Introduction

Windthrow of forest and woodland trees is common in Britain, where the effects of north Atlantic depressions are felt on average for more than 1 day each week. The tracks of these depressions most commonly pass near to the north and west, with the most extreme wind speeds experienced near the west coasts of Scotland, England and Wales. The most catastrophic damage to forested areas is expected to be caused by wind gust speeds greater than 40 m s$^{-1}$ (Quine, 1989), which relates to a mean hourly wind speed of $\sim 25$ m s$^{-1}$. Storms that produce such wind speeds are experienced on average once in 4 years in the north-west of Scotland (Benbecula) and once in $>$200 years in the south-east of England (Heathrow) (Troen and Petersen, 1989). This large difference in wind climate makes windthrow a frequent occurrence in the north and west of Scotland, but much rarer in the south and east of England. However, when damaging wind speeds are experienced in the most sheltered parts of Britain, the damage is sometimes greater than that caused by similar wind speeds in more exposed areas. For example, a storm in 1987, that produced its highest wind speeds (maximum gust recorded 51 m s$^{-1}$) across south-east England, damaged $\sim 3.9$ million m$^3$ of timber, representing 13–24 per cent of the standing volume of the affected area. In contrast, a
storm that produced similar wind speeds (maximum gust recorded 48 ms\(^{-1}\)) but tracked further north and produced its highest wind speeds across Wales and Western England in 1990 damaged ~1.3 million m\(^3\) of timber, representing <3 per cent of the standing volume in the affected areas (Quine, 1995). Such differences may be attributed to the attributes of the storms, the forest structure in the affected areas and from diseased or vulnerable trees standing longer in normally sheltered areas and then falling in the first severe storm. However, there is a generally held, but untested, assumption that such differences in wind damage may also reflect a stronger anchorage of trees that have grown in more exposed parts of the country (Quine et al., 1995).

‘Adaptive’ or ‘acclimative’ growth of trees in response to wind-induced mechanical stress has been reported for many years. Knight (1803) first reported that trees allowed to flex back and forth in one plane will increase their allocation of mass to the stem base and roots and that the stem base becomes elliptical in cross-sectional shape with the greatest diameter in the direction of flexing. Metzger (1893) formulated a hypothesis that the cambium in the tree stem produces new wood in a way that equalizes the mechanical stress on the outer surface—the ‘uniform stress hypothesis’. Although this hypothesis still generates debate (Morgan and Cannell, 1994), a number of authors (reviewed by Telewski, 1995) have described increased cambial growth as a direct response to mechanical stress. Plant growth responses to wind movement and other mechanical stress, termed ‘thigmomorphogenesis’ (Jaffe, 1973), are known to include changes in wood properties, reduced height growth, greater stem taper and development of smaller branches. The mechanisms of plant mechanoperception and response are reviewed and discussed by Telewski (2006).

There is an increasing understanding of the mechanisms of below-ground growth in response to mechanical stress. Roots move in the soil as a tree sways in the wind; for example, Hintikka (1972) described Norway spruce (Picea abies L.) roots in a clay soil lifting the surface by 13.6 mm for 3° of stem displacement and by 3.1 mm for 1° of stem displacement. Rizzo and Harrington (1988) found that movement of surface lateral roots was significantly and positively correlated with wind speed and with soil rootable depth.

Conifer species have been observed to allocate a larger proportion of total biomass below ground when they experience increased wind loading (Fritzschke, 1933; Nielsen and Mackenthun, 1991). Sitka spruce (Picea sitchensis (Bong.) Carr.) growing on exposed sites with shallow soils have been reported to allocate a larger proportion of this increased root biomass to the leeward side of the root system, relative to the prevailing wind direction (Nicoll et al., 1995; Nicoll and Ray, 1996). Ruth and Harris (1979) also described the largest supporting buttresses as being on the lee side of western hemlock (Tsuga heterophylla (Raf.) Sarg.) and Sitka spruce trees. Reduction of root secondary thickening has been induced in a number of experiments by preventing stem sway (Jacobs, 1939, 1954; Fayle, 1968; Wilson, 1975; Fayle, 1976). Nicoll and Gardiner (2006) exposed some Sitka spruce trees to increased light and wind movement by stand thinning and others to increased light but reduced wind movement by thinning and guying. Secondary thickening of the thinned trees was increased, compared with the thinned and guyed trees, in structural roots and parts of the stem near the base that would be expected to experience the greatest increase in mechanical stress.

Despite the considerable evidence of acclimative growth in response to mechanical stress, there is little known about the effects of this growth response on the strength or anchorage of trees. Stokes et al. (1997) found that 3-year-old Sitka spruce clonal cuttings that had been grown in a low-nutrient regime, and had been mechanically flexed for a growing season, required 2–47 per cent greater force to bend stems by 2.6° (depending on the clone) compared with unflexed trees, although there was no difference when trees were grown in a high-nutrient regime. Cucchi et al. (2004) found that 15- to 50-year-old Maritime pine (Pinus pinaster Ait.) trees on the edge of a forest stand had 20 per cent stronger anchorage than sheltered trees of equivalent size inside the stand; however, it is not clear to what extent this difference reflected acclimation to wind stress and to what extent it reflected the larger photosynthetic area of edge trees, providing proportionally more photosynthate for below-ground growth.

The ForestGALES model (Gardiner et al., 2004) developed for the management of forest stands for wind risk in Great Britain uses the
The overhanging weight of the crown, respectively.

Data were taken from the database of British tree-pulling experiments described by Nicoll et al. (2006). Trees in the database were aged between 15 and 56 years and were from 12 conifer species overturned in experiments conducted across Britain between 1960 and 2000. Only data from the most commonly overturned species, Sitka spruce, were used in this study and were available from 25 sites (Table 1).

To overturn a tree, a force was applied, using a winch, to the tree stem at a known height (Fraser and Gardiner, 1967; Nicoll et al., 2006), and the maximum load and the angle of stem inclination were recorded simultaneously. Once the tree had been pulled over, tree dimensions were recorded, including, height, diameter at breast height (1.3 m), crown spread and depth, stem mass, branch mass, total root depth and root–soil plate depth. The applied load was transformed into a critical turning moment at the tree base, allowing data from different tree-pulling experiments to be analysed together and related to tree allometric data. Selected trees were from the interiors of forest stands and no edge trees were included.

Critical turning moments \( (M_{\text{crit}}) \) for all trees were recalculated at the stem base, as follows:

\[
M_{\text{crit}} = M_{\text{applied}} + M_{\text{mass}},
\]

where \( M_{\text{applied}} \) (Nm) is the maximum turning moment applied by the winch and \( M_{\text{mass}} \) (Nm) is the turning moment resulting from the overhanging weight of the tree at the point when the maximum load was reached. \( M_{\text{mass}} \) and \( M_{\text{applied}} \) were calculated as follows:

\[
M_{\text{mass}} = m \times x,
\]

\[
M_{\text{applied}} = F \cos \theta_1 \times l,
\]

where \( m \) is the mass of the tree, \( x \) is the horizontal displacement of the tree at maximum load, \( F \) is the force applied by the winch, \( \theta_1 \) is the winch cable angle relative to horizontal and \( l \) is the height of the centre of mass at time of maximum load.

### Methods

#### Tree pulling data

The following equation to give the critical wind speed at the canopy top for overturning (Gardiner et al., 2000):

\[
ub_{\text{over}} = \frac{1}{kd} \left[ \frac{C_{\text{reg}} SW}{\rho G d} \right]^{1/2} \left[ \frac{1}{f_{\text{edge}} f_{\text{CW}}} \right]^{1/2} \ln \left( \frac{h - d}{z_0} \right),
\]

where \( k = 0.4 \) is Von Karman’s constant, \( D \) (m) is the average spacing between trees, \( \rho \) (kg m\(^{-3}\)) is the air density, \( G \) is an empirically derived gust factor, \( h \) (m) is mean tree height, \( d \) (m) is the zero plane displacement, \( z_0 \) (m) is the aerodynamic roughness, \( C_{\text{reg}} \), the anchorage coefficient, is a regression constant from turning moment against stem weight of overturned trees and \( SW \) (kg) is the stem weight of the tree. The factors \( f_{\text{edge}} \) and \( f_{\text{CW}} \) account for the position of the tree relative to the edge and the additional load due to the overhanging weight of the crown, respectively. The \( C_{\text{reg}} \) constants are derived from analysis of data from tree-pulling experiments conducted on almost 2000 trees of a range of conifer species and on a variety of soils and site conditions (Nicoll et al., 2006). The values of \( C_{\text{reg}} \) currently used within the ForestGALES model are applied uniformly for each soil group, regardless of the location of the forest and take no account of any possible change in anchorage as a result of acclimative growth in response to the wind climate. However, the large differences in root development that have been shown to result from acclimation to wind exposure (Nicoll and Ray, 1996), and the biomechanical implications of these differences (Nicoll, 2000), indicate that anchorage strength would be expected to improve with increasing exposure. Therefore, increases in wind exposure experienced by trees as they grow in different locations should relate to increases in the anchorage coefficient \( C_{\text{reg}} \).

In this study, we test the hypothesis that acclimative growth in response to wind improves the anchorage of trees in wind-exposed locations compared with equivalent-sized trees in sheltered locations. We then attempt to quantify the effect to allow its incorporation in forest wind risk models. The investigation is based on a reanalysis of existing tree anchorage data (Nicoll et al., 2006), including data on the wind climate of each experimental site as an additional factor.
For the purposes of this calculation, the centre of mass of the tree was placed at 0.5 tree height, and the stem was assumed to be a straight beam rotating around its base (Nicoll et al., 2006).

Soil data

Soil type was recorded at each experimental site using the British Forestry Commission soil classification system (Kennedy, 2002). Soils with similar physical properties were grouped together into four groups, i.e: A. free-draining mineral soils, B. gleyed mineral soils, C. peaty mineral soils and D. deep peat soils. As root depth is known to have a large influence on tree anchorage (Blackwell et al., 1990), each soil group was split into ranges of potential or actual rooting depths: 1. <40 cm, 2. 40–80 cm and 3. >80 cm.

Wind exposure score

The wind exposure of trees at each experimental site was assessed using the Detailed Aspect Method of Scoring (DAMS) system (Quine and White, 1993), which is a function of elevation, topographic exposure, aspect, funnelling effects and wind zone of the country. This score was derived using data from an analysis of the rates that standard cotton flags tattered (Lines, 1963) when exposed for 3-year periods in 1173 locations distributed across Britain (Quine and White, 1994). The rate of tatter is well correlated with average wind speed, and data from the tatter flag network provide the best estimates of windiness for Great Britain. To produce a DAMS score for a location, the wind zone score is combined with scores for elevation (linear 0–10 scale through zero, where score 10 = 500 m), Topex (the sum of eight principal compass point skyline angles)
and aspect (weighted to account for topographical funnelling as described by Quine and White (1993)). DAMS score, latitude and longitude for each tree-pulling experiment site used in this analysis are given in Table 1.

Statistical analysis

Data from trees that snapped during overturning, or for which visible root or stem rot was recorded, were excluded from the analysis. In a previous study, soil type and rooting depth were shown to influence the anchorage of Sitka spruce (Nicoll et al., 2006). A series of linear mixed models were fitted to compare the fixed effects of soil group, root depth and stem mass on critical turning moment. As data were collected from a number of forest sites, forests were modelled as random terms. Models were constrained such that the relationship between stem mass and turning moment passed through the origin, and trees were inversely weighted by their stem mass to account for the increasing variation in observed turning moment.

In this study, a new candidate explanatory variable, forest DAMS class, was added to the original data. A series of linear mixed models were fitted using the method of restricted maximum likelihood and any significant improvements to the previous model were identified. Soil group, root depth, stem mass, DAMS class and their interactions were considered to be fixed effects while forest sites nested within DAMS classes were modelled as random effects.

The inclusion of DAMS class within the linear mixed model created two potential problems. Firstly, it was considered desirable that, within the dataset of 25 forest sites (Table 1), there was replication of DAMS classes. Consequently, two forests with unique DAMS classes, Beddgelert (DAMS class 11) and Eredine (DAMS class 20), were excluded from the analysis. Secondly, it was important that DAMS class was defined as a factor with number of levels equal to the number of DAMS classes. Fitting DAMS class as a factor imposed the necessary property that the estimated random effects for forests within each DAMS class summed to zero. This was not the case if DAMS was defined as a continuous variable.

Possible linear and quadratic relationships between DAMS class and the stem mass/turning moment slope \( (C_{reg}) \) were analysed in the mixed model by fitting orthogonal polynomials to the DAMS factor class levels. Further interpretation of the relationship between DAMS class and \( C_{reg} \) was obtained by estimating Spearman rank correlation coefficients and by plotting the fixed effect model estimates of \( C_{reg} \) against their DAMS class. Results were obtained for each soil group/rooting depth combination.

Linear mixed models were fitted using the MIXED procedure of the SAS® software, version 9.1 (SAS Institute Inc., Cary, NC, USA). Orthogonal polynomials were estimated in SAS using the ORPOL function to account for the unequal distribution of DAMS class values.

Wind risk modelling

The effects of changes in \( C_{reg} \) on critical wind speed for overturning \( (u_{h,over}) \) and on the return time of these critical wind speeds in locations with different DAMS scores (DAMS 14, 16 and 18) were modelled for a ‘standard’ stand of trees using an adapted version of ForestGALES. ForestGALES provides a return period of the critical wind speed (Gardiner and Quine, 2000) based on Weibull \( \alpha \) and \( k \) for each DAMS class (Quine, 2000). \( C_{reg} \) values for shallow gleyed mineral soil (B1) from the original model that includes stem mass, soil group and rooting depth, but not DAMS, described by Nicoll et al. (2006), were run through ForestGALES and then replaced by values from the modelling exercise described here that includes DAMS as a fixed effect. The standard stand of trees was unthinned 55-year-old Sitka spruce planted at 1.7-m spacing on a Yield Class 16 site, i.e. showing an increment of 16 m\(^3\) ha\(^{-1}\) year\(^{-1}\).

Results

The effects of soil group and depth class on \( C_{reg} \) are described by Nicoll et al. (2006), and the current paper concentrates on how this is influenced by DAMS. In fitting the linear mixed models, stem mass was the most important variable in determining critical turning moment \( (M_{crit}) \) and
accounted for 63 per cent of the variance (Table 2). By adding soil group and depth class as fixed effects, 66.5 per cent of the variance was accounted for. Adding DAMS significantly improved the fit of the model \( (P<0.001) \), increasing the variance explained to 71.2 per cent (Table 2).

Correlations between DAMS class and the estimated \( C_{\text{reg}} \) coefficient showed positive correlation coefficients for all combinations of soil group and rooting depth (Table 3). This was highly significant, as the probability of all 12 correlation coefficients showing a positive relationship with DAMS class by chance, if there was no relationship, is \( P < 0.001 \). Significant individual correlations were found for gleyed mineral soil <40 cm depth and peaty mineral soils and deep peat soils >40 cm depth (Table 3). Similar significant probabilities were obtained by fitting orthogonal linear contrasts to the linear mixed model.

Plots of estimated anchorage coefficients \( (C_{\text{reg}}) \) against DAMS class show fitted linear relationships for all soil group and depth class combinations (Figure 1). These linear relationships were used to provide estimates of the effect of DAMS on \( C_{\text{reg}} \) for use in wind risk models (Figure 2).

Running ForestGALES for ‘standard’ stand characteristics with the \( C_{\text{reg}} \) value from Nicoll et al. (2006), that excludes the DAMS effect \( (C_{\text{reg}} = 112.08) \), gave a 21.73 ms\(^{-1}\) critical wind speed (Table 4). This wind speed has a return period of 143, 10 and 2 years at locations with DAMS 14, 16 and 18, respectively. When ForestGALES was given new \( C_{\text{reg}} \) values from Figure 2 for DAMS 14, 16 and 18, critical wind speed reduced for the more sheltered DAMS 14 site and increased for the windier DAMS 16 and 18 sites (Table 4). Correspondingly, the return periods of the critical wind speeds reduced by ~50 per cent at DAMS 14 to 69 years and more than doubled to 5 years at DAMS 18.

### Table 2: Residual degrees of freedom (df) and percentage of the variance accounted for by each of the fixed effects used in the model

<table>
<thead>
<tr>
<th>Fixed effect</th>
<th>Residual df</th>
<th>% Variance accounted for</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem</td>
<td>895</td>
<td>63.2</td>
</tr>
<tr>
<td>Stem soil</td>
<td>892</td>
<td>64.9</td>
</tr>
<tr>
<td>Stem depth</td>
<td>893</td>
<td>63.8</td>
</tr>
<tr>
<td>Stem soil depth</td>
<td>884</td>
<td>66.5</td>
</tr>
<tr>
<td>Stem soil depth DAMS</td>
<td>845</td>
<td>71.2</td>
</tr>
</tbody>
</table>

### Discussion

Trees have long been known to strengthen their anchorage when grown in wind-exposed locations. Knight (1803) stated that ‘If a tree be placed in a high and exposed situation, where it is much kept in motion by winds, the new matter which it generates will be deposited chiefly in the roots and lower parts of the trunk. ... The growth of the insulated tree on the mountain will be, as we always find it, low and sturdy, and well calculated to resist the heavy gales to which its situation constantly exposes it.’ More recently, considerable evidence has been published of various growth responses of trees and other plants to mechanical stress, both above ground (Jacobs, 1939; Rees and Grace, 1980; Valinger et al., 1994; Telewski, 1995) and below ground (Stokes et al., 1995; Nicoll and Ray, 1996; Stokes et al., 1997). However, improvements in anchorage in response to acclimative growth of trees have not previously been quantified. In parts of the world where the climate is windy enough to require that forests are managed to minimise losses to windthrow, such as in the UK and northern Europe, quantification of this effect seems essential.

Despite the need for risk models to include the effect of acclimative growth, available data and analysis tools have up to now been inadequate. The compilation of an extensive tree anchorage dataset (Nicoll et al., 2006) and developments in statistical modelling techniques have made an analysis of the influence of acclimative growth possible and we have quantified here the effect on tree stability for Sitka spruce, the most commonly grown conifer species in Britain. Interestingly, anchorage strength appears to increase linearly with wind exposure, indicating that Sitka spruce can continue to adapt to increasing mechanical perturbation even when it has already experienced considerable mechanical...
stress. Above-ground studies of American elm (Ulmus Americana L.) showed an exponential decrease in growth response with increasing amounts of stem flexing (Telewski and Pruyn, 1998), but in contrast, Honey locust (Gleditsia triacanthos L.) trees showed a linear dose–response to increasing wind speed (Telewski, et al., 1997). Dose–response curves have not been developed for any below-ground thigmomorphogenetic responses in either gymnosperms or angiosperms. However, results of an experiment where mechanical stress on Sitka spruce trees was manipulated by thinning and guy-ing (Nicoll and Gardiner, 2006) indicate that a decrease in height growth in response to increasing stress would be expected to correspond with a simultaneous increase in radial growth of the lower stem and structural roots. This will evidently provide a future research area with potential benefits

<table>
<thead>
<tr>
<th>Soil group: rooting depth (cm)</th>
<th>A. Free-draining mineral</th>
<th>B. Gleyed mineral</th>
<th>C. Peaty mineral</th>
<th>D. Deep peat</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. &lt;40</td>
<td>+0.700</td>
<td>+0.829</td>
<td>+0.700</td>
<td>+0.800</td>
</tr>
<tr>
<td></td>
<td>0.188</td>
<td>0.042</td>
<td>0.188</td>
<td>0.200</td>
</tr>
<tr>
<td>2. 40–80</td>
<td>+0.500</td>
<td>+0.600</td>
<td>+1.000</td>
<td>+0.900</td>
</tr>
<tr>
<td></td>
<td>0.391</td>
<td>0.208</td>
<td>&lt;0.0001</td>
<td>0.037</td>
</tr>
<tr>
<td>3. &gt;80</td>
<td>+0.200</td>
<td>+0.657</td>
<td>+1.000</td>
<td>+1.000</td>
</tr>
<tr>
<td></td>
<td>0.747</td>
<td>0.156</td>
<td>–</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

The significance level is shown in italics under each coefficient. There were insufficient data to calculate a significance level for peaty mineral soil with >80 cm rooting depth.
both to the understanding of tree acclimation and to the development of wind risk models. Overall, the finding that trees grown in sheltered parts of the country are relatively poorly anchored and, therefore, more vulnerable to windthrow if storms occur, may be used to improve our predictions of

![Figure 2](https://example.com/figure2.png)

*Figure 2. Turning moment against stem mass for each combination of soil group and rooting depth class. Soil groups A, B, C and D are free draining mineral, gleyed mineral, peaty mineral and deep peat, respectively. Rooting depth classes 1, 2, and 3 represent <40 cm, 40–80 cm and >80 cm, respectively. Regression lines represent the modelled predictions of $C_{reg}$ from Figure 1, for trees grown in locations with increasing wind exposure, i.e. DAMS scores 14, 16, 18 and 20. *Note: Regression lines are only shown for DAMS scores within the data range used to build each model. No lines are shown for C3 due to insufficient data points.*

<table>
<thead>
<tr>
<th>DAMS</th>
<th>$C_{reg}$ – A</th>
<th>CWS (ms$^{-1}$)</th>
<th>Return period (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>14</td>
<td>112.05</td>
<td>21.73</td>
<td>143</td>
</tr>
<tr>
<td>16</td>
<td>112.05</td>
<td>21.73</td>
<td>10</td>
</tr>
<tr>
<td>18</td>
<td>112.05</td>
<td>21.73</td>
<td>2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>DAMS</th>
<th>$C_{reg}$ – B</th>
<th>CWS (ms$^{-1}$)</th>
<th>Return period (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>14</td>
<td>103.91</td>
<td>20.91</td>
<td>69</td>
</tr>
<tr>
<td>16</td>
<td>118.22</td>
<td>22.34</td>
<td>16</td>
</tr>
<tr>
<td>18</td>
<td>132.52</td>
<td>23.61</td>
<td>5</td>
</tr>
</tbody>
</table>

Table 4: $C_{reg}$, critical wind speed (CWS) for overturning and return period of that wind speed for a standard stand of Sitka spruce trees grown on gleyed mineral soil with <40 cm rooting depth at locations with DAMS 14, 16 and 18

Standard trees were 55-year-old trees at Yield Class 16 grown at 1.7 m spacing. $C_{reg}$ – A uses the model that excludes DAMS as a fixed effect, while $C_{reg}$ – B includes DAMS as a fixed effect.
windthrow risk. However, if the underlying growth responses can be understood, this finding will also benefit the refinement of tree growth models, as it will allow wind exposure to be incorporated as an influence on allocation and growth.

The models described here for Sitka spruce can be directly incorporated into ForestGALES to provide revised return times for critical wind speeds that relate to the wind regime experienced by the forest stand during its growth. Data are likely to be insufficient to model the wind acclimation effect on anchorage for other species, but as the patterns of adaptive growth of roots have been observed to be similar in other species, it is reasonable to apply proportional changes in \( C_{\text{reg}} \) values to those provided by Nicoll et al. (2006). This will provide the best estimate of anchorage based on current knowledge, but should ultimately be replaced with factors derived from modelling of the development of root architecture (Coutts et al., 1999; Tobin et al., 2007) and associated biomechanical properties (Dupuy et al., 2005; Fourcaud et al., 2008).

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Conflict of Interest Statement

None declared.

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