Effects of early respacing on the density and microfibril angle of Sitka spruce wood

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Although significant advances have been made in modelling the effects of silviculture on wood properties, few models have been calibrated using data from long-term stand density or respacing experiments. In this study we examined the effects of early respacing on the density and microfibril angle (MfA) of Sitka spruce (*Picea sitchensis* [Bong.] Carr.) wood using samples taken from a fully-replicated 57-year-old trial located in Northern Ireland, which had been thinned at age 11 years. Using a mixed-effects modelling approach, radial profiles of density and MfA from four different respacing treatments (1.83 m × 3.66 m, 3.66 m × 3.66 m, 3.66 m × 5.49 m and 5.49 m × 5.49 m) were compared with those of timber from an unthinned control (1.83 m × 1.83 m). After accounting for radial position and ring width, we found significant differences in both density and MfA between respacing treatments. Mean predicted values of wood density for rings 40–50 were 400 and 494 kg m^{-3} for the widest respacing treatment and the unthinned control, respectively, and fell between these two extremes for the other respacing treatments. Predicted latewood proportions in ring 50 were 12 and 22 per cent, for the same respacing treatments, respectively. There was some evidence of an age-related decline in wood density in the two narrowest respacing treatments. While there was a significant effect of respacing on MfA variation, the trends between respacing treatments were less apparent. Overall, these results indicate that the timing of respacing treatments is an important consideration in Sitka spruce management; early and severe respacing should be avoided to avoid deleterious effects on wood density and MfA.

Introduction

Forest managers whose goal is to create a financial return from timber production generally want to know the impacts of their silvicultural practices on the quantity and quality of the timber raw material (Brazier, 1977). Control of tree spacing is one of the main methods by which a silviculturist can influence the quantity and quality of timber within forest stands (Smith *et al.*, 1997). Spacing influences a number of characteristics, including total standing volume, individual tree volume, tree taper, branch size, size of the juvenile wood zone, and wood density (Evert, 1971; Hamilton and Christie, 1974; Briggs and Smith, 1986; Smith *et al.*, 1997; Macdonald and Hubert, 2002). Forest managers can control tree spacing through any or all of the following: initial spacing at stand establishment, respacing (pre-commercial thinning) of normally-stocked stands, which is generally performed before canopy closure occurs (Rollinson, 1988), and thinning of older stands.

Thinning of planted Sitka spruce (*Picea sitchensis* Bong. Carr.) stands has declined in the United Kingdom (UK) since the 1960 s due to low financial returns (Rollinson, 1985). However, increased demand for fuelwood (i.e. harvest residues) in recent years has led to an increase in thinning in suitable stands (Whittaker *et al.*, 2011). Attempts to improve the economics of thinning through mechanisation (i.e. systematic thinning regimes) or by delaying operations to allow the trees to reach a larger size, while potentially leading to improvements in some wood quality characteristics e.g. reduced juvenile wood proportion, smaller branches, or increased wood density (Macdonald *et al.*, 2002), have often resulted in an increased risk of wind damage (Gardiner *et al.*, 1997). Therefore, in areas at high risk of wind damage, stands are generally managed under a 'no-thin' regime to maintain stand stability (Cameron, 2002). However, while reducing the potential for wind damage, 'no-thin' regimes do not afford the opportunity to improve the average wood quality within a stand by selecting those trees with superior

form. As a result, trees are on average smaller, and overall product recovery is generally reduced (Moore *et al.*, 2009). Instead, early respacing has been suggested as a way to increase mean tree size and possibly improve stand stability on sites where conventional commercial thinning is impractical (Rollinson, 1988). Compared with wide initial spacing, pre-commercial thinning provides an opportunity to improve average stand quality through early removal of trees with poor form (Briggs and Smith, 1986).

A key focus of previous research into Sitka spruce respacing was to quantify the effects of initial spacing and early respacing on volume production (Jack, 1971; Edwards and Grayson, 1979; Gallagher, 1980; Lynch, 1980; Kilpatrick, *et al.*, 1981; Rollinson, 1988; Deans and Milne, 1999) and factors such as branch size and frequency (Auty, *et al.*, 2012), which can influence product quality. Because of the negative relationship between tree vigour and wood density in Sitka spruce (Brazier, 1970a), coupled with the importance of density as an indicator of final product quality (CEN, 2016), several studies have also focused on the effects of spacing on both wood density (Brazier, 1970b; Gardiner and O'Sullivan, 1978; Savill and Sandels, 1983; Simpson and Denne, 1997; Deans and Milne, 1999; Gardiner *et al.*, 2011), and on the mechanical properties of sawn timber (Brazier *et al.*, 1985; Brazier and Mobbs, 1993; Moore *et al.*, 2009). In general, these studies have shown that wood from trees grown in widely spaced stands has lower average density, modulus of elasticity (MOE) and bending strength than wood from trees grown in more densely stocked stands.

In a 32-year-old replicated respacing experiment in Northern Ireland, Savill and Sandels (1983) found that mean Sitka spruce wood density decreased from 420 to 380 kg m^{-3} from the narrowest to the widest spacing treatment, respectively; however, only 12 per cent of the overall variation in wood density was attributed to the effect of respacing treatment, while 63 per cent was due to differences between trees within treatments. When this trial was harvested in 2006, the opportunity arose to collect detailed information about the effects of respacing on tree growth, branch characteristics and wood properties. A comparison of the branch characteristics between treatments was presented in Auty *et al.* (2012), while Moore *et al.* (2009) compared the mechanical properties of structural timber. The latter study found that wide respacing was associated with a statistically significant reduction in both the MOE and modulus of rupture (MOR) of structural timber, but there was no effect of respacing on wood density. The absence of a respacing effect on the density of structural-dimension timber suggests that differences in mechanical properties are likely due to variation in other factors, such as knot size and frequency, and microfibril angle (MfA), which are known to have a large influence on the mechanical properties of timber (Evans and Ilic, 2001; McLean *et al.*, 2010). In this paper, we adopt a statistical modelling approach for assessing treatment effects on the variation in wood properties, which has proved effective in several other studies (e.g. Jordan *et al.*, 2005; Leban and Haines, 1999; Schneider *et al.*, 2008; Auty *et al.*, 2014, 2016). While significant developments have been made in modelling the effects of silviculture on wood properties, the use of long-term stand density data or data from respacing experiments in such models is relatively rare. The use of mixed-effects models allows for quantification of multiple sources of variation (Gelman and Hill, 2006),

while the inclusion of both tree- and annual ring-level explanatory variables in the models allows for additional inference about the effects of growth rate on wood properties (e.g. Alteyrac *et al.*, 2007; Auty *et al.*, 2013). Inclusion of radial growth increments in the models means they can be integrated into growth and yield simulation systems to generate predictions of the effects of forest management practices on important final product properties (Houllier *et al.*, 1995).

The overall goal of this study was to compare the effects of early respacing on the radial variation in wood density and MfA in Sitka spruce using material from the experiment described above. A secondary objective was to develop nonlinear mixed-effects models to account for the radial variation in the wood properties under investigation, and to quantify any additional effects of growth rate on the variables of interest. Results from this study can also be used to further develop and refine wood quality simulation models that can be used to investigate the effects of factors such as site and silviculture on wood properties (Macdonald *et al.*, 2002).

Methods and materials

Experimental site

The study was conducted in an early respacing trial located on the Baronscourt Estate in County Tyrone, Northern Ireland (Lat. 54° 41′ N, Long. 7°26′ W, 140 m elevation). The stand containing the trial was planted in 1949 at an initial spacing of 1.83 m × 1.83 m (2990 trees ha^{-1}), and has a general yield class of 20, which corresponds to a maximum mean annual increment of 20 m^3 ha^{-1} yr^{-1} (Savill and Sandels, 1983). In 1960, the respacing trial was installed across a uniform 4 ha area within the original stand (Jack, 1971). Five respacing treatments were allocated to 25 plots of ~0.15 ha in size in a 5 × 5 Latin square design. This was achieved by systematically removing alternate rows and alternate trees within rows, as required. The five respacing treatments were planned to be 1.83 m × 1.83 m, 1.83 m × 3.66 m, 3.66 m × 3.66 m, 3.66 m × 5.49 m and 5.49 m × 5.49 m but the corresponding measured stand densities at the time of respacing were 2858, 1452, 725, 477 and 320 trees ha^{-1}, respectively. For brevity, we refer to the treatments by the equivalent square spacing used by Kilpatrick *et al.* (1981), i.e. ~1.9, 2.6, 3.7, 4.6, and 5.6 m.

A sample plot was established at the centre of each treatment unit. This initially consisted of 49 trees, but it was subsequently reduced to 25 (i.e. the inner 5 × 5 trees) in order to reduce measurement costs (Kilpatrick *et al.*, 1981). The trial was remeasured seven times between 1960 and 1979. Measurements until 1969 were presented in Jack (1971), while those made between 1960 and 1979 were presented in Kilpatrick *et al.* (1981). Since then, the stand was periodically remeasured up until and including 2004, when the stand was 55 years old. At that point, the total standing volume in the different respacing treatments ranged from 737 to 979 m^3 ha^{-1}, while mortality ranged from 3 to 60 per cent (Table 1).

Sampling

In 2006, when the stand was 57 years old, three trees were selected from the inner 25 trees in each plot for destructive sampling. The sample trees were selected on the basis of tree dominance with respect to stem diameter at breast height (DBH, cm) i.e. one dominant, one co-dominant and one intermediate tree from each plot. Only 24 plots were used since one plot had high levels of wind damage, which meant that the effective growing space available to the trees within it was no longer

Table 1 Stand-level characteristics for each respacing treatment and characteristics of the 72 felled trees and subsample of 30 trees selected for wood properties assessment

Attribute	Respacing treatment				
	1.9 m	2.6 m	3.7 m	4.6 m	5.6 m
Stand[1]					
Stand density (trees ha^{-1})	1134 (71)	922 (150)	581 (45)	435 (12)	310 (19)
Mortality (%)	60	37	20	9	3
DBH (cm)	29.1	33.5	41.3	46.5	51.2
Height (H, m)	32.8	34.5	34.9	36.2	35.8
H/DBH (m m^{-1})	113	103	85	78	70
Volume (m^3 ha^{-1})	859	923	979	880	737
Felled trees (n = 72)					
DBH (cm)	36.6 (5.0)	40.7 (5.2)	44.7 (6.6)	56.4 (5.3)	60.6 (9.6)
Height (m)	32.4 (2.7)	34.7 (1.8)	33.4 (2.2)	37.0 (1.0)	36.4 (2.1)
Live crown length (m)	9.0 (1.8)	10.2 (1.7)	10.2 (2.5)	14.1 (1.7)	14.8 (2.2)
Individual tree volume (m^3)	1.34 (0.4)	1.85 (0.5)	2.27 (1.0)	3.60 (0.6)	3.93 (1.4)
Branch index[2] (mm)	39 (3)	41 (3)	38 (3)	53 (3)	56 (7)
Silviscan-3 sample trees (n = 30)					
DBH (cm)	38.4 (2.4)	43.9 (5.3)	38.7 (4.9)	55.0 (4.7)	64.9 (10.1)
Height (m)	33.9 (1.2)	35.0 (1.3)	32.6 (2.1)	37.0 (0.7)	37.0 (1.7)
Wood density (kg m^{-3})	454.3 (85.7)	427.3 (74.9)	453.6 (76.7)	434.4 (81.3)	380.8 (64.4)
Latewood per cent (LW %)	13.1 (10.8)	10.2 (9.3)	11.4 (8.5)	8.6 (5.7)	5.9 (4.0)
Microfibril angle (MfA, °)	17.4 (6.0)	18.6 (6.7)	19.2 (6.5)	20.3 (6.4)	19.2 (6.5)

Where appropriate, standard errors of the mean are given in parentheses.
[1]Standard errors for stand-level characteristics are based on data from sample plots within each respacing treatment.
[2]Average diameter of the six largest branches per tree. Values are based on measurements made on one tree per plot.

representative of the prescribed respacing treatment. Overall, a total of 72 trees were sampled; 12 trees from the 4.6 m treatment and 15 trees from the other four treatments. These were the same trees that were sampled in the earlier studies by Moore *et al.* (2009) and Auty *et al.* (2012). After felling, total tree height (H, m) and the height to the lowest live branch and to the lowest live whorl were measured on each tree. Branch attributes, including diameter (mm), were measured along the stem of each sample tree, from which a branch index (mm) was calculated for each respacing treatment. This was defined as the mean diameter of the six largest branches per tree.

A 100-mm-thick disc was cut from each tree at breast height (1.3 m from the base of the stem), although in some instances the sampling height was adjusted to avoid branch whorls or obvious stem defects. In the laboratory, a pith-to-bark bar with dimensions of ~15 mm × 15 mm in the longitudinal and tangential direction was cut from each disc along a radial line extending from the pith to the cambium on the north side of the tree. These bars were conditioned at 20°C and 65 per cent relative humidity before being sent to Innventia AB (Stockholm, Sweden) for wood density and MfA determination using the SilviScan-3 instrument. Because resources only allowed for wood properties to be measured on 30 trees, one tree was selected from each plot (i.e. 24 trees in total) along with six additional trees that were selected at random, ensuring that six trees were sampled from each respacing treatment.

Measurement of density and MfA

A strip spanning the full radius was milled from each bar using a twin-blade precision sawing system. Each strip measured 7 mm in the longitudinal direction and 2 mm in the tangential direction. Solvent exchange was not carried out to remove extractives, due to the known low extractives content of Sitka spruce wood (Caron *et al.*, 2013). Strips were then conditioned at 40 per cent RH and 20°C, which corresponds to an equilibrium moisture content of 7–8 per cent. X-ray diffraction measurements were made at 50 μm resolution and the average MfA was determined over successive 5 mm intervals. Next, X-ray densitometry measurements were made on each sample at a resolution of 50 μm. The density profiles were used to identify annual growth ring boundaries and to define earlywood and latewood within each annual ring. Latewood was assumed when wood density was >80 per cent of the difference between the maximum and minimum values in each annual ring. Ring-level average values of density and MfA were calculated from the radial profiles, and these were examined for the presence of compression wood or other abnormal features. Rings containing obvious compression wood were removed from the MfA and density datasets in subsequent analyses. In addition, the last annual ring in each radial profile was removed before the analysis as annual growth was assumed to be incomplete at the time of data collection.

Data analysis

Radial variations in density and MfA and possible differences in these properties between respacing treatments were examined using non-linear mixed-effects models (Pinheiro and Bates, 2000). For each response variable, different fixed effects were used to model the radial variation and account for any treatment differences, while random effects were included to account for the hierarchical nature of the data (i.e. annual rings grouped within trees) and mutual dependence among observations. Hence a tree-level random effect was included in the models to allow fixed effects parameter estimates to vary around their mean values, giving a more precise estimation of parameter standard

errors (Lindstrom and Bates, 1990). Chi-squared based likelihood-ratio tests (LRT) were used to compare models and evaluate the significance of both fixed and random effects. Model performance was assessed by calculating the root mean square error (RMSE) and mean absolute percentage error (IEI %) from the fixed part of each model, while fit indices were calculated from the fixed, and fixed plus random parts of the models (Parresol, 1999). All models were fitted to the data using the R open source statistical software (R Core Team, 2016).

Modelling wood density

A number of different functional forms were tested for their ability to model the pith-to-bark radial trend in wood density. Initially, density was modelled as a function of cambial age (i.e. annual ring number from the pith) using the following equation, which is a modified version of the black spruce (*Picea mariana* (Mill.) B.S.P.) wood density model developed by Xiang *et al.* (2014):

$$DENS_{ij} = \alpha_0 e^{-\alpha_1 CA_{ij}} + \frac{\alpha_2 CA_{ij}}{\alpha_3 + CA_{ij}} + a_{2,i} + \varepsilon_{ij} \quad (1)$$

where $DENS_{ij}$ is the mean ring density (kg m^{-3}) of the *j*th annual ring in the *i*th tree, CA_{ij} is the cambial age (years) of the *j*th annual ring in the *i*th tree, and α_0, α_1, α_2 and α_3, are empirically determined parameters. Parameter α_0 denotes the intercept when CA_{ij} approaches a theoretical value of 0, and α_2 denotes the scale parameter of the early decrease in ring density. The within-group errors were assumed to be independent and normally distributed, with $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$. The first exponential term $\alpha_0 e^{-\alpha_1 CA_{ij}}$ has a value which decreases rapidly in the first few annual rings and then gradually approaches an asymptote close to zero. The second part of the equation is a Michaelis–Menten function where α_2 reflects the pseudo-asymptotic ring density of mature wood and α_3 denotes the rate of progression between this asymptote and a minimum value reached in the juvenile period (Xiang *et al.*, 2014). Parameter α_2 had both a fixed and a random component, hence $a_{2,i}$ is the estimated tree-level random effect of α_2. Other fixed effects parameters were also allowed to vary randomly, but the model with α_2 as the sole random effect provided the best fit to the data. The effect of respacing was examined by allowing each of the fixed effects parameters in the model to vary by respacing intensity, i.e. by including respacing as a categorical variable in the model. The overall significance of respacing was assessed using LRT to compare the model containing these terms to the reduced model equation (1). The significance of respacing on individual terms within the model was also examined.

To determine whether there was an effect of spacing on wood density over and above any effects on radial growth rate, a second model containing both ring number from the pith and annual ring width was fitted to the data. While the model developed by Gardiner *et al.* (2011) contains both these terms, the following model form provided a better fit to the data:

$$DENS_{ij} = \beta_0 e^{-\beta_1 CA_{ij}} + \frac{(\beta_2 + \beta_4 RW_{ij})CA_{ij}}{\beta_3 + \beta_5 RW_{ij} + CA_{ij}} + b_{2,i} + \varepsilon_{ij} \quad (2)$$

where RW_{ij} is the width (mm) of the *j*th annual ring in the *i*th tree, and β_0, β_1, β_2, β_3, β_4 and β_5, are the fixed effects coefficients. This model is similar to that given by equation (1) except that the α_2 and α_3 parameters were allowed to vary with ring width. Parameter β_2 had both a fixed component and a random tree component. As with equation (1), the effect of respacing was examined by allowing each of the fixed effects parameters in the model to vary by respacing intensity.

Modelling latewood proportion

The proportion of latewood in an annual ring was modelled as a function of ring number from the pith and respacing intensity. Because proportion data values fall between zero and one, latewood proportion was modelled using logistic regression with a binomial link function. In this model, the random effect of ring within tree was assumed to follow a beta distribution. This hierarchical generalised linear model was fitted using the *glmmADMB* package in the R statistical programming environment (Fournier *et al.*, 2012; Skaug *et al.*, 2014) and had the following form:

$$LW_{ij} = \gamma_0 + \gamma_1 CA_{ij} + \gamma_2 SP_{2.6} + \gamma_3 SP_{3.7} + \gamma_4 SP_{4.6} + \gamma_5 SP_{5.6} + c_{0,i} + \varepsilon_{ij} \quad (3)$$

where LW_{ij} is the proportion of latewood in the *j*th annual ring in the *i*th tree, and γ_0, γ_1, γ_2, γ_3, γ_4 and γ_5 are the empirically derived parameter estimates. $SP_{2.6}$, $SP_{3.7}$, $SP_{4.6}$ and $SP_{5.6}$ are indicator variables for the 2.6, 3.7, 4.6, and 5.6 m respacing treatments, respectively. Multiple pairwise comparisons between respacing treatments were made using Tukey's adjustment.

Modelling microfibril angle

The pith-to-bark radial trend in MfA within a tree was modelled as a function of cambial age using the logistic function presented in Jordan *et al.* (2005):

$$MfA_{ij} = \frac{\beta_0}{1 + e^{\beta_1 CA_{ij}}} + \beta_2 + b_{2,i} + e_{ij} \quad (4)$$

where MfA_{ij} is the cellulose MfA (°) in each annual growth ring, β_0 corresponds to an initial value parameter, β_1 is a rate parameter and β_2 is the lower asymptote (Jordan *et al.*, 2005). The $b_{2,i}$ term is the random effect estimate of parameter β_2 for the *i*th tree. The effect of respacing was examined by allowing each of the fixed effects parameters in the model to vary by respacing intensity.

To incorporate the effect of annual ring width on MfA, the β_2 parameter (i.e. the lower asymptote) in equation (4) was allowed to vary as a function of ring width, as follows:

$$MfA_{ij} = \frac{\beta_0}{1 + e^{\beta_1 CA_{ij}}} + \beta_2 + \beta_3 RW_{ij} + b_{2,i} + e_{ij} \quad (5)$$

where RW_{ij} is the width (mm) of the *j*th annual ring in the *i*th tree. An alternative model incorporating a ring width term, in the form of a modified Michaelis–Menten equation, was also fitted as it can account for the differential effect of annual ring width in juvenile and mature wood (Auty *et al.*, 2013). However, equation (5) proved to be a better fit to the data. Again, the effect of respacing was examined by allowing each of the fixed effects parameters in the model to vary by respacing intensity.

In fitting the models to the data, heteroscedasticity was modelled as a power function of the absolute values of cambial age, while for the wood density model, a first-order autoregressive correlation structure AR(1) was applied to model correlation among observations at successive cambial ages within each tree. For the MfA model, correlation was modelled using an autoregressive-moving average correlation structure (Pinheiro and Bates, 2000). More details about these variance and autocorrelation functions are given in Auty *et al.* (2013) and Jordan *et al.* (2005).

Results

Wood density

When averaged across all trees in each spacing treatment, the maximum value of wood density occurred in the first ring from

the pith, and ranged from 579 kg m^{-3} in the 5.6 m spacing to 620 kg m^{-3} in the 2.6 m spacing. This was followed by a decrease to an average minimum value of between 315 kg m^{-3} at ring 11 and 363 kg m^{-3} at ring 13 in the 5.6 and 3.7 m spacing treatments, respectively. After this, wood density gradually increased to quasi-asymptotic stable values between rings 30 and 35 (Figure 1). In the two closest spacing treatments there was some indication of a decline in wood density after ring 40, but this trend was not observed in the three widest treatments. There was a considerable amount of tree-to-tree variation in wood density with one tree in particular from the 4.6 m spacing treatment exhibiting quite marked departures from the general radial trend, possibly due to the presence of compression wood in some annual rings (Gardiner et al., 2011).

The model given by equation (1) was able to explain 35 per cent of the variation in wood density (69 per cent if tree-level random effects were included), and the overall effect of spacing was significant when incorporated into equation (1) (P-value for an LRT comparing the two models <0.001). More specifically, the α_1 and α_2 parameters differed significantly between spacing treatments, while the α_0 and α_3 parameters did not. Inclusion of

spacing terms in the model increased the amount of overall variation in wood density that could be explained to 49 per cent (70 per cent including random effects).

On average, annual ring width reached a maximum value between rings 6 and 10 from the pith and a minimum value close to the bark (Figure 2). Mean ring width was higher in trees from the two widest spacing treatments compared with those growing in the three narrowest spacing treatments, although by age 50 years ring widths in all but the widest spacing treatment had converged (Figure 2). There was a negative relationship between wood density and ring width, and the ring width terms were significant in the model given by equation (2). The latter model had a lower AIC value than the model containing only cambial age as an explanatory variable (equation (1)). This model was also able to explain a greater proportion of the variation in wood density (50 per cent with fixed effects only; 74 per cent including random effects). Parameter estimates for the fixed effects and standard deviations of the random effects for equation (2) are given in Table 2. The overall effect of spacing was significant when incorporated into equation (2) (P-value for an LRT comparing the two models <0.001). Parameters β_1, β_2 and
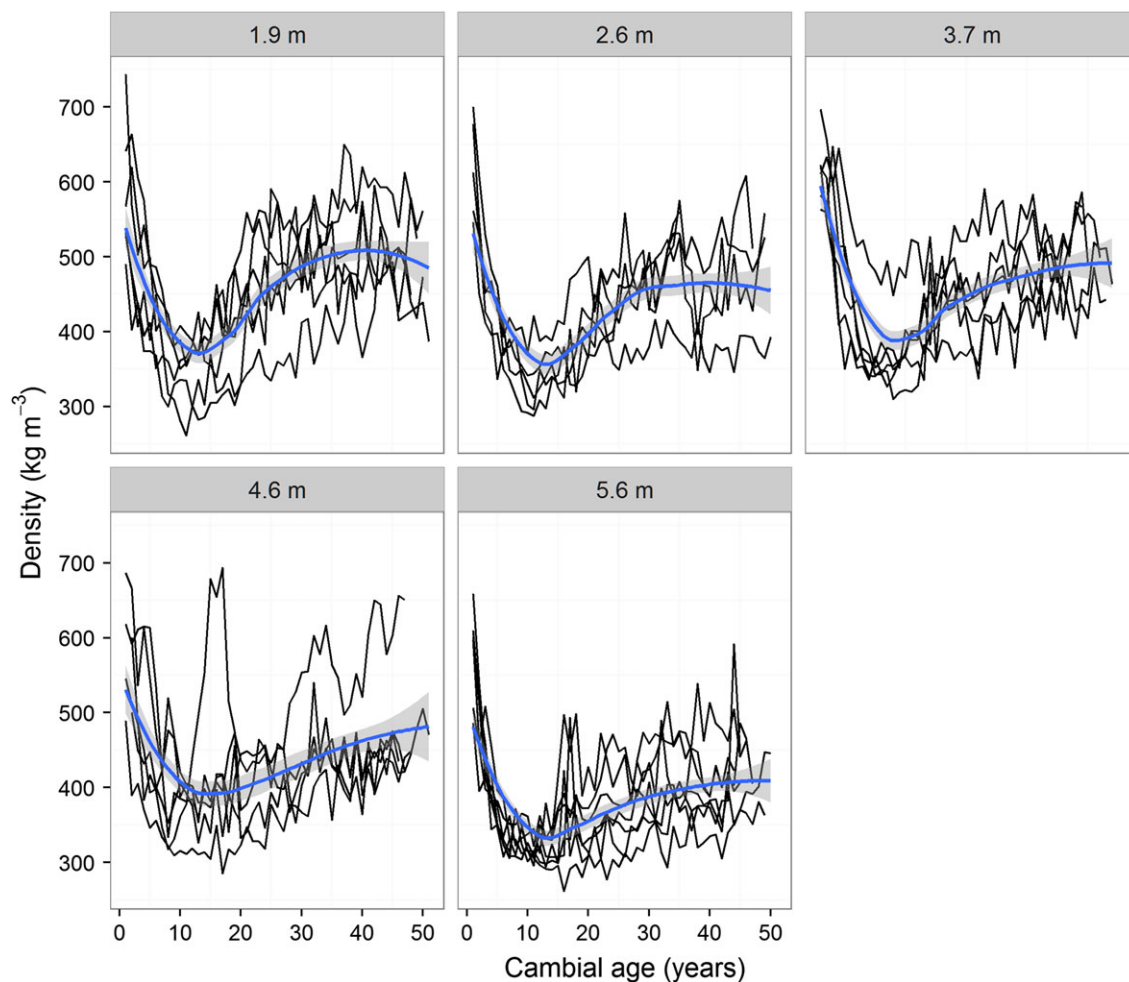

Figure 1 Radial variation in ring-level average wood density across the five respacing treatments. Black lines show the radial profiles for individual trees within each respacing reatment and the blue line corresponds to a locally-weighted regression (loess) fitted to the data. The standard error for this locally weighted regression is indicated by grey shading.
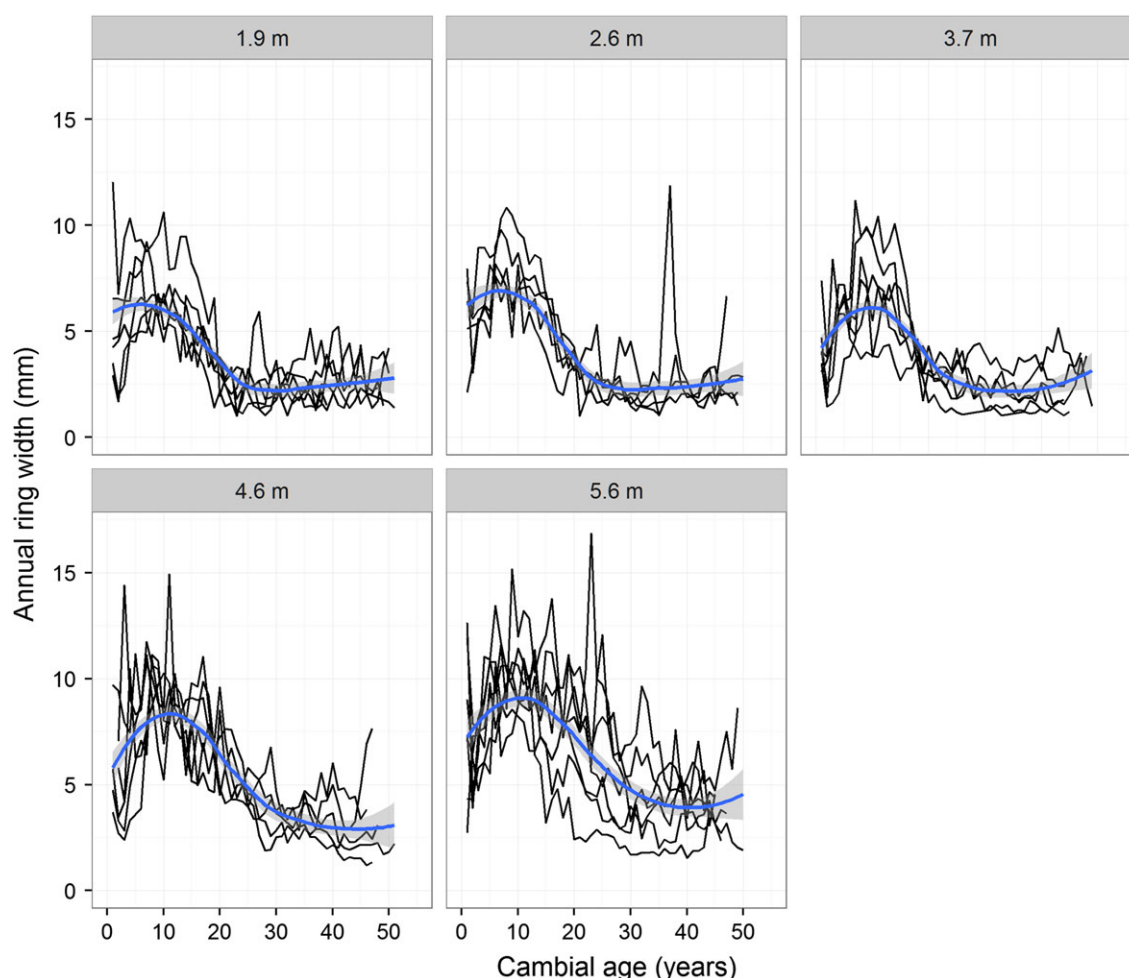
Figure 2 Radial variation in average ring width across the five respacing treatments. Black lines show the radial profiles for individual trees within each respacing treatment and the blue line corresponds to a locallyweighted regression (loess) fitted to the data. The standard error for this locally weighted regression is indicated by grey shading.

β_5 differed significantly between spacing treatments. Allowing these parameters to vary by spacing increased the amount of variation in wood density explained to 57 per cent (76 per cent with random effects). When the spacing term was included in the model fixed effects, the RMSE of equation (2) was 53.2 kg m^{-3} and IEI % was 9.4 per cent, compared with 58.5 kg m^{-3}, and 10.7 per cent, respectively, for equation (1).

Radial profiles of wood density were simulated for each spacing treatment using mean values of ring width for each ring number from the pith. Mean ring width values were predicted for each respacing treatment using nonlinear models of annual ring width as an exponential function of cambial age (parameter estimates not shown). Mean predicted values of wood density were 382 and 457 kg m^{-3} in the widest and narrowest spacing, respectively. Wood density for the other spacing treatments fell between these two extremes. Maximum predicted density values for each treatment were found in the ring adjacent to the pith (i.e. cambial age 1 year), minimum values at rings 10–13, and the mean values at a cambial age of ~25–28 years (Figure 3).

Because different parameters of the wood density model varied between respacing treatments, it was not possible to fully interpret the nature of its overall effect on wood density over and above the influence of cambial age and ring width. For this reason, we ran simulations whereby the model parameters estimated for each respacing treatment were used to predict wood density in the simulated growth data, i.e. using annual growth models developed using ring width data from each of the five respacing treatments in the experiment. The models for each spacing predicted that, after accounting for annual ring width, wood density would decrease progressively for a given cambial age as tree spacing increased (Figure 4A–E). This was the case no matter which growth model was used, although the magnitude of such variations differed between treatments. One clear trend was that wood density predictions were consistently much lower when predicted using the parameters estimated for the 5.6 m treatment, indicating that the ring width effect was smaller in the widest spacing than in the others.
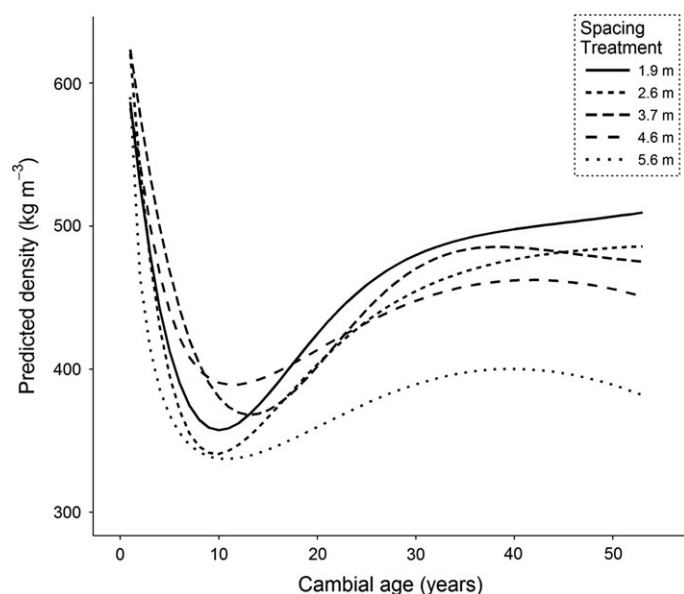
Latewood proportion

The proportion of latewood in an annual ring increased with increasing cambial age (Figure 5). The most significant differences

Table 2 Parameter estimates, associated standard errors, P-values and standard deviation of the random effects estimates for the final wood density model given by equation (2).

Fixed parameters	Estimate	SE	t-Value	P-value
β_0	657.399	12.646	51.985	<0.001
β_1 (Intercept)	0.215	0.022	9.843	<0.001
$\beta_{1,2,6}$	0.054	0.035	1.534	0.125
$\beta_{1,3,7}$	−0.063	0.026	−2.428	0.015
$\beta_{1,4,6}$	0.028	0.029	0.953	0.341
$\beta_{1,5,6}$	0.103	0.035	2.973	0.003
β_2 (Intercept)	586.340	22.589	25.956	<0.001
$\beta_{2,2,6}$	−48.356	29.426	−1.643	0.101
$\beta_{2,3,7}$	−4.916	29.692	−0.166	0.869
$\beta_{2,4,6}$	−38.070	28.577	−1.332	0.183
$\beta_{2,5,6}$	−97.295	27.446	−3.545	<0.001
β_3	3.536	0.631	5.605	<0.001
β_4	−10.124	2.321	−4.363	<0.001
β_5	0.744	0.236	3.158	0.002
$\beta_{5,2,6}$	−0.517	0.242	−2.141	0.032
$\beta_{5,3,7}$	0.517	0.452	1.145	0.252
$\beta_{5,4,6}$	−0.626	0.219	−2.864	0.004
$\beta_{5,5,6}$	−0.726	0.213	−3.411	0.001
Random parameters	Std. dev.			
$b_{2,i}$	42.991	*Tree*		
ε_{ij}	42.748	*Residual*		

Parameter estimates show the intercept (i.e. value for the 1.9 m respacing treatment) and additive coefficients for the other treatments relative to the 1.9 m treatment.

Figure 3 Radial profiles of ring-level average wood density for the five respacing treatments predicted using the model given by equation (2).

in latewood proportion were between the 5.6 and the 1.9 m respacing treatments ($P < 0.001$), and between the 5.6 and 3.7 m treatments ($P < 0.001$). The differences between the 5.6 m treatment and the 2.6 and 4.6 m treatments were also statistically significant ($P < 0.05$). Parameter estimates for the model given by equation (3) are given in Table 3. Predictions of latewood proportion for each respacing treatment are shown in Figure 6. On average, predicted latewood proportion increased from the widest to the narrowest respacing treatment. Trees growing at the 1.9 m spacing had ~20 per cent latewood in ring 50, while trees growing at the 5.6 m spacing had only 10 per cent latewood in the same ring.

Microfibril Angle

There was a general nonlinear decrease in MFA from an average value of ~30° at the pith (i.e. cambial age 1 year) to the mature wood region, where it reached a relatively constant value of ~16° (Figure 7). This decline was relatively rapid in the first 20 annual rings, before slowing down to the more stable values close to the bark. However, for a small number of trees the initial decrease was followed by an increase in MfA with increasing cambial age. When comparing models with a ring width term but no spacing term included, the fixed effects of equation (4) explained 54 per cent of the variation in MfA (70 per cent including random effects), compared with 50 per cent (62 per cent with random effects) for the Michaelis–Menten model.

The best performing model for MfA was the one given by equation (5), which was able to explain 59 per cent of the variation in MfA (76 per cent if tree level random effects were included). There was also a significant overall effect of respacing treatment on the β_1 and β_3 parameters of equation (5), and this model had the lowest AIC value of all the MfA models fitted. The RMSE of equation (5) was 4.2° and |E| % was 17.7°, compared with 4.4°, and 18.3°, respectively, for the equivalent Michaelis–Menten equation that included both spacing and ring width terms. Parameter estimates and standard deviations of the random effects for the final model of MfA variation (equation (5)) are given in Table 4.

Radial profiles of MfA were predicted for each respacing treatment using the same method as used for wood density. Over the first 20 annual rings from the pith, predicted MfA declined rapidly, and was consistently higher in the 4.6 and 5.6 m respacing treatments and lowest in the trees growing in the 1.9 m spacing (Figure 8). However, after reaching a minimum value at a cambial age of 35 years, predicted MfA in the narrowest spacing began to increase again towards the bark. This behaviour was also observed for predicted values in the 3.7 and 5.6 m spacings, where predicted MfA began to increase at rings 38 and 43 from the pith, respectively. In the 2.6 and 4.6 m treatments, predicted values continued to decrease or stabilise towards the bark.

Discussion

The effect of tree spacing on Sitka spruce wood density has been a source of considerable debate in British and Irish
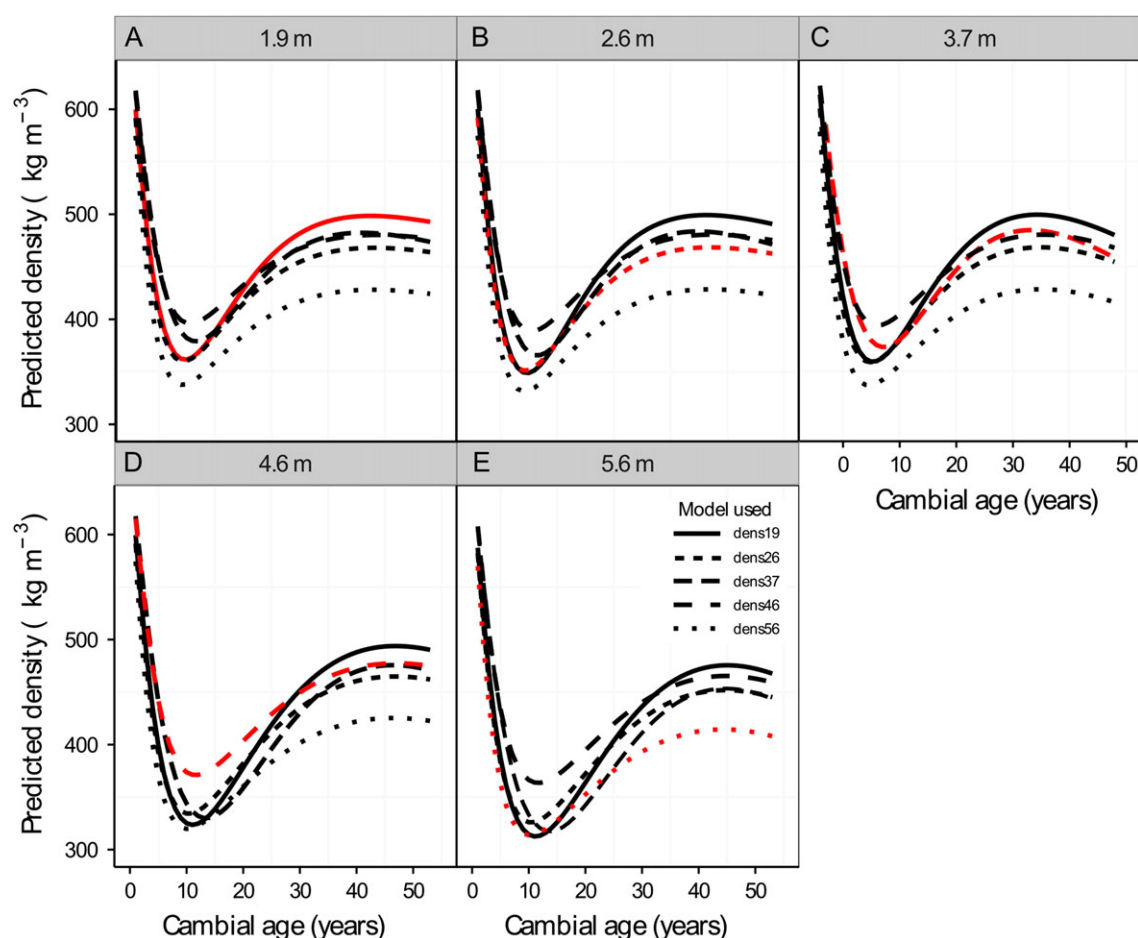
Figure 4 Wood density predictions on simulated data using growth models derived from ring width data from each respacing treatment (A–E). Each plot shows the predictions obtained using parameter estimates obtained from equation (2) and annual ring widths modelled using data from each respacing treatment. Red lines in each plot represent the true model for that particular spacing.

forestry. Our results confirmed the findings from previous studies (Brazier, 1970a, 1970b; Petty *et al.*, 1990; Simpson and Denne, 1997; Gardiner *et al.*, 2011), which showed that wood density was significantly lower in widely-spaced stands. In contrast to these earlier studies, which only covered a range of tree spacing from 0.9 m × 0.9 m up to 2.4 m × 2.4 m, our study covered a much wider range of spacing treatments. We also found that differences in wood properties between spacing treatments increased with cambial age. This is consistent with earlier results from the same experiment (Savill and Sandels, 1983) and also with studies in other conifer species, such as *Pinus radiata* D. Don (Watt *et al.*, 2011).

Despite finding no evidence of differences in wood density between treatments in an earlier study on structural timber from the same stand (Moore *et al.*, 2009), the results from this more detailed study show that significant differences exist, particularly in the two widest spacing treatments (i.e. 4.9 and 5.6 m). The study by Moore *et al.* (2009) measured density on blocks cut from structural timber with cross-sectional dimensions of 100 mm × 47 mm, and most of the variation in density occurred within trees or between trees within a plot, leaving less than 0.1 per cent of the variation due to differences among treatments. In contrast, more than 10 per cent of the variation

in bending strength and stiffness was attributed to differences between respacing treatments in the same study. The precise reason for these contrasting results is not known, but it may be an artefact of the original sampling scheme in the structural timber study (Moore *et al.*, 2009), in which two boards were selected from contrasting radial positions in each log. In the current study, the entire cross section of the tree was sampled to account for radial variation in wood properties. More generally, caution should be exercised when comparing ring-level wood properties measurements with those made on structural timber due to the much higher probability that the latter will contain defects (e.g. knots), which strongly influence mechanical properties.

This study found very similar radial patterns in wood density within Sitka spruce trees that have been described either qualitatively or quantitatively in earlier studies (Savill and Sandels, 1983; Petty *et al.*, 1990; Mitchell and Denne, 1997; Simpson and Denne, 1997; Gardiner *et al.*, 2011). Similar to the latter study, we found that that the radial variation in wood density within a tree could be modelled as a function of both ring number from the pith and annual ring width. We also found a negative relationship between ring width and wood density, which is consistent with the results from previous studies on Sitka spruce
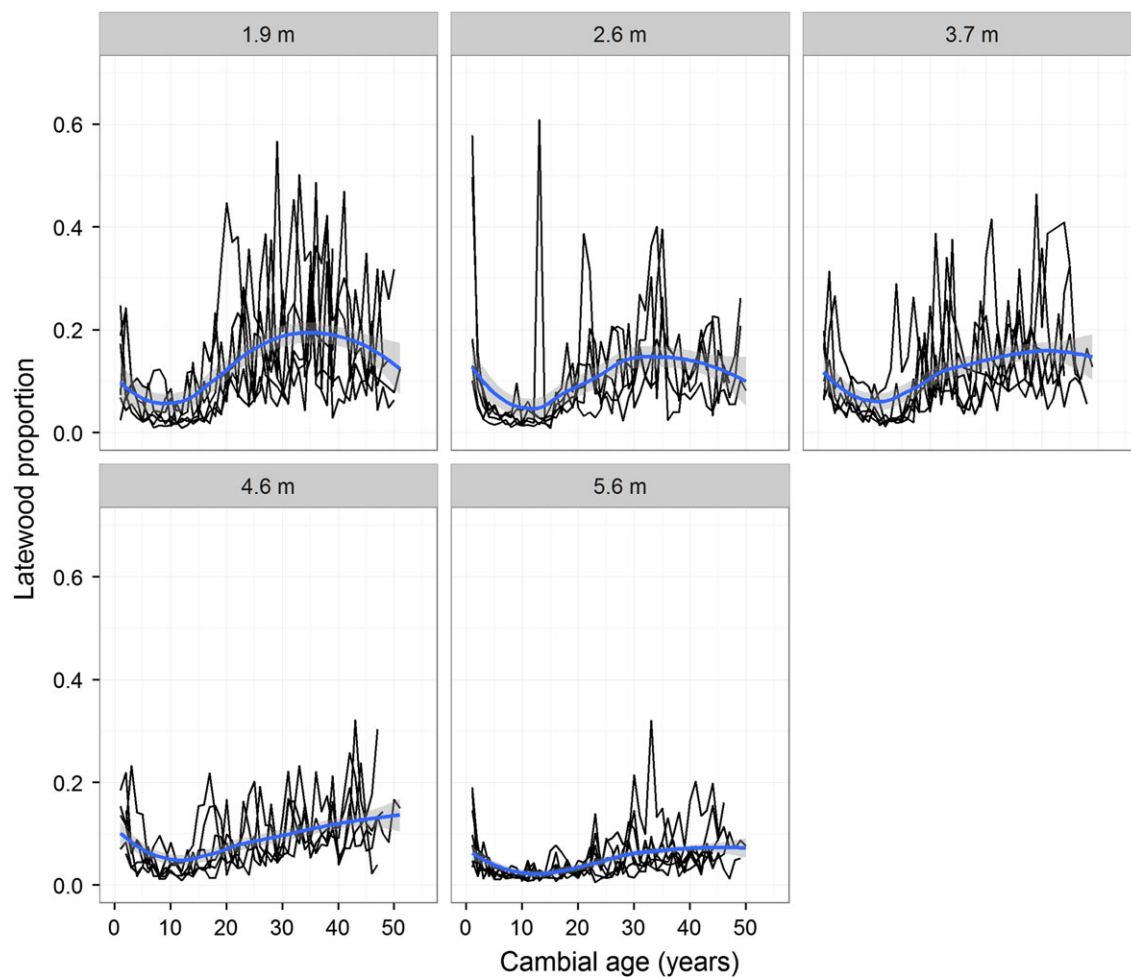
Figure 5 Radial variation in latewood proportion within an annual ring across the five respacing treatments. Black lines show the radial profiles for individual trees within each respacing treatment and the blue line corresponds to a locally-weighted regression (loess) fitted to the data. The standard error for this locally weighted regression is indicated by grey shading.

Table 3 Parameter estimates, associated standard errors, P-values and standard deviation of the random effects estimates for the final model of latewood proportion given by equation (3)

Fixed parameters	Estimate	SE	z-Value	P-value
γ_0	−2.636	0.091	−28.86	<0.001
γ_1	0.025	0.001	19.27	<0.001
γ_2	−0.219	0.126	−1.74	0.082
γ_3	−0.056	0.120	−0.47	0.642
γ_4	−0.290	0.122	−2.38	0.017
γ_5	−0.769	0.117	−6.55	<0.001
Random parameters	Std. Dev.			
$c_{0,i}$	0.187	*Tree*		
ε_{ij}	–	*Residual*		

(Brazier, 1970a, b; Gardiner and O'Sullivan, 1978; Petty *et al.*, 1990). The relationship between ring width and wood density has been a source of controversy in the scientific literature (Brazier, 1977), with some researchers claiming that such relationships are an artefact of the relationship between ring width and annual ring number from the pith (Larson, 1969). However, our results showed that there was a negative relationship between ring width and wood density at a given cambial age.

Although ring width is affected by tree spacing, we found that there was a still a significant effect of respacing treatment on wood density even after ring width was accounted for in the models. This indicates that existing models for predicting radial variation in Sitka spruce wood density (e.g. Gardiner *et al.*, 2011) may not be able to completely account for the effects of tree spacing, even if they contain a ring width term. The limited impact of ring width on predictions made using the growth model derived from the 5.6 m spacing (Figure 4E) could explain why spacing had a significant impact on wood density over and
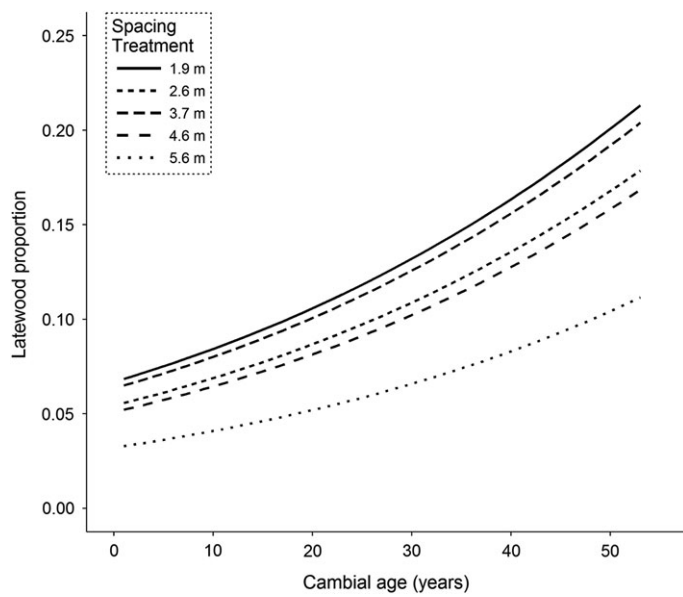
Figure 6 Radial profiles of ring-level latewood content for the five respacing treatments predicted using the model given by equation (3).

above the effects of cambial age and ring width. At such wide spacing, it is possible that wood density tends towards a minimum value that will be maintained even if the radial growth rate continues to vary among individual trees. This would suggest that the slowest-growing trees in the 5.6 m spacing (which are still fast-growing relative to trees in the narrower spacings) have already reached this threshold. The notion of a species-specific minimum wood density threshold seems biologically plausible given the requirement of xylem in mature trees to maintain both structural support and hydraulic conductance (Sperry, 2003). This idea is also compatible with the principle that ring average wood density is largely determined by the width of the earlywood, and the associated limited variation in the width of the denser latewood (Brazier, 1970a; Moore, 2011). Assuming constant density for both early- and latewood, this principle implies that the mean ring density should tend towards a lower asymptote at very large ring widths.

While the models developed in this study showed differences in wood density between spacing treatments, they do not provide any insight into why these differences exist. Although related to mechanical properties and structural support of the tree, it is also postulated that wood density is related to
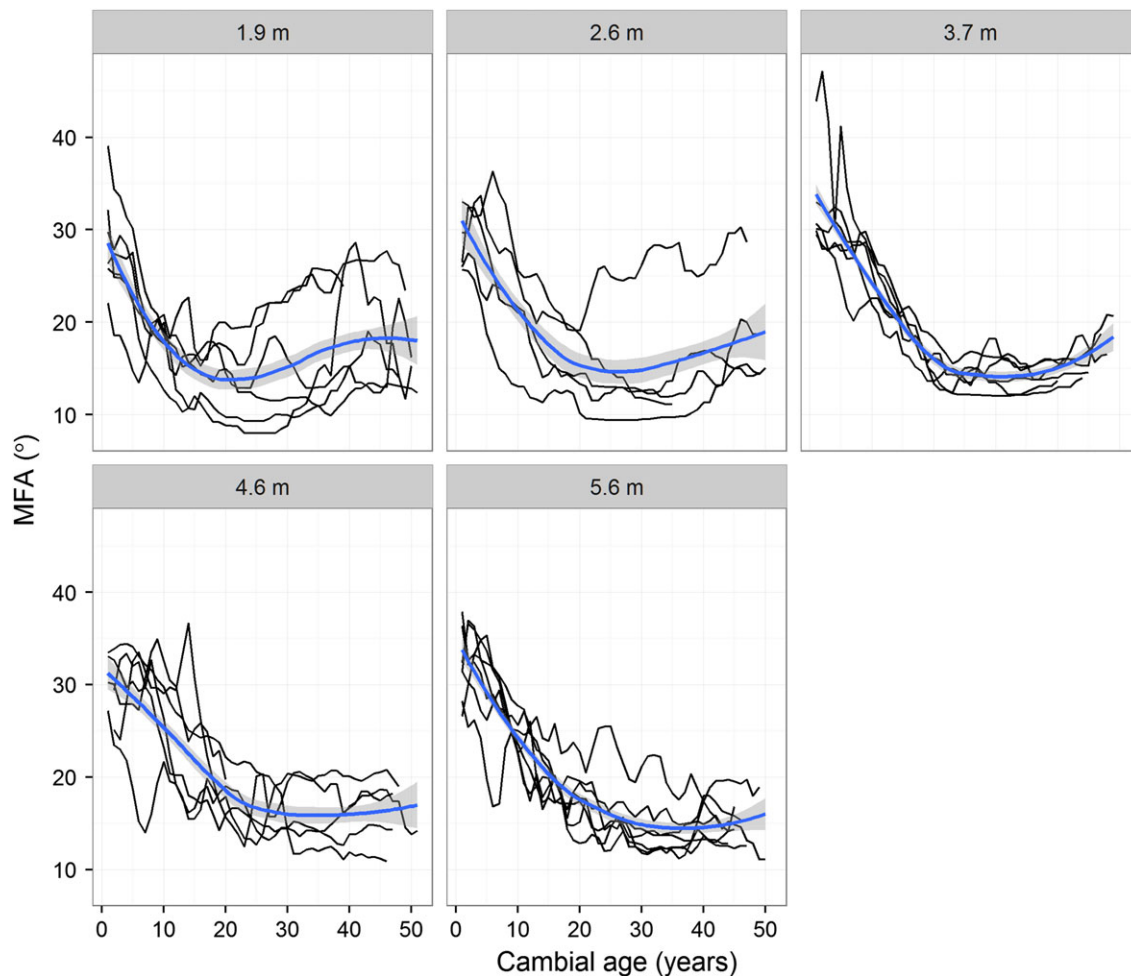

Figure 7 Radial variation ring-level average MfA across the five respacing treatments. Black lines show the radial profiles for individual trees within each respacing treatment and the blue line corresponds to a locally-weighted regression (loess) fitted to the data. The standard error for this locally weighted regression is indicated by grey shading.

Table 4 Parameter estimates, associated standard errors, P-values and standard deviation of the random effects estimates for the final model of MfA variation given by equation (5). Estimates for the β_1 and β_2 parameters show the intercept (i.e. value for the 1.9 m respacing treatment) and values for the other treatments relative to the 1.9 m treatment

| Fixed parameters	Estimate	SE	t-Value	P-value
β_0 (Intercept)	36.608	3.000	12.203	<0.001
β_1 (Intercept)	0.304	0.064	4.772	<0.001
$\beta_{1,2,6}$	−0.143	0.072	−1.981	0.048
$\beta_{1,3,7}$	−0.158	0.069	−2.277	0.023
$\beta_{1,4,6}$	−0.205	0.066	−3.103	0.002
$\beta_{1,5,6}$	−0.169	0.068	−2.493	0.013
β_2	14.720	0.636	23.150	<0.001
β_3 (Intercept)	0.412	0.069	5.971	<0.001
$\beta_{3,2,6}$	−0.407	0.096	−4.229	<0.001
$\beta_{3,3,7}$	−0.035	0.111	−0.320	0.749
$\beta_{3,4,6}$	−0.313	0.089	−3.525	<0.001
$\beta_{3,5,6}$	−0.152	0.081	−1.868	0.062
Random parameters	Std. Dev.			
$b_{2,i}$	2.598	Tree		
ε_{ij}	8.390	Residual		
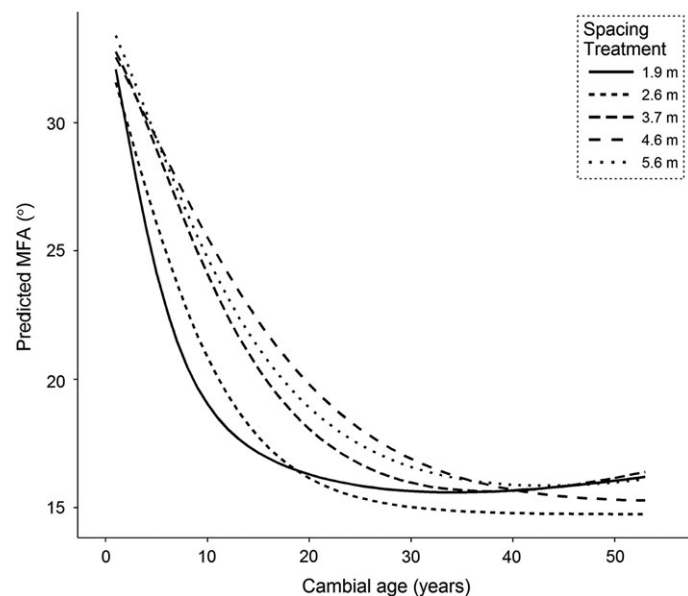
Figure 8 Radial profiles of ring-level average MfA for the five respacing treatments predicted using the model given by equation (5).

maintenance of hydraulic efficiency and to protect against implosion by negative pressure in the 'xylem pipeline' (Hacke et al., 2001). Larson (1969) also described a possible process through which spacing affects wood properties. His 'continuum' concept states that the development of a tracheid is determined by its distance from the crown, its age and its time of formation within a growth ring. Through this concept Larson

hypothesised that there should be a relationship between crown size and shape, and wood properties. Under more intense competition i.e. in closely-spaced stands, the rate of crown recession is expected to be greater and lateral spread reduced. Conversely, trees grown at wider spacing would be expected to have a larger crown and have a lower proportion of latewood in the lower part of the stem. In the widest spacing treatment in our study, trees had 10 per cent latewood in the outermost rings compared with 20 per cent in trees grown at the narrowest spacing. Brazier (1970a, b) found that the width of latewood in Sitka spruce annual rings was fairly constant across a radial profile, so that the proportion of latewood decreased with increasing ring width. We used a wood density threshold to define latewood, so examining relationships between latewood percentage and wood density in detail is potentially a circular argument. Further detailed studies on the anatomy of the wood cells formed under different spacing treatments are required to better understand the mechanisms through which tree spacing affects wood density, and especially the part of the variation that cannot be explained by the differences in ring width.

While the effects of tree spacing on wood density have been relatively widely studied, both in Sitka spruce and other species, relatively few studies have examined the effects of tree spacing on MfA. Watt et al. (2011) found a significant effect of tree spacing on MfA, but no consistent trend in the magnitude of this effect across different spacing treatments. Similarly, in the current study on Sitka spruce, while there was a significant effect of annual ring width on MfA, we also found a significant effect of respacing treatment on MfA over and above that of cambial age and ring width. This is consistent with similar results found in Scots pine (Pinus sylvestris L.) (Auty et al., 2013) and Norway spruce (Picea abies L. Karst.) (Herman et al., 1999). However, since only six trees were sampled from each spacing treatment in the current study, any samples that showed significant departures from the expected typical radial trend for MfA may have disproportionately influenced the results. In each of the two narrowest spacing treatments, at least one sample had an atypical pattern of radial variation. This may at least partially explain why mean MfA was higher in the outer rings in trees from the narrowest spacing treatment than in trees from the widest spacing.

In addition to the magnitude of wood properties, Larson (1969) also hypothesised that the radial pattern of variation in properties, in particular the transition from corewood to outerwood, would be affected by tree spacing. The spacing differences in this experiment were created by respacing plots that had been established at the same initial density, and respacing was done 11 years after the stands were planted. Therefore, differences in the size of the corewood zone would not be expected to be as large as they would have been had the treatments represented differences in initial spacing. However, Savill and Sandels (1983) measured the radial profile of wood density in the stand when it was 32 years old and concluded that the period of corewood formation did not cease until 1969, i.e. 20 years after the stand was planted and nine years after the respacing treatments were applied. The size of the corewood zone was much larger than the innermost 12 rings assumed by Brazier and Mobbs (1993) and, based on the diameter measurements presented in Kilpatrick et al. (1981), represented ~46 per cent of average

DBH (at time of felling) in the control plots, and 41 per cent of average DBH in the 5.6 m respacing treatment.

Conclusions

The results of this study support previous findings showing a significant effect of wide spacings on wood density and MfA, although differences in MfA between treatments were not large. While this study confirmed that wood properties are related to annual ring width at a given cambial age, our results showed that there are limitations associated with its use as a proxy for spacing. From a forest management perspective, early respacing to low residual stand densities will likely result in a considerable reduction in wood density, which is also associated with a reduction in the proportion of latewood in an annual ring. However, respacing to 2.6 or even 3.7 m is unlikely to have a detrimental effect on wood density and MfA over the life of the stand.

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Conflict of interest statement

None declared.

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