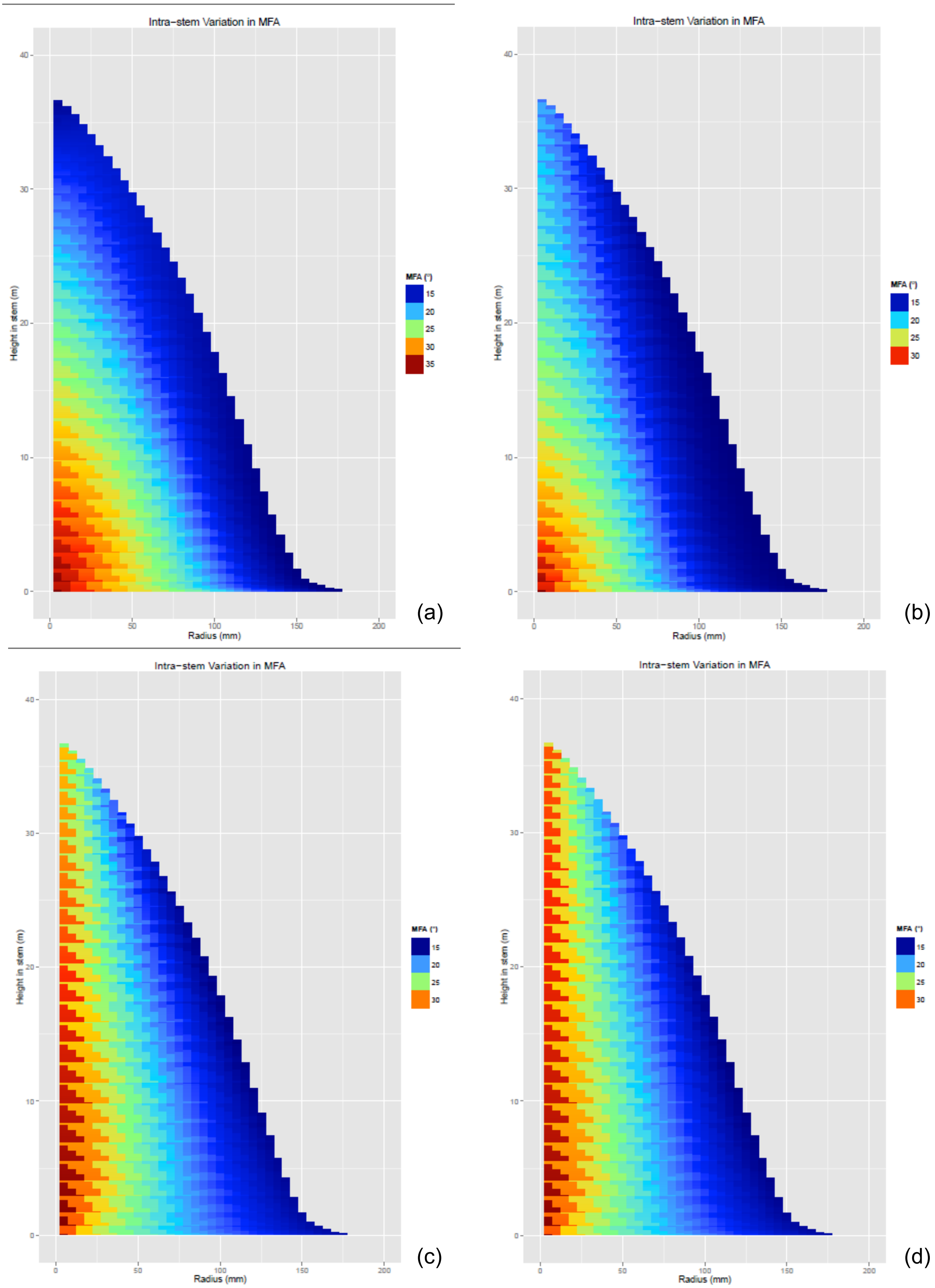

Figure 2. Intra-stem variation in MFA predicted by (a) a modified logistic function with a linear relative height term, (b) a logarithmic relative height term and (c) a modified Michaelis-Menten function with a linear relative height term and (d) a logarithmic relative height term. A constant ring width of 10 mm was assumed for these trees. Parameter estimates for the models are given in Table 6.

Table 6. 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	49.226	0.407	120.922	<0.001
α_1	0.152	0.002	73.340	<0.001
α_2	13.022	0.439	29.658	<0.001
α_3	-41.713	2.273	-18.353	<0.001
α_4	0.451	0.023	19.561	<0.001
α_5	2.898	0.469	6.172	<0.001
Eq. (7)				
α_0	20.059	1.006	19.948	<0.001
α_1	0.332	0.009	38.587	<0.001
α_2	13.425	0.434	30.964	<0.001
α_3	-14.064	0.538	-26.130	<0.001
α_4	0.078	0.004	19.559	<0.001
Eq. (8)				
β_0	-31.505	0.394	-80.040	<0.001
β_1	3.485	0.128	27.303	<0.001
β_2	39.708	0.630	63.005	<0.001
β_3	0.489	0.007	69.717	<0.001
β_4	-4.798	0.488	-9.842	<0.001
Eq. (9)				
β_0	-31.475	0.386	-81.482	<0.001
β_1	3.522	0.129	27.339	<0.001
β_2	36.240	0.673	53.846	<0.001
β_3	0.488	0.007	69.296	<0.001
β_4	-1.663	0.137	-12.106	<0.001

Spiral Grain

Most values of spiral grain angle were between -5° and +10°, with a few more extreme values (up to 20°) observed. A linear, or slightly curvilinear, trend in SGA was observed at all heights in the stem, with values of 5-6° observed in the first few growth rings from the pith decreasing to zero or becoming slightly negative with increasing ring number from the pith (Figure 3). As with MFA, most of the variation in SGA was due to radial variation within the stem (55%), with a further 23% due to vertical variation within the stem. Approximately 14% of the variation in SGA was attributed to differences between trees within a stand, with only 7% attributed to differences between sites.

The simple linear model (Eq. 3) appeared to perform the best of the three models evaluated and was able to predict approximately 26% of the variation in SGA based solely on the fixed effect of cambial age (61% including the random effects of site, tree and disc) (Table 7). This was slightly better than the amount of variation that could be explained by the models developed by Gjerdrum et al. [41] and Fonweban et al. [42] for Norway spruce and Sitka spruce, respectively. The simple linear model indicates that, on average, the value of SGA is approximately 6.7° adjacent to the pith and decreases by 0.3° with each additional growth ring out from the pith (Table 8). Therefore, the transition from a positive spiral grain angle to a negative angle is predicted to occur at approximately 21 annual rings from the pith.

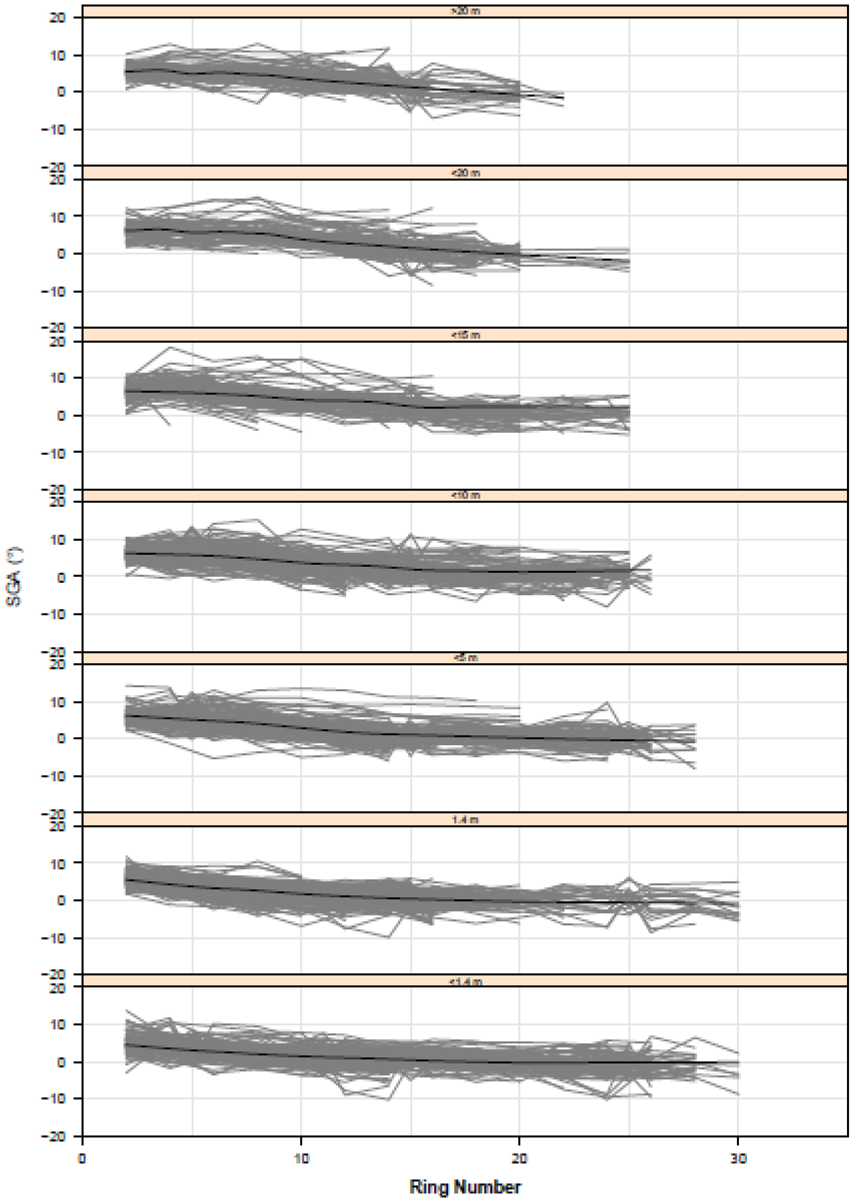

Figure 3. Radial profiles in SGA for discs taken at different heights within the stem. Each grey line represents the actual observations from an individual tree and the black line is a locally-weighted smoothing function (lowess) fitted to all observations.

Table 7. AIC, log-likelihood and fit indices for the models to predict SGA given by Eqs. 3-5.

Model	AIC	Log-likelihood	Fit indices (R^2)			
			Fixed	Site	Tree	Disc
Eq. (3)	147338	-73661	0.26	0.31	0.51	0.61
Eq. (4)	149165	-74575	0.22	0.28	0.48	0.61
Eq. (5)	148444	-74213	0.24	0.28	0.43	0.43

Table 8. Parameter estimates and associated standard errors (s.e.) and tests of significance for the models given by Eqs. 3-5.

Parameter	Estimate	s.e.	t-value	p-value
Eq. (3)				
γ_0	6.708	0.156	42.883	<0.001
γ_1	-0.310	0.003	-121.942	<0.001
Eq. (4)				
δ_0	8.506	0.161	52.775	<0.001
δ_1	-2.316	0.020	-117.628	<0.001
Eq. (5)				
ω_0	7.299	0.095	77.009	<0.001
ω_1	-2.357	0.153	-154.468	<0.001
ω_2	-0.059	0.001	-62.263	<0.001

Modelling Variation in SGA with Height

Relative height terms were added to the models given by Eq. 3-5 following the same approach adopted for MFA. In the two linear models (Eqs. 3&4), terms representing both the relative height and the interaction between relative height and cambial age were added to the model, while in the nonlinear model given by Eq. (5) relative height terms were added to each of the parameters, i.e.

$$y_{ijkl} = \gamma_0 + \gamma_1 CA_{ijkl} + \gamma_2 HT_{rel,ijk} + \gamma_3 HT_{rel,ijk} CA_{ijkl} + c_{0,i} + c_{0,ij} + c_{0,ijk} + \varepsilon_{ijkl} \quad [10]$$

$$y_{ijkl} = \gamma_0 + \gamma_1 CA_{ijkl} + \gamma_2 \log HT_{rel,ijk} + \gamma_3 \log HT_{rel,ijk} CA_{ijkl} + c_{0,i} + c_{0,ij} + c_{0,ijk} + \varepsilon_{ijkl} \quad [11]$$

$$y_{ijkl} = \delta_0 + \delta_1 \log CA_{ijkl} + \delta_2 HT_{rel,ijk} + \delta_3 HT_{rel,ijk} \log CA_{ijkl} + d_{0,i} + d_{0,ij} + d_{0,ijk} + \varepsilon_{ijkl} \quad [12]$$

$$y_{ijkl} = \delta_0 + \delta_1 \log CA_{ijkl} + \delta_2 \log HT_{rel,ijk} + \delta_3 \log HT_{rel,ijk} \log CA_{ijkl} + d_{0,i} + d_{0,ij} + d_{0,ijk} + \varepsilon_{ijkl} \quad [13]$$

$$y_{ijkl} = \left((\omega_0 + o_{0,i} + o_{0,ij} + o_{0,ijk}) + \omega_3 HT_{rel,ijk} + (\omega_1 + \omega_4 HT_{rel,ijk}) CA_{ijkl}\right) e^{(-(\omega_2 + \omega_5 HT_{rel,ijk}) CA_{ijkl})} + \varepsilon_{ijkl} \quad [14]$$

$$y_{ijkl} = \left((\omega_0 + o_{0,i} + o_{0,ij} + o_{0,ijk}) + \omega_3 \log HT_{rel,ijk} + (\omega_1 + \omega_4 \log HT_{rel,ijk}) CA_{ijkl}\right) e^{(-(\omega_2 + \omega_5 \log HT_{rel,ijk}) CA_{ijkl})} + \varepsilon_{ijkl} \quad [15]$$

Adding relative height terms to the linear model given by Eqs. (10) & (11) increased the proportion of variation in SGA that was explained by these models to approximately 30% (Table 9). This was greater than the amount of variation explained by the addition of height terms to the nonlinear models given by Eqs. (14-15), but slightly less than the amount of variation explained by the log-linear models given by Eqs. (12-13). However, based on the AIC criterion, the "best" model for explaining the intra-stem variation in SGA is given by Eq. 11. The model given by Eq. (10) had a very similar AIC and also produced similar predictions of SGA, while the models given by Eqs. (12) & (13) only produced positive estimates of SGA, and those given by Eqs. (14) and (15) produced some very large negative estimates of spiral grain (up to -10°). Therefore, the linear models given by Eqs. (10) and (11) were preferred. The parameter estimates for these models are given in Table 10 and predicted intra-stem patterns in SGA for a modelled tree are given in Figure 4. This shows that the inner part of the tree has values of SGA of approximately 7-8° with SGA increasing with height up the stem for a given cambial age. SGA decreases with increasing cambial age with the lowest values found near the base of the tree. Negative (right-hand) values of SGA are only found at the outermost part of the base of the tree. This pattern confirms what has been described qualitatively in the literature (e.g.[31]).

Table 9. AIC, log-likelihood and fit indices for the models to predict SGA given by Eqs. 10-15.

Model	AIC	Log-likelihood	Fit indices (R^2)			
			Fixed	Site	Tree	Disc
Eq. (10)	49898	-24939	0.29	0.35	0.56	0.58
Eq. (11)	49829	-24904	0.30	0.36	0.57	0.59
Eq. (12)	50003	-24991	0.29	0.35	0.56	0.59
Eq. (13)	50012	-24996	0.29	0.36	0.57	0.59
Eq. (14)	51143	-25561	0.27	0.34	0.50	0.50
Eq. (15)	51087	-25532	0.29	0.36	0.36	0.36

Table 10. Parameter estimates and associated standard errors (s.e.) and tests of significance for the models given by Eqs. 10 & 11.

Parameter	Estimate	s.e.	t-value	p-value
Eq. (10)				
γ_0	5.831	0.278	20.955	<0.001
γ_1	-0.367	0.006	-57.453	<0.001
γ_2	1.556	0.218	7.126	<0.001
γ_3	0.341	0.027	12.779	<0.001
Eq. (11)				
γ_0	7.319	0.282	25.920	<0.001
γ_1	-0.199	0.013	-15.505	<0.001
γ_2	0.835	0.070	11.914	<0.001
γ_3	0.073	0.008	9.483	<0.001

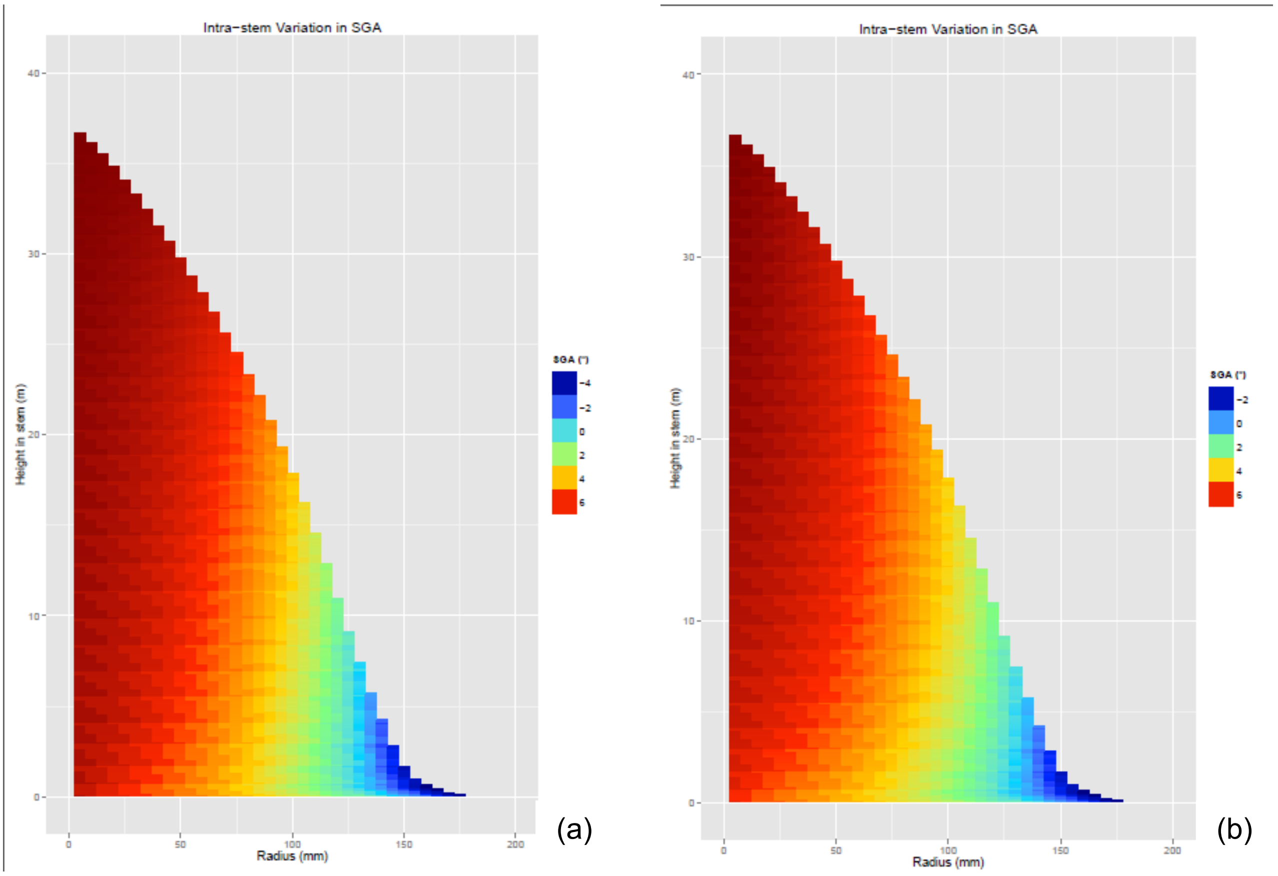

Figure 4. Intra-stem pattern in SGA predicted by a modified logistic function with (a) a linear relative height term and (b) a logarithmic relative height term. Parameter estimates for the two models are [redacted]

General Discussion and Further Work

One of the central goals of the Intensive Forests Systems (IFS) project is to develop a system to predict end product performance and to be able to link this to the growth and management of forests. This system consists of three main parts:

(1) a suite of tools (PQSim), principally employing finite element methods, to evaluate the qualities (stiffness, stability) of individual products (timber) based on 3-dimensional descriptions of wood quality variation;
(2) a statistical model, dependent on forest management decisions (site, silviculture genetics) that, in conjunction with a growth model, stochastically predicts the internal wood property distributions for individual trees; and
(3) a destructive sampling programme that collects the data required to parameterise the statistical model at acceptable cost.

In order to achieve this, better models are required to predict the fundamental wood properties in relation to tree age, site and silviculture. At present the mathematical modelling framework is not sufficiently well developed that it can produce realistic representations of the internal wood properties of trees. However, models such as STANQUA [34, 47], and the national wood density and modulus of elasticity models [48, 49] that predict ring-level average values are able to provide useful information for forest managers on the implications of their decisions on wood quality.

The work reported here extends the suite of wood properties that can be predicted, based on site and tree age, and also summarises one of the most comprehensive datasets on MFA and SGA for a single species anywhere in the world. While the dataset covered a wide range of sites and growing conditions in New Zealand, the predominant source of the variation in both MFA and SGA occurred within the stems of the sampled trees, with less than 15% of the variation occurring between sites. The variation in MFA between sites was considerably greater than the variation in SGA. The “best” models developed in this study were able to explain about 60% of the variation in MFA, but only about 32% of the variation in SGA. This 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. More detailed analysis is needed to understand this variation and to be able to account for it in wood properties models.

The models developed here have quantified much of our previous knowledge about intra-stem variation in MFA and SGA. Modern visualisation tools that are contained in most statistical analysis packages make it possible to display the 2-dimensional patterns in these properties in a way which makes it easy to readily comprehend. These visualisations highlight the issue of corewood in radiata pine, which has both high MFA and high SGA. Solid timber cut from this region of the tree will have low stiffness and a high propensity to twist, so will be unsuitable for many appearance and structural applications.

Through coupling the models developed in this study to a growth model within the Forecaster framework, the effects of different management practices and site productivity on the size of this corewood zone could be examined. 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 and/or SGA above a certain threshold. Such an approach could be implemented within Forecaster, where it is currently not possible to provide visualisations of the internal wood properties in the same way that has been done in this paper. This would also provide a quantitative measure that forest managers could use to compare regimes.

While site-level variation was relatively small, particularly for SGA, it is still considered worthwhile to investigate this further as previous studies have shown that both MFA and SGA are affected by exposure to wind [42, 50]. Other site factors, such as soil type and rainfall distribution may also be important. Similarly, genetics is also likely to affect both of these properties as previous studies [redacted] very diverse, with many of the trees from open-pollinated families that it is unlikely to see a genetic effect over and above the other sources of variation in the dataset, although the model forms developed here could be used to test for genetic differences in trials established for this purpose. Given that site-level variation in MFA is relatively small, we hypothesise that differences in modulus of elasticity that are observed across New Zealand[49] are driven by differences in wood density. This hypothesis could be tested using the WQI benchmarking dataset, which contains density, MFA and SilviScan-derived modulus of elasticity[10] for 17 sites throughout New Zealand.

The modelling approach developed here could also be used as the basis for analysing the data obtained from the destructive sampling project, although this has the added complexity that it also includes circumferential variation. However, the simpler models developed here could be used to subtract the “baseline” variation in MFA and SGA from the destructively sampled trees, with more detailed analysis focusing on modelling the patterns of residual variation that remain. If this residual variation is essentially random and has a similar structure between different trees and sites, then this could greatly simplify the development of the intra-stem property maps needed to drive the product quality simulations.

It is clear from this and other studies that both spiral grain and microfibril angle are

a) regular features of the juvenile core of radiata and many conifers, and
b) they are significantly adversely affected by increased growth rates[18, 44, 46, 54, 55].

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 through spacing (except at the extremes), but more conservative thinning may give more uniform final crops with better average stem form and branches. Gains may also be achieved through improved genotypes and several researchers have already estimated the heritability of key wood quality traits and hence the role that tree breeding has to play in improving wood quality[52, 56-58].

We did not examine silvicultural influences on internal wood properties distributions in this study, but analysis of data from replicated silvicultural trials[18, 59] has shown that control of tree spacing does have a significant influence on MFA and wood stiffness and that it is not necessary to go to extremes of stocking to achieve gains. Previous analysis has also shown that the effect of site and silvicultural practices, particularly initial spacing and thinning on wood stiffness can be interpreted through their impact on tree slenderness, i.e. the ratio of height to diameter at breast height[49]. While it would have been desirable to test this approach using a broader dataset, this was not done here as height was not directly measured on the vast majority of sample trees, but was instead predicted from sectional measurements made along the stem. As a result, we 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.

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APPENDICES

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:

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

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 dbh 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 and SGA data were collected. The compatible volume and taper equation for the direct sawlog regime developed by Katz et al. (1984)[1] 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, 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 dbh trees were probably overestimated, especially for large diameter (greater than 50 cm) trees that had the topmost disc sampled at only 10 m above the ground.

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