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Effect of early release from intense competition within high density natural regeneration on the properties of juvenile and mature wood of 40-year-old Sitka spruce (*Picea sitchensis* (Bong.) Carr.)

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Abstract

• **Context** While numerous studies have considered the effects of initial planting spacing on wood properties, little is known about the properties of trees grown from dense natural regeneration and the effects of early release from competition.
• **Aims** This study examined 40-year-old Sitka spruce (*Picea sitchensis* (Bong.) Carr.) trees originating from regeneration with an initial density $\sim 27,000$ stems ha^{-1} .
• **Methods** Treatments were a control of natural regeneration with no interventions and regeneration re-spaced to two metres (height ~ 1.6 m). Density and strength measurements were made on the juvenile and mature wood.
• **Results** No differences were observed in density, modulus of elasticity (MOE) and modulus of rupture (MOR) between the juvenile and mature wood of the control trees. By contrast, the juvenile wood of re-spaced trees was less dense and had a lower MOE than the mature wood.

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Contribution of the co-authors The second author was involved with setting up the project and providing guidance throughout. The third and fourth authors carried out most of the field work. The first author proposed the study, set up the funding, carried out most of the data analysis and drafted the paper.

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• **Conclusion** The control trees revealed a uniformity of properties across the juvenile and mature wood zones, unlike the re-spaced treatment. Re-spaced trees appear to adapt to their new environment by producing more thin-walled conductive tissue and lowering overall cell wall density that continues from the juvenile to mature wood. Higher compression wood levels in the control trees are thought to be linked to stem slenderness.

Keywords Sitka spruce · Natural regeneration · Re-spacing · Wood properties · Juvenile wood

1 Introduction

Natural regeneration of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) has become a common feature of many clear-felled sites in Scotland and is increasingly seen as a potentially cost-effective alternative to replanting (Macdonald et al. 2010). On open sites where conditions are favourable, Sitka spruce is capable of regenerating at high stocking densities of over 100,000 stems per ha (Clarke 1992). Current management recommendation for dense, naturally regenerated Sitka spruce is to re-space to around 2,000–2,500 stems per ha when the stands are 1.5–2 m in height (Mason 2010). However, it is not known what effect early re-spacing has on future wood properties of Sitka spruce. Investigations examining wood formation in trees released from intense competition by re-spacing are relatively rare. Renninger et al. (2006) studied 12–18-year-old Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees released from suppression and found that, in addition to greatly increased growth, earlywood width was around four times greater following release and wood density declined by 20 and 11 % for Douglas fir and western hemlock, respectively,

although the authors pointed out that density remained within acceptable limits for typical applications.

Trees within young, densely stocked stands are likely to experience a period of restricted growth (Oliver and Larson 1996) that in turn may influence the size and properties of the juvenile core (Cregg et al. 1998; Renninger et al. 2006). Juvenile wood in conifers is generally thought to form during the first 10–20 growth rings from the pith and is associated with timber of lower stiffness or modulus of elasticity (MOE), strength or modulus of rupture (MOR) and dimensional stability (e.g. Dinwoodie 2000). While the boundary between juvenile and mature wood is gradual and varies depending on species, it is thought to occur around rings 12 and 13 in both Sitka spruce (Brazier and Mobbs 1993; Cameron et al. 2005) and Norway spruce (*Picea abies* (L.) Karst.) (Pape 1999). A greater proportion of juvenile wood in the stem is associated with wider initial spacing (e.g. Brazier and Mobbs 1993; Moore et al. 2009), and its extent is exacerbated by high growth rates (Macdonald and Hubert 2002; Cameron et al. 2005). There is evidence that MOE of juvenile core wood of *Pinus radiata* (D. Don.) increases with increasing stocking density from less than 1,000 stems per ha to around 2,500 (Lasserre et al. 2004; Waghorn et al. 2007), and similar results have been found in spacing studies in other species (e.g. Wang and Ko 1998; Zhang et al. 2002). A study by Moore et al. (2009) considered the effect of an early noncommercial thinning or re-spacing of planted Sitka spruce, initially spaced at 1.83×1.83 m to a series of wider spacings up to 5.49 m at age 11 years, on the physical and mechanical properties of structural timber. They found that MOE and MOR declined with increased spacing, but density remained unaffected. These studies are based on much wider initial spacings than typically observed for naturally regenerated seedlings, and comparisons should be treated with caution.

Although dominant trees will eventually emerge from densely stocked stands (Oliver and Larson 1996), the high inter-tree competition will force trees to invest resources into height growth at the expense of stem and root development, creating slender trees. Compression wood has been associated with dense stands (Pillow and Luxford 1937) and is a serious defect in sawn timber (Timell 1986; Panshin and de Zeeuw 1980). It is thought to form as a result of phototropic movements in response to the intense competition for light (Barger and Ffolliott 1976). It is hypothesised that trees are more likely

to lean as a result of these movements to exploit the limited space in a crowded canopy, resulting in compression wood forming to negate the imbalance (Reader and Kurmes 1996; Cameron and Thomas 2008). The relationship between early intense competition experienced in naturally regenerated stands of Sitka spruce and the presence of compression wood has not been studied. The aim of this investigation was to study the wood properties of 40-year-old Sitka spruce grown from densely stocked, natural regeneration with and without early re-spacing.

2 Methods

2.1 Study site and treatments

The study site was located in Ae Forest in Dumfries and Galloway (55° 12' N, 3° 37' W). The topography is level to slightly sloping to the west and south with a mean elevation of 214 m. Soils are mainly peaty ironpans with smaller areas of surface water gleys. Annual mean rainfall is 1,380 mm. The site has a history of wind damage, and after the extensive damage to the existing stand in a storm in 1968, the remaining trees were felled shortly afterwards. Extensive natural regeneration colonised the site and a randomised experiment was set up in 1973 with the original aim of studying the effects of re-spacing on growth (Mason 2008). The experimental area consisted of approximately 1.6-m-tall regeneration of Sitka spruce (probably Queen Charlotte Islands provenance) with an average stocking density of 27,000 stems ha⁻¹ into which four re-spacing treatments (selective and mechanical re-spacing, with and without chemical follow-up treatment of unwanted re-growth) and a control (no re-spacing). Only the selective re-spacing (selected for superior height and re-spaced to 2 m without chemical treatment) and control treatments were used in this study (Table 1). Records show that by 1997, the stocking density had declined in the control treatment over time as a result of self-thinning to a density not greatly different to that of the re-spaced treatment (2,700 stems ha⁻¹ c.f 1,900 stems ha⁻¹) (Mason 2008). The experiment was closed in 2006 as a result of extensive wind and snow damage resulting in a loss of two of the three blocks. The current study used the treatment plots (0.1 ha in size) from

Table 1 Description of treatments used in the study

Treatment	Description
Control (no re-spacing)	Natural regeneration (~27,000 stems ha ⁻¹) arising from clear-felling in 1968–1969; no re-spacing and left un-thinned until end of experiment
Re-spaced	Natural regeneration (~27,000 stems ha ⁻¹) arising from clear-felling in 1968–1969, with trees re-spaced in 1973 (~1.6 m tall) for superior height vigour at approximately 2-m square spacing, with the remainder being cut at or near ground level; left un-thinned until end of experiment

the remaining undamaged block. The assumptions made for the statistical analysis are discussed in Section 2.4.

2.2 Sample trees and measurements

Tree diameter was measured within the treatment plots to determine the diameter range. The first quartile was not used since these trees were suppressed and unlikely to reach sawlog dimensions. Sixteen trees from each treatment (i.e. 32 trees in total) were randomly selected from the remaining quartiles and felled in 2008. Due to the difficult conditions at the site and time constraints on the felling operation, it was not possible to measure height and DBH of the sample trees.

2.3 Preparation of wood samples

A half metre stem section was removed from each of the butt logs with the base of sections at approximately 1.5 m from stump height and placed in a covered, well-aired store for initial drying. Due to internal defects, one of the stem sections could not be used in the analysis of wood properties. The 50-cm-long stem sections were air-dried for 3 months. Two 10-cm discs were removed before the remaining section was sawn through in a longitudinal direction down the middle of the log to reduce radial and tangential stresses associated with cracking and splitting. All samples were placed in a dehumidifying room and equilibrated to 12 % moisture content.

2.4 Measurements of wood properties

Figure 1 shows the location of the test samples used in the experiment. Compression wood was measured on 3-mm cross-sectional slices (15 and 16 each from the control and re-spaced treatments) removed from stem sections, soaked for

48 h and placed on a transmitted light table. Compression wood appears as an opaque brown-red colour (Pillow 1941). The relatively indistinct colour of the latewood in Sitka spruce makes identification of compression wood relatively straight forward. Confirmation of the presence of compression wood was made by taking thin transverse sections from the 'coloured' and 'normal' areas of the sample discs and examining these under a microscope. Observations made on samples from the 'coloured' wood revealed cells with thick walls in both early and late wood, and rounded tracheids with intercellular spaces feature characteristic of compression wood (e.g. Dinwoodie 2000). The area of compression wood was measured and expressed as a proportion of stem cross-sectional area. Due to the difficulties in visually identifying compression wood, no distinction was made in the intensity observed. Grain angle measurements were made on 10-cm-thick discs split longitudinally through the pith in a north-south direction. Grain angle was measured on the open face of one of the halves using a modified protractor fitted with a pendulum (Brazier 1965). This was done by first levelling the stem section so that its outer stem surface was vertical. The angles at the 9th (juvenile) and 20th (mature) rings on both sides of the pith were measured and average values determined.

Small clear samples (20×20×300 mm) were cut from the remaining part of the stem section: four samples each from the juvenile and adult wood—based on an approximate boundary between juvenile and adult wood at rings 12 to 13 from the pith (Cameron et al. 2005) (Fig. 1). Samples from the juvenile and mature wood were centred on the 9th and 20th rings, respectively. There were 120 and 128 samples available for the control and re-spaced treatments respectively. MOE and MOR were determined by three-point bending on an Instron 4483 strength testing machine according to the procedure described by Desch and Dinwoodie (1996). Samples were

Fig. 1 Source of wood samples from the 50-cm stem sections used for measurements on compression wood, grain angle, ring width, density, MOE and MOR. Measurements are in millimetres

oriented with the grain perpendicular to the load. MOE and MOR were calculated from the results of the static bending test. A small 20-mm section was removed from the ends of the tested small clear samples and density determined by the water displacement method (Olesen 1971).

Radial-longitudinal microscopic sections were prepared from the samples used to directly measure density for the measurement of microfibril angle (MFA). This was done by measuring the angle of the ‘slits’ of the cross-field bordered pits on captured images using ImageJ software (vs 1.42, NIH, USA). Given the time-consuming nature of these measurements, samples were used from ten randomly selected trees from each treatment. A minimum of five slides were prepared from each wood sample, and between three and ten MFAs, measurements were made from each slide. Average values for each wood sample were used in the statistical analysis.

2.5 Itrax measurements

Samples were also analysed using a scanning X-ray densitometer Itrax Multiscanner (Cox Analytical Systems, Gothenburg) system. Radially diametric longitudinal sections were cut from each sample disc. The samples were prepared in an automated precision twin-blade circular saw to produce pith-to-bark strips measuring 2 mm in the longitudinal direction and 20–30 mm tangentially. Before scanning, the specimens were conditioned in the Itrax chamber at approximately 20 °C and 10–15 % relative humidity for several hours, resulting in a testing moisture content of approximately 4 %. A digital micrometre was used to record the thickness (nearest 0.001 mm) at four positions along the length of each sample to account for dimensional variation along the sample length. Samples were scanned in the radial-longitudinal direction at 50- μ m resolution. A cellulose propionate wedge of known density and thickness was scanned with the samples in order to calibrate the density measurements from each batch. The attenuated X-ray beam was recorded by an electronic detector, and the resulting greyscale image (microradiograph) was analysed using WinDENDRO image analysis software

(Régent Instruments Inc., Quebec City, Canada), which converts the grey intensity levels to actual density values for each annual ring using the average thickness of each sample. WinDENDRO demarcates annual ring boundaries and calculates the minimum and maximum density and the mean earlywood and latewood density values for each ring, which depends on a user-defined threshold setting. Density values were not weighted by ring surface area.

2.6 Statistical analyses

Due to the experimental limitations described above, a number of assumptions were made regarding the statistical analysis. The two treatment plots (no re-spacing and re-spaced) were used as discrete populations from which the samples were randomly selected ($N_1=16$; $N_2=16$). Given that the two plots (populations) were physically separated, it was assumed that the treatments were independent of each other. It was also assumed that the uniformity of the site conditions would allow environmental effects to be ignored. Statistical analysis involved one-way analysis of variance between treatments (no re-spacing and re-spaced) and between wood types (juvenile and mature wood). Means, standard errors of the means and p values were calculated for all variables using IBM SPSS Statistics version 19 (SPSS 2010). Associations among the measured parameters of juvenile and mature wood were carried using Pearson correlations. MFA data were normalised using a log10 transformation before statistical analyses.

3 Results

3.1 Directly measured wood properties

Values for the directly measured wood properties associated with timber stiffness and strength are shown in Table 2. The juvenile and mature wood of the control treatment was significantly denser than that observed in the re-spaced treatment.

Table 2 Mean values for density (directly measured on wood samples), modulus of elasticity (MOE) and modulus of rupture (MOR) of juvenile wood (1–12 rings from pith) and mature wood (13+ rings from pith) from naturally regenerated Sitka spruce originally established with and without re-spacing

Treatment	No. of trees	Density (g cm^{-3})			MOE (N mm^{-2})			MOR (N mm^{-2})		
		Juvenile	Mature		Juvenile	Mature		Juvenile	Mature	
Control (no re-spacing)	15	0.40 (0.010)	0.42 (0.012)	NS	8,375 (325.2)	9,173 (424.2)	NS	62.7 (2.87)	64.1 (3.16)	NS
Re-spaced	16	0.35 (0.010)	0.38 (0.010)	*	7,196 (294.1)	8,544 (397.0)	*	54.0 (2.31)	56.0 (2.36)	NS
		**	*		*	NS		*	NS	

Standard errors are in parentheses

NS not significant

* $p<0.05$; ** $p<0.01$ and *** $p<0.001$ indicate differences between treatments and between juvenile and mature wood characteristics

There was no difference in the density, MOE and MOR between the juvenile and mature wood of the control treatment. The mature wood of the re-spaced treatment was denser and stiffer (MOE) than the juvenile wood. The re-spaced treatment had a lower density in both the juvenile and mature wood than the control treatment. MOE and MOR were also lower in the re-spaced trees in comparison with the control.

3.2 Itrax-derived wood properties

Figure 2 shows the variation in mean annual radial increment over time for each treatment measured using the Itrax Multiscanner. Since the lower surface of the sample stem sections were located 1.5 m from the base of the tree, the lowest cambial age on the graph approximately represents the time when the re-spacing treatment occurred. Re-spacing had the effect of enhancing growth for around five or so years following the intervention; then, it declined to form a level slightly below that of the control trees. The control treatment had a lower mean ring width in the juvenile wood and higher in the mature wood in comparison with the re-spaced treatment (Table 3). The width of earlywood and latewood within the juvenile and mature zones are best described when expressed as a percentage of the annual ring as latewood. There is no difference between treatments for the proportion of mature wood, whereas the control treatment had a higher proportion of latewood in the juvenile zone in comparison with the re-spaced treatment.

The Itrax-derived values for mean ring density (Table 4) indicated that the juvenile wood of the re-spaced treatment had a lower density than that of the control, whereas there were no differences between treatments in mature wood mean

Fig. 2 Variation in mean ring width with ring number from the pith from two stands of Sitka spruce; control treatment of naturally regenerated Sitka spruce without re-spacing and re-spaced to 2-m square spacing when 1.5-m average height (Bars ± 1 s.e.)

ring density. When considering the early- and latewood individually, there were no differences in density of the earlywood in both the juvenile and mature wood between treatments, whereas latewood density was lower in both the juvenile and mature wood of the re-spaced treatment in comparison with the control.

3.3 Juvenile wood proportion, grain angle and compression wood content

The control treatment had a significantly lower proportion of juvenile wood in comparison with the re-spaced treatment (Table 5). There were no differences in grain angle at the 9th (juvenile wood) and 20th (mature wood) rings between treatments. There was significantly more compression wood associated with the control treatment in comparison with the re-spaced treatment.

3.4 Microfibril angle

Microfibril angle (MFA) was significantly lower in the juvenile wood of the control treatment in comparison with the re-spaced treatment (Table 6). There were no differences in MFA in the mature wood between treatments. While there was the anticipated lower MFA observed in the mature wood in comparison with the juvenile wood, this was only significantly different for the re-spaced treatment.

3.5 Correlations

Correlations made on all data highlighted strong positive relationships between MOE and MOR ($r=0.80$), directly measured density ($r=0.84$), mean ring density (Itrax) ($r=0.80$), and negative correlations between MOE and ring width ($r=-0.51$) and earlywood ring width ($r=-0.54$) (c.f latewood $r=-0.14$). Increasing ring width had a strong negative effect on MOE of the juvenile wood of the re-spaced trees ($r=-0.74$), whereas it had no effect on the control trees ($r=-0.19$). Increasing ring width had a strong negative effect on the proportion of latewood formed in the juvenile wood of the control and re-spaced treatments ($r=-0.63$ and -0.66 , respectively); however, the association was weaker in the mature wood ($r=-0.38$ and -0.25 , respectively). Compression wood content was significantly correlated with mature wood ring width and early wood width ($r=0.55$ and 0.51 , respectively), whereas similar associations were not evident in the juvenile wood ($r<0.06$). Compression wood was not associated with density, MOE and MOR ($r=-0.05$, -0.16 and -0.07 , respectively). There were no significant associations between grain angle and other wood properties for both treatments. Separate correlations carried out on the sub-sample of MFA data for all treatments indicated relatively weak relationships with MOE for the juvenile wood of the control treatment ($r=-0.36$) and

Table 3 Itrax-derived mean values for ring width, earlywood width, latewood width and late wood proportion within the juvenile wood (1–12 rings from pith) and mature wood (13+ rings from pith) from naturally regenerated Sitka spruce originally established with and without re-spacing

Treatment	No. of trees	Ring width (mm)			Earlywood width (mm)			Latewood width (mm)			Latewood proportion (%)		
		Juvenile	Mature		Juvenile	Mature		Juvenile	Mature		Juvenile	Mature	
Control (no re-spacing)	15	4.6 (0.22)	2.8 (0.17)	***	3.5 (0.20)	1.9 (0.16)	***	1.1 (0.04)	0.9 (0.08)	*	26.1 (0.96)	34.5 (2.37)	**
Re-spaced	16	5.5 (0.18)	2.3 (0.11)	***	4.3 (0.19)	1.5 (0.10)	***	1.1 (0.05)	0.7 (0.06)	***	22.3 (1.15)	34.3 (1.69)	***
		**	**		**	*		NS	*		*	NS	

Standard errors are in parentheses

NS not significant

* $p < 0.05$; ** $p < 0.01$ and *** $p < 0.001$ indicate differences between treatments and between juvenile and mature wood characteristics

the mature wood of the re-spaced treatment ($r = -0.41$). All other correlations were very weak ($r < -0.17$).

4 Discussion

While there were limitations to this study, primarily due to the availability of only one replicate of the experiment and that the sampling was made at one height within the tree, it has nevertheless highlighted some interesting consequences of high initial stocking densities and early re-spacing on wood properties of Sitka spruce. These findings have practical implications for the management of dense natural regeneration. The initial phase of growth of the control treatment (no re-spacing) was restricted by the intense inter-tree competition; however, the stand did not move into a period of stagnation seen in some species (Oliver and Larson 1996). In its native range in North America, local dominants within dense Sitka spruce regeneration have been observed to emerge at an early age (Peterson et al. 1997). In the current study, trees within the control treatment clearly encountered intense early competition that resulted in restricted growth during the period of juvenile wood development (Table 3 and Fig. 2); however, the greater ring width recorded in these trees during the mature phase of growth (rings 13+ from pith) in comparison with the

re-spaced trees may point to local dominants emerging from the dense regeneration at a relatively early stage, based on the view that dominants are more vigorous than their immediate neighbours. The juvenile wood formed in the control trees under these conditions had values of density, MOE and MOR similar to those of the mature wood (Table 2), whereas density and MOE of the juvenile wood of the re-spaced trees were inferior to those of the mature wood. McLean et al. (2011) observed a broadly similar effect in a study on the wood properties of several naturally regenerated tropical species from primary forest and the same species growing under more widely spaced plantation conditions.

Given that grain angle was too low in both treatments to significantly influence strength (e.g. Dinwoodie 2000) and that the use of ‘defect-free’ samples removed the influence of knots (presence of compression wood was not taken into account), density is likely to be an important factor in determining MOE. The observed differences in directly measured wood density between treatments were relatively small; however, comparatively small changes in density can be associated with considerably larger changes in mechanical properties (Zhang 1997). Microfibril angle (MFA) is also known to be an important factor in determining stiffness in Sitka spruce wood (McLean et al. 2010). While in the current study, MFA was significantly lower in the control in comparison with the re-spaced treatment (Table 6), MFA and MOE were only weakly

Table 4 Itrax-derived mean values for ring density, earlywood density and latewood density within the juvenile wood (1–12 rings from pith) and mature wood (13+ rings from pith) from naturally regenerated Sitka spruce originally established with and without re-spacing

Treatment	No. of trees	Ring density (g cm^{-3})			Earlywood density (g cm^{-3})			Latewood density (g cm^{-3})		
		Juvenile	Mature		Juvenile	Mature		Juvenile	Mature	
Control (no re-spacing)	15	0.43 (0.009)	0.45 (0.016)	NS	0.35 (0.008)	0.35 (0.013)	NS	0.63 (0.009)	0.62 (0.020)	NS
Re-spaced	16	0.39 (0.011)	0.43 (0.014)	NS	0.34 (0.008)	0.35 (0.011)	NS	0.59 (0.012)	0.57 (0.015)	NS
		*	NS		NS	NS		**	*	

Standard errors are in parentheses

NS not significant

* $p < 0.05$; ** $p < 0.01$ and *** $p < 0.001$ indicate differences between treatments and between juvenile and mature wood characteristics

Table 5 Mean values for disc diameter, proportion of disc area within juvenile wood (1–12 rings from pith), grain angle measured at the 9th (within juvenile wood) and 20th rings (within mature wood) and

compression wood content (% of sample disc area) of naturally regenerated Sitka spruce originally established with and without re-spacing

Treatment	No. of trees	Disc diameter (cm)	Juvenile wood proportion (rings 1–12) (%)	Grain angle 9th ring (°)	Grain angle 20th ring (°)	Compression wood (%)
Control (no re-spacing)	15	19.0 (0.86)	32.2 (4.15)	1.7 (0.31)	1.6 (0.34)	26.5 (4.62)
Re-spaced	16	19.1 (0.83)	43.5 (3.47)	2.5 (0.34)	2.4 (0.43)	10.7 (1.85)
		NS	*	NS	NS	**

Standard errors are in parentheses

NS not significant

* $p < 0.05$; ** $p < 0.01$ and *** $p < 0.001$ indicate differences between treatments and between juvenile and mature wood characteristics

correlated. This suggests that variations in MFA observed between treatments did not seem to explain the differences in stiffness observed.

The most likely reason for the observed lower density and corresponding reduction in the strength properties of the wood of the re-spaced trees in comparison with the control is the significantly lower proportion of latewood observed in the juvenile wood of the re-spaced trees (Table 3). Renninger et al. (2006) observed the relationship between increasing growth rate following release from suppression and a decrease in the proportion of latewood and a corresponding decline in density in Douglas fir and western hemlock. The trees used in their investigation were much younger (<20 years old) than used in the study reported here (~40 years old) suggesting that their findings primarily relate to the juvenile zone. The cause of this reduction in density and mechanical strength in the re-spaced trees is thought to be a result of the dramatic change in the growing environment following release from suppression. Released trees will rebalance their leaf area with the sapwood area, so as leaf area and photosynthetic capacity increases, sapwood area also increases (Renninger et al. 2007). The process of increasing water transport capacity is achieved by increasing the area of sapwood by increasing annual ring

width and/or making the wood produced more conductive. An increase in ring width has to be balanced by the limits of the resources available to make the new wood and this may result in a decline in density, and making wood more conductive requires a lower proportion of latewood to form also reducing density (Domec and Gartner 2002). This was observed in the current study where, in comparison with the control trees, there was less latewood formed in the juvenile wood of the re-spaced trees (Table 3) and this latewood was less dense (Table 4). This difference in latewood density was also observed in the mature wood. It has been reported that trees under moisture stress initiate latewood earlier than well-irrigated trees (e.g. Cregg et al. 1998) and it is possible in the current study that the dense regeneration on an open site could have been affected by moisture stress leading to the earlier formation of latewood. A greater proportion of latewood would result in higher wood densities in suppressed trees and a greater water storage capacity given that latewood has a higher storage capacity than earlywood (Domec and Gartner 2002).

The higher level of compression wood observed in the control trees compared with the re-spaced trees may be due to the slenderness of the stems and the greater propensity to sway and bend (e.g. Timell 1986). A slenderness ratio (height/diameter) of greater than 80 is considered to be unstable, and a ratio of over 100 is identified as a value that places trees at high risk of damage (Burschel and Huss 1987; Oliver and Larson 1996). It is likely that the lack of conventional thinning was the cause of the very slender stems observed rather than the effects of initial treatments. Height and diameter data from the same experiment described by Mason (2008) reveals that by 1986, 13 years after the start of the experiment when the estimated age of the trees was around 17 years old (based on the assumption that most of the regeneration established immediately following the clearance of the site in 1968 and 1969), the slenderness ratio of the control trees was 125 whereas it was only 93 in the re-spaced stand. These values indicate that trees within the control treatment were very slender at a young age and therefore more prone to bending within the canopy, and hence the higher level of compression

Table 6 Mean values for microfibril angle measured at the 9th (within juvenile wood) and 20th rings (within mature wood) of naturally regenerated Sitka spruce originally established with and without re-spacing

Treatment	No. of trees	Microfibril angle (°)		
		Juvenile	Mature	
Control (no re-spacing)	10	20.7 (2.08)	16.3 (2.10)	NS
Re-spaced	10	26.8 (2.04)	15.2 (0.84)	***
		*	NS	

Measurements were carried out on a sub-sample of 10 randomly selected trees. Statistical analyses were carried out on transformed data. Standard errors are in parentheses

NS not significant

* $p < 0.05$; ** $p < 0.01$ and *** $p < 0.001$ indicate differences between treatments and between juvenile and mature wood characteristics

wood observed in the stems (Table 5) formed to correct this lean (Barger and Ffolliott 1976; Reader and Kurmes 1996). Given that height growth is important to trees subject to competition for light and commands the second highest priority for photosynthates after respiration (Smith et al. 1997), it is not surprising that trees in dense stands are forced to overcome competition through height growth, with the possibility of the stems bending towards the available light (Barger and Ffolliott 1976; Reader and Kurmes 1996). Higher growth rate in un-thinned stands is known to be associated with greater compression wood formation (Cameron and Thomas 2008), and this concurs with findings in the current study where compression wood content was significantly correlated with increasing ring width and early wood width in the mature wood ($r=0.55$ and 0.51 , respectively). Interestingly, compression wood was not associated with density, MOE and MOR, which may suggest that it was in a relatively mild form.

Watt et al. (2006) examined MOE, density and stem slenderness in relation to critical buckling height in young *P. radiata* trees. They hypothesised that, for a given mass, increasing slenderness will result in greater compressive stresses in the stem and that trees react to this increased loading by forming wood with a higher MOE, possibly through a reduction in the MFA of the cell wall. An increase in MOE would in turn increase the critical compressive stress that the stem can withstand before it buckles under its own weight. While the effects of slenderness on wood properties were not the primary focus in the current study, the findings presented here are consistent with the theory that trees may be reacting to increased loading for a given stem diameter by altering the properties of the wood to compensate, resulting in the observed higher levels of density and stiffness in the juvenile core of the control trees.

The data presented here suggest that very early re-spacing may lead to the development of a relatively large juvenile core of wood that is less stiff than if the regeneration was left untouched. It appears that dominants should be allowed to emerge naturally in dense natural regeneration and that an early thinning should be carried out only after the main period of juvenile wood formation—say at between 15 and 20 years old depending on growth rate—to promote stem taper and growth of the mature wood. It is recognised, however, that thinning such dense stands will be problematical. Thinning should continue at regular intervals to maintain stand stability and growth rate (Cameron 2002). Further research is required on other sites to support these initial findings and to better understand the relationship between initial stocking density, early re-spacing and wood properties in naturally regenerated stands.

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References

- Barger RL, Ffolliott PF (1976) Factors affecting occurrence of compression wood in individual ponderosa pine trees. *Wood Sci* 8:201–208
- Brazier JD (1965) An assessment of the incidence and significance of spiral grain in young conifer stems. *Forest Prod J* 15:308–312
- Brazier JD, Mobbs ID (1993) The influence of planting distance on structural wood yields of unthinned Sitka spruce. *Forestry* 66:333–352
- Burschel P, Huss J (1987) *Grundriß des Waldbaus*. Verlag Paul Parey, Hamburg and Berlin, 352 pp
- Cameron AD (2002) Importance of early selective thinning on the development of long-term stand stability and improved log quality: a review. *Forestry* 75:25–35
- Cameron AD, Thomas K (2008) Effect of thinning on the development of compression wood in stems of Corsican pine. *Eur J For Res* 127: 247–251
- Cameron AD, Lee SL, Livingston AK, Petty JA (2005) Influence of selective breeding on the development of juvenile wood in Sitka spruce. *Can J For Res* 35:2951–2960
- Clarke GC (1992) The natural regeneration of spruce. *Scott For* 46:107–129
- Clegg BM, Dougherty PM, Hennessey TC (1998) Growth and wood quality of young loblolly pine trees in relation to stand density and climatic factors. *Can J For Res* 18:851–858
- Desch HE, Dinwoodie JM (1996) *Timber—structure, properties, conversion and use*, 7th edn. Macmillan, Basingstoke, 320 pp
- Dinwoodie JM (2000) *Timber: its nature and behaviour*, 2nd edn. E & FN Spon, New York, 257 pp
- Domec JC, Gartner BL (2002) How do water transport and water storage differ in coniferous earlywood and latewood? *J Exp Bot* 53:2369–2379
- Lasserre JP, Mason EG, Watt MS (2004) The influence of initial spacing on corewood modulus of elasticity in a clonal experiment of 11-year-old *Pinus radiata* D. Don. *N Z J For* 49:18–23
- Macdonald E, Hubert J (2002) A review of the effects on timber quality of Sitka spruce. *Forestry* 75:107–138
- Macdonald E, Gardiner BA, Mason WL (2010) The effects of transformation of even-aged stands to continuous cover forestry on conifer log quality and wood properties in the UK. *Forestry* 83:1–16
- Mason WL (2008) Natural regeneration of Sitka spruce in the Forest of Ae: development over 25 years. *Scott For* 62:2–9
- Mason WL (2010) Respacing naturally regenerating Sitka spruce and other conifers. Forestry Commission Practice Note FCPN016
- McLean JP, Evans R, Moore JR (2010) Predicting the longitudinal modulus of elasticity of Sitka spruce from cellulose orientation and abundance. *Holzforschung* 64:495–500
- McLean JP, Zhang T, Bardet S, Beauchêne J, Thibaut A, Clair B, Thibaut B (2011) The decreasing radial wood stiffness pattern of some tropical trees growing in the primary forest is reversed and increases when they are grown in a plantation. *Ann For Sci* 68:681–688
- Moore J, Achim A, Lyon A, Mochan S, Gardiner B (2009) Effects of early re-spacing on the physical and mechanical properties of Sitka spruce structural timber. *For Ecol Manag* 258:1174–1180
- Olesen PO (1971) The water displacement method. A fast and accurate method of determining the green volume of wood samples. *For Tree Improve Aboric Horsholm* 3:3–23
- Oliver CD, Larson BC (1996) *Forest stand dynamics*. John Wiley and Sons Inc., New York, 520 pp
- Panshin AJ, de Zeeuw C (1980) *Textbook of wood technology*, 4th edn. McGraw-Hill, New York, 722 pp

- Pape R (1999) Effects of thinning regime on the wood properties and stem quality of *Picea abies*. Scand J For Res 14:38–50
- Peterson EB, Peterson NM, Weetman GF, Martin PJ (1997) Ecology and management of Sitka spruce: emphasising its natural range in British Columbia. UBC Press, Vancouver, 336 pp
- Pillow MY (1941) A new method of detecting compression wood. J For 39:385–387
- Pillow MY, Luxford RF (1937) Structure, occurrence and properties of compression wood. US Department of Agriculture Technical Bulletin 546. 32 pp
- Reader TG, Kurmes EA (1996) The influence of thinning to different stocking levels on compression wood development in ponderosa pine. For Prod J 46:92–100
- Renninger HJ, Gartner BL, Meinzer FC (2006) Effects of release from suppression on wood functional characteristics in young Douglas fir and western hemlock. Can J For Res 36:2038–2046
- Renninger HJ, Meinzer FC, Gartner BL (2007) Hydraulic architecture and photosynthetic capacity as constraints on release from suppression in Douglas fir and western hemlock. Tree Physiol 27:33–42
- Smith DM, Larson BC, Kelty MJ, Ashton PMS (1997) The practice of silviculture: applied forest ecology, 9th edn. John Wiley & Sons, New York, 537 pp
- SPSS (2010) IBM SPSS Statistics vs. 19. Chicago, US
- Timell TE (1986) Compression wood in gymnosperms. Springer, Berlin, 2150 pp
- Waghorn MJ, Mason EG, Watt MS (2007) Influence of initial stand density and genotype on longitudinal variation in modulus of elasticity for 17-year-old *Pinus radiata*. For Ecol Manag 252:67–72
- Wang SY, Ko CY (1998) Dynamic modulus of elasticity and bending properties of large beams of Taiwan-grown Japanese cedar from different plantation spacing sites. J Wood Sci 44:62–68
- Watt MS, Moore JR, Facon J-P, Downes GM, Clinton PW, Coker G, Davis MR, Simcock R, Parfitt RL, Dando J, Mason EG, Brown HE (2006) Modelling the influence of stand structural, edaphic and climatic influences on juvenile *Pinus radiata* dynamic modulus of elasticity. Forest Ecol Manag 229:136–144
- Zhang SY (1997) Wood quality: its definition, impact and implications for value-added timber management and end uses. In Timber Management Toward Wood Quality and End-Product Value. S.Y. Zhang, R. Gosselin and G. Chauret (eds). Proceedings of the CTIA/IUFRO International Wood Quality Workshop, Quebec City. Part I. pp 17–39
- Zhang SY, Chauret G, Ren HQ, Desjardins R (2002) Impact of initial spacing on plantation black spruce lumber grade yield, bending properties and MSR yield. Wood Fibre Sci 34:460–475