

PREDICTING THE BRANCHING PROPERTIES OF SITKA SPRUCE GROWN IN GREAT BRITAIN*

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(Received for publication 1 November 2005; revision 6 June 2006)

ABSTRACT

Predictions of the branching characteristics of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) were made as part of the development of a timber properties simulation tool. For each annual growth unit, non-linear modelling was used to describe the average number of branches and their associated diameter, insertion angle, and probability of being alive. The parameters for the model were obtained using the branching characteristics of 60 trees collected from a range of locations across Scotland and northern England. The non-linear equations describing the branching properties gave an adequate representation of the mean of each branch property from the top to the base of the tree. Analysis of the residuals around the stem revealed that branches grew bigger on the south side but were more numerous on the north side. The predictions used a total of only six predictor variables that can be obtained from normal mensurational data and from the height growth history of the trees. Yield tables could hence be used to run two simulations of typical Sitka spruce stands managed under a thinning or no-thinning regime. As expected, the effect of thinning was to increase branch diameter, to lower the height at which branches die, and to increase the number of branches without having any effect on their insertion angle. After incorporation of clear-wood properties, the model will be used to predict the properties of sawn battens.

Keywords: branching; knots; wood quality modelling; *Picea sitchensis*.

* Based on a paper presented at IUFRO WP S5.01.04 Fifth Workshop on Wood Quality Modelling, 20–27 November 2005, Waikeke Island, New Zealand

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INTRODUCTION

The silviculture of Sitka spruce in Great Britain has undergone significant changes over the last 50 years (Mason 1993). From the 1920s until the 1940s, Sitka spruce was planted on relatively fertile, sheltered soils at spacings of 1.0–1.5 m. In contrast, from the 1960s to the early 1980s there was rapid afforestation with the use of cultivation and/or herbicides that allowed planting on higher, more exposed sites with initial spacings increased to 2.0–2.4 m and with greater use of systematic thinnings. Over the next 20 years the supply of softwood timber from British conifer plantations is expected to double to around 16 000 000 m³ (Smith *et al.* 2001) and the majority of this will be Sitka spruce (~70%) typically harvested over a rotation of 40 years. As plantations established since the 1960s come into production, the characteristics and properties of timber being harvested are changing. There are concerns about decreasing wood density, larger juvenile cores, increased area and frequency of knots, increased incidence of compression wood, and poorer stem form.

Currently, the practical implications of these changes on timber utilisation cannot be easily quantified. Furthermore, there are no tools available to guide British foresters as to the effect of their silvicultural decisions on the future timber quality of stands, which is of increasing importance with the increased use of alternative silvicultural systems. It was considered that the best approach to provide predictions of these characteristics within a reasonable time frame was through computer modelling. A series of classical-style field experiments would be too expensive, take too long, and provide only information about the specific situations studied. This paper focuses on the part of a timber quality model which is designed to predict the effect of site quality and silviculture on the branching properties of Sitka spruce.

As trees grow in diameter, branches become incorporated in the stem, thus creating knots which locally deviate and distort wood fibres. Knots are important factors in weakening structural timber as they lead to stress concentrations and because checking often occurs around them during drying (USDA 1999). Their negative effect on stress grading results has long been recognised in Sitka spruce (Brazier 1986; Maun 1992). The extent of this effect depends on the proportion of the cross section of the batten which is occupied by a knot, its position in the batten (lumber), and on whether it is live (intergrown) or dead (encased) (USDA 1999). In turn, such properties are dictated by the position in the stem where the batten came from and by the history of how branch size, number, insertion angle, and condition (live or dead) evolved as the tree was growing.

A decision was made to follow the modelling approach developed by Colin & Houllier (1992). Their approach describes the branch characteristics in a tree from variables which can be obtained from a combination of stand inventory data and growth model predictions (i.e., current tree height and diameter and yearly

increments). An advantage is that the model is hence independent of a knowledge of the history of silvicultural interventions, which is often unavailable. This facilitates integration with growth models such as the one presented by Houllier *et al.* (1995).

This paper describes the results of this modelling effort by (1) presenting the parameters of the model as obtained using a 60-tree sample from a range of locations across Scotland and Northern England, (2) plotting the predicted values along the stem of a typical 40-year-old Sitka spruce tree, and (3) showing the effect of thinning on these predictions.

MATERIALS AND METHODS

Location of the Sample Trees

All the trees studied were of Queen Charlotte Island provenance. The details of the sample sites are given in Table 1.

Measurement Methodology

Branch characteristics were measured following the method of Colin & Houllier (1992). The north and west sides were marked on the standing tree with spray paint. Once the sample tree was felled, the paint marks were extended along the length of the stem. Then, a 30-m measuring tape was stretched from the apex of the tree to the butt end and a series of measurements were made on all whorls in the following sequence:

- The distance from the bottom of the growth unit to the top of the tree was recorded (D_{top} , m).
- The number of branches at the whorl position and the number of branches between this and the next whorl down were counted separately. In the remainder of the text, the former will be referred to as “whorl” branches and the latter as “inter-whorl” branches.
- The status (i.e., live or dead) of each branch was recorded.
- The diameter of the stem was measured at the bottom of the growth unit (immediately above the next whorl of branches) using a diameter tape.

The following additional measurements were recorded on every second whorl (*see* details in Fig. 1):

- Using a measuring tape, the distance (in the longitudinal axis of the tree) between the position of the top of the growth unit and the position of the base of each branch was recorded (D_{whorl} , m).
- The horizontal (Φ_h , cm) and vertical diameters (Φ_v , cm) of each branch were measured in axes perpendicular to the longitudinal axis of the branch.

TABLE 1—Sample sites showing stand characteristics. Yield Class estimated from Edwards & Christie (1981).

Site	Location	Planting year	Age at felling (years)	Yield Class	Number of trees sampled	Initial spacing (m)	Mean height (m)	Mean diameter (cm)
Kershope 50	55°06'10"N 2°47'42"W NY493 790	1986	13	Too young to assess	6	2.0	7.8	12.0
Eddleston	55°46'24"N 3°13'22"W NT233 540	1985	16	Too young to assess	6	2.0	10.1	15.3
Glentress 67	55°42'04"N 3°15'45"W NT207 460	1970	30	16	6	2.0	14.5	18.2
Kersope 34	55°07'17"N 2°42'11"W NY552 811	1967	32	18/20	6 6	1.8 2.4	18.8 18.4	18.8 22.7
Hawkhope Burn	55°12'30"N 2°27'20"W NY710 905	1964	35	16	6	1.7	16.3	21.1
Highfield	55°13'00"N 2°24'30"W NY740 915	1963	36	16	6	1.7	17.6	19.6
Harecairn Moss	55°12'00"N 2°24'04"W NY745 896	1954	46	14	6	1.7	21.2	22.1
Glengarry	57°04'00"N 2°53'10"W NH251 009	1935	65	18/20	6 6	1.8 2.4	32.6 32.1	38.1 37.2

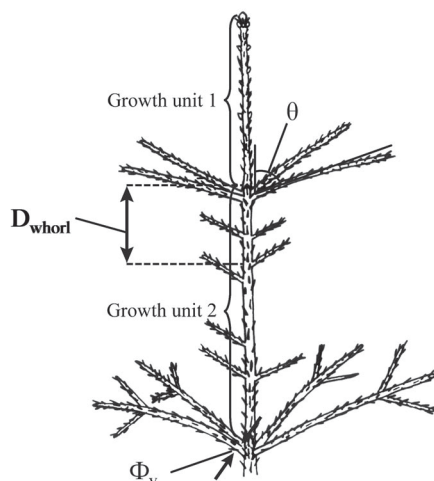


FIG. 1—The branching structure of Sitka spruce and how some of the branching variables were measured. Φ_v is the vertical diameter of the branch. D_{whorl} is the distance between the base of the branch (at its geometrical centre) and the top of the growth unit (indicated by a scar on the bark). θ is the insertion angle of the branch. Adapted from Cochrane & Ford (1978).

- The angle of insertion (θ , degrees) of the branch into the stem was measured with a protractor positioned at the base of the branches. It was experimentally defined as the angle between the axis of the stem and the centre of the branch at a 5-cm distance from the stem.
- The azimuth direction of the branch (α , degrees) was estimated by holding a circular protractor beside the stem and aligning it using the paint marks.

By subtracting D_{top} values from two successive whorls, we obtained the lengths of each growth unit (U_{length} , m).

Modelling Approach

The model uses non-linear equations to describe the changes in branch characteristics along the stem. The shapes of these equations were based mainly on those used by Colin & Houllier (1992) but adjusted on the basis of previous experiences and published information on the branching habits of Sitka spruce (Cannell 1974; Cochrane & Ford 1978).

Insertion angle

$$\theta = i_{\theta} e^{-\frac{a_{\theta}}{b_{\theta} - h_r}} \quad [1]$$

where a_{θ} , b_{θ} , and i_{θ} are empirically determined parameters, and

$$h_r = \frac{H - D_{top}}{H} \quad [2]$$

where H (m) is the height of the tree.

Number of branches

$$N = i_N U_{length}^{a_N} e^{-b_N D_{top}} \quad [3]$$

where a_N , b_N , and i_N are empirically determined parameters.

Branch condition

$$P_{live} = \left[\frac{1}{1 + e^{-(a_l + b_l U_{\#})}} \right] \quad [4]$$

where P_{live} is the probability of a branch being alive, a_l and b_l are empirically determined parameters, and $U_{\#}$ (dimensionless) is the growth unit number (starting with 1 at the apex of the tree (*see* Colin & Houllier 1992)).

Branch diameter

$$\Phi = a_{\Phi} + i_{\Phi} [1 - h_r] \cdot e^{-b_{\Phi} h_r} \quad [5]$$

where Φ represents either Φ_h or Φ_v and a_{Φ} , b_{Φ} , and i_{Φ} are empirically determined parameters. Note that Equation 5 only predicts the average (whorl or inter-whorl) branch diameter in a growth unit.

The parameters of each equation were inferred using the NLIN procedure in SAS (1990). This procedure looks for an optimal combination of parameter values through iterations. The Levenberg-Marquardt fitting algorithm was used to perform the iterations. A model for each of the 60 study trees was fitted first. The parameters so obtained were then analysed through linear regression using the REG procedure. The effects of the diameter at breast height (DBH , m), tree height (H , m), and the $H:DBH$ (dimensionless) ratio were tested on each parameter using the following model:

$$y = \alpha + \beta \cdot DBH + \gamma \cdot H + \delta \cdot H : DBH + \varepsilon \quad [6]$$

where y represents parameters a , b , or i in Equations 1 to 5; α , β , γ , and δ are parameters; and ε is the residual error. Only the significant parameters were retained. This meant that in each equation, the parameters (a , b , and i) would be used either as constants if no significant effects were detected or as functions of DBH , H , $H:DBH$ or any possible combination of these variables, provided their effect was statistically significant ($p < 0.05$). Separate equations were derived for whorl and inter-whorl branches.

Link to Growth Model

The rationale behind this model is that branch characteristics can be predicted using a combination of the current stem characteristics and the height growth history of

the trees. This implies that predictions of external branching characteristics can be made at any height in a tree using only six variables: U_{length} , $U_{\#}$, D_{top} , DBH , H , $H:DBH$. Most variables can be obtained from normal inventory data but U_{length} has to be obtained from detailed tree measurements or by using a height growth model. The yield tables of Edwards & Christie (1981) were used for this purpose.

The results were displayed by plotting each branch characteristic along the height of a 40-year-old Sitka spruce planted on a yield class 14 site with an initial spacing of 1.7 m. Two simulations were made: one where the stand was left unthinned and one where the stand was subjected to a series of intermediate thinnings applied every 5 years (Table 2). Note how the intermediate thinnings alter the final mean diameter at breast height of the crop. The predictions obtained from the model are intended to describe the branching properties of the average tree from each simulation.

RESULTS

Distribution Along the Stem

No effect of tree size was found on any of the parameters in Equation 1 (Table 3). Therefore, no effect of thinning could be seen on branch insertion angle in the simulation (Fig. 2). The angles of both whorl and inter-whorl branches decrease very rapidly at the top of the tree and then decrease slowly and linearly towards the base. All along the stem whorl branches are shown to grow at a more upward angle than inter-whorl branches with an almost constant difference (≈ 13 degrees).

All parameters from Equation 3 were found to vary with either DBH , H , or $H:DBH$ (Table 4). Thinned trees had a few more whorl and inter-whorl branches (Fig. 3). The differences were of the order of 0.3 to 0.5 whorl and inter-whorl branches per growth unit. There was an almost constant number of inter-whorl branches at the top of the tree down to half tree height, and they began to decrease in number rapidly towards the base. In contrast, whorl branches were more numerous close to the base of the tree.

Because the parameters from Equation 4 were found to vary as a function of DBH (Table 5) an effect of thinning could be observed in branch status (Fig. 4), for both whorl and inter-whorl branches. Thinning lowered the height at which the probability of a branch being alive went from effectively 1 to 0. This change in status always occurred higher in the tree for inter-whorl branches than for whorl branches.

The parameters from Equation 5 were not influenced by tree size for inter-whorl branches but they varied with DBH and H for whorl branches (Table 6). Thinning caused both the horizontal and vertical diameters of whorl branches to increase, particularly at mid-height in the tree where the increase approached 0.5 cm (Fig. 5). The vertical diameter was slightly higher than the horizontal diameter of whorl

TABLE 2—Stand characteristics for the two simulations (extracted from Edwards & Christie 1981). *BA* is the basal area, *Vol* is the volume, and *MAI* is the mean annual increment.

Age	Main crop						Yield from thinnings						Cumulative production		
	<i>H</i> (m)	Trees/ha	Mean <i>DBH</i> (cm)	<i>BA</i> (m ² /ha)	<i>Vol</i> (m ³ /ha)	Trees/ha	Mean <i>DBH</i> (cm)	<i>BA</i> (m ² /ha)	<i>Vol</i> (m ³ /ha)	Trees/ha	Mean <i>DBH</i> (cm)	<i>BA</i> (m ² /ha)	<i>Vol</i> (m ³ /ha)	<i>MAI</i> (m ³ /ha)	
No thinning															
17	6.9	3321	10	25	62								62	3.7	
22	9.8	3010	12	37	134								134	6.1	
27	12.7	2809	14	45	223								223	8.3	
32	15.4	2427	16	51	321								321	10	
37	17.9	2107	18	56	418								418	11.3	
Intermediate thinning															
17	6.9	3321	10	25	62	0	0	0	0	0	0	0	62	3.7	
22	9.8	2038	13	26	85	972	12	10	49	49	10	49	134	6.1	
27	12.7	1358	16	28	127	680	13	9	49	49	9	49	225	8.3	
32	15.4	1003	20	31	181	355	16	7	49	49	7	49	328	10.2	
37	17.9	791	23	34	239	212	19	6	49	49	6	49	435	11.8	

TABLE 3—Model parameters for the insertion angles of whorl and inter-whorl branches.

	α	β	γ	δ
Inter-whorl				
$a_{\theta I}$	0.0013 (0.00034)			
$b_{\theta I}$	0.99 (0.0008)			
$i_{\theta I}$	85.6 (0.25)			
Whorl				
$a_{\theta W}$	0.0028 (0.00030)			
$b_{\theta W}$	1.00 (0.0010)			
$i_{\theta W}$	72.87 (0.17)			

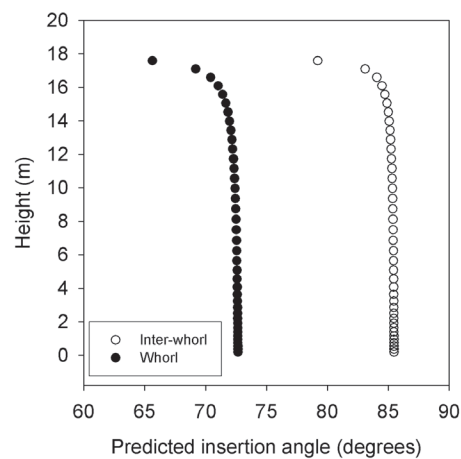


FIG. 2—Average branch insertion angles for each growth unit in a 40-year-old Sitka spruce.

TABLE 4—Model parameters for the number of branches in each whorl or inter-whorl.

	α	β	γ	δ
Inter-whorl				
a_{NI}	0.71 (0.25)	-0.56 (0.52)		0.0034 (0.0021)
b_{NI}	0.023 (0.0042)			
i_{NI}	12.49 (0.75)		-0.18 (0.032)	
Whorl				
a_{NW}	0.19 (0.024)			
b_{NW}	-0.089 (0.011)	0.072 (0.019)		0.00055 (0.00008)
i_{NW}	5.71 (0.26)		-0.084 (0.011)	

branches, whereas the two were indistinguishable in inter-whorl branches. The diameters of inter-whorl branches increased slowly and linearly from the top to the base of the simulated trees. Whorl branches increased in diameter from the top of the tree and then started decreasing before mid-height was reached.

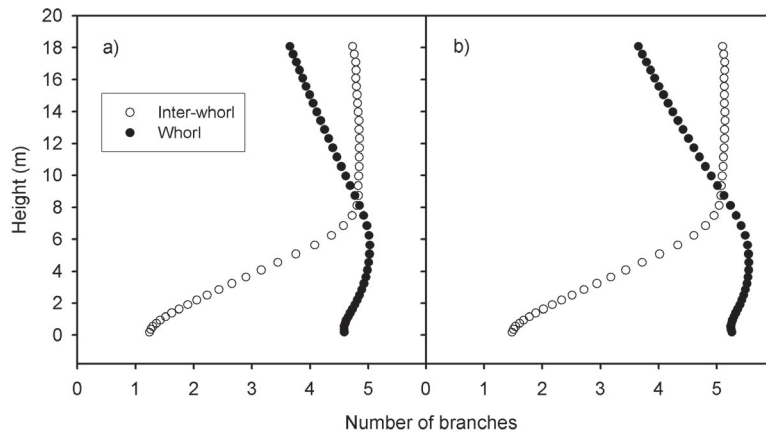


FIG. 3—Average branch numbers in each growth unit; (a) No thinning, (b) Intermediate thinning, no delay.

TABLE 5—Model parameters for the probability of a whorl and inter-whorl branch being alive.

	α	β	γ	δ
Inter-whorl				
a_{1I}	6.32 (0.30)			
b_{1I}	-0.73 (0.037)	0.89 (0.057)		
Whorl				
a_{1W}	4.94 (0.29)		0.15(0.013)	
b_{1W}	-0.58 (0.026)	0.48 (0.046)		

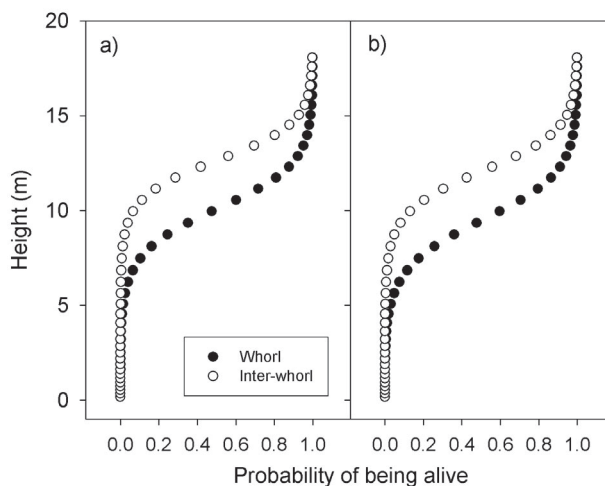


FIG. 4—Probability of a branch being alive for each growth unit; (a) No thinning, (b) Intermediate thinning, no delay.

TABLE 6—Model parameters for the vertical and horizontal diameters of whorl and inter-whorl branches.

	α	β	γ	δ
Horizontal – Inter-whorl				
$a_{\Phi HI}$	0.69 (0.023)			
$b_{\Phi HI}$	-0.38 (0.025)			
$i_{\Phi HI}$	0.35 (0.24)			
Horizontal – Whorl				
$a_{\Phi HW}$	0.63 (0.034)			
$b_{\Phi HW}$	-2.37 (0.063)		-0.0085 (0.0023)	
$i_{\Phi HW}$	0.21 (0.043)	4.28 (0.16)	-0.012 (0.0021)	
Vertical – Inter-whorl				
$a_{\Phi VI}$	0.70 (0.023)			
$b_{\Phi VI}$	-0.36 (0.026)			
$i_{\Phi VI}$	0.34 (0.26)			
Vertical – Whorl				
$a_{\Phi VW}$	0.65 (0.041)			
$b_{\Phi VW}$	-2.39 (0.065)		-0.0084 (0.0024)	
$i_{\Phi VW}$	0.22 (0.045)	4.36 (0.16)	-0.013 (0.0022)	

* In Tables 3 to 6, the values between brackets represent the asymptotic standard deviations of the parameter estimates. α , β , γ , δ are the parameters used in Equation 6.

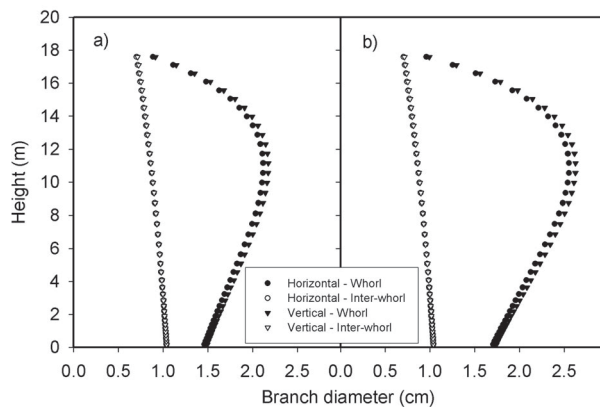


FIG. 5—Average branch diameters in each growth unit; (a) No thinning, (b) Intermediate thinning, no delay.

Model Residuals

When analysed by azimuth direction, the model residuals showed that, on average, branch diameter was under-predicted on the south side of the trees but over-predicted on the north side (Fig. 6). For the purpose of this analysis the residuals were not investigated directly but as a proportion of the predicted diameter. This is

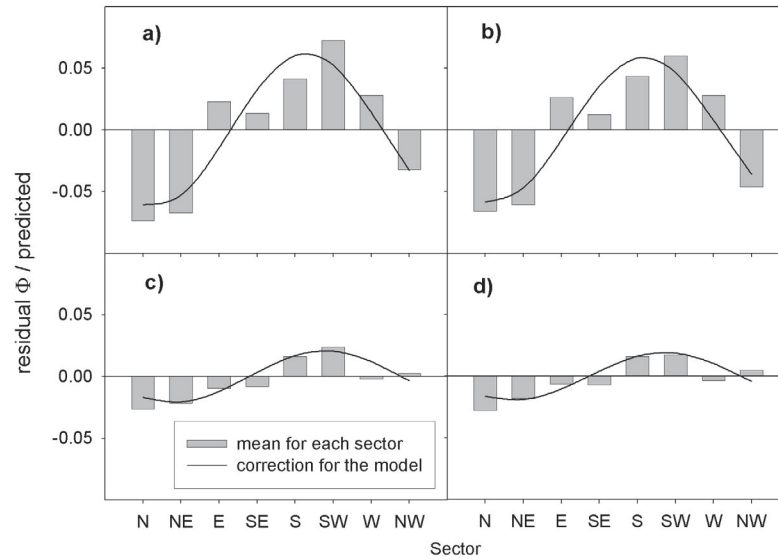


FIG. 6—Average ratios of residual over predicted values for branch diameters in 45-degree sectors; (a) inter-whorl horizontal diameter, (b) inter-whorl vertical diameter, (c) whorl horizontal diameter, (d) whorl vertical diameter. Φ represents branch diameter.

because it made sense to assume that the extent of an effect of azimuth direction would be related to the size of the branch. We found this proportional difference to be higher for inter-whorl branches than for whorl branches.

As a result of this investigation, we suggest that a cosine function could take the observed effect into account. Equation 5 would thus be transformed into:

$$\Phi = (a_{\theta} + i_{\Phi} [1 - h_r] \cdot e^{-b_{\Phi} h_r}) \cdot (1 + p \cos(\alpha + d)) \quad [7]$$

where α is expressed in radians and p and d are the experimentally determined parameters (Table 7).

On the other hand, more branches were measured overall on the north side of trees (plotted in four 90-degree sectors in Fig. 7). No function was used to describe the directional effect but eventual predictions could be weighted for each 90-degree sector according to the numbers presented in Fig. 7.

Plotting the residuals against growth unit number showed that the chosen functions gave an adequate representation of the mean of each branch property from the top to the base of the tree (Fig. 8). The only notable exceptions were for the insertion angle and number of inter-whorl branches: insertion angle was over-predicted at the very top of the tree but it was slightly under-predicted for the rest of the upper half of the tree; the model under-predicted the number of branches at the top of the tree and, conversely, over-predicted in the middle.

TABLE 7—Parameters for Equation 7. The values of the a_ϕ , b_ϕ , and i_ϕ parameters can be found in Table 6.

	Horizontal		Vertical	
	Inter-whorl	Whorl	Inter-whorl	Whorl
p	-0.062	-0.021	-0.059	-0.019
d	-0.23	-0.62	-0.14	-0.57

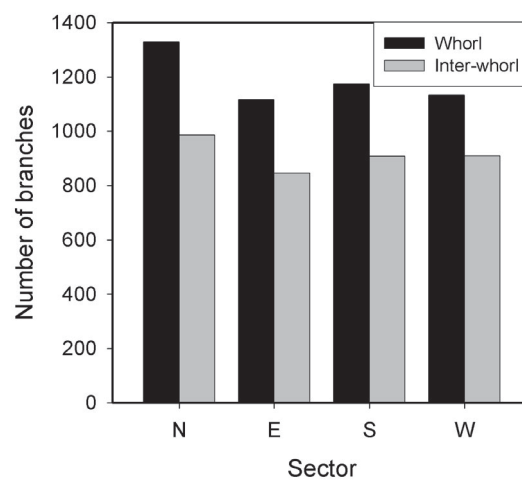


FIG. 7—Total number of branches measured in the experiment by sector.

DISCUSSION

Variations in Properties

The model description of how branching properties vary along a Sitka spruce stem corresponds well to our knowledge of the branching habits of this species. Cannell (1974) had already illustrated the strong tendency of Sitka spruce to produce numerous whorl and inter-whorl branches, often more than 10 in a year. He observed that it produced around three times as many first-order branches as lodgepole pine (*Pinus contorta* Dougl.). In this respect Sitka spruce is, unsurprisingly, more similar to Norway spruce (*Picea abies* Karst.). Colin & Houllier (1992) predicted slightly higher numbers of (whorl and inter-whorl) branches in a 38-year-old Norway spruce, but similar numbers of whorl branches.

In that study, as in the current one, the number of whorl branches was fairly constant along the stem although the number of inter-whorl branches clearly decreased towards the base. This implies that only self-pruning of inter-whorl branches had started taking place at this stage in the tree development. Even for the oldest of our sample stands it was not considered necessary to model the height of the first branch

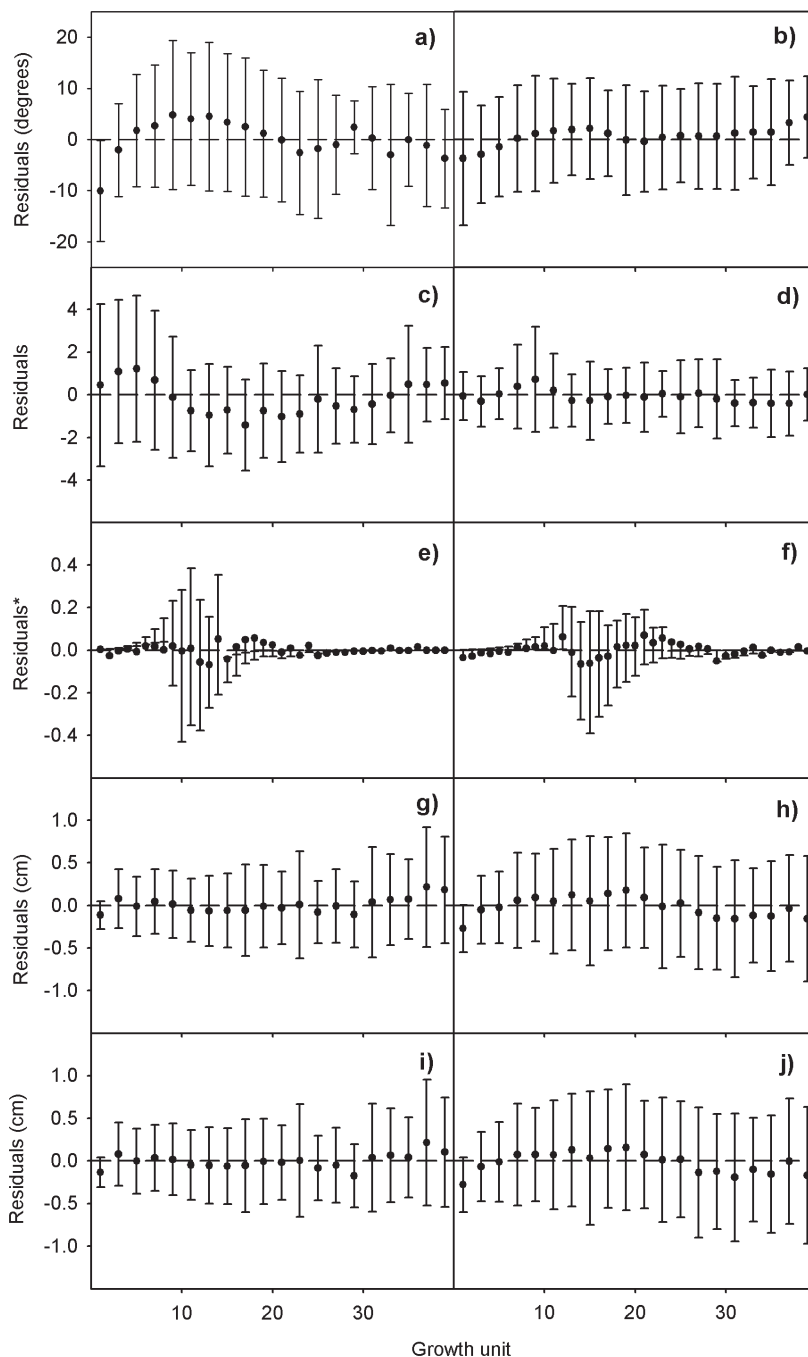


FIG. 8—Mean residuals and their standard deviations for the first 40 growth units; (a) inter-whorl insertion angles, (b) whorl insertion angles, (c) inter-whorl branch numbers, (d) whorl branch numbers, (e) inter-whorl probabilities of being alive, (f) whorl probabilities of being alive, (g) inter-whorl horizontal branch diameter, (h) whorl horizontal branch diameter, (i) inter-whorl vertical branch diameter, (j) whorl vertical branch diameter. Growth unit 1 is at the top of the tree.

* Due to the binomial nature of the branch condition data, the 25th and 75th percentiles were plotted instead of the standard deviation.

as the trees had, in effect, no lower clear bole. The practical implication of this behaviour is that, under current silvicultural systems, characterised by rotation lengths rarely exceeding 45–50 years, clear wood can only be obtained through pruning. This may explain the long history of interest in the subject in Britain (for a complete discussion *see* Henman 1963).

As predicted in our simulation, Cochrane & Ford (1978) observed inter-whorl branch angles to be bigger than those of whorl branches in young Sitka spruce trees, although the difference we predicted was smaller. This seems related mainly to the fact that they observed most inter-whorl branches to point downwards. The parameters from Equation 1 show that our model predicts that insertion angles remain smaller than 90° along any stem, meaning that on average the branches point upwards. The downward increase in angle corresponds well to what was predicted by Colin & Houllier (1992) for Norway spruce, although their model predicted a bigger difference between the top and the base of the tree. Lemieux *et al.* (2001) reported that lower branches in black spruce (*Picea mariana* [Mill.] B.S.P.) first point upwards and gradually change to point downwards. If the difference in branch insertion angles between the top and the base of a tree is taken as an indirect measure of knot straightness, the results suggest that Sitka spruce has generally straighter knots than these other two species of spruce.

The average diameters of whorl and inter-whorl branches modelled in this study are very similar to those modelled by Colin & Houllier (1992). The shape of the top-to-base profile is also in accordance with them and with the ones described by Makinen & Song (2002) for Scots pine (*Pinus sylvestris* L.) and Maguire *et al.* (1994) for Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco). This profile implies that the largest whorl branches are located in the middle section of the trees and smaller ones are found near the base. However, as pointed out by Vestol & Hoibo (2001), the effect of the latter on the properties of battens might be just as detrimental since they are more likely to be dead. In fact, branch condition should be at least partly responsible for the smaller branch diameters observed near the base. Lemieux *et al.* (2001) observed a reduction in knot diameter as a result of branch death inside black spruce butt logs.

Interestingly, inter-whorl branches did not show the same peak at mid-height but a slow, steady increase from top to base. A possible explanation comes from the fact that the bigger whorl branches will shade the inter-whorl branches, hence slowing their diameter growth. The process is possibly more severe close to mid-height, where whorl branches are bigger, than at the base of the tree. It is reasonable to assume that the same process explains why inter-whorl branches are likely to die earlier.

Our observation that branches are non-uniformly distributed around the stem tends to support the hypothesis that some environmental factors bias the distribution of

knots around the stem (Lemieux *et al.* 1997). In the Northern Hemisphere crowns have been observed to be generally weighted asymmetrically towards the south (Rouvinen & Kuuluvainen 1997; Skatter & Kucera 1998). However, there seem to be inconsistencies in how this is reflected in the distribution of diameters and numbers of branches around the stem. Results from other studies do not corroborate our observation that knot diameter peaks in the south to south-west direction but that more branches grow in the northern quadrant. Conversely, Lemieux *et al.* (2001) found that black spruce trees in Canada had more knots in the southern direction but those in the northern side were on average bigger. Lemieux *et al.* (1997) reported knot volume to be higher in the southern and south-eastern portions of Norway spruce logs from Finland due to the presence of larger and more numerous knots. The fact that no general trend can be identified suggests that the position of the sun at higher latitudes is unlikely to be the main driver for the observed biases. The reality of what drives the production of branches and their subsequent growth is more complex, with factors such as ground slope, exposure direction, and the presence of a forest edge likely to have an important role (Grace *et al.* 1999).

Maguire *et al.* (1994) highlighted the need to understand branch distribution around the stem. The type of function that we used to model this effect could arguably be used to model the frequency distribution of knots around the stem in the study of Lemieux *et al.* (1997) but would not be adequate to explain their measured distribution of diameters. The more elaborate concepts used in phyllotaxy — the study of the arrangement of leaves on the axis of a plant — could help further the understanding of the arrangement of branches around the stem (Pont 2001).

Modelling Approach and Link to Yield Model

It is acknowledged that silvicultural interventions can have a major impact on branch characteristics but we assume they can be taken into account indirectly through their effect on stem morphology (a combination of diameter at breast height and height) at a given age. Our simulation of two thinning regimes can be regarded as a preliminary examination of this assumption. It is encouraging to see that the results were in accordance with what was expected. Increased branch (or knot) size is a widely acknowledged effect of thinning (e.g., Brazier 1986; Maguire & Kershaw 1991; Makinen 1999). Likewise, a lowering of the live crown is expected after thinning. The fact that our predicted increase was small seems to be in accordance with the observations of Makinen (1999). Although it is known to be mainly related to the height growth of the parent shoot (Cannell 1974; Colin & Houllier 1992), an increase in branch initiation would also be expected as a result of improved light conditions in thinned stands (Maguire *et al.* 1994). Because our predictions were very similar for the thinned and unthinned simulations at the top

of the tree, it is also plausible that the increased numbers resulted from a difference in self-pruning. How this process is influenced by thinning is, however, poorly understood (Makinen 1999). In contrast to the other properties, the insertion angles of the branches were not affected by thinning, as was also observed by Deleuze *et al.* (1996) in Norway spruce.

Despite the model seeming to be successful in predicting the effect of a sequence of thinnings, a few minor modelling artefacts were observed. For example, the higher branch diameter at the base of thinned trees than in unthinned trees seems illogical. This is because the branches at the base of thinned and unthinned trees were all below the predicted height of the first live whorl at the time of first thinning and would therefore have all stopped growing. This artefact occurred as a result of the branch condition model and the branch diameter model being derived independently. To account for this, we intend to insert logical constraints between the equations when they are included in our timber properties simulator for Sitka spruce.

In conclusion, it can be said that Sitka spruce branch characteristics show substantial within-stem variability. The main practical implication of this variability is that it offers potential for improved grade yield of timber sawn from such trees (Samson 1993; Lemieux *et al.* 1997). It is therefore desirable that this model be developed to describe the impact of knots on the properties of the sawn timber. The necessary steps to make this possible are:

- (1) Estimate internal knot characteristics. Because predictions can be made at any time in the development of a tree, this can be achieved by considering that the branching characteristics of year t become the internal characteristics of year $t+1$. Such predictions would have to be tested against real measurements of knots.
- (2) Make the model stochastic, i.e., capable of describing the variability at different levels. The within-whorl variation needs to be described if virtual battens are to be modelled. This can only be achieved by also quantifying the variability within trees, between trees, and between stands (Colin & Houllier 1992). Adding a random tree effect to the models might be helpful for this purpose (Garber & Maguire 2005).
- (3) Amalgamate the branching model with a model describing the properties of the clear wood. Such a model is currently under development at Forest Research (Gardiner *et al.* 2002).
- (4) Integrate with a batten performance model. Such algorithms have already been developed by Maun (1992).

ACKNOWLEDGMENTS

The authors would like to thank Elspeth Macdonald, Jason Hubert, Franka Brüchert, and Francis Colin who initiated and encouraged this work. We wish to express particular thanks to Shaun Mochan, Keijo Heikkila, Joanna Forbes, Dave Clark, and the numerous Technical Support Unit staff who helped with the measurements in the field. Thanks also to David Vinué Visús for ensuring the quality of the database and to Monica De Ioanni for drawing Fig. 1. We are grateful for funding from the Scottish Forestry Trust (John Eadie Fellowship) which enabled the third author to instigate this work.

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