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Variation of radial wood properties from genetically improved Sitka spruce growing in the UK

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There is little information about the impacts of past Sitka spruce (*Picea sitchensis* [Bong.] Carr.) tree breeding on wood properties because the emphasis has traditionally been on improving stem form and growth rates. This study used both SilviScan and mechanical testing to investigate the radial variations in wood stiffness, bending strength, density and microfibril angle in defect-free samples taken from the first United Kingdom progeny trial to reach merchantable size. We tested for differences in these radial patterns of variation in half-sibling progeny of three plus trees originally selected for superior growth rate and stem form against a non-selected control. Large differences in all of the properties were observed with radial position, with properties generally being less desirable in the corewood. Significant undesirable differences between the improved families and the control were found for stiffness, strength and microfibril angle. There was no significant relationship between wood density and stiffness in samples taken from the inner part of the tree, where stiffness was more closely associated with microfibril angle. Overall, previous selections for growth rate and/or stem form have compromised timber properties. It is recommended that current breeding programmes focus on corewood stiffness to prevent further degradation in the wood properties of the future timber supply.

Introduction

Sitka spruce (*Picea sitchensis* [Bong.] Carr.) is the most commonly planted commercial tree species in the UK (Forestry Commission, 2014), where it is grown on a rotation of ~40 years. A breeding programme for Sitka spruce has existed in the UK since the 1960s, with the primary focus on improving the growth rate, stem form and branching characteristics (Fletcher and Faulkner, 1972). However, little consideration was given to the wood properties, other than knot size, that can affect the quality grade and hence value of the timber. Lee (1999) showed that the breeding programme was successful in its aim to increase growth and improve stem form. However, this has been accompanied by reduced wood density (albeit estimated with a Pilodyn (Cown, 1978)), which is a grade-determining property for structural timber (CEN, 2003). Lee (1999) also noted that planting faster growing selectively bred material would lead to shorter rotations with a larger proportion of juvenile wood, more suitably termed corewood (Burdon *et al.*, 2004), in the final crop. Lee (1999) echoed earlier advice of Brazier (1967) and Thompson (1992) who suggested that the properties of the corewood should be more limiting than the properties of outerwood for timber performance. Therefore, breeding efforts should concentrate on improving corewood properties. Apiolaza (2009) proposed that this can be further used as an advantage to breeding for better quality wood, as trees can be selected at a young age, thereby shortening the generation cycle and accelerating breeding programmes. It is, therefore, important to consider the effects of selective breeding on the radial variation in grade-determining wood properties.

Wood density, stiffness and strength are the three wood properties used by architects and engineers in design specifications and are, therefore, given equal weighting when assigning structural timber to a strength class (CEN, 2003). It is the nature of the grading system that one of these three properties will always be limiting and constrains timber to a particular grade. In the current study, it is wood stiffness that is most of interest, because previous studies (e.g. Moore *et al.*, 2013) have shown that it is the property that generally limits UK Sitka spruce timber to the C16 grade (CEN, 2003), whereas the wood density and wood strength are normally sufficient for the higher C18 and C20 grades, respectively. Wood stiffness primarily depends on wood density, which relates to the amount of wood material present in a given volume, and microfibril angle (MFA) (Evans and Ilic 2001; McLean *et al.*, 2010), which here refers to the mean orientation of cellulose microfibrils in the S2 wood cell wall layer. Typically wood stiffness is observed to increase with wood density (Kollmann and Cote, 1968; Zobel and van Buijtenen, 1989; McLean *et al.*, 2010) and decrease with MFA (Cowdrey and Preston, 1966; Evans and Ilic, 2001; McLean *et al.*, 2010). Empirical relationships that combine density and MFA are used as a basis to predict stiffness with a high degree of success (Evans and Ilic, 2001; McLean *et al.*, 2010). As instrumentation such as SilviScan (Evans, 1999) has made it possible to resolve measurements of wood density and MFA on an annual ring basis, studies have examined the radial evolution of these two properties as a proxy for wood stiffness in spruce breeding programmes (e.g. Gräns *et al.*, 2009; Steffenrem *et al.*, 2009; Lenz *et al.*, 2011; Chen *et al.*, 2014). However, Alteyrac *et al.* (2006) had previously used mechanical testing in combination with SilviScan and found that only MFA was important for wood stiffness. Therefore, the use of wood density, possibly even in combination with MFA, to estimate wood stiffness could be flawed. We propose that this discrepancy arises due to the complex radial wood density profile in spruce (e.g. Gardiner *et al.*, 2011) and, therefore, that the relationship of both wood density and MFA with wood stiffness should be considered with respect to radial position. This is an important matter for tree breeders, as stiffness or MFA is more difficult and costly to measure than wood density. Furthermore, if the aim is indeed to improve the corewood properties, then we need to ensure that the most appropriate method is used. In this study, we investigated the radial variation in the key wood properties affecting structural timber grade (i.e. stiffness, strength and density) in a Sitka spruce progeny trial. Additionally, by measuring the properties of defect-free wood samples, we determined whether wood density or MFA had the greater influence on the radial variation in wood stiffness in order to help guide the future of spruce breeding programmes.

Material and methods

The study was undertaken using material from the same experiment as Moore *et al.* (2009), which is briefly summarized here. The experiment was a family by plot-size trial planted in 1968 at Kershope Forest, Cumbria, UK (latitude 55° 05′ N; longitude 2° 50′ W, 190 m elevation). Trees were planted at 1.8 × 1.8 m square spacing in a mix of plot sizes and shapes, where plots denote families; however, we only used the larger square plots containing 4 × 4, 5 × 5 and 6 × 6 trees. The families investigated were half-siblings chosen to represent improvements over nonselected trees of Queen Charlotte Island (QCI) origin, used as a control. Family 2 was selected for improved stem straightness, Family 3 was selected for improved vigour and Family 4 was selected for improved (Pilodyn estimated) density. Hereafter, families and the control are referred to as treatments.

Twelve 36-year-old trees from each treatment with diameter at breast height of at least 18 cm (i.e. large enough to produce sawlogs) were randomly sampled across the range of diameters present in each treatment. This sampling was unbalanced with respect to the experimental design at the time of planting as it was independent of the blocking in the original experimental design. The characteristics of all trees and the 12 sampled trees from each of the 4 treatments are given in Table 1. The 12 trees per treatment ($n = 48$) were additional to the 36 trees per treatment ($n = 144$) sampled for the determination of structural timber properties described in Moore *et al.* (2009). The north side of each selected tree was marked with a line for the future reference orientation of disc and clear wood samples. The trees were felled, and a 1-m-long log was cut from each tree ($n = 48$) starting at 2 m above the base of the tree. In addition, a disc was cut at breast height (1.3 m) from each tree.

Mechanical properties of small clear specimens

From each of the logs, small defect-free wood specimens were prepared with dimensions of 20 × 20 × 300 mm in their radial, tangential and longitudinal directions, respectively. One log from Family 2 did not yield any defect-free specimens. These specimens were cut from the pith to the bark along four cross sectional radii, from two perpendicular diameters, and the ring numbers from the pith for each specimen were recorded. A total of 603 specimens were prepared, and these were tested to determine MOE and bending strength (modulus of rupture – MOR) in accordance with BS 373 (BSI, 1957). Prior to testing, specimens were conditioned to 12 per cent moisture content in a controlled-environment chamber at 65 per cent RH and 20°C. The moisture content of each specimen was measured immediately prior to testing using a capacitance-based non-contact moisture meter (Model FMV, Brookhuis Micro-Electronics BV, The Netherlands). Mass and volume of each specimen were recorded and used to calculate density.

Specimens were tested in three-point bending using a universal testing machine (Model H5KT, Tinius Olsen Ltd, Redhill, England) with the distance

Table 1 Sample and stand-level characteristics (mean values) of the four treatments selected for further measurement

Treatment	Sample tree characteristics ('12 trees per treatment')				Stand-level characteristics ('all living trees per treatment')			
	DBH (cm)	Height (m)	HLB^1 (m)	HCB (m)	DBH (cm)	Yield class	Survival^2 (%)	Basal area (m^2 ha^{-1})
QCI (control)	24.9 (3.8)	24.2 (1.5)	15.3 (1.4)	16.7 (1.4)	20.7^a	22	50	56
Family 2 (straighter)	23.7 (3.7)	24.6 (1.6)	15.5 (1.5)	16.8 (1.6)	22.2^b	24	67	84
Family 3 (faster growth)	23.8 (4.2)	23.6 (1.5)	15.2 (2.1)	17.0 (1.2)	22.2^b	24	61	79
Family 4 (higher density)	21.5 (3.8)	23.8 (1.4)	15.2 (0.9)	16.5 (1.1)	19.9^a	22	64	66

Stand-level data are from Mochan *et al.* (2008). Standard deviations for sample tree characteristics are given in parentheses.

[1] HLB and HCB are the height to the lowest live branch and height to the lowest live whorl, respectively.

[2] Survival is calculated as per cent of remaining stems per hectare from an initial planting density of 3136 stems ha^{-1}.

[a,b] Figures with different superscripts are significantly different at $P \leq 0.05$. No superscripts indicate significance tests either not carried out or no differences were found between any of the treatments.

between support points set at 280 mm. The rate of loading was set at 6.6 mm min^{-1}, and deflection of the specimen was measured from the crosshead displacement of the testing machine. MOE and MOR were calculated using the standard equations for beam bending under three-point loading as presented in BS 373 (BSI, 1957). Measurements made on small clear specimens cannot be related to a single growth ring like higher-resolution SilviScan measurements. We reflected this using categorization of the small clear samples according to their radial position, based on ring number from the pith (i.e. cambial age). Samples that did not contain any rings older than 7 years were classified as 'corewood', whereas samples that did not contain any rings younger than 15 years were classified as 'outerwood'. All other samples were deemed to be intermediate between these two categories and classified as 'transition' wood. The sample numbers according to treatment and age classification are shown in Table 2 and for analysis we refer to these categories as 'radial positions'.

Ring-level density and MFA measurements

Measurements of density and MFA were made using the SilviScan-3 instrument at Innventia AB, Stockholm. Resources only permitted SilviScan analysis of 9 discs per treatment, which were randomly selected from the 12 breast height discs available for each tree within each of the 4 treatments ($n = 36$). A pith-to-bark sample strip was cut from each disc along a radial line extending from the pith to the cambium on the north side of the tree. This strip had dimensions of 7 mm in the longitudinal direction and 2 mm in the tangential direction and was prepared in accordance with the requirements for SilviScan measurements (Evans *et al.*, 1999). All strips were Soxhlet extracted with acetone to remove the resins, which could affect the measurements, then conditioned at 40 per cent RH and 20°C within a climate controlled room to reach an equilibrium moisture content of 7–8 per cent.

Radial profiles of ring average wood density were determined for each strip using X-ray absorption at 50 μm resolution, and the average MFA was determined over successive 5-mm intervals using X-ray diffraction (Evans, 1999). The presence of compression wood or other defects (e.g. small knots), visually identified on the samples that were produced, caused abnormalities in the data and resulted in the exclusion of five profiles from further analysis. In total, data from 31 of the 36 radial strips were used in the comparison of MFA between treatments.

MFA of destructively tested small clear specimens

In order to directly investigate the influence of MFA and density on the stiffness of the small clear specimens in this study, short sections 7 × 20 × 2 mm (longitudinal × radial × tangential) were cut from a random subsample ($n = 69$) of the small clear specimens used to determine mechanical properties. MFA was determined using the SilviScan instrument at CSIRO, Melbourne (Evans, 1999; Evans *et al.*, 1999).

Table 2 Number of small clear samples used for mechanical testing according to treatment and radial position category

Radial position	QCI control	Family 2	Family 3	Family 4	Sum
Corewood	46	57	77	65	245
Transition	76	59	91	72	298
Outerwood	24	12	12	12	60
Total	146	128	180	149	603

Data analysis

Radial variations in wood properties and possible differences in these properties between treatments were examined using mixed effects models (Pinheiro and Bates, 2000), in which a nested structure was assumed for the random effects. These random effects represent the original experimental design and consisted of block, plot within block and tree within plot. Fixed effects were used to account for the radial variation in these properties and to investigate treatment differences, as described in more detail in the following section. All models were fitted to the data using the maximum likelihood method in the nlme package (Pinheiro *et al.*, 2013) within the open source statistical software R version 3.1.2 (R Core Team, 2014). To test the significance of treatment differences, models (described below) containing treatment terms were compared with a reduced model without any treatment terms by likelihood-ratio tests (Pinheiro and Bates, 2000).

Mechanical properties and wood density

The radial trends in mechanical properties, such as wood stiffness (e.g. Leban and Haines, 1999), and wood density (e.g. Gardiner *et al.*, 2011) are usually described with nonlinear models. In our study the sampling strategy focused on producing a series of sequential specimens extending outwards from the centre of the tree and, therefore, no outerwood specimens were obtained from some trees. As a result, we were not able to observe the asymptotic value that typically occurs in these properties in all trees. For this reason, and because we have categorized samples to account for the measurement resolution, we used the following linear model to investigate possible differences in clear wood mechanical properties and wood density between treatments:

$$y = \mu + \alpha_1 + \alpha_2 + \alpha_1.\alpha_2 + b_1 + b_2 + b_3 + \varepsilon, \tag{1}$$

where y is the property value, μ is the overall mean, α_1 is the fixed effect of the radial position, α_2 is the fixed effect of the treatment, $\alpha_1.\alpha_2$ is the interaction within treatment and radial position, b_1 is the random effect of block, b_2 is the random effect of plot within block, b_3 is the random effect of tree within plot within block and ε is the residual error. The random effects and residual errors were assumed to be independent and multivariately normally distributed. Models were progressively simplified to leave only significant fixed effects in a minimum adequate model, where a likelihood ratio test was performed at each simplification step in order to determine the significance ($\alpha = 0.05$) of the inclusion of the main effects or interaction terms. Residuals of the final models were checked for homogeneity of variance, before considering significant ($\alpha = 0.05$) differences in parameter estimates.

Microfibril angle

To gain a more detailed understanding of how MFA varied in the radial direction within a tree and how this pattern may differ between treatments, the pith-to-bark radial trend in MFA within a tree was modelled as a function of ring number from the pith. Jordan *et al.* (2005) presented a logistic function for this purpose, which has also been used successfully to model MFA variation with ring number for Scots pine (*Pinus sylvestris* L.) growing in the UK (Auty *et al.*, 2013). However, this equation contains an unnecessary sigmoidal component in the denominator and, therefore, we simplified it to produce the following exponential model:

$$\mathrm{MFA} = \frac{\beta_0}{e^{\beta_1 \mathrm{Ring}}} + \beta_2, \tag{2}$$

where Ring is the ring number from pith (analogous to cambial age in years), β_0 corresponds to an initial value parameter, β_1 is a rate parameter and β_2 is the lower asymptote. Using this function to determine the significance of treatment in mixed effects, two of the parameters, the rate and the asymptote, should be allowed to vary randomly within each level of grouping (i.e. block, plot within block, tree within plot within block). However, our subsampling for this analysis did not include enough samples from each block or plot within block. In fact in the majority of cases, only one tree was sampled per plot according to the experimental design at time of planting. Therefore, we could only consider tree as a random effect. Auty *et al.* (2013) allowed the asymptote only to vary randomly with comparable random effects, with the justification that it assumes a constant value at all cambial ages, but here we achieved a better model fit by also allowing the rate to vary with the groupings. The final model used in the analysis was therefore:

$$\mathrm{MFA} = \frac{\beta_0 + \alpha_0}{e^{(\beta_1+\alpha_1+b_1)\mathrm{Ring}}} + \beta_2 + \alpha_2 + b_2 + \varepsilon, \tag{3}$$

where α_0 is the fixed effect of treatment on the initial value β_0, α_1 is the fixed effect of treatment on the rate β_1, b_1 is the random effect of tree on the rate β_1, α_2 is the fixed effect of treatment on the asymptote β_2, b_2 is the random effect of tree on the asymptote β_2 and ε is the residual error. The random effects and residual errors were assumed to be independent and multivariately normally distributed. The model residuals were checked for homogeneity of variance, and the significance ($\alpha = 0.05$) of the main effect of treatment was assessed using a likelihood ratio test.

Results

Mechanical and physical properties of small clear specimens

Of the 603 small defect-free specimens produced from 47 trees, 245 (41 per cent) were from the corewood zone, 298 (49 per cent) were from the transition zone and 60 (10 per cent) were from outerwood zone (Table 2). Only 25 of the 47 trees (53 per cent) contained at least one sample from the outerwood zone. Across all treatments, values of MOE ranged from 3.26 up to 12.8 GPa, with a mean of 6.78 GPa. Within a tree, there was an ~1.5-fold increase (5.8–8.3 GPa) in MOE from corewood to outerwood. A significant difference in MOE was observed between radial positions ($P < 0.001$), where MOE increased by ~2 GPa between corewood and transition wood and then by a further 1 GPa between transition wood and outerwood (Figure 1). The inclusion of treatment was significant ($P = 0.027$) in a likelihood ratio test, and each treatment was ~0.8 GPa lower than the QCI control ($P < 0.020$). The inclusion of the interaction between radial position and treatment was non-significant ($P = 0.560$) in a likelihood ratio test indicating that the effect of treatment on MOE did not vary with radial position. The correlation between average corewood MOE and average transition wood MOE across all trees was 0.79 (we did not examine the correlation with outerwood due to the lack of outerwood samples).

Across all treatments, values of MOR ranged from 12.3 MPa up to 105.6 MPa, with a mean of 58.8 MPa. MOR and MOE were strongly and linearly related ($R^2 = 0.61$). A significant difference in MOR was observed between radial positions ($P < 0.001$), where MOR increased by ~8 MPa between corewood and each successive radial position (Figure 1). The inclusion of treatment was significant ($P = 0.047$) in a likelihood ratio test, and the model estimates showed that Family 2 was ~8 MPa lower than the QCI control ($P = 0.009$) and Family 3 was ~6 MPa lower than the control ($P = 0.044$). The interaction between radial position and treatment was non-significant ($P = 0.262$) in a likelihood ratio test, showing that the effect of treatment on MOR did not vary with radial position. The correlation between average corewood MOR and average transition wood MOR across all trees was 0.88 (we did not examine the correlation with outerwood due to the lack of outerwood samples).

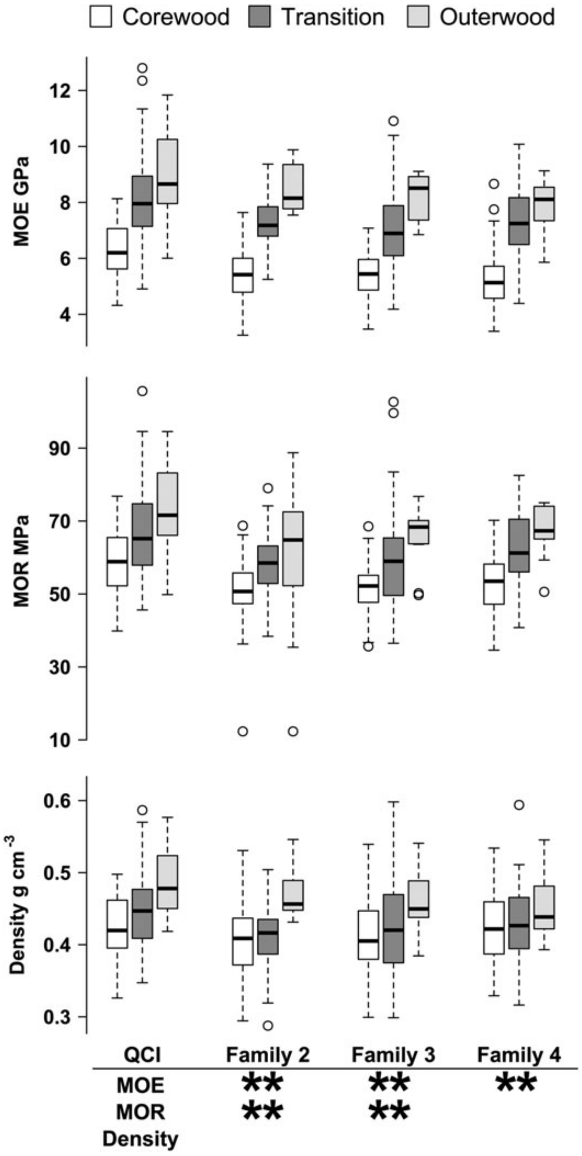

Figure 1 Box and whisker plots showing the variation in modulus of elasticity (top), modulus of rupture (middle) and wood density at 12% moisture content (bottom) by treatment and radial position. Significant ($\alpha = 0.05$) differences between the families and the control are indicated with an ** by property under the *x*-axis labels.

For wood density at 12 per cent moisture content, values ranged from 0.21 g cm^{-3} up to 0.67 g cm^{-3}, with a mean of 0.42 g cm^{-3}. MOR and wood density were moderately linearly related ($R^2 = 0.46$). A significant difference in wood density (Figure 1) was observed between radial positions ($P < 0.001$), where wood density increased significantly ($P < 0.001$) by ~0.06 g cm^{-3} between corewood and outerwood. The difference between corewood and transition wood was not significant ($P = 0.073$). Despite visual evidence that a difference may exist between the improved families and the QCI control, where the improved families appeared to have lower density than the control, the inclusion of treatment was non-significant ($P = 0.190$) in a likelihood ratio test. Mean differences between the improved families and the control were of the order of 0.03 g cm^{-3}, but standard deviations within treatments were larger and of the order of 0.05 g cm^{-3}. The interaction between radial position and treatment was non-significant ($P = 0.797$) in a likelihood ratio test, showing that the effect of treatment of treatment did not vary with radial position. The correlation between average corewood density and average transition wood density across all trees was 0.25 (we did not examine the correlation with outerwood due to the lack of outerwood samples).

Ring-level density and microfibril angle

Across all trees, a nonlinear decrease in MFA was observed from an average value of ~32° at the pith (i.e. cambial age of one year) to the outerwood region where it generally reached a relatively constant value of ~12° (Figure 2). A decrease in wood density with increasing cambial age was observed during the first 7 years of growth, followed by an increase above this age. In the corewood region, MFA was observed to decrease by ~10°, followed by a 6–7° decrease in the transition zone and then became more stable in the outerwood zone. The highest value of density was observed at the beginning of the corewood zone, whereas the lowest value was observed at the beginning of the transition zone. It then increased at a constant rate until ~20 years. The inclusion of treatment as a fixed effect in the model given by equation (3) was significant ($P < 0.001$). There were significant differences in the initial MFA between the QCI control, Family 3 ($P = 0.033$) and Family 4 ($P = 0.013$) (Figure 3). Both of these families had an estimated initial value of MFA 3° higher than the QCI control. There was no evidence of a difference in the radial profile of MFA between Family 2 and the QCI control.

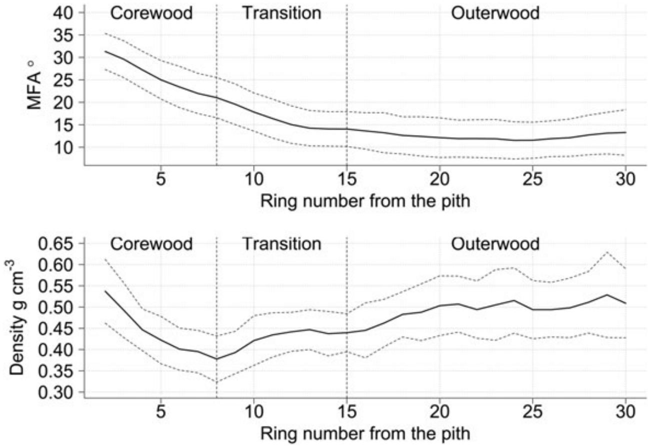

Figure 2 Radial variation in MFA (top) and mean ring density at 8% moisture content (bottom). The solid lines represent the mean of all 31 samples at each ring number, and the dashed lines represent plus (above mean) and minus (below mean) one standard deviation. The vertical lines delineate the radial positions of 'corewood', 'transition' wood and 'outerwood' used in the examination of mechanical properties.

Relationship between MOE, MFA and wood density

For the subset of small clear specimens for which MFA measurements were additionally obtained, MOE is plotted against MFA and wood density in Figure 4. The relationship between MOE and wood density in Sitka spruce was weak ($R^2 = 0.16$) when all samples were considered together with the lines from the least squares fits differing according to the radial position category (Figure 4). Including a term for radial position (here corewood or non-corewood) in a generalized linear model for a MOE response produced a significant interaction ($P = 0.002$) between wood density and radial position that justified looking at the radial positions separately. There was no significant relationship between density and MOE for corewood specimens, again using the definition of the first 7 years growth. On the other hand, for non-corewood samples, the relationship was strong ($R^2 = 0.77$). For MFA, the differences in relationships with MOE were less pronounced than those for the relationships with wood density. Including radial position in a generalized linear model for the MOE response produced a significant interaction ($P = 0.038$) between MFA and radial position that justifies looking at the two categories separately. Compared with the relationship between MOE and

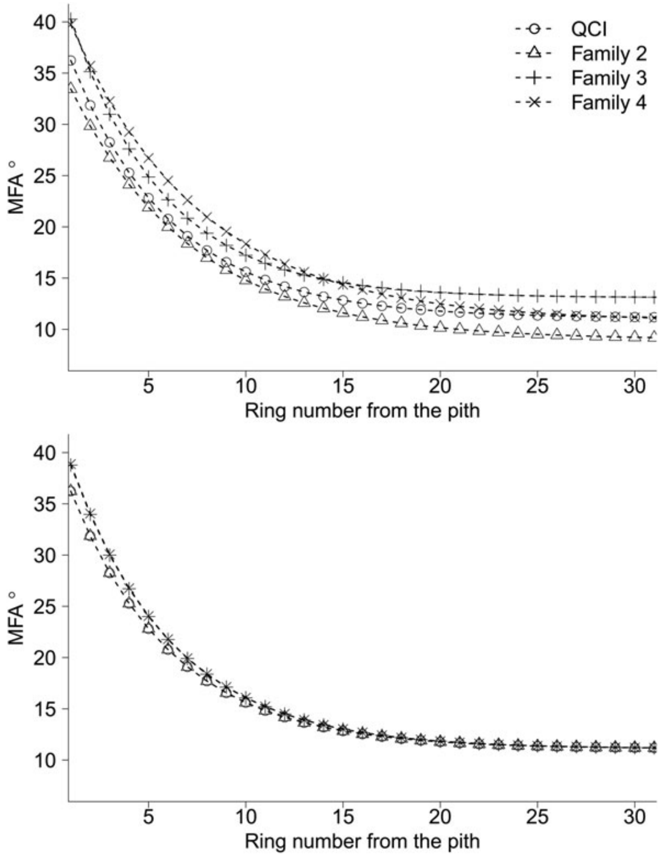

Figure 3 (Top) Models fitted to the radial trends in MFA for each treatment included a parameter for starting value, rate and lower asymptote. Family 3 ($P = 0.033$) and Family 4 ($P = 0.013$) were found to have significantly higher MFA at the starting value than the QCI control, there were no other differences in parameter values. (Bottom) The models showing only the significant differences.

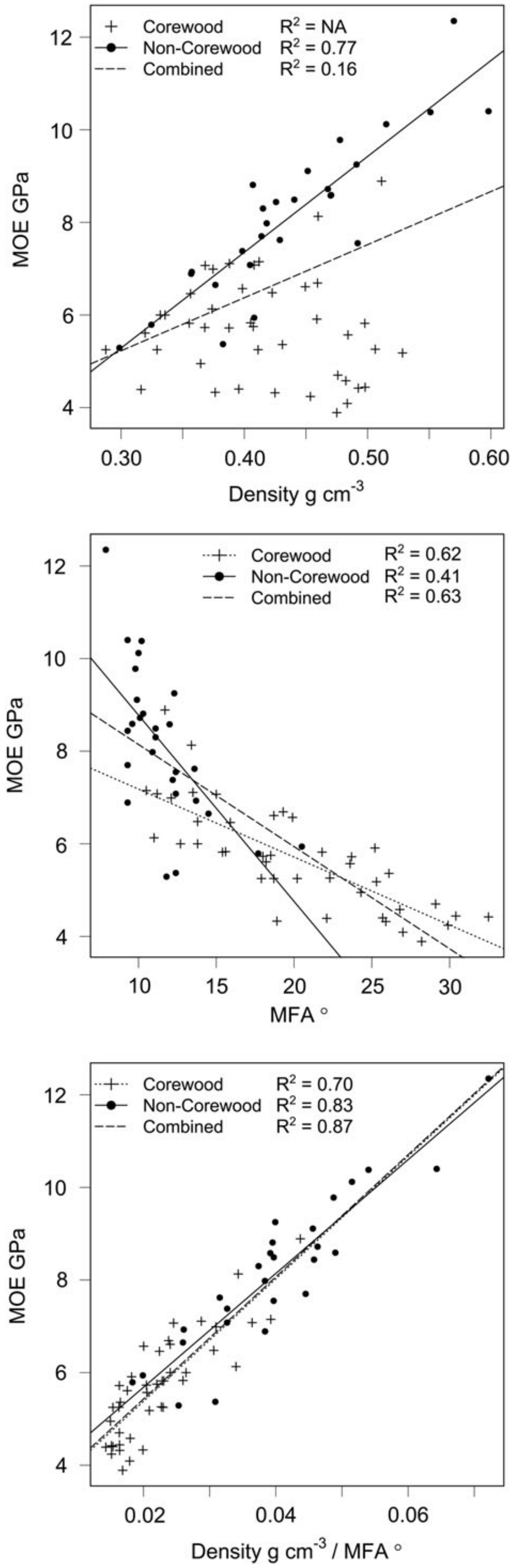

Figure 4 The relationship between MOE and wood density (top), MFA (middle) and density/MFA (bottom) in the clear wood of Sitka spruce ($n = 69$). Lines represent the best fit linear regressions, drawn where appropriate with coefficients of determination (R^2).

wood density, the relationship between MOE and MFA for the non-corewood samples was weak ($R^2 = 0.41$), whereas for corewood samples, it was moderate ($R^2 = 0.62$). For all samples considered together, the relationship remained moderate ($R^2 = 0.63$), but visually this would appear to be driven by the greater range of MFA for the corewood samples. For all samples together, the best indication of MOE was obtained when density was divided by MFA ($R^2 = 0.87$). In this case, there was little change between the best fit lines and the interaction with radial position was non-significant ($P = 0.144$) in a generalized nonlinear model, showing the same relationship is valid for both categories.

Discussion

The results are consistent with those from earlier studies on structurally sized UK Sitka spruce timber (Moore *et al.*, 2009, 2013), which showed that MOE is the property that most limits its use in structural applications. The lower mean MOE compared with the values obtained by Moore *et al.* (2009) (mean = 7.9 GPa) is most likely due to the fact that the samples in the current study mainly represent wood that was produced in the early life of the tree (Burdon *et al.*, 2004). Here the sampling strategy was focused on obtaining information on the radial variation in wood properties, and hence the majority of the samples came from the region close to the pith, with only 10 per cent of samples produced from the outer portion of the tree and not all trees having outerwood samples. It is clear in this study, as well as other studies in the literature (e.g. Leban and Haines, 1999; Koponen *et al.*, 2005; Antony *et al.*, 2012), that timber stiffness in conifers is lower in the corewood compared with the outerwood. The amount of corewood and the properties of that corewood will therefore have correspondingly negative impacts on the properties of timber populations from even-aged planted coniferous forests. These results support the argument that should rotations become shorter due to faster growth of selectively bred or improved material then the properties of the corewood will become increasingly important.

When considering differences in clear wood properties between the treatments, it was shown that previous maternal selection based on growth and stem form have resulted in lower stiffness and strength of the wood, at least in the inner parts of the tree. We did not see a significant interaction between treatment and radial position when examining the mechanical properties, which suggests that treatment differences existed throughout the profile. However, our sampling strategy for the mechanical tests did not produce many outerwood samples, and the asymptotes or upper levels usually seen in these properties (e.g. Leban and Haines, 1999) were not yet apparent in our trees. Therefore, our results are most relevant to the mechanical properties up to 15 rings from the pith, which we have classified as the outer edge of the transition wood. In this region, it was clear that there were treatment differences in stiffness (and strength), but not significant differences in wood density. Like Cameron *et al.* (2005), we observed that MFA was higher in the corewood of a faster growing family of Sitka spruce; however, only the starting value of MFA was significantly higher in the faster growing treatment indicating that any genetic difference was lost in the outerwood.

By combining SilviScan data with destructive mechanical testing on a sample set with a high proportion of corewood specimens, we were able to observe the changing relative contributions of wood density and MFA to wood stiffness across the radial profile. The strong correlation between MFA and corewood stiffness is as expected based on established theory (Cowdrey and Preston, 1966; Cave, 1968) and numerous observations for other species (e.g. Megraw, 1985; Cave and Walker, 1994). The strong empirical relationship between stiffness and density/MFA is also as expected (Evans and Ilic, 2001). The lack of an observed relationship between wood density and stiffness in the corewood zone is similar to results reported by Lenz *et al.* (2011) for white spruce (*Picea gluaca* (Moench) Voss). We hypothesize that this is because density decreases for the first seven rings from the pith in spruce, a trend that is not observed in pines (e.g. Auty *et al*., 2014). The reasons for this initial decrease in density with radial position are not certain, though it has been suggested that it might be due to shorter fibres in the wood in the first few rings from the pith (Elliott, 1970), and/or it is possibly part of a physiological response to flexing of the young stems (e.g. Telewski, 1989). Irrespective of what causes the initial high density, it does not seem to convey higher stiffness to the wood and MFA was a much better proxy for corewood stiffness. Contrary to Lenz *et al.* (2011), who suggested that MFA remained well correlated to estimated MOE throughout the radial profile, we found that the strength of the relationship decreased considerably outside of the corewood region. Our measurements agree more closely with the theory proposed by Cave (1968), where at an MFA of ~10°, there is little further effect on MOE.

Our findings show that when using proxies for MOE in spruce breeding, it is important to consider which part of the tree is being examined. For example, selection based on outerwood MFA is unlikely to lead to improvements in corewood stiffness, and selection based on corewood density is unlikely to lead to improvements in wood stiffness in any part of the radial profile. Selection based on outerwood density may lead to improvements in outerwood stiffness, but outerwood stiffness is unlikely to be the grade-limiting factor for structural timber.

Conclusions

Stiffness is the mechanical property that generally limits the strength class that UK grown Sitka spruce structural timber can achieve. Previous maternal selections for better stem form and growth in tree breeding programmes have had a negative impact on the wood stiffness of the progeny, apparently through an increase in MFA with changes in wood density having no observable impact. There could be undesirable consequences for the future UK spruce timber supply if tree breeders do not take account of wood stiffness in current tree improvement programmes. Because it is the stiffness of the wood produced by the young tree that is the major problem, there is the potential to accelerate breeding programmes by focussing on improving the mechanical properties of young trees.

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Conflict of interest statement

None declared.

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