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Modelling the effect of spacing and site exposure on spiral grain angle on Sitka spruce (Picea sitchensis (Bong.) Carr.) in Northern Britain

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Large grain angles in timber can have a negative effect on wood quality by reducing dimensional stability, strength properties and performance, and causing twisting and warping in sawn timber and poles. In this study, we assessed the impact of tree spacing and site exposure on grain angle, based on the measurements from 360 discs cut from Sitka spruce (Picea sitchensis (Bong.) Carr.) trees from Northern Britain (Scotland and Northern England). The results show that planting on sites exposed to strong prevailing winds, planting at wider spacing or undertaking heavy thinning can significantly increase spiral grain angle. Using the mixed-effect model, we found that between-tree variation ranged from 3.6 to 33.3 per cent, variation due to disc position within the tree ranged from 5.7 to 47.8 per cent; and between-ring variations within discs ranged from 0 to 38.5 per cent. Residual variation ranged from 25.7 to 64.8 per cent. Grain angles are greater at the juvenile stage than at the mature stage of wood development. A non-linear model, developed to predict grain angle, explained only 16 per cent of total variation in grain angle, despite the inclusion of several stand covariates into the model. Although the mixed-effect model improved the root mean square error (RMSE) by 26 per cent, and the coefficient of determination ($R^2$) rose to 53 per cent, its usage requires that a sample of grain angle measurements be made on the particular site for model calibration. The silvicultural response to reduced grain angle would be to plant at closer spacing and delay thinning or thin lightly, or to avoid planting Sitka spruce on very exposed sites. Given that grain angle is highly heritable, a further option is to reduce grain angle through selective breeding.

Introduction

Spiral grain in trees has fascinated scientists for over 150 years (see Rauchfuss and Speer, 2006), not only because of its visible presence, but also because of its negative effects on timber quality and value. It occurs when the tracheids deviate from the longitudinal axis of the stem (Harris, 1989; Hansen and Roulund, 1998a). Spiral grain in wood can cause shrinkage and warping of boards and planks and also decreases the strength of timber (Hannrup et al., 2002). It reduces dimensional stability (Johansson et al., 1994), strength (Kollmann and Coté, 1984; Pape, 1999;) and stiffness in wood (Desch and Dinwoodie, 1996) and, therefore, the value (Northcott, 1965) and suitability of timber for a number of applications (Pape, 1999; Raymond, 2002; Sepúlveda et al., 2003). It increases longitudinal shrinkage within the juvenile core (Cown, 1999), and reduces strength in compression, tension and bending in wood (Kollmann and Coté, 1984). It causes twisting of poles and posts in service (Paul, 1956; Phillips, 1978) and may decrease specific elasticity which is an important property for musical instruments (Huang and Chen, 1997). Economic losses due to grain angle are thought to be considerable, especially if trees are harvested and subsequently found to be unusable for timber because of severe angles (Harris, 1989; Danborg, 1994a; Kliger, 1997; Skatter and Kučera, 1997; Rauchfuss and Speer, 2006). Twist, which has been described as the most severe type of distortion and which causes downgrading and rejection of a significant proportion of timber, is strongly correlated with spiral grain (Stevens and Johnson, 1960; Forsberg and Warenswj, 2001; Hannrup et al., 2002). Maclaren (2002) quotes Cown who stated that “it has been documented that the greatest source of drying degrade in processing young logs is twist as a direct result of spiral grain in excess of 5 degrees”. Danborg (1994a) found that the severe twisting of boards of Norway spruce (Picea abies (L.) Karst.) and Sitka spruce (Picea sitchensis (Bong.) Carr.), are induced by spiral grain and is most pronounced in small-dimension boards near the pith.

Various hypotheses have been put forward concerning the origin and function of grain angle in trees. It is now widely accepted that the origin and formation of spiral grain can be
linked to cell division taking place in the cambial region (Harris, 1973, 1989; Zagorska-Marek and Little, 1986; Włoch et al., 2002). Three cell division processes are believed to contribute to the development of spiral grain (Hejnówicz and Zagorska-Marek, 1974): the frequency of pseudo-transverse antinodal divisions (PAD) in the vascular cambium (Hejnówicz and Romberg, 1979; Hejnówicz, 1980); intrusive growth resulting from the relative orientation of the pointed tips of elongated cambial derivatives (Bannan, 1966; Harris, 1973; Kubler, 1991; Larson, 1994); and imperfect periclinal divisions and orientation of fusiform cambial cells (FCC) (Harris, 1973; Savidge and Farrar, 1984). Furthermore, ethylene production in wood is also said to influence or even initiate spiral grain formation (Rauchfuss and Speer, 2006). Spiral grain is furthermore under considerable genetic control, although its expression seems to be at least partly dependent on the environmental factors affecting tree growth. Harris (1989) states that the propensity of trees to twist is controlled by heritable factors, but that its expression is dependent on the local environment. Most researchers accept that spirality is highly heritable or under stronger genetic influence than environmental control, and that there is no strict causal relationship between environmental conditions and grain angle direction (Harris, 1965). Although a number of environmental factors like wind (Eklund and Sall, 2000), temperature, soil nutrient status, rainfall, slope and exposure (Smythies, 1915; Rault and Marsh, 1952), altitude (Champion, 1935; Rault and Marsh, 1952), and temperature, soil nutrient status, rainfall, slope and exposure (Smythies, 1915; Rault and Marsh, 1952), altitude (Champion, 1935; Rault and Marsh, 1952) and the earth’s rotation have been proposed as possible causes of grain angle, none adequately explains its occurrence. Furthermore, as research increases into these causal environmental factors, there appears to be an increase in controversies, inconsistencies and inconclusive findings (see Acuna and Murphy, 2006; Rauchfuss and Speer, 2006).

There are two main hypotheses for the functional role of spiral grain in trees although neither hypothesis has been conclusively validated (Eklund and Sall, 2000). One suggestion is that spiral grain ensures better water and nutrient distribution within the tree (Vité, 1967; Kubler, 1991), while another is that spiral grain could be an adaptation of trees to withstand the weight of snow and strong winds (Skatter and Kucera, 1997).

Both forest managers and the timber industry are concerned about the negative impacts of spiral grain on timber performance and value, and the ways to minimize its development. Research has therefore been undertaken to assess and quantify these impacts on various timber species. However, only a few studies have been undertaken for British-grown Sitka spruce (Picea sitchensis (Bong.) Carr.) (e.g. Brazier, 1965; Tranquart, 1995). The aim of the present study was to assess the effects of tree spacing and site exposure on grain angle, and to develop a spiral grain model for British grown Sitka spruce. Our working hypothesis is that increased tree spacing and site exposure in Sitka spruce plantations both contribute to an increase in grain angle.

Materials and methods

Study sites and data collection

The data for this study were collected from Sitka spruce stands at Kershope, Glengarry, Glentress, Lochaline and Benmore Forests (Figure 1). All Sitka spruce progenies were of Queen Charlotte Island (QCI), British Columbia origin. The sites were chosen to cover a range of ages, spacing and site exposure; site summary data are presented in Table 1. Site exposure was assessed using the detailed aspect method scoring (DAMS) system detailed in Quine and White (1994). The stands at Benmore (1 and 2), Lochaline (1 and 2), Glentress and Kershope (2) Forests were planted at initial spacing of 2 m; while at Glengarry, 0.9, 1.4, 1.8 and 2.4 m spacings were used. At Kershope (1) Forest, the stands were initially planted at 1.8 m spacing, and re-spaced at age 17 to 2.4 m (systematic removal of 50 per cent of trees: removal of every second row, 3.4 m (by a systematic removal of 75 per cent of trees: removal of every second and third rows and every third tree in remaining rows) and 4.9 m (by a systematic removal of 89 per cent of trees: removal of every second and third rows and every second and third trees in the remaining rows) (see Rollinson (1988) p4 and Gardiner et al. (1997) p235). More detailed descriptions of the study sites can be found in Rollinson (1988), Gardiner and Macdonald (2005), Achim et al. (2006) and Fonweban et al. (2011). The protocol for selecting disc locations within the tree can be found in Gardiner and Macdonald (2005) and Gardiner et al. (2011).

Grain angle was assessed on cross-sectional discs of 10–15 cm thickness. At Benmore and Lochaline, two discs were cut at around 4 and 10 m height from each tree, at Glengarry discs were cut at 3 m, and subsequently at 3 m intervals along the tree stem; while at Glentress, Kershope (1) and (2) discs were cut at 1, 3 and at 3 m intervals along the stem. The discs were dried to 12 per cent moisture content and then split through the pith in the North–South direction using a hydraulically powered ram and blunt blade (see Figure 2).

The grain angle was measured at ring number 1 and then at the 5th, 10th, 15th, 20th rings, etc. from the pith at Glengarry Forest. At Benmore and Lochaline Forests, ring measurements were made at ring number 1 and then on the 6th, 11th, 16th, 21st rings, etc. from the pith. At Glentress and Kershope (2) Forests measurements were taken at ring numbers 1, 2, 4, 6, 8, 10, 12 etc. from the pith outwards, while at Kershope (1) measurements were taken at ring numbers 1, 2, 4, 5, 6, 7, 8, 9, 10 and at 5 ring intervals thereafter. The grain angle was measured with an angle gauge protractor on the split surface (Figure 2) from the pith to bark, following a method described by Tranquart (1995). Each measurement was taken on opposite radii for each ring and the mean was calculated to eliminate errors originating from tilt in stem disc arising during crosscutting and sample preparation (Brazier, 1965). By definition, a left hand grain (grain going from bottom right to top left on the tree) is designated as positive (+ve) and a right hand grain (bottom left to top right) is designated as negative (–ve). In this study, the overwhelming majority of grain angles were left hand and we considered the grain angles only in absolute terms, given that the magnitude of the angle (deviation) is what affects timber performance. Data were collected on a total of 360 discs from 180 sample trees from the eight stands. Table 1 presents summary statistics for grain angle for the study sites.

Data analysis and model development

The data collected were analysed to assess the impact of between tree spacing and site exposure on grain angle, and second, to model grain angle trends in Sitka spruce. Mixed modelling was used to analyse the data, having site, spacing, tree, disc position and ring number (class) as class variables. The effect of spacing, disc height and ring number were considered as fixed, while tree effects were considered random. The linear mixed model procedure in SAS (SAS, 2004; Littell et al., 2006) was used. The general model for analysis for each site was:

\[
y_{ijkl} = \mu + S_i + T_{ij} + D(T)_{jk} + R(D)_{kl} + e_{ijkl}
\]

where \(y_{ijkl} = \) grain angle measurement; \(\mu = \) overall mean; \(S_i = \) ith spacing; \(T_{ij} = \) jth tree within the ith spacing; \(D(T)_{jk} = \) the kth disc within the jth tree; \(R(D)_{kl} = \) the kth ring within the kth disc; \(e_{ijkl} = \) error.
The proc mixed procedure with the options for a Satterthwaite test was implemented in SAS (SAS Institute Inc., 2004). Measurements were grouped in five ring intervals starting from the pith.

In order to develop a model to predict grain angle variation or trends, some statistical models were tested and the best selected. This was an extension of the grain angle modelling work begun by Mavrou (2007) for Lochaline and Benmore forests to also include Kershope, Glengarry and Glentress Forests. Plots of mean grain angle versus ring number from the pith to bark were used to observe if there were any discernible trends that could be modelled. The plots showed a general initial increasing trend in grain angle with ring number from the pith, reaching a maximum, and then decreasing, either rapidly or slowly towards the bark, depending on the study site. Similar trends have been observed for Sitka spruce in Denmark (Hansen and Roulund, 1998a) and for Norway spruce in Sweden (Pape, 1999; Hannrup et al., 2002). However, in some sites (e.g. Glentress) no clear pattern was observed. Also when plots were made for individual trees, some did not show clear patterns, while some maintained high positive grain angles over prolonged periods of growth. This presented serious problems in obtaining an appropriate general model for grain angle.

Based on a comparative assessment of five models, Mavrou (2007) found that the following model was best for predicting grain angle of Sitka spruce:

$$\text{GA} = (a_1 + a_2 \log \text{RN}) \cdot \exp(-a_3 \cdot \text{RN})$$

where \(\text{GA}\) = grain angle (degrees); \(\text{RN}\) = ring number from the pith; \(a_1, a_2, a_3\) = coefficients to be determined.

Figure 1 Location of study sites in Northern Britain.
In the present study, two additional models were tested:

\[
GA = a_1 \cdot \exp(-a_2/RN) + a_3
\]

and

\[
GA = a_1 \cdot RN^{a_2} \cdot \exp(-a_3 RN)
\]

Model (2) is a modified Schumacher model (Schumacher, 1939) and Model (3) is the generalized exponential or “Hugershoff” function used in dendrochronology for growth-trend estimation (Warren, 1980; Schweingruber, 1987). The models were adjusted to grain angle data using the non-linear regression procedure in SAS (SAS Institute Inc., 2004) and were compared using the RMSE. Residual plots were also made to see whether there were any noticeable trends of residuals with ring number. Further fitting of the models was undertaken by including tree and site variables in the models and testing whether there were any significant improvements. Variables examined included: spacing, altitude, DAMS scores, age, relative disc height (RH = disc height/tree height) and disc diameter (Disc_Diam). Based on the correlations obtained, the following modified versions of Models (1), (2) and (3), henceforth referred to as (1'), (2') and (3'), were refitted to the data:

\[
GA = [(a_1 + a_2 \cdot \text{Spacing}) + a_3 \cdot \text{RH} + a_4 \cdot \text{DAMS}] \cdot (\beta_1 + \beta_2 \cdot \text{Age}) \cdot \log RN \cdot \exp[-(\delta \cdot RN) + \varepsilon_i]
\]

(1')

\[
GA = [a_1 + a_2 \cdot \text{RH} + a_3 \cdot \text{DAMS} + a_4 \cdot \text{Disc_Diam} + a_5 \cdot \text{Spacing}] \cdot \exp(-\beta/RN) + \delta + \varepsilon_i
\]

RN

(2')

\[
GA = [a_1 + a_2 \cdot \text{Spacing} + a_3 \cdot \text{RH} + a_4 \cdot \text{Disc_Diam}]RN^\delta \cdot \exp[-(\delta \cdot \text{DAMS})RN + \varepsilon_i]
\]

(3')

The best two models were further refitted using non-linear mixed-effects modelling techniques to see if this could lead to further improvements. Mixed modelling was used because the tree ring data collected within each disc are not independent and are probably correlated, thus invalidating the assumptions of independence and identically distributed errors (\(e \sim iid(0,\sigma^2)\)) in ordinary least squares (OLS) regression analysis. Mixed-effects modelling assumes that some or all the parameter estimates have fixed and random components, and incorporates these effects in the regression analysis. We used the per cent NLINMIX macro in SAS (SAS Institute Inc., 2004; Littell et al., 2006; Wolfinger, 2007) to fit the mixed-effects models. Akaike’s information criterion (AIC),

Table 1 Stand characteristics and summary statistics for grain angle

<table>
<thead>
<tr>
<th>Site</th>
<th>Stand characteristics</th>
<th>Absolute grain angle; summary statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Altitude (m)</td>
<td>Age at felling (years)</td>
</tr>
<tr>
<td>Kershope (1)</td>
<td>246</td>
<td>32</td>
</tr>
<tr>
<td>Kershope (2)</td>
<td>220</td>
<td>13</td>
</tr>
<tr>
<td>Glengarry</td>
<td>152</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td>152</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td>152</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td>152</td>
<td>65</td>
</tr>
<tr>
<td>Glentress</td>
<td>410</td>
<td>30</td>
</tr>
<tr>
<td>Lochaline (1)</td>
<td>150</td>
<td>48</td>
</tr>
<tr>
<td>Lochaline (2)</td>
<td>152</td>
<td>48</td>
</tr>
<tr>
<td>Benmore (1)</td>
<td>310</td>
<td>42</td>
</tr>
<tr>
<td>Benmore (2)</td>
<td>310</td>
<td>42</td>
</tr>
</tbody>
</table>

¹DAMS = detailed aspect method scoring (Quine and White, 1994); YC = yield class NA = data not available; N(·) = number of trees with total number of ring measurements (in brackets).

Figure 2 Split disc and the apparatus used for measuring grain angle.
Schwarz's Bayesian information criterion (BIC), and the $-2 \log$-likelihood were used as goodness-of-fit statistics to compare the models.

This final fitting resulted in the selection of Model (3′) as the best model for describing grain angle in Sitka spruce (see Table 6 in the Results section for details). The final model form is:

$$GA_{ij} = [(\alpha_1 + u_{1i}) + \alpha_2 \text{Spacing} + \alpha_3 \text{RH} + \alpha_4 \text{Disc Diam}] \cdot RN^{\beta(u_{2i})} \cdot \exp\left[(-[(\delta + u_{3i}) \cdot \text{DAMS} \cdot RN] + (\lambda + u_{4i})RN + e_{ij})\right] \tag{4}$$

where the $\alpha_{i}$s, $\beta$, $\delta$ and $\lambda$ are fixed-effects parameters and $u_i$s are the random-effects parameters and $e_{ij}$ is the random error. The UN (UNstructured) covariance structure option (cf. Littell et al., 2000, 2006) was used to obtain the variance-covariance estimates for the random-effects parameters.

### Results

#### Variation of grain angle with spacing

The results for Glengarry Forest (Table 2 and Figure 3) indicate that the 1.4 m spacing has the highest initial mean grain angles (for $RN \leq 5$) followed by the 0.9 and 2.4 m spacings, while the 1.8 m spacing has the lowest. However, the differences were not significant ($P \leq 0.05$). Initial grain angles in the 2.4 m spacing are higher than those for the 1.8 m spacing, but rapidly decreased, becoming the lowest. Overall, the 1.4 m spacing has a significantly higher mean grain angle (2.55°), followed by the 1.8 (2.19°) and 0.9 m spacings (2.17°); while the 2.4 m spacing had the lowest mean value (0.71°). The mean trends for all spacing reach a maximum around ring number 10, and thereafter, begin to decline towards the tree bark (Figure 3).

Table 3 and Figure 4 present the results of analysis and mean trends in grain angles for Kershope (1) Forest. The trees in the 3.4 m spacing had the highest mean grain angle followed by trees in the 4.9 m spacing, while trees in the 1.8 and 2.4 m spacings had lower values. The results for all rings taken together showed the same trends. Again, grain angles seemed to peak around ring number 10, followed by decreasing trends in mean angles for all spacings.

#### Variation of grain angle between sites

In order to assess the site effect on grain angle, we selected the 2 m spacing which was common to most sites. For Glengarry and Kershope (1), we used the 1.8 m spacing as being closest to the 2 m spacing. Table 4 indicates highly significant differences ($P < 0.0001$) in mean grain angles between sites, while Figure 5 shows mean trends. For the first five rings ($RN \leq 5$), trees at Kershope (1 and 2) had the highest mean grain angles (2.54° and 2.39°, respectively), followed by trees at Glentress (1.88°) and...
between ring numbers 5 and 10 (5 < RN ≤ 10), with Benmore and Lochaline showing higher values, and Glengarry and Glentress showing the lowest values. For ring numbers up to 20, the trees at Benmore (2) and Kershope (1) had the highest mean angles, while Glentress had low overall values. A further analysis of variance (ANOVA) irrespective of spacing indicated that the trees at Kershope had the highest mean grain angle followed by trees at Benmore (2), and trees at Glentress had the lowest angles.

**Between- and within-tree variation of grain angle**

Analysis of variance was also undertaken to determine whether there were any between- and within-tree variation in grain angle. The factors tested were spacing, tree, disc position within the tree and ring number. Table 5 gives the percentage variation due to each factor, based on the mixed model analysis for each forest. Between-tree variation ranged from 3.6 per cent (Kershope (2)) to 33.3 per cent (Lochaline (2)), while variation due to the disc position within the tree ranged from 5.7 per cent (Lochaline (1)) to 47.8 per cent (Glentress). There were also between-ring variations within discs ranging from 0 per cent (Glentress and Lochaline(1)) to 38.5 per cent for Benmore (2). Residual (unexplained) variation ranged from 25.7 per cent (Kershope (1)) to 64.8 per cent (Lochaline(1)).

**Variation of grain angle with height**

Plots of mean grain angles with the disc height class (plots not included) did not show any particular trend in most cases, except for Glentress and Kershope (1) (1.8 and 4.9 m spacings) where decreasing trends in grain angle with height were observed, and Glengarry (1.4 and 2.4 m spacing) which gave an increasing trend in grain angle with disc height. ANOVA for disc height indicated no significant differences for Lochaline (1 and 2), Benmore (1 and 2) and Kershope (1) (2.4 and 3.4 m spacing); while significant differences were obtained for Glentress, Glengarry and Kershope (1) (1.8 and 4.9 m spacings).

Table 3 ANOVA for grain angle for spacing by ring number in Kershope

<table>
<thead>
<tr>
<th>Ring number class</th>
<th>Spacing</th>
<th>1.8 m × 1.8 m</th>
<th>2.4 m × 2.4 m</th>
<th>3.4 m × 3.4 m</th>
<th>4.9 m × 4.9 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>RN ≤ 5</td>
<td></td>
<td>2.52</td>
<td>2.36</td>
<td>3.19</td>
<td>2.74</td>
</tr>
<tr>
<td>5 &lt; RN ≤ 10</td>
<td></td>
<td>2.94b</td>
<td>2.88b</td>
<td>4.68a</td>
<td>3.73ab</td>
</tr>
<tr>
<td>10 &lt; RN ≤ 15</td>
<td></td>
<td>2.82b</td>
<td>2.40c</td>
<td>4.31a</td>
<td>3.58ab</td>
</tr>
<tr>
<td>15 &lt; RN ≤ 20</td>
<td></td>
<td>2.86</td>
<td>2.33</td>
<td>3.86</td>
<td>3.89</td>
</tr>
<tr>
<td>20 &lt; RN ≤ 25</td>
<td></td>
<td>2.25ab</td>
<td>2.13</td>
<td>3.79</td>
<td>2.88ab</td>
</tr>
<tr>
<td>Global</td>
<td></td>
<td>2.55b</td>
<td>2.46b</td>
<td>3.71a</td>
<td>3.20ab</td>
</tr>
</tbody>
</table>

Letters are presented only for rows where there are significant differences between means (P ≤ 0.05).

Figure 4 Variation of the mean grain angle with the ring number and spacing for Kershope forest.
Model development

Results for the non-linear regression of Models (1), (2) and (3) gave very close values of RMSEs of 1.461, 1.464 and 1.465, respectively. Furthermore the overlaid plots for model predictions on the original data, as well as the overlaid plots of residuals did not show any appreciable differences in trends for the three models. For all models, however, the RMSE values, as well as the magnitude of the residuals indicated a large amount of unexplained variation in grain angle, an indication that the use of ring number alone as an explanatory variable in the model is not sufficient to account for most of the variation in grain angle. In addition the ANOVA in the previous section revealed a lot of within- and between-tree variations and most of this variation remains unexplained. Refitting of the models by including tree and site variables (see methodology) resulted in a slight reduction in RMSE values from 1.46 for Model (1) to 1.40 for Model (1’) ($R^2 = 0.15$); from 1.46 for Model (2) to 1.39 for Model (2’) ($R^2 = 0.16$) and from 1.47 for Model (3) to 1.40 for model (3’) ($R^2 = 0.16$). Further analysis involved refitting Models (2’) and (3’) using non-linear mixed-effects modelling techniques to see whether this led to further improvements.

Table 4  ANOVA for grain angle of Sitka spruce in various forests

<table>
<thead>
<tr>
<th>Ring number class</th>
<th>Kershope 1</th>
<th>Kershope 2</th>
<th>Glentress</th>
<th>Glengarry</th>
<th>Lochaline 1</th>
<th>Lochaline 2</th>
<th>Benmore 1</th>
<th>Benmore 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>RN ≤ 5</td>
<td>2.54a</td>
<td>2.39a</td>
<td>1.88b</td>
<td>1.62bc</td>
<td>1.26d</td>
<td>1.25d</td>
<td>1.19d</td>
<td>0.99d</td>
</tr>
<tr>
<td>5 &lt; RN ≤ 10</td>
<td>2.70b</td>
<td>3.29a</td>
<td>1.72c</td>
<td>2.29bc</td>
<td>3.21a</td>
<td>2.81b</td>
<td>3.03ab</td>
<td>3.16a</td>
</tr>
<tr>
<td>10 &lt; RN ≤ 15</td>
<td>2.88a</td>
<td>3.56a</td>
<td>1.79b</td>
<td>2.65ab</td>
<td>2.91a</td>
<td>2.57b</td>
<td>2.88a</td>
<td>3.23a</td>
</tr>
<tr>
<td>15 &lt; RN ≤ 20</td>
<td>2.92a</td>
<td>1.59bc</td>
<td>2.59b</td>
<td>2.43b</td>
<td>2.13bc</td>
<td>2.59b</td>
<td>2.59b</td>
<td>3.06a</td>
</tr>
<tr>
<td>20 &lt; RN ≤ 25</td>
<td>2.25b</td>
<td>0.88c</td>
<td>2.59b</td>
<td>2.01b</td>
<td>1.67bc</td>
<td>2.18b</td>
<td>2.18b</td>
<td>3.31a</td>
</tr>
<tr>
<td>25 &lt; RN ≤ 30</td>
<td>1.25b</td>
<td>1.83b</td>
<td>1.83b</td>
<td>1.83b</td>
<td>1.71b</td>
<td>2.22b</td>
<td>2.22b</td>
<td>2.92a</td>
</tr>
<tr>
<td>30 &lt; RN ≤ 35</td>
<td></td>
<td>1.83b</td>
<td>1.64b</td>
<td>1.90ab</td>
<td></td>
<td>1.72 b</td>
<td>1.72 b</td>
<td>2.46a</td>
</tr>
</tbody>
</table>

Different letters on the same row indicate significant differences between means ($P \leq 0.05$).

Figure 5  Mean spiral grain angle variation from the pith to bark (spacing ~2 m).
model grain angle in Sitka spruce. Table 6 shows parameter estimates and fit statistics for Model (4) together with a form without DAMS. In fitting the model, the unstructured covariance structure was assumed. Model fitting with other error structures (e.g. first-order autoregressive (AR1), TOEP and SPOW), gave higher values of AIC, BIC and RMSE. The improvement in terms of reduced RMSE values ranges from 25.5 to 26.1 per cent. The residual plots (not included) did not portray any apparent trend with predicted values, and we therefore concluded that there was no violation of the homogeneity of variance assumption. Graphical displays of the trends in grain angle with ring number as well as predicted versus observed grain angles (not included) also show an improvement in model predictions using the mixed-effects modelling approach.

**Discussion**

**Variation of grain angle with spacing**

The results for Glengarry Forest show an overall higher mean grain angle for the 1.4 m spacing followed by the 1.8 and 0.9 m spacings, while the 2.4 m spacing had the lowest mean grain angle. There are no clear trends between the grain angle and spacing. From plot descriptions (Tracey, 1988), the 0.9 and 1.4 m spacings are located at the base of the slope and on fertile soil and have a more sheltered exposure, while the 1.8 and 2.4 m spacings are located on the upper part of the slope, are more exposed and on less fertile soils. Harris (1989, pp. 90–93) cites instances where fast growth resulted in increased grain angle; others where the slow growth rate also led to increased grain angle, and some where grain angle was independent of the growth rate. Hence, the fertility gradient may not provide enough explanation. The 0.9 and 1.4 m spacings were also thinned, while the 1.8 and 2.4 m spacings were unthinned. Thinning will have modified the spacings in the 0.9 and 1.4 m spacings, and may have led to higher grain angles than in the 2.4 m spacing. Although the 2.4 m spacing had coarse lower branches (Tracey, 1988), which could obstruct or reduce the effect of strong winds, this might not be sufficient to explain why it has lower grain angle than the others. It is also worth noting that the Glengarry experiment is well sheltered (very low DAMS score of 11) and so the effect of exposure might be minimal. Also, because the slope was facing north and the prevailing winds are from the south-west, all the spacings would have been equally sheltered and the effect of early thinning may be more important.

Contrary to the results obtained from Glengarry, those from Kershope show that trees at wider spacings (3.4 and 4.9 m) had higher grain angles than closer spacings (1.8 and 2.4 m) (Table 3 and Figure 4). The Kershope (1) site in contrast to the Glengarry site faces the prevailing wind and the DAMS is higher (15) and so spacing effects may be more prominent here. Therefore, even though there may be no clear or discernible trend between the spacing and grain angle (e.g. in Glengarry), there are indications that re-spacing from 1.8 to 3.4 and 4.9 m in Kershope (1) (see Rollinson, 1988) might have resulted in noticeable increases in grain angles. Becker and Wabst (1993) reported that variation in the grain angle of trees was higher in a thinned stand than in an unthinned stand. Bergstedt and Jørgensen (1997) observed that heavy thinning contributed to maintaining a high grain angle or increased it, while Pope (1999) obtained similar results for Norway spruce after a single heavy thinning (removal of 60 per cent of the basal area of a stand). In the present study, we found that re-spacing (thinning) from 1.8 to 3.4 m and 4.9 m in Kershope (1) resulted in a marked increase in spiral grain. However, in stands where the thinning intensity was light, for example, from 1.8 to 2.4 m spacing in Kershope (1), there was no marked effect on the grain angle of Sitka spruce. This is in agreement with Pope (1999) who also observed that light thinning did not have any impact on grain angle.

**Variation of grain angle between sites**

The results indicate that Kershope and Benmore (2) forests had, on average, higher grain angles than the other sites, and that Glen- tess forests had the lowest values. While the higher grain angle values in Benmore (2) and Kershope could be due to their altitudes (310 m and 220–246 m, respectively) or exposure compared with Lochaline (80–150 m), and Glengarry (152 m); it is not clear why Glen- tess at 410 m, and with a high DAMS score, has the lowest grain angle. However, the location of Glen- tress with an eastern aspect could be a possible explanation based on Smythies (1915) who observed that Chir fir (Pinus roxburghii Sarg.) growing on northern and eastern aspects in India had lower grain angles than trees on the western and southern aspects. However, this still cannot be conclusive given that Canning (1915), Champion (1924) and Rault and Marsh (1952) found no relationship between the aspect and grain angle (see Harris, 1989: page 80). It is also possible that stands at higher altitudes have low grain angles, as was the case for Caribbean pine (Pinus caribaea var. caribaea Morlet) trees grown in Fiji which had low grain angles (<3.4°) at altitudes <300 m compared with higher grain angles (between 4.7° and 6.6°) at low altitudes (Cown et al., 1983: in Harris, 1989, page 83). However, apart from these exceptions, it is generally held that trees growing at high altitudes or more exposed sites tend to develop extreme values of grain angle (Harris, 1989). The general tendency observed is that planting on exposed sites (e.g. Lochaline) at 2 m spacing may result in mean grain

<table>
<thead>
<tr>
<th>Forest</th>
<th>Variation in grain angle (per cent)</th>
<th>Total residual variation (per cent)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Between trees</td>
<td>Due to disc within tree</td>
</tr>
<tr>
<td>Glengarry</td>
<td>18.4</td>
<td>37.1</td>
</tr>
<tr>
<td>Kershope (1)</td>
<td>8.2</td>
<td>40.4</td>
</tr>
<tr>
<td>Kershope (2)</td>
<td>3.6</td>
<td>46.9</td>
</tr>
<tr>
<td>Glen- tress</td>
<td>15.2</td>
<td>47.8</td>
</tr>
<tr>
<td>Lochaline (1)</td>
<td>29.5</td>
<td>5.7</td>
</tr>
<tr>
<td>Lochaline (2)</td>
<td>33.3</td>
<td>11.0</td>
</tr>
<tr>
<td>Benmore (1)</td>
<td>28.3</td>
<td>10.9</td>
</tr>
<tr>
<td>Benmore (2)</td>
<td>21.3</td>
<td>6.2</td>
</tr>
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</table>
angles as high as 4–5° (similar to the 3.4 and 4.9 m re-spacings on a moderately exposed site at Kershope (1)). However, this observation needs to be confirmed with further studies, given the wealth of contradictory literature on this subject. We also have to acknowledge the fact that we do not know how sheltered the trees were by other parts of the forest; and we do not have long-term wind measurements at these sites to say exactly how exposed they were (DAMS on its own may not be a good enough indication of overall exposure). Also, it would appear that the environmental factors considered are not particularly strong in their control of grain angle.

Variation of grain angle with height

No general trends were obtained for the variation in grain angle with height. While decreasing trends were observed in trees at some forests, increasing trends were observed in others. Similar conflicting evidence was reported by Northcott (1957). Acuna and Murphy (2006) also cite cases where the grain angle is shown to decrease with height (for red alder: Alnus rubra Bong.), to be unaffected by height (for western hemlock: Tsuga heterophylla) and to increase with height (for ponderosa pine: Pinus ponderosa P. and C. Lawson). It is not clear why the grain angle should vary in such an unpredictable manner with height. Pedini (1990) quoted in Tranquart (1995) reported a decrease in grain angle with increasing height in Sitka spruce growing in Denmark.

Model development

The non-linear least square (NLS) models, even after including tree and stand variables, explained barely 16 per cent of variation in grain angle. Acuna and Murphy (2006) found no statistically significant relationship (in Douglas fir: Pseudotsuga menziesii (Mirb.) Franco) between the grain angle and tree height, aspect, elevation and over-bark diameter and their model developed using these variables only explained 3 per cent of the variation in grain angle. This was the only grain angle model we found in the literature to compare our findings with. The low level of variation accounted for by our model implies that the ring number alone accounts for little variation in grain angle. The ring distance from the pith could be another possible variable to use in the model; however, this was not measured in this study. Harris (1989, p. 56) pointed out that grain angles tend to show

### Table 6 Parameter estimates and fit statistics for non-linear mixed models (Model 4) for Sitka spruce grain angle

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter estimate</th>
<th>Standard error</th>
<th>Variance</th>
<th>VC*</th>
<th>RMSE</th>
<th>−2 LLK</th>
<th>AIC</th>
<th>BIC</th>
<th>R²</th>
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<tr>
<td>Model (4)</td>
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</tr>
<tr>
<td>α₀</td>
<td>2.04570</td>
<td>0.22820</td>
<td>1.0623</td>
<td>M (see below)</td>
<td>1.0307</td>
<td>9489.0</td>
<td>9525.0</td>
<td>9582.0</td>
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<td>α₁</td>
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<td></td>
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<td>Model (4) excluding DAMS</td>
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<tr>
<td>α₀</td>
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<td>0.22840</td>
<td>1.0438</td>
<td>M1 (see below)</td>
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<td>9485.4</td>
<td>9521.4</td>
<td>9521.7</td>
<td>0.5469</td>
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<td>α₁</td>
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<td>0.07615</td>
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<td>α₂</td>
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<td>0.16850</td>
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<td>λ</td>
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</table>

VC* = variance–covariance matrix: diagonals represent variances, while the off-diagonals represent covariances between u₁, u₂, u₃ and u₄.

\[
M = \begin{pmatrix}
  u_1 & u_2 & u_3 & u_4 \\
  u_2 & u_{12} & u_{13} & u_{14} \\
  u_3 & u_{31} & u_{32} & u_{34} \\
  u_4 & u_{41} & u_{42} & u_{43}
\end{pmatrix}
\]

\[
M_1 = \begin{pmatrix}
  u_1 & u_2 & u_3 & u_4 \\
  u_2 & u_{22} & u_{23} & u_{24} \\
  u_3 & u_{32} & u_{33} & u_{34} \\
  u_4 & u_{42} & u_{43} & u_{44}
\end{pmatrix}
\]
Practical implications

The mean grain angles measured were generally <5° and according to Cowan’s rule of thumb (see MacIora, 2002), this would not lead to serious downgrade in sawn timber. However, this conclusion was based on the experiments with Radiata pine. For Sitka spruce, we do not have similar measurements; although a detailed study on Norway spruce (see Lönnroth and Klijger, 2000) shows that grain angles >3° can cause serious problems in sawn timber.

Silvicultural treatments including initial spacing and thinning are undertaken in order to improve tree growth and timber yields. By doing so, various wood properties like grain angle are affected. Because the grain angle has a negative impact on timber quality, it is important to know how silvicultural practices may be modified in order to reduce the magnitude of grain angle in trees. Given that most impact and variation of grain angle occurs during the juvenile stage (most often within the first 10 years) of stand development (also see Pape, 1999; MacIora, 2002), it is important to know what steps can be taken to minimize grain angle at this stage. Since heavy thinning or re-spacing appears to increase the grain angle considerably, it may be preferable to avoid such practices; to plant at close spacings, and delay thinning or thin lightly until the most valuable lower part of the stem has passed out of the period with the highest grain angles (typically 30 years). This could help to reduce the maximum grain angle which usually occurs within the first 10–15 growth rings. Although later thinnings might increase the grain angle, it seems most likely that the main impact would be to reduce the rate of change from left-handed spiral grain towards a right-handed grain angle (Pape, 1999).

Because most of the variation in spiral grain is hereditary, another way to minimize grain angle could be to use genetic or clonal selection. Hansen and Roulund (1997, 1998b) observed that Sitka spruce clones have a high degree of genetic heritability, with individual broad-sense heritabilities of ~0.5 and narrow-sense heritabilities of 0.63 and 0.78 for two clones of Sitka spruce in Denmark. Cahanal (1985, 1987) states that grain angle in Sitka spruce in Britain is under a high level of genetic control. Tranquart (1995) also reported a strong genetic component in the grain angle of Sitka spruce in Britain, which means that there is good potential for improvement through breeding. Grain angle has been included as a selection criteria in the breeding programme of Sitka spruce in Denmark (Roulund, 1990; Hansen and Roulund, 1998a; Hansen, 1999) and in the initial selection of Sitka spruce plus trees in the UK (Lee, 1999). Given the strong genetic effects, it is therefore obvious that any predictive model for spiral grain based only on tree and environmental variables may not explain much of the intrinsic variability in grain angle.

Conclusion

The aim of this study was to assess the impact of spacing and site exposure on spiral grain, and to develop a spiral grain angle model for British grown Sitka spruce. The results indicate that planting on sites exposed to prevailing winds, planting at wider spacing or undertaking heavy thinning can significantly increase grain angle. The impact of grain angle is greater at the juvenile stage of wood formation (first 10–15 rings) than at the mature stage. Between-tree variation ranged from 3.6 per cent (Kershope (1)) to 64.8 per cent (Lochaline (2)), while variation due to the disc position within the tree ranged from 5.7 per cent (Lochaline (1)) to 47.8 per cent (Glenfesh). There were also between-ring variations within discs ranging from 0 per cent (Glenfesh and Lochaline(1)) to 38.5 per cent for Benmore (2). Residual (unexplained) variation ranged from 25.7 per cent (Kershope (1)) to 64.8 per cent (Lochaline(1)). Sites with higher windiness scores had higher initial grain angles which quickly reached a maximum and then declined rapidly as the wood becomes mature, while those with lower windiness scores had low initial grain angles which increased more slowly and remained higher into the mature wood. A silvicultural implication of these findings would be to plant at closer initial spacings (<2 m) and delay thinning or only thin lightly until trees are ~30 years. It would also be best to avoid planting on highly exposed sites (>DAMS of 15) if structural timber with low tendency to twist is required. However, because of the dominating genetic control of grain angle it would also be advisable to undertake proper clonal selection, given that grain angle appears to be highly heritable. A NLS model developed to predict grain angle explained only 16 per cent of total variation in grain angle, despite the inclusion of several covariates into the model. The low variation explained by the model confirms the strong genetic control of grain angle, and that environmental factors only explain a small amount of its variation. Even though the use of a mixed-effect model improved the RMSE by 26 per cent, and the $R^2$ value rose to 53 per cent, the benefits in the use of mixed models can only be derived if the model user has additional sample data to calibrate the model.
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Conflict of interest statement
None declared.

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Quin, C.P. and White, I.M.S. 1994 Using the relationship between rate of tatter and topographic variables to predict site windiness in Upland Britain. Forestry 67, 245–256.


