Original article

Branchiness of Norway spruce in north-eastern France: modelling vertical trends in maximum nodal branch size

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Summary — This paper is part of a study which aims at proposing a new method for assessing the wood quality of Norway spruce from northeastern France. One component of this method is a wood quality simulation software that requires detailed inputs describing tree branchiness and morphology. The specific purpose of this paper is to present a model that predicts maximum limbsize at various points along the stem. The dependent variable of the model is the maximum diameter per annual growth unit. The independent variables are the relative distance from the growth unit to the top of the stem and some combinations of standard whole-tree measurements and general crown descriptors. The equation is a segmented polynomial with a join point at the height of the largest branch diameter for each tree. First, individual models are fitted to each sample tree. Then a general equation is derived by exploring the behaviour of the individual tree parameters of the polynomial model as functions of other individual tree attributes. Finally the model is validated on an independent data set and is discussed with respect to biological and methodological aspects and to possible applications.

branchiness / crown ratio / modelling / wood resource / wood quality / *Picea abies*

Résumé — **Branchaison de l'épicéa commun dans le Nord-Est de la France : modélisation du diamètre maximal des branches verticillaires le long de la tige.** *Cet article s'insère dans un projet qui vise à proposer une méthode d'évaluation de la qualité de la ressource en épicéa commun du Nord-Est de la France. Ce projet s'appuie notamment sur un logiciel de simulation de la qualité des sciages (Leban et Duchanois, 1990) qui nécessite une description détaillée de la morphologie et de la branchaison de chaque arbre. Cet article a pour but de proposer un modèle de prédiction de la distribution du diamètre des branches le long de la tige. La variable prédite est le diamètre maximal de branche par unité annuelle de croissance. Les variables indépendantes du modèle sont la distance de l'unité de croissance à l'apex ainsi que des combinaisons des variables dendrométriques usuelles et des descripteurs globaux du houppier. L'équation est non linéaire et segmentée autour d'une valeur critique qui correspond à la position de la plus grosse branche de l'arbre. On ajuste d'abord un modèle individuel pour chaque arbre échantillonné. Puis on construit un modèle global à partir d'une analyse du comportement des paramètres du modèle individuel en fonction d'autres caractéristiques dendrométriques. Ce modèle est ensuite validé sur un jeu de données indépendantes. On discute finalement des propriétés de ce modèle tant au plan méthodologique et biologique qu'au plan de ses possibilités d'utilisation.*

branchaison / houppier / modélisation / ressource en bois / qualité du bois / **Picea abies**

INTRODUCTION

Description and modelling of tree branchiness may be carried out in various contexts: growth and yield investigations, silvicultural and genetic experiments, logging and wood quality studies. The analysis and the prediction of branch size (*ie* branch diameter) is obviously one of the most important features of branchiness studies. Several authors have already considered the limbsize at various heights: Madsen *et al* (1978), at 2.5, 5 and 7.5 m from ground level; Hakkila *et al* (1972), at 70% of the total height, De Champs (1989), at the fourth and eighth whorl counted from tree base; Maguire and Hann (1987), at the point where the radial extension of the crown is at its maximum.

Other authors (Ager *et al* (1964) and Western (1971) in Kärkkäinen (1972) *op cit*; Kärkkäinen (1972), Uusvaara (1985)) observed the relationship between limb size and the distance from the top of the stem. However, few studies have tried to model this vertical trend and predict the maximum limbsize anywhere along the stem (Maguire *et al*, 1990, on Douglas fir).

This study aims to develop a limbsize model that links standard whole-tree measurements (age, total height, diameter at breast height) to the required inputs of a wood quality simulation software (Simqua; Leban and Duchanois, 1990). This software requires information on stem taper, ring width patterns and branching structure (insertion angle, diameter, number of nodal and internodal branches). It can then simulate the sawing process for any board sawn from any stem for which this detailed information is available. It can further simulate lumber grading by examination of the 4 faces of each board and application of grading rules (for instance, French grading rules for softwood lumber).

This sofware and the results of the present study will be integrated into a system for predicting the quality of the coniferous wood resources from the data recorded by regional or national forest inventories. This project deals specifically with Norway spruce in northeastern France (ENGREF, INRA, UCBL, 1990).

Until now the project has focused on mid-size with a diameter at breast height *(DBH)* ranging between 15 and 35 cm. There are 2 reasons for this choice: 1), this size range will provide most of the stems that will be harvested in the coming decades; 2), the prediction of the quality of these logs is important because they may either be sawn or utilized as pulpwood.

Applications of this study are not limited to this particular project, since branching structure can also be related to growth modelling. Indeed, crown development and recession are intimately linked to wood yield through the interactions between branch size, leaf area and carbon assimilation rate. Therefore, information on branch size at various stages of stand development provide an insight into the dynamic interactions between stem and crown.

MATERIAL AND METHODS

Study area

All the trees were sampled in the Vosges department, in the northeastern part of France where Norway spruce stands are mostly located in the Vosges mountains, at elevations ranging from 400 to 1 100 m. The approximate annual precipitation is between 800 and 2 200 mm while mean temperature ranges from 8 to 5 °C. Snow is abundant above 800–900 m.

In the pre-Vosgian hills, sandstone with voltzite prevails on the western side, while much diversity appears (limestone, clay, sandstone) on the eastern side. The lower Vosges, between 350 and 900–1 000 m, are composed of triassic

limestones, which produce acid soils covered by forests, and also permian limestones, which yield richer soils that are seldom occupied by forests. The high Vosges are composed of granites of various kinds, producing primarily rich soils, although these soils can sometimes be poor to very poor (Jacamon, 1983).

Sampling

Three subsamples were collected, 2 for building the model and the third one for its validation. The trees of the 2 first subsamples were measured after felling whereas the last subsample was obtained by climbing the trees.

Subsample 1

The sample trees (between 30 and 180 years of age) came from public forests managed by the ONF (Office National des Forêts). In 1988, 10 trees without severe damage from late frosts and/or forest decline (in upper elevations) were sampled in 10 stands, for which the current density ranged between 500 and 1 500 stems per ha. The past silviculture of these stands was unknown.

Subsample 2

In 1989, 16 trees were removed by thinning in a private experimental plantation, managed by AFOCEL (Association Forêt-Cellulose). This stand represents a fairly intensive silvicultural regime when compared with usual practices carried out in non experimental stands. The seedlings (6 years in the nursery) were installed in 1961 and then thinned in 1974, 1983 and 1989.

Subsample 3

For 9 of the 10 stands belonging to the first subsample, and for 7 trees in each of these stands, the diameter of the thickest whorl branch per annual shoot was collected up to the maximum height that it was possible to reach by climbing.

Figure 1 shows the frequency of samples trees by diameter at breast height, total stem height, total age and crown ratio (for an exact definition of the latter parameter, see the *Statistical analysis* section).

Data collection

For the first 2 subsamples, the following variables were measured:
– the length of each annual shoot and the distance from the top of the tree to the upper bud scale scars (measured to the nearest 2 cm);
– the diameter over bark for each whorl branch (*ie* having a diameter > 5 mm) with a digital caliper (to the nearest mm and at a distance from the bole that was approximately equal to one branch diameter);
– the "height to the live crown" which was defined as the height from the base of the tree to the first whorl including more than three-quarters of green branches (modified from Maguire and Hann, 1987, *op cit*);
– the total height of the stem and the diameter at breast height;
– the age by counting the number of rings at the stump after felling.

For the third subsample, only the diameter of the thickest whorl branch, instead of the diameter of each whorl branch, was measured.

Statistical analysis

Two kinds of data were used: "the branch descriptors" and the "whole-tree descriptors". The latter were the standard tree measurements and different crown heights and crown ratios:

AGE = total age of the tree (in years);

DBH = diameter (of the stem) at breast height (in cm);

H = total height of the stem (in cm);

H/DBH = ratio between H and DBH;

$HFLB$ = height to the first live branch (in cm);

$HBLC$ = height to the base of the live crown as previously defined (in cm);

HC = average of the 2 previous heights, $HFLB$ and $HBLC$ (in cm);

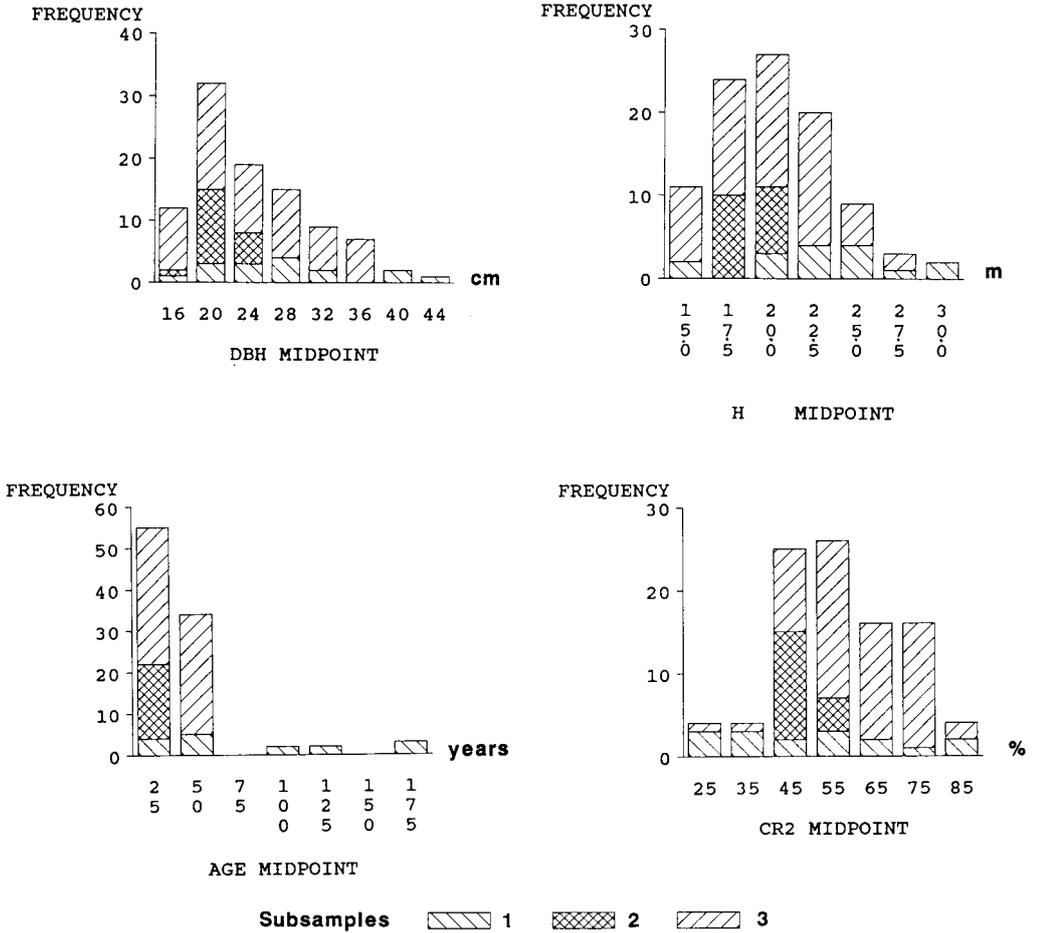$$CR1 = 100 \, \frac{H - HBLC}{H} \ \text{(in \%)}$$

Fig 1. Frequency distribution of the sample trees by diameter at breast height *(DBH)*, total stem height *(H)*, total age *(AGE)* and crown ratio *(CR 2)*.

$$CR2 = 100 \frac{H - HC}{H} \text{ (in \%)};$$

$$CR3 = 100 \frac{H - HFLB}{H} \text{ (in \%).}$$

The "branch descriptors" were relative either to an individual branch or to the whorl (or to the annual shoot) where the branch is located:

X = absolute distance from the upper bud scale scars of the annual shoot to the top of the stem (in cm)

$XR = 100 \, X/H$ = relative distance from the upper bud scale scars of the annual shoot to the top of the stem (in %).

DBR = diameter of the branch (in cm).

In the nonlinear models that were tested, we focused on the prediction of the diameter of the thickest branch per annual shoot, *DBRMAX*.

The independent variables (*ie* the predictors) were the whole-tree measurements as well as the absolute and relative distances to the top [1].

The analysis was carried out in 4 steps:

First step: We tried to model the variation of *DBRMAX* along each stem with individual equations (one per tree) according to the relative distance to the top of the stem, *XR*:

$$DBRMAX_{i,j} = f(XR_{i,j}; \Theta_i) + \varepsilon_{i,j} \qquad (1)$$

where *i* denotes the *i*th tree, *j* the *j*th annual shoot, Θ_i the model parameters specific to the *i*th tree and $\varepsilon_{i,j}$ random homoscedastic and non autocorrelated variable.

Second step: We analyzed the variability of the parameters Θ_i in relation to the whole tree descriptors and then tried to fit temporary equations of the following type:

$$\Theta_i = g(DBH_i, H_i, AGE_i, H_i/DBH_i, CR1_i, CR2_i,$$
$$CR3_i, HFLB_i, HBLC_i, HC_i, \psi) + \eta_i \qquad (2)$$

where ψ denotes the global model parameters common to all trees and η_i a random error.

Third step: We moved from the individual models towards a global model by progressively replacing the Θ_i parameters in (1) by their predictions (equation 2). We finally obtained models of the following form:

$$DBRMAX_{i,j} = f(XR_{i,j}, \Theta(DBH_i, H_i, AGE_i,$$
$$H_i/DBH_i, CR1_i, ...; \psi)) + \varepsilon_{i,j} \qquad (3)$$

These global models were then compared with the individual ones in order to check that there was no great loss in accuracy. These 3 first steps only used the data from the first 2 subsamples.

Fourth step: We used the data of the third subsample to validate the model and then put the 3 data sets together and re-estimated parameters for a final global model.

RESULTS

Individual models

Several preliminary models were explored and tested. A modified Chapman–Richards equation was one of the best:

$$DBRMAX = \beta \gamma XR ((XR/\alpha)^{-1/\gamma} - 1)$$

(*ie* the differential form of the usual Chapman–Richards model with α, β and γ being parameters: $\alpha > 0$, β and $\gamma \geq 1$).

However, it did not adequately describe the peak of the experimental curve around the thickest branches of the stem. Indeed, the prediction of the thickest branch of the tree was not efficient, either for the location of this branch along the stem or for its diameter.

By observing the actual *DBRMAX* distribution along the stem, the idea was proposed to choose a segmented second order polynomial model (Max and Burkhardt, 1975; Tomassone *et al*, 1983, p 119–122; with a join point value (ξ) which is the location of the estimated thickest branch:

$$DBRMAX = \alpha XR + \beta XR^2 \text{ if } XR < \xi \qquad (4)$$
$$DBRMAX = \alpha \xi + \beta \xi^2 + \gamma (XR-\xi)^2 \text{ if } XR \geq \xi$$

where α, β, γ and ξ are constrained parameters: $\alpha > 0$, $\beta < 0$, $\gamma < 0$ and

$$\xi = -\frac{\alpha}{2\beta} \qquad (5)$$

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[1] The data were analysed using the SAS Statistical Package (version SAS 6.03) on a Compaq 386/25 computer with 8 Mbytes extended memory and on a SUN 4/330. Nonlinear regressions were fitted with the PROC NLIN procedure using ordinary least squares. Since the number of parameters was fairly high (up to 11), the procedure sometimes converged to a local rather than to a global minimum of the error sum of squares. We therefore tried different starting values in order to avoid that kind of problem. Moreover the mutual interdependence of observations coming from the same tree –*ie* the within-tree autocorrelation of successive branch sizes– implies that the error estimates of the nonlinear regressions are probably biased and that the usual asymptotic statistical tests are not exact. This matter is currently under consideration but it is not examined in this paper.

This model has the following properties (see fig 2): a) the model and its first-order derivative are continuous; b) α/H is the slope of the *DBRMAX* over the *X* curve at the top of the tree (*ie* α is the slope of the *DBRMAX* over the *XR* curve): α/H is therefore related to the geometry of the top of the crown; c) $X_0 = \xi.H$ is the distance between the top of the stem and the location of the thickest branch; d) the thickest branch of the stem has a predicted value noted Max *(DBRMAX)*:

$$\text{Max}(DBRMAX) = -\frac{\alpha^2}{4\,\beta} \qquad (6)$$

This model was fitted independently for each tree. Since the model contains only 3 independent parameters (*ie* 4 basic parameters related by equation 5), estimates of β were derived from the estimates of α and ξ by using equation (5). Figure 3 shows how the model fits to the data for 2 different trees (a relatively good and a relatively bad fit). For the worst fit, the model slightly underestimates the greatest diameter and there is a small discrepancy between the observed and predicted locations of the thickest branch.

Construction of a single global model

At first, we tried to predict the estimated values of Max*(DBRMAX)* and ξ (*ie* the diameter and the location of the thickest branch of the *i*th tree). Among various
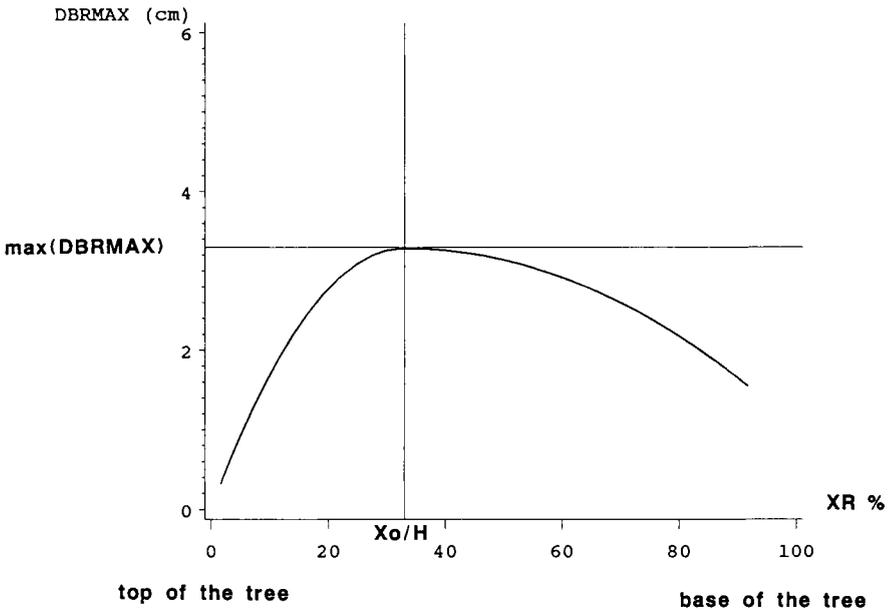

Fig 2. Mathematical properties of the segmented second order polynomial model. Model: $DBRMAX = \alpha\,XR + \beta\,XR^2$ if $XR < \xi$; $DBRMAX = \alpha\,\xi + \beta\,\xi^2 + \gamma(XR - \xi)^2$ if $XR \geq \xi$ with α, β, γ and ξ parameters: $\alpha > 0$, $\beta < 0$, $\gamma < 0$ and $\xi = -\alpha/(2\beta)$. *DBRMAX*: diameter of the thickest branch per growth unit (in cm); XR = relative distance of the upper limit of the growth unit to the top of the stem (in %); ξ: relative distance of the thickest branch of the tree to the top of the stem; Max*(DBRMAX)* = $-\alpha^2/(4\beta)$ = diameter of the thickest branch of the stem. The model and its first-order derivative are continuous.
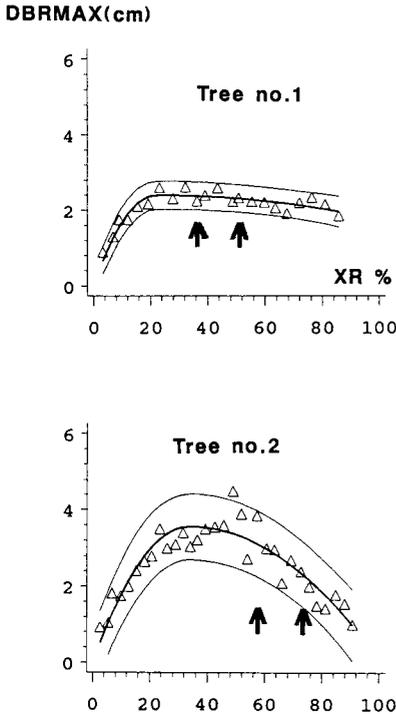
DBRMAX(cm)

Fig 3. Prediction of the maximum limbsize per annual growth unit *(DBRMAX)* by individual tree models (see equations 1, 4 and 5)): example of 2 trees. These 2 trees represent the most accurately (tree No 1) and most poorly fitted trees (tree No 2). *XR*: relative distance of the upper limit of the growth unit to the top of the stem (in %); central bold curve: predicted values; extreme normal curves: 95% confidence intervals around the mean predicted values; triangles: experimental data (one point per annual shoot); arrows: positions of the base of the live crown and of the first live branch.

combinations of 1, 2, 3 or more whole-tree descriptors, the best fit for ξ was given by:

$$\xi = a_0 + a_1\,CR\,2 \qquad (7)$$

(Statistics of fit: $R^2 = 0.73$; $RMSE = 5.4\%$ (root mean squared error); $P > F = 0.001$)

a_0 was not significantly different from 0; this parameter was therefore removed in further analysis.

Since the best prediction of Max *(DBRMAX)* was not as good, we decided to incorporate equation (7) into the individual models by substituting for ξ. We then reestimated the parameters α and γ of model (4) in order to investigate the possible relationships between α and γ and to predict these parameters by using the whole-tree parameters (β was not directly estimated but was deduced from α and ξ by using equation 5).

Among various combinations, the best equations were:

$$\alpha = a_2 + a_3\,CR\,2 + a_4\,DBH + a_5\,AGE \qquad (8)$$

(Statistics of fit: $R^2 = 0.96$; $RMSE = 0.012$; $P > F = 0.000\ 0$)

$$\gamma = a_6 + a_7\,CR\,2 + a_8\,DBH \qquad (9)$$

(Statistics of fit: $R^2 = 0.77$; $RMSE = 0.000\ 14$; $P > F = 0.000\ 1$)

The regression expressions of ξ, α and γ (eq 7, 8 and 9) were then introduced in the individual models to form a global model which was estimated simultaneously for all the trees of the first 2 subsamples. After some modifications due to high correlations between some parameters, the model form was:

$$DBRMAX = \alpha\,XR + \beta\,XR\,^2 \text{ if } XR < \xi \qquad (10)$$
$$DBRMAX = \alpha\xi + \beta\,\xi^2 + \gamma\,(XR-\xi)^2 \text{ if } XR \geq \xi$$

with: $\xi = a_1\,CR\,2$

$\alpha = a_2 + a_3\,CR\,2 + a_4 DBH + a_5\,AGE$

$$\beta = -\frac{\alpha}{2\,\xi}$$

$\gamma = a_6 + a_7\,CR\,2 + a_8\,DBH$

(Statistics of fit for 699 observations and 26 trees: $RMSE$ = 0.36 cm; $P > F$ = 0.0001)

The parameter values and their standard errors were estimated as follows in table I.

The 2 estimated asymptotic correlations among parameter estimates with the highest absolute value were: $r(a_8, a_6)$ = –0.95 $r(a_7, a_8)$ = –0.75.

Comparison between the tree-by-tree model and the overall model

Although the hypotheses necessary for its application are likely to be at least partially violated (there is a within-tree autocorrelation and the within-tree error is not rigorously homoscedastic) we used an F statistic to test the loss of precision between models (4) and (10). We noted SSE, the sum of squared residuals, obtained after the nonlinear adjustments: the sum of SSE for the 26 individual models was: 64.0 (with 621 degrees of freedom); SSE for the overall model was: 90.6 (with 691 degrees of freedom).

Although the root mean squared error was not very different between the 2 mod-

Table I. Parameter values and their standard errors.

Parameter	Estimated value	Asymptotic standard error
a_1	5.62 10^{-1}	1.14 10^{-2}
a_2	2.17 10^{-1}	9.47 10^{-3}
a_3	–2.85 10^{-3}	9.48 10^{-5}
a_4	4.86 10^{-3}	4.05 10^{-4}
a_5	7.68 10^{-4}	1.08 10^{-4}
a_6	1.21 10^{-3}	1.32 10^{-4}
a_7	–1.36 10^{-5}	1.13 10^{-6}
a_8	3.73 10^{-5}	4.10 10^{-6}

els ($RMSE$ = 0.32 cm for model 4 vs $RMSE$ = 0.36 cm for model 10), the value of the F statistic was fairly high (F = 3.69) according to the high degrees of freedom (ie 70 and 621). Thus it appeared that the global model was slightly but significantly less accurate than the set of individual models and that a part of the within- and between-tree variation of branch size could not be predicted by the tested whole-tree descriptors and by the relative distance to the top of the tree.

VALIDATION

Validation on the third subsample

At first, we checked how the global model (10) previously adjusted on 26 trees predicted the $DBRMAX$ distribution for the 60 trees of the validation sample (ie we used the parameter values given above). The difference between actual and simulated values (observed $DBRMAX$ minus predicted $DBRMAX$) and the square of this difference were calculated for each observation (a total of 1 728 observations). We obtained the following results:

– the mean difference was –0.229 cm, which indicates that the model overestimated limbsize for the validation sample;

– the sum of squared differences was 771.68, which gives a root mean squared difference equal to 0.66 cm which is considerably higher than the $RMSE$ obtained for the 26 trees of the first two samples.

Global fit of the same model with all tree subsamples

The root mean squared error for the 2 427 observations and the 86 trees was: 0.49

cm. The parameter values and their standard errors were estimated in table II.

The estimated asymptotic correlation among parameter estimates with the highest absolute value was: $r(a_6, a_7) = -0.73$.

Improvement of the global model for the third subsample

Using the same strategy as described in *Construction of a single global model* for the 60 trees of the third subsample we first obtained:

$$\xi = b_1 + b_2\ CR3 + b_3\ H \qquad (7')$$
(Statistics of fit: $R^2 = 0.62$;
$RMSE = 9.6\%$; $P > F = 0.000\ 0$)

$$\alpha = b_4 + b_5\ CR3 + b_6\ H/DBH + b_7\ HFLB \quad (8')$$
(Statistics of fit: $R^2 = 0.82$;
$RMSE = 0.038$; $P > F = 0.000\ 0$

$$\gamma = b_8 + b_9\ CR3 + b_{10}\ DBH + b_{11}\ H \qquad (9')$$
(Statistics of fit: $R^2 = 0.65$;
$RMSE = 0.000\ 34$; $P > F = 0.000\ 0$

The global model was then reestimated using these equations; it provided a root mean squared error equal to 0.49 cm.

Development of a global model for the 3 subsamples

The model obtained in *Improvement of the global model for the third subsample* above was finally adjusted to the 2 427 observations coming from all 86 trees. The root mean squared error was 0.47 cm with the following parameter values (since b_4 and b_{11} were not significantly different from zero, these parameters were removed) (table III).

The estimated asymptotic correlation among parameter estimates with the highest absolute value was: $r(b_5, b_6) = -0.82$. The fit of this model for 2 different trees is illustrated in figure 4.

If adjusted to the 26 trees of the first 2 subsamples, this model provides a root mean squared error equal to 0.37 cm which is fairly similar to the 0.36 cm given in *Construction of a single global model*. Thus this last model was considered as the best compromise for the whole data set.

Table II. Parameter values and their standard errors.

Parameter	Estimated value	Asymptotic standard error
a_1	$5.95\ 10^{-1}$	$8.52\ 10^{-3}$
a_2	$2.18\ 10^{-1}$	$5.30\ 10^{-3}$
a_3	$-2.34\ 10^{-3}$	$6.63\ 10^{-5}$
a_4	$4.32\ 10^{-3}$	$1.43\ 10^{-4}$
a_5	$2.90\ 10^{-4}$	$6.75\ 10^{-5}$
a_6	$5.78\ 10^{-4}$	$4.80\ 10^{-5}$
a_7	$-1.36\ 10^{-5}$	$7.29\ 10^{-7}$
a_8	$-1.19\ 10^{-5}$	$1.41\ 10^{-6}$

Table III. Parameter values and their standard errors.

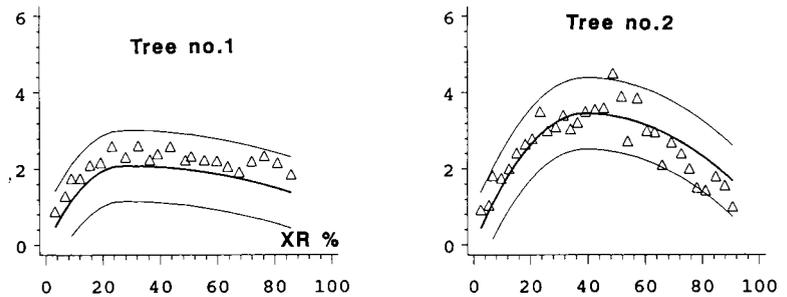| Parameter	Estimated value	Asymptotic standard error
b_1	4.718	1.26
b_2	$5.406\ 10^{-1}$	$1.55\ 10^{-2}$
b_3	$-2.436\ 10^{-3}$	$3.94\ 10^{-4}$
b_5	$2.244\ 10^{-3}$	$5.05\ 10^{-5}$
b_6	$-1.540\ 10^{-3}$	$5.43\ 10^{-5}$
b_7	$2.274\ 10^{-4}$	$5.16\ 10^{-6}$
b_8	$6.429\ 10^{-4}$	$5.64\ 10^{-5}$
b_9	$-1.168\ 10^{-5}$	$7.59\ 10^{-7}$
b_{10}	$-1.163\ 10^{-5}$	$1.64\ 10^{-6}$

DBRMAX(cm)

Fig 4. Prediction of the maximum limbsize per annual growth unit *(DBRMAX)* by a global model (see Improvement of the global model for the third subsample and Development of a global model for the 3 subsamples): for same trees as in figure 3. A comparison with figure 3 shows: 1), that the global model may either fit as well as the individual model (tree No 2) or fit worse than the individual model (tree No 1); 2), that the width of the confidence intervals are broader for tree No 1 and similar for tree No 2. *XR*: relative distance of the upper limit of the growth unit to the top of the stem (in %); central bold curve: predicted values; extreme normal curves: 95% confidence intervals around the mean predicted values; triangles: experimental data (one point per annual shoot).

DISCUSSION

Biological interpretation

The predominant effect of the distance from the tip, also observed and modelled by Madgwick *et al* (1986), Maguire *et al* (1990, *op cit*)) is actually the result of different complementary aspects:

– softwood species present a conical crown, due to a strong apical dominance;

– the effect of the age of the branch: older branches are located far away from the tip;

– at a certain distance from the tip, the branches belong to the part of the crown where mutual inter-tree interference occurs (shading and stress marks);

– further down, the branches belong to the part of the crown where sunlight exposure

is very restricted so that their growth is nearly stopped, and near the ground they are dead.

Consequently, the first part of the model with a curvilinear form predicts limbsize from the tip of the stem to approximately the base of the live crown: qualitatively, the second degree polynomial equation takes into account the intrinsic geometry of the crown as well as the beginning of the effects of the mutual inter-tree shading. The second part of the model which is also a second degree polynomial describes the part of the crown that goes from the base of the live crown to the dead branches.

The estimated values of a_1, b_1, b_2 and b_3 parameters indicate that the thickest branch seems to be actually located higher than the base of the living crown (*eg* a_1 = 0.56 in *Construction of a single global model*). Since the maximum of the curve is

generally quite flat, there is a wide portion of the stem where maximum limbsize per whorl is nearly constant. However, this point should be analysed further to check whether the difference between ξ and base of the living crown is due to an inadequacy of the model or to an early effect of the competition that precedes crown recession.

Concerning the overall model established for the 3 subsamples (see *Development of a global model for the 3 subsamples*), we noticed: 1) a slight overestimation of the *DBRMAX* for the smallest trees (*ie* for most trees which have a *DBH* < 16 cm; and 2) a slight but systematic underestimation for the trees which are located in edge conditions or in stands installed on sites with steep slopes. This is probably due to the fact that the standard whole-tree measurements introduced in the model cannot take into account the relative over-development of the branches that are oriented towards the best sunlight conditions.

Moreover the model underestimated slightly but frequently the maximum limbsize for the trees of the AFOCEL stand. This is not really surprising since: 1), the weight of these trees in the whole data set is relatively small; and 2), they belong to a stand which has been submitted to a more intensive silviculture than the others (*ie* the spacing conditions of these trees have been more favourable to their growth). Again, it is likely that the model does not reflect their increased exposure to sunlight.

The crown ratio *CR 3* and the height to the first live branch *(HFLB)* turned out to be the best crown parameters when we tried to validate the model. This is probably due to the fact that the proportion of trees located in stands with steeper slopes (> 20 °C) is higher in this part of the data set. Steep slopes introduce an asymmetry in the crown and produce a greater differ-

ence between the height to the base of the live crown (as previously defined) and the height to the first five branch; the thickest branches are located nearer to this latter height.

For the first 2 samples, the crown ratio *CR 2 (ie* the ratio $100.(H-HC)/H$) was the best predictor. When considering this reduced data set the weight of the trees belonging to the AFOCEL stand is high (16 trees / 26 trees) in the regression analysis. Since this stand is more homogeneous (*ie* the total heights of the trees are very similar) and the slope is gentle, the crowns are nearly symmetrical and have a regular external shape; hence, the difference between *CR 2* and *CR 3* does not vary much from one tree to another.

Therefore all these remarks seem to be consistent. The distribution of the maximum limbsize per annual growth unit along the stem appears to be sensitive to the symmetry of the crown and to the sunlight exposure conditions.

Comparison with other models

Maguire *et al's* model (Maguire *et al,* 1990, *op cit*) focuses on young Douglas fir trees from plantations before crown closure and, hence, where the base of the live crown is very near to ground level. The shape of their model is curvilinear rather than linear from tip down to stem base. This is consistent with the fact that, even without intertree competition for light, the growth of the lower branches is reduced (Mitchell, 1975).

Due to younger ages and the open-grown condition of Maguire *et al's* trees, it is difficult to compare their results with ours. However it is important to note that their model does not separate the within- and between-tree variabilities, since the dimensions of the trees are not taken into account. This might at least partially ex-

plain the great variance around their model and why our first attempts (not reported here) to model branch size variation along the stem without including whole-tree descriptors were not conclusive.

Vertical distribution of branch diameter and growth conditions

Site growth conditions (*eg* site index) are partially hidden in the model by the use of relative depth into the crown as an independent variable. To predict the actual size of the branches, for instance in the merchantable part of the stem, it is necessary to return to the absolute values of depth in the crown which are linked with height growth and therefore with site conditions.

Tree growth conditions are also determined by the current and initial stand densities, by the silvicultural practices and by the competitive status of the tree. The main effect of the stand management is reflected in crown development which is, at least partially, included in the proposed model through crown ratio variables. Nevertheless, as already observed for widely spaced trees (*ie* AFOCEL stand) or for edge trees, the overall model does not describe perfectly the trees submitted to favourable or asymmetrical sunlight exposure.

The growth conditions at high elevations imply branch and leader damage which are caused by late frost and snow weight. For some trees we indeed observed that the model does not describe the peak of the empirical curves very well. This fact could be explained, at least partly, by the occurrence of "ramicorn branches" that attain greater diameters than other branches. Although these branches are very important in lumber grading, they have not been analysed in this study be-

cause of the absence of a good definition in terms of limb size and insertion angle, and because their occurrence cannot be predicted with deterministic models.

Vertical distribution of branch diameter and genetic origin

On different families of a Polish provenance studied by Van de Sype (personal communication), he observed that independently of growth vigour, branches are proportionally thicker for certain families than for others. Such differences have also been established by Cannell and Bowler (1977) on *Picea sitchensis*. Our sampled trees probably belong to the same genetic origin (*ie* the same provenance): the Gérardmer provenance. It will therefore be important to check whether a part of the residual variability around the model may be attributed to genetic effects. This will be done by fitting the model to various provenances.

As cited by Schmidt-Vogt (1977) and also observed by Hakkila (1971), different patterns of branchiness exist: brush form, comb form, flat form, with narrow or wide lateral extension. Do these patterns have a strong influence on the accuracy of our model? Using our field notes we were not able to establish an actual effect of branch form. In fact, only three trees presented comb-shaped branches and these trees were accurately modelled. During future sampling, such characteristics will have to be noted again.

Utilization of the model

First, it must be emphasized that the model was developed in order to predict the mean vertical trend in maximum limb size at a point of time and that it does not repre-

sent the dynamics of the branching structure (*ie* branch growth and crown recession). This point may partly explain the difference that was observed between ξ and the base of the living crown (see *Biological interpretation section*). Above all, it implies that the direct application of the model to the outputs of a tree growth model may lead to some inconsistencies between the successive predictions of maximum limb size at a given height for the same tree.

One interesting feature of this model is that it provides relatively good estimates of the maximum branch diameters along the stem as well as quantitative indications about the variability around these predictions. Although the underlying statistical assumptions are probably violated, the confidence intervals (see figs 3, 4) provide rough estimates of extremes in limbsize. As previously stated, a more rigorous statistical analysis recognizing autocorrelated and heteroscedastic errors was outside of the scope of this paper and will now be performed. Information about the variability around the model could then be used in Monte-Carlo simulations to provide probabilistic inputs to SIMQUA rather than purely deterministic predictions.

The proposed model has been established for mid-size trees (15 cm $\leq$ *DBH* $\leq$ 35 cm) in even-aged stands. It cannot be extrapolated to smaller or bigger trees without further validation. Indeed, the behaviour of the model for bigger trees is unknown and the slight overestimation for the smallest trees indicates that the model should be improved for small and young trees. Its application to uneven-aged stands or to steep slopes should also be avoided due to the highly asymmetrical development of the crown in these conditions.

One other practical problem is that measurement of crown ratio is rarely performed in operational surveys (*eg* National Forest Survey data) so that *CR* 2 or *CR* 3 values will have to be estimated from other whole-tree descriptors (*eg AGE, DBH, H*). This procedure will probably introduce a major source of variability which has not been assessed in this study.

The model has several other applications as well:

– for logging operations and for standing or felled tree grading, information about the height of the thickest branch or about the height to a given branch size are very useful. For instance, in the Soviet Union (Arlauskas and Tyabera, 1986) or in Finland (Hakkila *et al*, 1972, *op cit*; Leban, 1989) the size of the branches combined with the length of the merchantable logs determine the quality and value of trees;

– for pruning, the choice of the tools as well as the assessment of the costs also require information about the size of the branches that would be removed by different pruning lifts (Riou-Nivert, personal communication);

– lastly, due to the close links between maximum or mean whorl limbsize and branch length, our model could be used to predict the external shape of the crown.

CONCLUSION

Since the estimated confidence intervals are relatively broad around the predicted limbsize values and since lumber grading rules are heavily dependent on the maximum limbsize in boards, trees with similar whole-tree descriptors may actually produce different grades. Thus, the accuracy of limbsize predictions is crucial when attempting to apply such models to operational inventory data to estimate wood product quality.

Our approach provides an insight into this question, but there are still many im-

portant points to be addressed: 1), the improvement of the accuracy of the proposed model by taking into account more precisely the effects of site and silvicultural treatments; 2), the analysis of the genetic variability of limbsize distributions; 3), a more rigorous statistical analysis of the regression models; 4), the proposal of probabilistic simulation procedures that use the information provided about the residual variability around the model; 5), and a dynamic approach of branching structure that would allow the establishment of a direct and consistent link with growth and yield models.

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