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# Effects of early respacing on physico-mechanical properties of naturally regenerated *Picea sitchensis* in Great Britain

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## Abstract

Natural regeneration can reduce costs compared with replanting. However, its use requires knowledge about how either active or passive management will affect the balance between quality and quantity in the timber supply. This study aimed to quantify the effects of respacing on volume recovery and wood properties. Two British forest experiments using *Picea sitchensis* with various respacing distances and an un-respaced control were assessed 21–22 years after the treatments were applied. Tree dimensions were measured and used to quantify slenderness, merchantable volume, and sawlog volume. Wood properties were assessed on a sub-sample using mechanical testing. Generalised linear mixed models were used to examine differences between treatments and sites. Respacing decreased slenderness and increased relative sawlog volume and branch size. Wider respacing reduced wood strength and the widest respacing reduced wood stiffness. Respacing did not affect wood density. However, at the relatively low productivity sites considered here, respacing to 2.1 m represented the best compromise for current markets. In summary, not respacing improved some wood properties but reduced tree stability and the proportion and volume of sawlogs, which will negatively affect forest value.

**Key words:** Sitka spruce, wood quality, sawlog volume, slenderness, natural regeneration

## Introduction

The two main considerations when growing any crop are the quantity of the product achieved at harvest and the suitability of that crop for the designated market. When applied to coniferous trees with a target market of structural sawn wood products, the quantity is the volume suitable to produce sawlogs (i.e., logs of large enough dimensions for producing sawn wood), and the suitability of the wood is determined by comparing the stiffness, strength, and density quality grades, such as EN 338 (CEN 2016) in Europe. Knots, the remnants of branches in trees, are also important "defects" affecting usability and appearance of wood and are consequently a further grading parameter. The volume of wood produced is in fact a composite metric of both tree growth and survival. The quantity of sawlogs and the quality of the wood, collectively the physico-mechanical properties of trees, can be manipulated through silviculture. This is the overarching theme of the study.

In Britain and Ireland, the main tree species used for timber production is Sitka spruce (*Picea sitchensis* (Bong.) Carr.) due to its rapid growth and adaptability to a wide range of sites. Most timber forests are even-aged and planted to achieve 2500 stems ha$^{-1}$ at age 5 or 2 m square spacing. This planting density was derived from the extensive study of Brazier and Mobbs (1993), who determined that a 2.0 m initial spacing (2500 stems ha$^{-1}$) produced Sitka spruce trees with the right balance of growth rate and wood properties for structural timber. Clearfelling takes place at around 40 years and the next rotation is established by replanting and following the same practice. However, the ecology of Sitka spruce is such that it is well-adapted to regenerating in the disturbed soil and woody debris of harvested sites (Peterson et al. 1997). In the British Isles, such regeneration following clearfell can be profuse with plant densities exceeding 300 000 ha$^{-1}$ (Clarke 1992; von Ow et al. 1996). Therefore, there is a move in large parts of the timber-growing regions of Great Britain to exploit this tendency for natural regeneration and there is a requirement for practical research on how to manage it.

If the main objective of a forest is timber production, respacing of natural regeneration is recommended (Nixon and Worrell 1999; Mason 2010). The advice is simple: to respace to the same uniform layout (2500 stems ha$^{-1}$) as a planted forest when the trees are about 1.5–2.0 m in height. Again, this is related to the compromise point in the trade-off between growth and wood properties identified by Brazier and Mobbs (1993). However, this has not yet been investigated with observations based on forest experiments and this

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is the purpose of our study. A further consideration is that not respacing, a "passive" management option, is popular because it comes at no immediate cost. There are consequentially substantial areas of passively managed natural regeneration in Great Britain. As the downstream costs of this passive management have not yet been fully considered, a further purpose of this study is therefore to additionally consider the impacts of *not* respacing.

Initial (or planting) spacing is known to affect tree diameter (Brazier and Mobbs 1993; Simic et al. 2017), branch/knot size (Brazier and Mobbs 1993), stiffness (Brazier and Mobbs 1993; Simic et al. 2017), and wood density (Brazier and Mobbs 1993; Simic et al. 2017). Qualitatively comparable results are shown for other plantation conifer species black spruce (*Picea mariana* (Mill.) BSP) (Zhang et al. 2002), radiata pine (*Pinus radiata* D.Don) (Lasserre et al. 2009), jack pine (*Pinus banksiana* Lamb.) (Hébert et al. 2016), loblolly pine (*Pinus taeda* L.) (Clark et al. 2008), Norway spruce (*Picea abies* (L.) H. Karst) (Johansson 2008), and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Rais et al. 2014). Studies consistently show that wider initial spacing reduces competition between trees, resulting in increased diameter growth and branch size while reducing wood density, stiffness, and strength. Respacing dense natural regeneration has a similar effect to initial spacing on tree growth (Stokes and Kerr 2013), but little is known about wood properties. One preliminary study (Cameron et al. 2014) suggested that passive management might offer advantages for wood properties, particularly in that there could be no difference between the juvenile corewood and outerwood (Burdon et al. 2004) parts of the stem, which could essentially negate the negative connotations of juvenile corewood (Zobel and Sprague 1998) for wood utilisation. The available literature does not adequately address sawlog production from a base of high stem density natural regeneration for a target market of primary processors intending to produce structural timber. To do this, it is necessary to simultaneously consider both volume and all of the most important wood properties (i.e., wood density, stiffness, and strength) for structural timber. A simultaneous consideration of volume recovery and wood properties will be done within this study, in addition to an investigation in the radial (i.e., pith to bark) trends of the wood properties.

A final aspect that we will consider is the implications of passive management of dense natural regeneration on tree stability. Tree stability is important for survival and therefore volume at harvest. The buckling of trees under their own weight is described according to Euler's (1757) critical load calculation, adapted to trees by Greenhill (1881), as presented in Dargahi et al. (2019). The biomechanics of this can be simplified to two components, tree slenderness, or the ratio of height to diameter, and wood stiffness. A slenderer tree has an increased risk of buckling and for trees of equivalent slenderness, a stiffer tree has a decreased risk of buckling. Tree slenderness is also an important consideration for wind stability, a constant and real risk in the Sitka spruce-growing regions of Great Britain. Wind risk is relatively well-studied in these areas (Hale et al. 2015) and it is well understood that more slender trees are at increased risk of breakage (Peltola et al. 2000). Further, self-buckling and breaking is a common occurrence with snow loading, where trees are unable to support the weight of snow in addition to their own weight (reviewed in Nykänen et al. 1997). When snow occurs in the British Isles, mainly in Scotland, it is frequently a rapid accumulation of wet, heavy snow due to the oceanic climate. Stokes and Kerr (2013) observed heavy snow damage in un-respaced Sitka spruce regeneration 17 years after the previous clearfell. Therefore, there are reasonable concerns about stability of passive management of natural regeneration and it follows that tree survival will be affected by slenderness and it should be considered in forest management.

The aims of this study are to evaluate the effects of active or passive management of high stem density natural regeneration on the quantity and quality of wood produced. We will do this by making appropriate measurements on forest experiments of Sitka spruce in Great Britain as the case study. Specifically, we (i) quantified the effects of not respacing natural generation and various respacing distances on sawlog volume recovery, merchantable volume recovery, and wood properties; and (ii) examined the impact of not respacing on tree slenderness and therefore forest stability. We hypothesised that not respacing would lead to a significant decrease in sawlog recovery, increased stem slenderness, and improved wood properties, including less radial variation in those properties. This study will allow direct recommendations to be made for the management of Sitka spruce forests in the British Isles.

## Material and methods

### Study sites and experimental layout

The forest experiments were located in Fernworthy Forest, Dartmoor, England (50.641 °N, 3.908 °W) and Radnor Forest, Wales (52.286 °N, 3.165 °W) and are described in Table 1. These experiments were described at earlier periods by Stokes and Kerr (2013). The previous stands of Sitka spruce were clear-felled in the mid-1980s (Table 1) and the sites were left uncultivated and with no removal of residues. Within 5 or 6 years, profuse natural regeneration of Sitka spruce occurred resulting in stocking of approximately 50 000 stems $ha^{-1}$ at Dartmoor and 72 000 stems $ha^{-1}$ at Radnor.

Respacing treatments were applied in 1991 to 1.8 × 1.8 m, 2.1 × 2.1 m, and 2.6 × 2.6 m (hereafter "1.8 m," "2.1 m", and "2.6 m"), with non-respaced controls. Trees were selected for retention on the basis of good stem form, relative height, and dominance. Tree age assessment indicated that advance regeneration had been occurring for several years prior to overstorey removal (Stokes and Kerr 2013). The layout was a randomised block design with four replications. Individual treatment plots were 0.1 ha in area (31.6 × 31.6 m) with a central 0.02 ha (14.1 × 14.1 m) "measurement" plot.

For this study, the number of replicate treatment plots available at Radnor was reduced as one control plot, two 1.8 m plots, and one 2.1 m plot were lost to mechanical damage, whilst a further control plot was lost recently to snow damage. In addition, one 2.1 m plot at Dartmoor was excluded from destructive sampling since stand basal area was

**Table 1.** Description of the study sites, treatments.

| | Dartmoor | Radnor |
|---|---|---|
| Location | Dartmoor, Devon, SW England | Knighton, Powys, Mid Wales |
| Stand area (ha) | 1.3 | 2.0 |
| Elevation (m, ASL) | 420 | 470 |
| Aspect | SE | NNW |
| Approximate slope | Constant 13% | Varied around 35% |
| Soil type | Podzol (very acidic) | Upland brown earth (freely draining, slightly acidic) |
| Lithology | Igneous, granite | Sedimentary, slate |
| Mean annual rainfall | 1600 mm | 1100 mm |
| Clear-felled | 1986 | 1985 |
| Treatments | Control | Control |
| | 1.8 m | 1.8 m |
| | 2.1 m | 2.1 m |
| | 2.6 m | 2.6 m |
| Initial stocking density when treatments applied (stems $ha^{-1}$) | 50 000 | 72 000 |
| Treatments applied | October 1991 (one growing season after Radnor) | January 1991 |
| Mean tree age at treatment | 7 (range 3–11) | 4 (range 2–8) |
| Date sample trees felled | March 2013 | February 2013 |
| Mean age of sample trees | 28 | 26 |

so low that any removals would have influenced the desired longer-term study of the treatment.

## Measurements on standing trees and calculation of volume recovery

All trees in the 0.1 ha individual treatment plots were assessed for survival and were measured for stem diameter at breast height (DBH; taken at 1.3 m above ground level) using a diameter tape. Only trees of merchantable roundwood dimensions were included, i.e., ≥7 cm DBH.

Within the central 0.02 ha measurement plots, diameter quartiles were applied and five trees per quartile were randomly selected, giving a total of 20 trees per plot to ensure a representative range of tree sizes in the analyses. Small trees (<10 cm DBH) of limited commercial value and trees with defects (e.g., forks, bends) were excluded. Tree height was measured using a Haglöf Vertex IV ultrasonic hypsometer (Haglöf Inc. Sweden). Branch diameter was measured using Vernier callipers on the largest diameter branch closest to 2.0 m stem height, perpendicular to longitudinal branch axis.

Stem "slenderness" was calculated as the ratio of tree height (m) to DBH (m); it is consequentially dimensionless. Single tree volume was calculated with the use of a stem taper function developed by Fonweban et al. (2011) and tested for wider application by Manso et al. (2022) to predict stem diameters at 10 cm intervals from the ground to the tree tip:

$$(1)\quad d_i = dbh.x^{\left[0.7580+0.2954(z-1)+3.3279.e^{-12.0326z}\right]}$$

$$x = \frac{h_t - h_i}{h_t - 130}$$

$$z = \frac{h_i}{h_t}$$

where $d$ is the stem diameter at height $h_i$ and $h_t$ is the total tree height, all in cm. Volume of each interval section was calculated as the volume of a frustrum of cone with base at height $i$ and top at height $j$; the sum of these section volumes equates to total tree volume.

$$(2)\quad \sum_{i=0}^{t-10}\sum_{j=10}^{t} v_{ij} = \frac{\pi\left(h_j - h_i\right)}{3} \times \left(\frac{{d_j}^2 + {d_i}^2}{4} + \frac{d_j.d_i}{2}\right)$$

The use of a taper function in this way offers an advantage over the standard equations in Matthews and Mackie (2006) and Matthews et al. (2016) as we can (i) derive sawlog volume and merchantable volume by restricting the sum to sections where $d_j \geq 14$ cm and $d_j \geq 7$ cm, i.e., the minimum top diameters overbark accepted locally for sawlogs and roundwood, respectively; (ii) derive the individual stem lengths associated with the sawlog volume and merchantable volume and then; (iii) by using eq. 1 and eq. 2, we can censor trees that did not produce a minimum merchantable sawlog length (we used 2.1 m) so that they did not appear to produce any real sawlog volume.

## Measurement of wood properties

Lowest diameter quartiles were excluded from destructive testing since the trees were of insufficient size to produce test samples of suitable dimensions. At each site ($n = 2$), 15 trees per treatment ($n = 4$) were selected randomly for destructive testing, with five trees from each of the three upper diameter quartiles and approximately even numbers from each replicate. Therefore 60 trees were tested at each site with a total of 120 trees used to assess wood properties. Logs of 60 cm length were cut from each stem, their bases at approximately 1.5 m stem height and centred on the inter-whorl section to limit the presence of knots. North and west faces were marked

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using paint to ensure consistent orientation during sample processing. This was so that any effects of wind on the wood properties, such as the formation of flexure wood (Telewski 1995), would therefore be consistent across trees.

Logs were air-dried for 3 months, then sawn longitudinally through the pith into western and eastern halves to relieve drying stress and prevent splitting. During sample preparation, the intention was to remove two "clearwood" test samples of dimensions 300 mm × 20 mm × 20 mm from each half; one from the inner stem and one from the outer, making a total of four samples per tree. Outer samples were to be aligned to the outermost growth ring (ring ranges 17–23 for Dartmoor and 16–22 for Radnor). Inner samples were to be centred on the ninth ring from the pith, where possible. This definition of inner and outerwood samples was as close as possible to the study by Cameron et al. (2014). However, because stem diameter was frequently prohibitively small, inner samples were often taken from the immediately adjacent radial position to the outer sample creating a possible overlap. To account for this, the age range of the rings within each sample was recorded and used to calculate mean age, which was included as a continuous, explanatory variable in the analysis. Where possible, additional samples were also prepared in radially adjacent positions to the original, predefined sample positions. A total of 698 test samples were obtained, from which 445 were suitably defect-free to use as clearwood.

Prepared samples were conditioned to constant mass in a TAS *Eco* Environmental Chamber (Temperature Applied Sciences, Worthing, England) at 65% relative humidity and 20 °C to achieve a nominal 12% moisture content at testing. Weight was recorded on removal from the chamber and volume measured with width and depth determined using Vernier callipers, based on means of three readings at equal intervals along the length. Wood density was calculated by dividing mass by volume. Samples were tested for bending stiffness and strength, defined as the modulus of elasticity (MOE) and modulus of rupture (MOR), respectively. Tests were undertaken in a three-point flexural configuration with a span of 280 mm, using a H5K-S benchtop test machine (Tinius Olsen Ltd., Redhill, England). These were performed according to BS 373 (BSI 1957) with the orientation of growth rings parallel to the direction of load. Deflection was measured using the displacement of the cross head. MOE and MOR were calculated using QMAT software (version 5.11; Tinius Olsen Ltd., Redhill, England).

## Statistical analyses

The major analyses of data used general-linear mixed modelling techniques (Pinheiro and Bates 2000) with the aim of determining whether the treatment effects were significant.

The general-linear mixed effect models for the measurements made on trees (DBH, height, slenderness, volume, and branch size) had the following form:

$$y_{ijkl} = \mu + \alpha 0_i + \alpha 1_j + \alpha 0_i.\alpha 1_j + \beta 0_k + \epsilon_{ijkl} \quad (3)$$

where $y$ is the observed tree property of tree $l$ in treatment $i$ from replicate $k$ in site $j$, $\mu$ is the overall mean, $\alpha 0$ is the fixed effect of respacing treatment $i$, $a_1$ is the fixed effect of site $j$, $\beta 0$ is the random effect of replicate $k$, and $\epsilon$ is the residual error. In the case of single tree volume, the response was log transformed prior to analysis and in the case of sawlog volume, the distributions were zero-inflated by the trees that did not produce any sawlogs. A two-stage or "hurdle" model strategy was therefore employed. Prior to the analysis of the nonzero data by the above general-linear mixed model, the hurdle model was first used to determine probability of a tree producing a sawlog by considering the binary response:

$$z_{ijkl} \begin{cases} 1 & \text{if the } ijkl-\text{th tree produces a sawlog} \\ 0 & \text{otherwise} \end{cases} \quad (4)$$

And estimating the probability $p$ that a sawlog will be produced with a generalised logistic mixed-effects model where

$$p = \mathrm{P}\left(z_{ijkl} = 1\right) \quad (5)$$
$$\log it\,(p) = \gamma 0 + \left(a0_i + a1_j + a0_i.a1_j + \beta 0_k\right).\gamma 1$$

The $\gamma$ parameters describe the linear relationship to the log-odds of producing a sawlog. It follows that the expected sawlog volume per treatment can be predicted as the product of the probability of that treatment produced a sawlog, determined in eq. 5, and the expected sawlog volume from that treatment, determined in eq. 4 from the truncated data.

The models for the measurements made on wood samples (wood density, MOE, and MOR) had the following form:

$$y_{ijklmn} = \mu + \alpha 0_i + \alpha 1_j + \alpha 2 + \alpha 0_i.\alpha 1_j + \alpha 0_i.\alpha 2 + \beta 0_k + \beta 1_{kl} + \beta 2_{klm} + \epsilon_{ijklmn} \quad (6)$$

where $y$ is the observed wood property of sample $n$ within orientation $m$ within tree $l$ in treatment $i$ within replicate $k$ within site $j$, $\alpha 2$ is the continuous fixed effect of mean ring number, $\beta 1$ is the random effect of tree, $\beta 2$ is the random effect of orientation (i.e., east or west radius), and $\varepsilon$ is the residual error. $\alpha 0$, $\alpha 1$, and $\beta 0$ are as described previously for eq. 3.

Analyses were conducted within *R* (version 4.2.2; R Core Team 2022) using the *nlme* package (version 3.1–160; Pinheiro et al. 2022) and the *lme4* package (Bates et al. 2015). Models were fitted by Maximum Likelihood as this allows comparisons of models with different fixed effects. The full mixed models given above were fitted to the data and a stepwise reduction of the models was conducted using likelihood ratio tests ($\alpha = 0.05$) until only significant fixed effects remained (the minimum adequate model). These stepwise reductions started with the highest-level interaction terms, meaning individual variables could not be removed if they were significant in an interaction. Final model residuals were checked for homogeneity of variance. With the exception of the generalised linear hurdle model (eq. 5), an *F*-test in Analysis of variance (ANOVA) was performed on the minimum adequate model to examine significance of the fixed effects and multiple *post-hoc* Tukey comparisons were made on the minimum adequate models using the *emmeans* package (version 1.8.4–1, Lenth 2023), where the degrees of freedom were calcu-

**Table 2.** Summary of stand (i.e., full treatment plot) growth parameters at the Dartmoor and Radnor study sites, 21 and 22 growing seasons, respectively, after respacing treatments were applied.

| Site | Treat. | Mean tree age (years) | n. trees assessed (stems <7 cm DBH excluded) | Stem density (trees ha$^{-1}$) (% of control) | Mean DBH (cm) (stems <7 cm DBH excluded) | Mean height of sample trees (m) (based on measurements made on 20% of trees) |
|---|---|---|---|---|---|---|
| Dartmoor | Control | 28 | 289 | 3613 | 13 | 16.5 |
| | 1.8 m | 28 | 201 | 2513 (70%) | 14 | 17.0 |
| | 2.1 m | 28 | 154 | 1925 (53%) | 16 | 16.5 |
| | 2.6 m | 28 | 134 | 1675 (46%) | 18 | 18.0 |
| Radnor | Control | 26 | 105 | 4650 | 12 | 17.5 |
| | 1.8 m | 26 | 118 | 2950 (63%) | 16 | 18.0 |
| | 2.1 m | 26 | 125 | 2083 (45%) | 19 | 16.5 |
| | 2.6 m | 26 | 111 | 1388 (30%) | 20 | 19.0 |

**Note:** Excludes all live stems <7 cm DBH. DBH, diameter at breast height.

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lated by the containment method and $p$ values were multiplicity adjusted for each comparison. Where the interaction term between treatment and site was significant in likelihood ratio comparisons, *post-hoc* Tukey comparisons were made by site. Examples of the entire process can be consulted in Appendix A.

# Results

## Survival

In the interval since respacing (21–22 years), relative natural mortality in the control plots occurred at similar rates in both sites: stem density reduced by 93% at Dartmoor and 94% at Radnor (data not shown). However absolute stem densities in the respacing treatments and the control were not consistent between sites (Table 2). Radnor had a higher initial stem density and there was a more marked decrease relative to the control at this site than at Dartmoor (Table 2). Further, the widest respacing treatment at Radnor had fewer surviving trees than the equivalent at Dartmoor.

## DBH and height

DBH and height by treatment and site are shown in Fig. 1. For DBH, the interaction between site and treatment ($p < 0.001$) was significant by inclusion in a likelihood ratio comparison ($\chi^2(3) = 18.349$, $p < 0.001$). The single effects of treatment ($F_{[3,1219]} = 88.211$, $p < 0.001$) and site ($F_{[1,6]} = 9.229$, $p = 0.023$) were significant in ANOVA. Using multiple comparison: at both sites all respacing treatments had significantly larger DBH than the control ($p < 0.001$) and in general, wider respacing treatment had larger DBH than correspondingly narrower ones ($p \leq 0.045$), with the exception that the difference between the 2.1 and 2.6 m respacing treatments was not significant at Dartmoor ($p = 0.250$). For tree height, the inclusion of the interaction between treatment and site was significant in the likelihood ratio comparison ($\chi^2(3) = 12.565$, $p < 0.006$). In ANOVA the simple effect of treatment was significant ($F_{[3,526]} = 20.965$, $p < 0.001$), but site was not ($F_{[3,526]} = 0.005$, $p = 0.944$). The general result in multiple comparison was that the 2.6 m respacing treatment had taller trees than the other treatments and this difference was of the order of 1 to 2 m ($p \leq 0.005$), with the exception that there was no difference between the 2.1 and 2.6 m respacing treatments at Dartmoor ($p = 0.281$).

## Stem slenderness

Tree slenderness is plotted by treatment and site in Fig. 2. In the likelihood ratio test, the inclusion of the interaction of treatment and site was not significant ($\chi^2(3) = 1.531$, $p = 0.675$), but the inclusion of both simple effects was (Site $\chi^2(1) = 6.552$, $p = 0.011$; Treatment $\chi^2(1) = 64.938$, $p < 0.001$). In multiple comparison, Dartmoor had significantly more slender trees than Radnor (difference = 0.07, $p = 0.018$). Every treatment was significantly ($p <= 0.012$) less slender than the control. The estimated control slenderness was 1.05, while the treatments were estimated at 0.97, 0.88, and 0.89 for the 1.8, 2.1, and 2.6 m respacing treatment, respectively. The 2.1 and 2.6 m respacing treatments were less slender than the 1.8 m treatments ($p \leq 0.001$), but there was no difference between the 2.6 and 2.1 m treatments ($p = 0.830$).

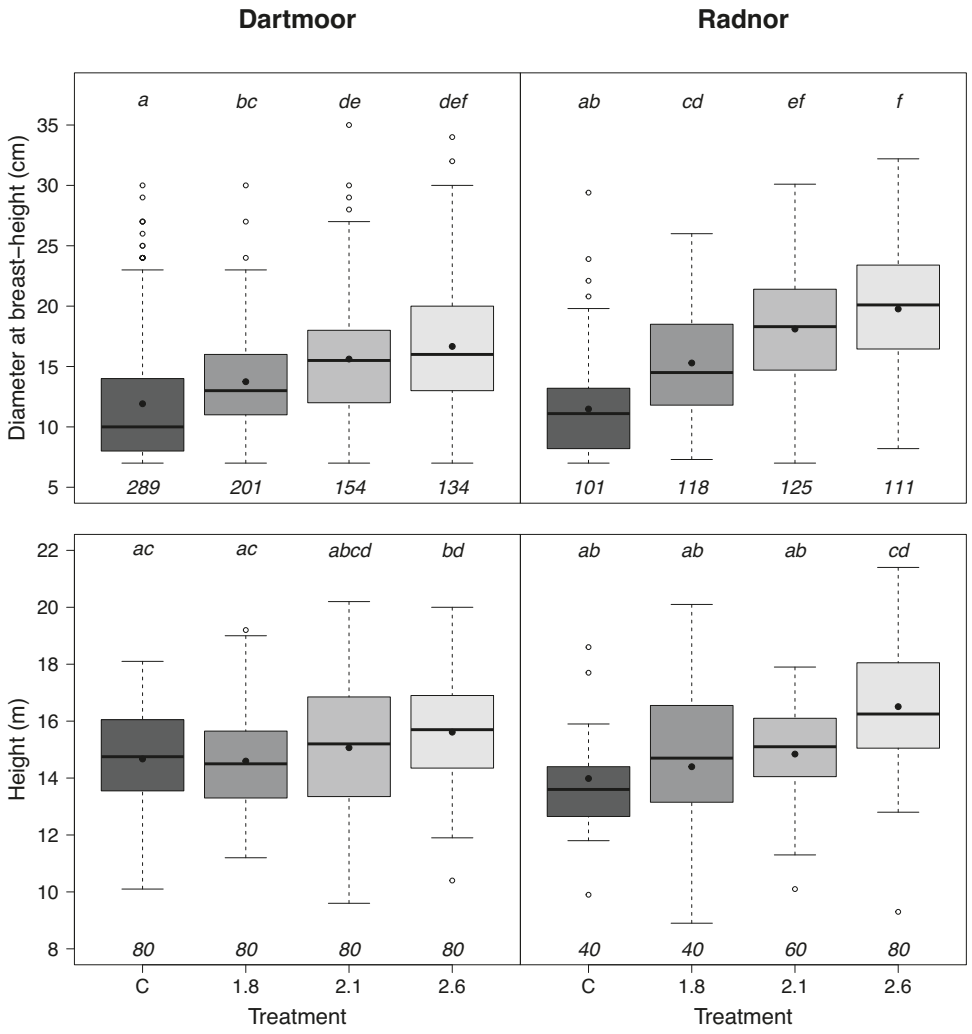
## Single tree merchantable volume

Single tree volume is plotted by site and treatment in Fig. 2. A large variation in single tree volume can be observed within the treatments, as well a clear positive skew (Shapiro Wilk $p$ value < 0.001), a logarithmic transformation, was used in further analysis. The interaction between treatment and site was not significant in the likelihood ratio test ($\chi^2(3) = 7.312$, $p = 0.063$); in further reduction, it was not necessary to include site in the model ($\chi^2(1) = 3.760$, $p = 0.053$), but treatment was significant for inclusion ($\chi^2(1) = 73.188$, $p < 0.001$). In multiple comparison, the respacing treatments >1.8 m had significantly ($p \leq 0.015$) greater single tree volumes than the control. Otherwise, the 2.1 and 2.6 m treatments were greater than the 1.8 m ($p \leq 0.003$) but not different from each other ($p = 0.8858$). The expected values per treatment at each site are also given in Table 3.

## Sawlog volume recovery

Sawlogs are defined as logs with a top diameter of ≥14 cm over bark and ≥2.1 m in length; these dimensions ensure they can be used to produce structural timber. Overall, 58% ($n = 313$) of the examined trees produced a sawlog. The prob-

**Fig. 1.** (top) DBH of all trees > 7 cm DBH according to respacing treatment at each site and (bottom) height of a subset of trees according to respacing treatment at each site. The numbers below each box provide the number of trees represented in each category, while the compact letter display of significant differences between groups are given above each box. • represents the estimated marginal mean for each group according to the mixed models used in the analysis.

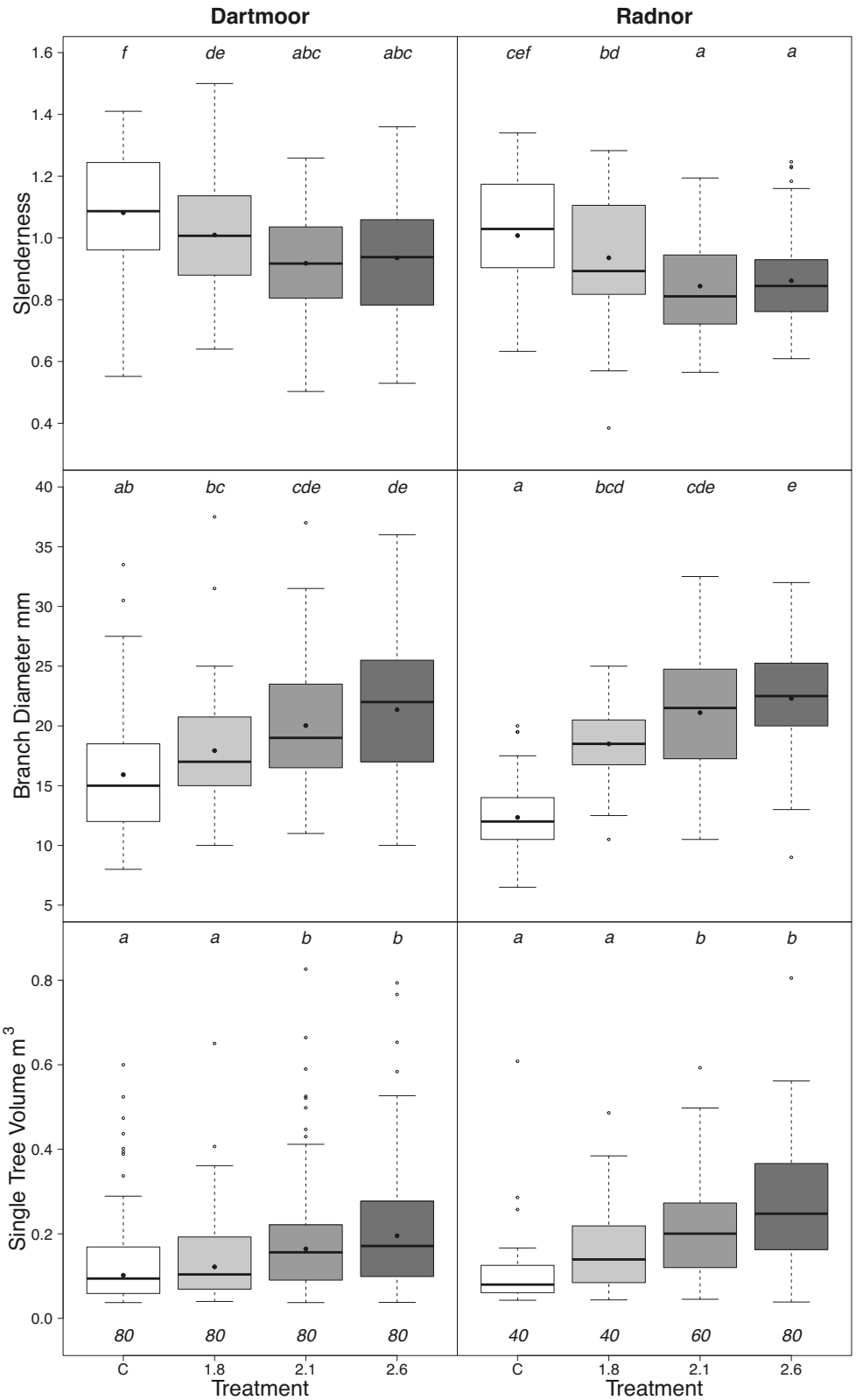



abilities of producing a sawlog, and the geometric mean values per site and per treatment are given in Table 3. The geometric mean was used as the data were not normally distributed, which is also why these were log transformed prior to analysis in mixed models. The inclusion of the interaction between treatment and site was significant in the hurdle model ($\chi^2(3) = 8.65$, $p = 0.034$). The respacing treatments all had higher probabilities of producing sawlogs than the controls at both sites, but this difference was only significant for the 2.1 and 2.6 m treatments (Wald test $z = \geq 1.987$, $p \leq 0.047$). When considering the truncated data where trees that did not produce a sawlog were excluded, the fully specified model could be reduced to only treatment ($\chi^2(3) = 14.427$, $p = 0.002$); the interaction between treatment and site ($\chi^2(4) = 2.495$, $p = 0.645$), plus site ($\chi^2(1) = 2.316$, $p = 0.128$), could be removed. Here the *post-hoc* test found that the 2.6 m respacing treatment produced higher sawlog volume than the control and 1.8 m treatments ($p \leq 0.029$). The expected values per treatment are used to illustrate the outcomes at each site (Table 3). At Dartmoor the 1.8 m respacing treatment yielded a similar amount of sawlog volume per hectare to the control, but this was not the case at Radnor where the control was lower and the 1.8 m treatment was higher (about 1.6 times the same treatment at Dartmoor). The conclusion on this aspect was therefore that the 2.1 m treatment was the minimum respacing distance to produce a high yield of sawlog volume across both sites.

The most similar stem density between the two sites was found at 2.1 m spacing, which is also closest to the 2.0 m square standard spacing of Sitka spruce in these regions. If we consider that the time since clearfell was 38 years, then the mean annual volume increment during this period for the 2.1 m spacing was 8.3 $m^3 \cdot ha^{-1} \cdot year^{-1}$ at Dartmoor and 9.0 $m^3 \cdot ha^{-1} \cdot year^{-1}$ at Radnor.

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**Fig. 2.** (top) Stem slenderness (the ratio of height to diameter), (middle) single tree merchantable volume (i.e., where the stem is ≥ 7 cm) and (bottom) thickest branch diameter (at 2.0 m stem height) according to respacing treatment at each site excluding trees <7 cm DBH. The numbers below each box provide the number of trees represented in each category, while the compact letter display of significant differences between groups are given above each box. • represents the estimated marginal mean for each group according to the mixed models used in the analysis.




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**Table 3.** A simulation of merchantable volume (≥7 cm) and sawlog volume (≥14 cm) returns based on results of this study (measurement plots only).

| Site | Treat. | Stems Ha$^{-1}$ | Mean tree volume [i] ($m^3$) | Plot volume per Hectare [ii] ($m^3 \cdot ha^{-1}$) | Probability of tree producing a sawlog [iii] (%) | Sawlog volume per tree[iv] | Volume of sawlogs per hectare [v] ($m^3 \cdot ha^{-1}$) |
|---|---|---|---|---|---|---|---|
| Dartmoor | C | 3613 | $0.10_a$ | 368 | $36_a$ | $0.14_a$ | 177 |
| | 1.8 | 2513 | $0.12_b$ | 306 | $45_b$ | $0.13_a$ | 153 |
| | 2.1 | 1925 | $0.16_c$ | 316 | $60_b$ | $0.17_{ab}$ | 195 |
| | 2.6 | 1675 | 0.20 cd | 327 | $65_b$ | $0.19_b$ | 212 |
| Radnor | C | 4650 | $0.10_a$ | 473 | $26_a$ | $0.14_a$ | 165 |
| | 1.8 | 2950 | $0.12_b$ | 359 | $61_b$ | $0.13_a$ | 243 |
| | 2.1 | 2083 | $0.16_c$ | 342 | $65_{bc}$ | $0.17_{ab}$ | 229 |
| | 2.6 | 1388 | 0.20 cd | 271 | $75_c$ | $0.19_b$ | 203 |

**Note:** The subscript letters denote Tukey groups. [i]These are the expected values from the appropriate generalised linear model.
[ii]This is the product of the mean tree volume and stems ha$^{-1}$.
[iii]These are determined from the hurdle model.
[iv]These are the expected values based on the generalised linear model of the truncated data.
[v]This is the product of stems ha$^{-1}$, probability of producing a sawlog and mean sawlog volume per tree.

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## Branch diameter

Branch diameter (Fig. 2) ranged from 7.0 to 38.0 mm with a mean of 19.1 mm and a standard deviation of 5.4 mm. A large variation can be observed within treatments. The inclusion of the interaction between treatment and site was significant in the likelihood ratio comparisons ($p < 0.002$). ANOVA then showed that the simple effect of treatment was significant ($F_{[3,526]} = 56.567$, $p < 0.001$), while site was not ($F_{[1,6]} = 0.016$, $p = 0.903$). According to the multiple comparison, every treatment had significantly ($p \leq 0.036$) larger branches than the control; there was no difference between the 2.1 and 2.6 m treatments ($p \geq 0.265$). Despite the significant interaction term, the *post-hoc* test showed the differences were qualitatively the same at both sites, but the differences between treatments and the controls were relatively greater at Radnor.

## Wood properties

MOE is plotted by site in Fig. 3. The interactions between treatment and ring number ($\chi^2(3) = 0.976$, $p = 0.807$) and treatment and site ($\chi^2(3) = 4.593$, $p = 0.204$) were not significant in the likelihood ratio comparison. In further reductions, the inclusion of site ($\chi^2(7) = 13.521$, $p = 0.060$) was not significant, while the inclusion of treatment was significant by inclusion ($\chi^2(9) = 24.94$, $p = 0.003$). Ring number had a positive effect on MOE (Fig. 3). The only treatment that was significantly different from the control was the 2.6 m respacing (0.70 GPa lower, $p < 0.006$).

MOR is plotted by site in Fig. 3. The interaction between site and treatment was significant ($p < 0.001$), but the interaction between treatment and ring number was not ($\chi^2(3) = 0.022$, $p = 0.999$). In ANOVA, the single effects of site ($F_{[1,6]} = 10.054$, $p = 0.019$) and treatment ($F_{[3,252]} = 8.712$, $p < 0.001$) were significant. The expected value of MOR was 3.71 MPa higher at Dartmoor. Ring number had a positive effect on MOR (Fig. 3). In multiple comparison, the only treatments that were significantly different from the control were the 2.1 and 2.6 m respacing treatments at Radnor only (≥10.67 MPa lower, $p < 0.007$).

Wood density is plotted by site in Fig. 3. The interaction between treatment and site was significant by inclusion in the likelihood ratio comparison ($\chi^2(3) = 17.339$, $p < 0.001$). In ANOVA of the reduced model, the simple term for site was significant ($F_{[1,6]} = 18.436$, $p = 0.005$), but treatment was not ($F_{[3,254]} = 2.604$, $p = 0.052$). The expected value of wood density was 34 kg·m$^{-3}$ higher at Dartmoor. Ring number had a negative effect on wood density (Fig. 3) meaning wood density decreased with ring number.

A more detailed description of the analysis and the results on wood properties is included in Appendix A.

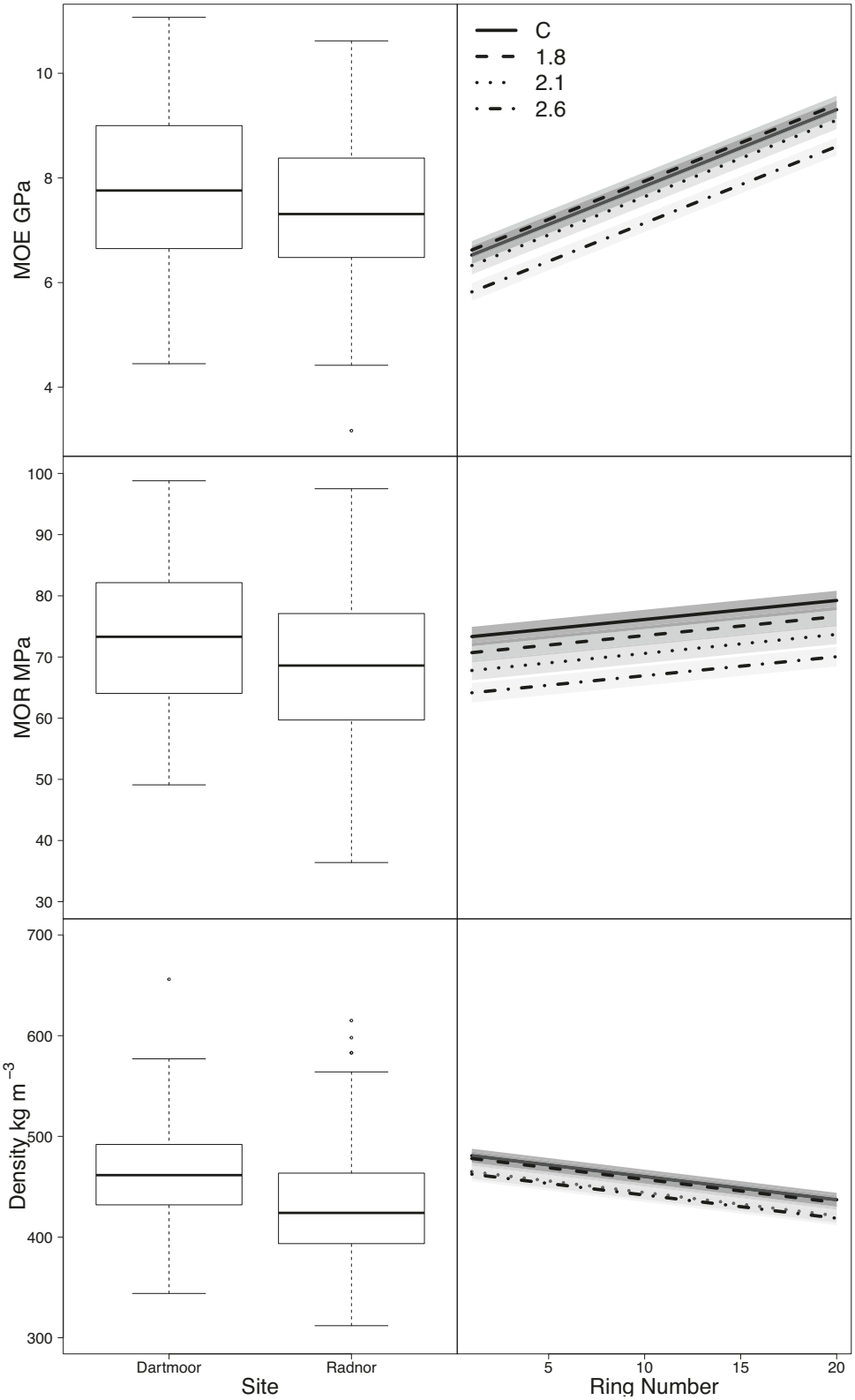
# Discussion

We aimed to quantify the effects of respacing distance on slenderness as a proxy for tree stability, volume recovery, and wood properties of naturally regenerated Sitka spruce for the purpose of aiding forest management decisions relating to growing suitable material for wood-based forest products. Specifically, we sought to determine whether the wood properties might be improved by sustained, intense early competition via the management option of not respacing natural regeneration (passive management), and what any trade-offs might be in terms of stem slenderness and sawlog volume recovery. To examine this, measurements were made on trees and samples collected from two long-term respacing experiments.

## Tree survival, size, and shape

In the un-respaced controls, survival was comparable to that reported in other studies of Sitka spruce (e.g., Nelson 1990; Mason 2010), therefore they can be considered representative of the resource. The density of remaining trees was equivalent to 3600 ha$^{-1}$ at Dartmoor and 4650 ha$^{-1}$ at Radnor, equating to 1.7 and 1.5 m square spacings (although spacing regularity was not considered). Coincidentally, these values are close to the target planting densities commonly used for Sitka spruce in plantations during the mid-20th Century (Hibberd 1991). However, because we followed standard op-

**Fig. 3.** (Top) (Left) MOE plotted by site and (right) the trends in MOE plotted by ring number and treatment. (Middle) the same applied to MOR and (bottom) to wood density. The trends are derived from the general-linear mixed-model analysis described in the text with errors denoted by the standard error of the estimates. Not all of the differences between treatments are significant and in some cases, they were significant at one site only. MOE, modulus of elasticity; MOR, modulus of rupture.




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erational forest measurement practices in Great Britain (i.e., stems <7 cm DBH were not assessed), our data did not include information on the large quantity of dead and very small diameter stems present, particularly in the controls, and the actual plant densities in the control plots will be higher than our figures suggest. These small trees would ultimately further decrease harvesting efficiency (Ackerman et al. 2022) and increase costs above what can be derived from the values reported here.

Respacing had an obvious benefit for tree growth, increasing single tree diameter within the snapshot in time approach adopted here. Responses appeared to differ between sites, but the sites were not identical in terms of environment nor the resulting stem density. It is also presumed that genetic differences exist between the sites. Overall, DBH increased progressively in response to respacing distance. This was amplified at Radnor, where differences in stem density between controls and respacing treatments were greater than at Dartmoor. Overall respacing effects on stem diameter were consistent with studies on tree spacing observed by previous researchers (e.g., Cregg et al. 1988; Nelson 1991; Deans and Milne 1999). Tree height was also affected by respacing with height increasing relative to control in the widest respacing treatment, which is consistent with results from an earlier study at the same sites (Stokes and Kerr 2013). Over enough time, it is possible that each treatment would be capable of producing trees with the same DBH, with the relatively closer spacings taking comparatively longer. This could not be considered within this study, but a distance-dependent growth model (e.g., Thurnher et al. 2017), or even a stand-level model that could account for such low spacing in the control could be used to examine how long this would take in each treatment, which could in turn be weighed against economics and increased length of exposure to wind risk for example.

When we consider the shape of the tree stems as slenderness, the differences in height between treatments were relatively inconsequential compared to diameter. Therefore, there were marked differences in slenderness between successive respacing treatments. Stem slenderness is inversely proportional to the so-called safety factor (Watt et al. 2006; Waghorn and Watt 2013), where more slender stems are at greater risk of buckling under their own weight, even without additional weight from snow, particularly if MOE does not increase to compensate for the increased slenderness, as would normally be expected (Watt et al. 2006). Our results for MOE, considered with other wood properties later in this dicussion, suggested only the 2.6 m treatment had lower MOE than the other treatments, but our results also showed that diameter and slenderness changed between successive treatmtents. Therefore, according to these results, not respacing at all carries an increased risk of forest damage through the self-buckling of trees and consequential loss of total volume. However, the consensus among forest wind risk studies and simulations is that higher plant densities are at less of a risk due to increased shelter (i.e., although individual tree stability is low, stand stability is high) (Hale et al. 2015). These studies are not generally calibrated with observations for such dense forests, e.g Gardiner et al. (1997) tested a maximum of 3222 stems. If the pattern holds true in the dense natural regeneration studied here, while the trees are individually more at risk, the high density of plants means that the stands should be stable so long as the stand remains intact. If gaps start to open, for example due to snow damage, then the forest will likely be more vunerable to subsequent storm damage as the remaining stems are prone to breakage.

## Merchantable volume and sawlog volume recovery

Our aim here was to quantify the effect of respacing on volume production and contrast it to the passive option of not respacing. If merchantable volume is considered according to current practices of growth and yield (e.g., Stokes and Kerr 2013), then the reduced tree size in high plant densities is usually at least compensated for by an increased number of stems per hectare. We consider that this is overly simplistic, and a change of approach in the evaluation of these forests is needed. Ultimately, if many more stems need to be harvested to obtain the same volume, then the operations at the end of the forest management cycle are inefficient (Ackerman et al. 2022) and will lead to higher costs and lower returns. When the target is sawlog production for sawn wood products, then logs of certain sizes are required and this should be reflected in the evaluation.

We addressed the question about how many logs of at least a minimum threshold size could be produced by employing a technique to estimate the probability of sawlog production from each of the treatments based on the use of a stem taper profile from the literature (Fonweban et al. 2011), which has elsewhere been shown to be robust enough for wider uses (Manso et al. 2022). We used arbitrary, but realistic, definitions of sawlogs as the minimum thresholds. The analysis could in principle be extended to logs of any target dimensions. We used this technique to quantify the proportion of stems producing sawlogs and, in this case, our results indicate higher proportions of suitably dimensioned stems in respaced treatments and, in absolute terms, greater volumes of sawlogs on a per hectare basis. Therefore, a higher number of stems did not compensate for the small trees. Respacing to 2.1 m can be seen to effectively increase the volume of sawlogs in a given area over the time period considered here. In our example, this was between 10% and 30% dependent on the site, for harvesting 15% and 45% of the number of stems to get that volume. The probability of producing a saw log is much more important in determining this than single tree volume. This information could be used to examine cost–benefit scenarios of respacing treatments.

Both sites considered in this study were relatively low yielding. If the ratio of volume with respect to the time since clearfell is considered for the 2.1 m treatments, then the volume produced at the two sites would be similar to the returns expected from an even-aged, unthinned stand of yield class 10 of the same age, where yield class is used as a measure of site productivity in British forestry (Matthews et al. 2016). This is low for Sitka spruce in Great Britain. Moreover, a cost–benefit analysis relating to active or passive management will be sensitive to the probability of producing sawlogs and the volume of those sawlogs, which in turn could reasonably be

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expected to be related to site productivity, especially in the respaced treatments. The effects of site productivity on the control are uncertain, but it seems plausible that the stem occlusion stage will be reached faster at least. Further studies are required to quantify the effect of site productivity over a wider range of site productivities, preferably in a way that allows calibration for a simulator that can be applied over the range of site productivities where the debate of active vs. passive management of natural regeneration applies.

## Wood properties

In relation to sawn timber for construction, we hypothesised that un-respaced control trees would have superior wood properties to those in respaced treatments, and that there would be less difference in the measured wood properties between the inner and outer parts of the tree. Respacing, to any distance, was found to increase thickest branch diameter at 1.8–2.0 m height in the stem, which, in turn, would increase the size of knots (Manso et al. 2020). The findings support those of previous researchers that branch/knot size is governed primarily by initial spacing (e.g., Savill and Sandels 1983) or respacing distance (Auty et al. 2012). Therefore, respacing can be considered to have a negative effect on knot size.

Respacing also had negative effects on MOE, but lesser effects on wood density and MOR, where there was a limited effect at once site only. For British-grown Sitka spruce, MOE is the most important property (Moore et al. 2013), but in this study a decrease in MOE was significant only at 2.6 m respacing where the difference in MOE between the 2.6 m respacing and the control is around the order of 1 GPa, which is more than enough to affect the grade of any timber produced (CEN 2016). Another study on Sitka spruce (Auty et al. 2018) showed that wood density and microfibril angle, the two factors that can determine wood stiffness (Mclean et al. 2010), were negatively affected by respacing. The study by Auty et al. (2018) did not begin with dense natural regeneration, but rather a planted forest at 1.8 m square spacing. Further, in the study by Auty et al. (2018), respacing treatments extended up to a 5.6 m respacing treatment. The two studies complement each other in the sense that wider respacing will have an effect.

On one hand, the results on respacing generally agree with Brazier and Mobbs (1993) finding that 2.0 m spacing is the maximum without unacceptable impacts on wood properties. On the other hand, it does not agree in the sense that there is no continual "improvement" in wood properties at increasingly closer spacing. A possible explanation might be the natural variability of spacing in natural regeneration. Our study did not measure competition indices between individual plants in the un-respaced control for example, and it is possible that some individuals had wider equivalent spacing than 1.8 m at the time of sampling due to mortality (i.e., self-thinning). Additionally, both sites in this study were at relatively high elevations (Table 1); the tree line in Great Britain is generally considered to be at about 500 m asl and, according to combined spatial data on the public forest estates (Forestry Commission 2019*a*, 2019*b*; Natural Resources Wales 2019), the median elevation for Sitka spruce is 244 m asl, the 75th percentile is 323 m asl, and 95th percentile is 434 m asl. Elevation has been shown to have a negative effect on wood stiffness (Moore et al. 2009) and could be one reason that the higher elevation site (Radnor) appeared to have lower stiffness in this study. Moreover, the fact that both sites were growing at relatively high altitude means that the physical environment rather than the competitive growing environment (or silviculture) may have limited mechanical wood properties.

Our study also examines an important element of the high stem density control plots, namely the radial variation in wood properties in such dense forests and how there might be no difference in wood properties between the innermost and outermost parts of the tree. We hypothesised that in respaced treatments, the mechanical wood properties of the inner part of the stem would be inferior to those of the outer stem wood. We further considered that there would be less of a difference between the inner and outer wood of the control relative to other treatments based on an earlier study by Cameron et al. (2014). Cameron et al. (2014) observed no difference between the stiffness of the juvenile corewood and outer maturewood. We investigated this by considering the interaction between treatment and ring number. Had the analysis showed that this interaction term was significant, it would have indicated that the slope of the line that describes the radial trend in MOE (MOR and wood density for that matter) were different between the treatments and the control. However, the interaction was not significant for any of the measured wood properties. Further, the parameter estimates remained clearly positive or negative rather than almost zero (i.e., weakly positive or negative).

In these data, MOE and MOR increased with radial position as expected. Density decreased with radial position, which is also expected since Sitka spruce has a density profile that decreases from pith to a minimum around ring seven, then increases towards the bark (Gardiner et al. 2011; Auty et al. 2018). Our density data did not contain measurements from the outer part of the tree (i.e., beyond 20 rings) and therefore only the decrease was observed. Further the complex radial trend in wood density was probably smoothed towards a simple linear decrease due to the low spatial measurement resolution, in that the samples contained many rings. We know a linear function would not normally be appropriate for this species, but the age of the sample material and the nature of the experiment can reasonably explain why it was observed here. The most important point is that the radial trend in any of these three properties did not vary between the control and the respacing treatments. Our results therefore suggest that the previously observed trends in the radial trends of MOE and MOR (Moore et al. 2011; McLean et al. 2015) also occur in dense natural regeneration and we have rejected our hypothesis that the dense natural regeneration would have more favourable juvenile corewood in the site conditions investigated here.

It would seem reasonable to state that respacing to 2.1 m will produce a good compromise in the trade-off between growth and stiffness. However, we would raise the question about whether better site-adapted silvicultural interventions could be possible based on local growth and wood proper-

ties. To fully understand this, a further study on natural regeneration is required that spans a wider range of environments, and particularly elevations. We would therefore also recommend that due to the differences in tree size, future studies on respacing should make use of continuous pith to bark sampling of physical and mechanical properties that can be resolved at the tree ring level (e.g., McLean et al. 2015, Gil-Moreno et al. 2023). This would allow more precise modelling of the radial trends in wood properties in a way that could be more reliably linked to growth models.

### The benefits of planting vs. natural regeneration and added value from respacing

It is appropriate to consider the economic and other benefits of using natural regeneration as opposed to planting on the sites studied. Compared to planting these sites, regeneration offered savings of all site preparation and planting costs, but incurred the costs of respacing. On one hand, for planted sites costs would typically be for mechanical mounding and manual planting (i.e., labour plus the costs of plants). On the other hand, respacing costs are essentially those of a motor-manual precommercial thinning. According to Davies and Kerr (2014), the relative cost of respacing to planting is 51%, or respacing is essentially half of the price of (re)planting. However, planting would normally make use of "improved" plant material from tree breeding programs, which offers considerable gains in growth rate (Manso et al. 2022). This is a relatively important potential disadvantage when using natural regeneration; the parents of the next generation are not controlled for favourable growth rates (assuming the seed trees are open pollinated) and the seedling position is not specifically chosen/optimised. It is worth considering that these sites are at the lower end of the productive scale (i.e., they would have a low site index) and it could reasonably be questioned if significant growth gains would be achieved here even with superior genotypes. Given the relatively longer return period for the investment made at planting on low productive sites, it might be possible to save money and make use of natural regeneration with appropriate respacing. Indeed, studies elsewhere have shown that planting only really makes sense on more productive sites (Simonsen 2013; Lula et al. 2021). Similar studies have not been made in our study region. Another possible benefit to using natural regeneration on relatively less productive sites is that it can avoid any potential supply issues from tree nurseries, making sure that available nursery material can go to the more productive sites as a priority.

When it comes to decision about respacing, the benefits to managers are clear. Sitka spruce is quite shade-tolerant (Bianchi et al. 2018), meaning that it will survive for a reasonably long time in dense conditions. In this study, the densities of the control plots (we measured only the number of stems < 7 cm DBH) were approximately 1.5–2 times higher than normal planting densities (about 2500 stems $ha^{-1}$) even after 22 growing seasons. Applying the respacing treatment could almost be described as the difference between having a merchantable stand, i.e., approaching harvestable dimensions, after 22 years or not. The costs of precommercial thinning (therefore respacing) increases with stand growth due to the increased time consumption for the motor–manual operation (Kaila et al. 2006). Such costs are not typically estimated for such late stand-developmental stages. Nonetheless, it is highly likely that trying to do any kind of remediation of un-respaced stands with these characteristics at this late stage, i.e., trying to convert them towards a more productive stand environment favouring larger single trees, is likely to be more expensive than it would have been to plant the stand to begin with. Of course, the natural forests of Sitka spruce in native lands see these kind of growth patterns (Peterson and Martin 1997), and eventually they become mature forest structures, probably after centuries (Alaback 1982; Deal et al. 1991). The value in such stands is likely to be for other purposes than timber production (Deal et al. 2014), and in this respect, those other values would likely be higher if landscape restauration was to occur with native species.

## Conclusions

This study has quantified outcomes from the early respacing of high density, naturally regenerated Sitka spruce and provided insights into active or passive management of that regeneration. Improved diameter growth following respacing led to increased tree size and considerable increases in sawlog volume per hectare for a given period of time. While there are some unfavourable effects of respacing, mainly an increase in branch diameter, which would result in greater knot sizes, the trade-off in forest stability or sawlog volume is likely to be too great a price to pay for a reduced knot size. If respacing is restricted to no greater than 2.1 m between plants, then there should be no detrimental impact on wood mechanical properties. However, further work is required to include a wider variety of sites that consider environmental effects and the full range of site productivity classes where this might be applied.

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## Data availability
Data generated or analysed during this study are available from the corresponding author upon reasonable request.

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## Competing interests
The authors declare there are no competing interests.

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## Appendix A

In this study, general-linear mixed models were used to investigate the effect of respacing treatment on the stiffness (modulus of elasticity or MOE), strength (modulus of rupture or MOR) and wood density of small clear specimens. In this section, summary statistics of the data used (Table A1), the minimum adequate models following stepwise reduction (Table A2), and the parameters obtained in the model fitting process (Table A3, Table A5, Table A7) are detailed alongside some *post-hoc* Tukey comparisons (Table A4, Table A6, Table A8). The purpose is to provide a detailed and transparent analysis through demonstration. This analysis supports the main text. However, the results of these analyses are not of wider interest. As the models only served in the detailed interpretation of the data collected in the study. Therefore, they are presented as an Appendix A for those with a special interest in the methods of analysis.

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**Table A1.** Summary statistics of samples used to assess wood properties with respect to the experimental treatments using general-linear mixed models.

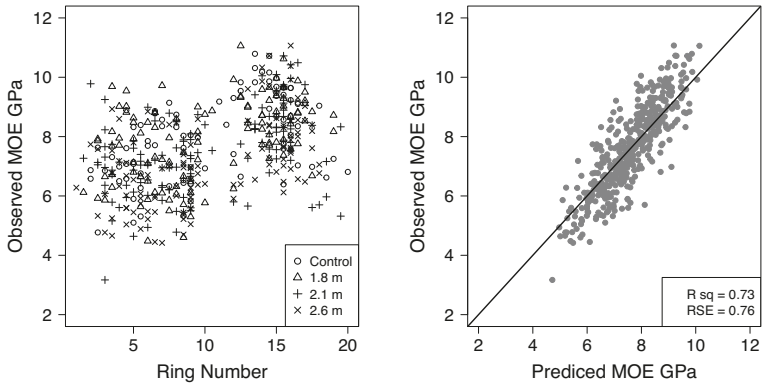
| | Dartmor | | | | Radnor | | | |
|---|---|---|---|---|---|---|---|---|
| Site treatment variable | Control | 1.8 m | 2.1 m | 2.6 m | Control | 1.8 m | 2.1 m | 2.6 m |
| Number of trees | 14 | 15 | 15 | 15 | 13 | 14 | 13 | 15 |
| Number of specimens | 55 | 53 | 66 | 58 | 33 | 56 | 61 | 63 |
| Minimum ring number | 2.0 | 1.5 | 2.5 | 2.5 | 2.0 | 2.5 | 1.5 | 1.0 |
| Maximum ring number | 19 | 19 | 19.5 | 18 | 20 | 17.5 | 18.5 | 17.5 |
| Mean ring number | 9.6 | 10.2 | 10.5 | 10.5 | 11.3 | 10.0 | 9.8 | 10.1 |
| Mean MOE GPa | 7.88 | 8.34 | 7.66 | 7.4 | 8.26 | 7.45 | 7.4 | 6.85 |
| SD MOE GPa | 1.53 | 1.25 | 1.5 | 1.69 | 1.09 | 1.32 | 1.29 | 1.09 |
| Mean MOR MPa | 73.9 | 77.1 | 70.8 | 72.1 | 79.2 | 70.1 | 68.9 | 61.8 |
| SD MOR MPa | 12.5 | 9.4 | 11.3 | 10.7 | 11.3 | 11.3 | 10.5 | 10.5 |
| Mean density kg·m$^{-3}$ | 453 | 479 | 452 | 467 | 466 | 438 | 432 | 412 |
| SD density kg·m$^{-3}$ | 45 | 40 | 46 | 48 | 52 | 60 | 48 | 52 |

**Table A2.** Demonstration of the stepwise reduction of the fully specified model (eq. 6) through the backwards elimination of categorical fixed effects by sequential likelihood-ratio ($\chi^2$) comparisons.

| Step | Fixed effects | Removal | DF | $\chi^2$ | $p$ |
|---|---|---|---|---|---|
| 0 | $\alpha0.\alpha1 + \alpha0.\alpha2 + \alpha0 + \alpha1 + \alpha2$ | | 16 | | |
| 1a | $\alpha0.\alpha1 + \alpha0 + \alpha1 + \alpha2$ | $\alpha0.\alpha2$ | 13 | 0.976 | 0.807 |
| 1b | $\alpha0.\alpha2 + \alpha0 + \alpha1 + \alpha2$ | $\alpha0.\alpha1$ | 13 | 4.593 | 0.204 |
| 2 | $\alpha0 + \alpha1 + \alpha2$ | $\alpha0.\alpha1 + \alpha0.\alpha2$ | 10 | 5.576 | 0.472 |
| 3a | $\alpha0 + \alpha2$ | $\alpha0.\alpha1 + \alpha0.\alpha2 + \alpha1$ | 9 | 13.521 | 0.060 |
| 3b | $\alpha1 + \alpha2$ | $\alpha0.\alpha1 + \alpha0.\alpha2 + \alpha0$ | 7 | 24.943 | 0.003 |

**Notes:** For convenience only the fixed effects are shown ($\alpha0$ = Treatment, $\alpha1$ = Site, $\alpha3$ = Ring Number, $\alpha3$ is a continuous variable). The reduction process stops when a significant difference is found as that fixed effect should not be removed. In this case, the final model fixed effects are given in step 3a; the full model is given as eq. A1.

**Fig. A1.** (Left) MOE of individual specimens plotted against ring number with treatments differentiated by different symbols and (right) MOE of individual specimens plotted against the predicted values from the same specimens using the general-linear mixed model derived in the study. MOE, modulus of elasticity.




The effect of respacing treatment on MOE was tested using a general-linear mixed model approach where the model was reduced from the fully specified model (eq. 6) to the minimum adequate model based on likelihood-ratio tests for the significance of an inclusion of the fixed effects (Table A2).

The minimum adequate form of the model as found to be:

$$y_{ijklmn} = \mu + \alpha0_i + \alpha2 + \beta0_k + \beta1_{kl} + \beta2_{klm} + \epsilon_{ijklmn} \quad \text{(A1)}$$

where $y$ is the observed MOE of sample $n$ within orientation $m$ within tree $l$ in treatment $i$ within replicate $k$ within site $j$, $\alpha0$ is the fixed effect of treatment $i$, $\alpha2$ is the continuous fixed effect of mean ring number, $\beta0$ is the random effect of replicate $k$, $\beta1$ is the random effect of tree $l$, $\beta2$ is the random effect of orientation $m$ (i.e., east or west radius) and $\varepsilon$ is the residual error. The random effects are not of interest in this study per se; they are used as

**Table A3.** Parameter estimates for the general-linear mixed model [A1].

| | | Value | SE | DF | $t$ | $p$ |
|---|---|---|---|---|---|---|
| Fixed effects | $\mu$ | 6.38 | 0.21 | 255 | 30.31 | <0.01 |
| | $\alpha 0$ Treat 1.8 m | 0.10 | 0.22 | 255 | 0.43 | 0.67 |
| | $\alpha 0$ Treat 2.1 m | −0.20 | 0.23 | 255 | −0.89 | 0.38 |
| | $\alpha 0$ Treat 2.6 m | −0.70 | 0.21 | 255 | −3.31 | <0.01 |
| | $\alpha 3$ | 0.15 | 0.01 | 255 | 16.62 | <0.01 |
| | | SD | | | | |
| Random effects | $\beta 0$ | 0.20 | | | | |
| | $\beta 1$ | 0.84 | | | | |
| | $\beta 2$ | 0.18 | | | | |
| | $\epsilon$ | 0.85 | | | | |

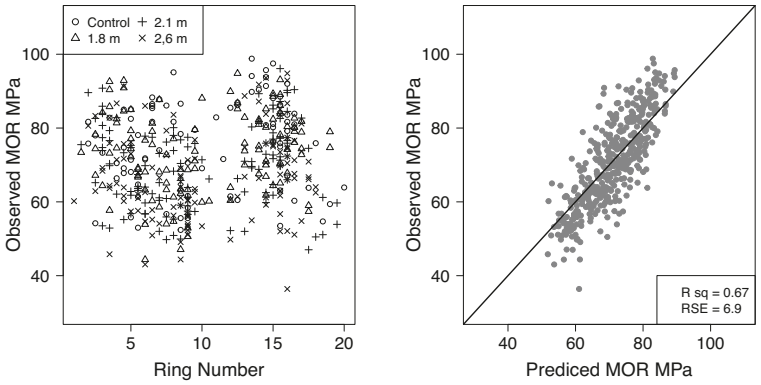
**Note:** The $\mu$ term is the estimate for the control treatment.

**Table A4.** Multiple post-hoc Tukey comparisons on the treatment effects on the general-linear mixed model [A1].

| Comparison | Difference GPa | SE | DF | $t$ ratio | $P$ |
|---|---|---|---|---|---|
| Control—1.8 m | −0.10 | 0.23 | 255 | −0.432 | 0.973 |
| Control—2.1 m | 0.20 | 0.23 | 255 | 0.887 | 0.812 |
| Control—2.6 m | 0.70 | 0.21 | 255 | 3.312 | 0.006 |
| 1.8–2.1 m | 0.30 | 0.21 | 255 | 1.429 | 0.483 |
| 1.8–2.6 m | 0.80 | 0.20 | 255 | 4.057 | <0.001 |
| 2.1–2.6 m | 0.50 | 0.22 | 255 | 2.325 | 0.095 |

**Notes:** Effects are averaged over site as there was no significant interaction between site and treatment and the effect of treatment is thus considered the same at both sites. $p$ values are multiplicity adjusted and the denominator degrees of freedom (DF) are calculated using the containment method.

**Fig. A2.** (Left) MOR of individual specimens plotted against ring number with treatments differentiated by different symbols and; (right) MOR of individual specimens plotted against the predicted values from the same specimens using the general-linear mixed model derived in the study. MOR, modulus of rupture.




a convenient way to account for the experimental design only. MOE is plotted against ring number by treatment in Fig. A1. The parameter estimates for the model are provided in Table A3, and the multiple comparisons between respacing treatments and the control in Table A4. The model fit is visually presented in Fig. A1 alongside the fit statistics.

The effect of respacing treatment on MOR was similarly tested and the minimum adequate form of the model was found to be:

$$\text{(A2)}\quad y_{ijklmn} = \mu + \alpha 0_i + \alpha 1_j + \alpha 2 + \alpha 0_i.\alpha 1_j + \beta 0_k + \beta 1_{kl} + \beta 2_{klm} + \epsilon_{ijklmn}$$

where $y$ is now the observed MOR and all other variables are as described for eq. A2. MOR is plotted against ring number by treatment in Fig. A2. The parameter estimates for the model

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**Table A5.** Parameter estimates for the general-linear mixed model [A2].

| | | Value | SE | DF | $t$ | $p$ |
|---|---|---|---|---|---|---|
| Fixed effects | $\mu$ | 71.17 | 2.18 | 252 | 32.65 | <0.01 |
| | $\alpha$0 Treat 1.8 m | 2.13 | 2.68 | 252 | 0.79 | 0.43 |
| | $\alpha$0 Treat 2.1 m | −0.42 | 2.58 | 252 | −0.16 | 0.87 |
| | $\alpha$0 Treat 2.6 m | −1.27 | 2.58 | 252 | −0.49 | 0.62 |
| | $\alpha$1 SiteR | 3.71 | 3.17 | 6 | 1.17 | 0.29 |
| | $\alpha$3 | 0.31 | 0.08 | 252 | 3.89 | <0.01 |
| | $\alpha$0:$\alpha$1 1.8 m:Radnor | −9.5 | 4.08 | 252 | −2.33 | 0.02 |
| | $\alpha$0:$\alpha$1 2.1 m:Radnor | −10.26 | 4.16 | 252 | −2.47 | 0.01 |
| | $\alpha$0:$\alpha$1 2.6 m:Radnor | −15.85 | 3.89 | 252 | −4.07 | <0.01 |
| | | SD | | | | |
| Random effects | $\beta$0 | 0 | | | | |
| | $\beta$1 | 7.68 | | | | |
| | $\beta$2 | 0 | | | | |
| | $\epsilon$ | 7.7 | | | | |

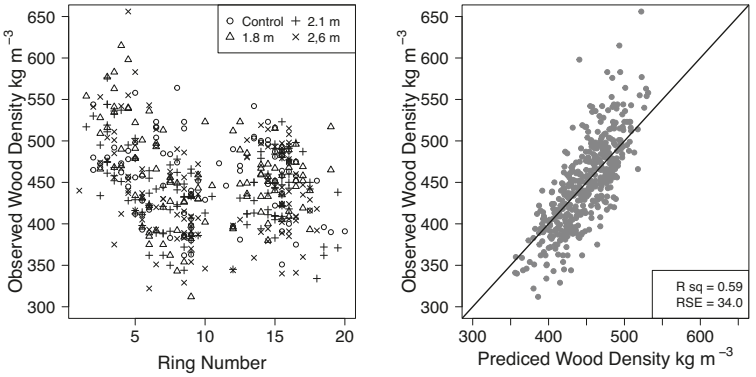
**Notes:** The $\mu$ term is the estimate for the control treatment at the Dartmoor site. The random effects are not of interest in this study per se, they are used as a convenient way to account for the experimental design only.

**Table A6.** Multiple post-hoc Tukey comparisons on the treatment effects on the general-linear mixed model [A2].

| Site | Comparison | Difference | SE | DF | $t$ ratio | $p$ |
|---|---|---|---|---|---|---|
| Dartmoor | Control—1.8 m | −2.13 | 2.68 | 252 | −0.79 | 0.86 |
| | Control—2.1 m | 0.42 | 2.58 | 252 | 0.16 | 1.00 |
| | Control—2.6 m | 1.27 | 2.58 | 252 | 0.49 | 0.96 |
| | 1.8–2.1 m | 2.54 | 2.77 | 252 | 0.92 | 0.80 |
| | 1.8–2.6 m | 3.39 | 2.69 | 252 | 1.26 | 0.59 |
| | 2.1–2.6 m | 0.85 | 2.69 | 252 | 0.32 | 0.99 |
| Radnor | Control—1.8 m | 7.38 | 3.08 | 252 | 2.40 | 0.08 |
| | Control—2.1 m | 10.67 | 3.26 | 252 | 3.27 | 0.01 |
| | Control—2.6 m | 17.11 | 2.91 | 252 | 5.89 | <0.01 |
| | 1.8–2.1 m | 3.30 | 2.56 | 252 | 1.29 | 0.57 |
| | 1.8–2.6 m | 9.74 | 2.37 | 252 | 4.10 | <0.01 |
| | 2.1–2.6 m | 6.44 | 2.84 | 252 | 2.27 | 0.11 |

**Notes:** Effects are examined by site as there was a significant interaction between site and treatment. $p$ values are multiplicity adjusted and the denominator degrees of freedom (DF) are calculated using the containment method.

**Fig. A3.** (Left) Wood density of individual specimens plotted against ring number with treatments differentiated by different symbols and (right) wood density of individual specimens plotted against the predicted values from the same specimens using the general-linear mixed model derived in the study.




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**Table A7.** Parameter estimates for the general-linear mixed model [A3].

| | | Value | SE | DF | $t$ | $p$ |
|---|---|---|---|---|---|---|
| Fixed effects | $\alpha 0$ Intercept | 480.24 | 9.62 | 254 | 49.91 | 0 |
| | $\alpha 0$ Treat 1.8 m | 17.34 | 11.55 | 254 | 1.5 | 0.13 |
| | $\alpha 0$ Treat 2.1 m | 3.25 | 11.17 | 254 | 0.29 | 0.77 |
| | $\alpha 0$ Treat 2.6 m | 17.14 | 11.21 | 254 | 1.53 | 0.13 |
| | $\alpha 1$ SiteR | 5.72 | 13.8 | 6 | 0.41 | 0.69 |
| | $\alpha 3$ | −2.3 | 0.38 | 254 | −6 | 0 |
| | $\alpha 0$:$\alpha 1$ 1.8 m:Radnor | −40.29 | 17.73 | 254 | −2.27 | 0.02 |
| | $\alpha 0$:$\alpha 1$ 2.1 m:Radnor | −38.32 | 17.75 | 254 | −2.16 | 0.03 |
| | $\alpha 0$:$\alpha 1$ 2.6 m:Radnor | −71.06 | 16.84 | 254 | −4.22 | 0 |
| | | SD | | | | |
| Random effects | $\beta 0$ | 4.79 | | | | |
| | $\beta 1$ | 28.2 | | | | |
| | $\beta 2$ | 0 | | | | |
| | $\epsilon$ | 37.53 | | | | |

**Notes:** The intercept term is the estimate for the control treatment at the Dartmoor site. The random effects are not of interest in this study per se, they are only used as a convenient way to account for the experimental design.

**Table A8.** Multiple post-hoc Tukey comparisons on the treatment effects on the general-linear mixed model [A2].

| Site | Comparison | Value | SE | DF | $t$ | $p$ |
|---|---|---|---|---|---|---|
| Dartmoor | Control—1.8 m | −17.3 | 11.5 | 254 | −1.50 | 0.44 |
| | Control—2.1 m | −3.3 | 11.2 | 254 | −0.29 | 0.99 |
| | Contorl—2.6 m | −17.1 | 11.2 | 254 | −1.53 | 0.42 |
| | 1.8–2.1 m | 14.1 | 11.8 | 254 | 1.19 | 0.63 |
| | 1.8–2.6 m | 0.2 | 11.6 | 254 | 0.02 | 1.00 |
| | 2.1 m - 2.6 m | −13.9 | 11.5 | 254 | −1.21 | 0.62 |
| Radnor | Control—1.8 m | 23.0 | 13.4 | 254 | 1.71 | 0.32 |
| | Control—2.1 m | 35.1 | 13.8 | 254 | 2.54 | 0.06 |
| | Contorl—2.6 m | 53.9 | 12.5 | 254 | 4.30 | 0.00 |
| | 1.8–2.1 m | 12.1 | 11.2 | 254 | 1.08 | 0.70 |
| | 1.8–2.6 m | 31.0 | 10.6 | 254 | 2.93 | 0.02 |
| | 2.1–2.6 m | 18.9 | 12 | 254 | 1.57 | 0.40 |

**Notes:** Effects are examined by site as there was a significant interaction between site and treatment. $p$ values are multiplicity adjusted and the denominator degrees of freedom (DF) are calculated using the containment method.

are provided in Table A5, and the multiple comparisons between respacing treatments and the control in Table A6. The model fit is visually presented in Fig. A2 alongside the fit statistics.

Finally, the effect of respacing treatment on wood density was tested in the same fashion and the minimum adequate form of the model was found to be:

$$(A3)\quad y_{ijklmn} = \mu + \alpha 0_i + \alpha 1_j + \alpha 0_i.\alpha 1_j + \alpha 2 + \beta 0_k + \beta 1_{kl} + \beta 2_{klm} + \epsilon_{ijklmn}$$

where y is now the observed wood density of an individual specimen and all other variables are as described in for eq. A3. Wood density is plotted against ring number by treatment in Fig. A3. The parameter estimates for the model are provided in Table A7, and the multiple comparisons between respacing treatments and the control in Table A8. The model fit is visually presented in Fig. A3 alongside the fit statistics.

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