

## Branchiness of Norway spruce in northeastern France: predicting the main crown characteristics from usual tree measurements

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**Summary** — This paper is part of a study proposing a new method for assessing the quality of wood resources from regional inventory data. One component of this method is a wood quality simulation software that requires detailed input describing tree branchiness and morphology. The specific purpose of this paper is to construct models that predict the main characteristics of the crown for Norway spruce. One hundred and seventeen spruce trees sampled in northeastern France have been described in detail. The position of the different parts of the crown, the size, the insertion angle, the number and the position of the whorl branches have been predicted as functions of usual whole-tree measurements (*ie* diameter at breast height, total height, total age) and of the position of the growth unit along the stem (*ie* distance to the top, and number of growth units counted downward or upward) for branchiness prediction. The most efficient predictors of crown descriptors have been established and preliminary models are proposed.

**branchiness / *Picea abies* Karst / modelling / wood quality / crown ratio / wood resources**

**Résumé** — Branchaison de l'épicéa commun dans le Nord-Est de la France : prédiction des principales caractéristiques du houppier à partir des mesures dendrométriques usuelles. Cette étude s'insère dans le cadre d'un projet qui vise à proposer une nouvelle méthode d'évaluation de la qualité de la ressource à partir des données issues d'un inventaire forestier régional. Ce projet s'appuie notamment sur un logiciel de simulation de la qualité des sciages qui nécessite une description détaillée de la morphologie et de la branchaison de chaque arbre. Cet article concerne spécifiquement l'épicéa commun et vise à proposer des modèles de prédiction des principales caractéristiques du houppier à partir des données dendrométriques usuelles. Cent dix sept épicéas échantillonnés dans le Nord-Est de la France sont décrits en détail. La position des différentes zones du houppier, le diamètre, l'angle d'insertion, le nombre et la position des branches verticillaires sont prédits à partir des variables dendrométriques usuelles (diamètre à 1,30 m, âge et hauteur totale) et de la position de l'unité de croissance considérée le long de la tige (distance à l'apex, âge ou numéro de l'unité de croissance) pour la prédiction de la branchaison. Les variables dendrométriques les plus efficaces (pour la prédiction) sont mises en évidence et des modèles préliminaires sont proposés.

**branchaison / *Picea abies* Karst / modélisation / qualité du bois / houppier / ressources en bois**

## INTRODUCTION

The current interest in branchiness studies for forest trees is linked to several complementary factors: i) the search for a better description of the role of the crown compartment in growth and yield studies (Mitchell, 1969, 1975; Väisänen *et al*, 1989) and in forest decline evaluation (Roloff, 1991); ii) the need for rationalizing harvesting, logging and industrial operations which are affected by limb size (Hakkila *et al*, 1972); iii) the necessity of assessing the influence of silvicultural practices on the quality of wood products which depends partially on knottiness (Kramer *et al*, 1971; Fahey, 1991).

These considerations are well illustrated by the recent development of several models that predict both the growth and the wood quality in artificial stands (*eg* Mitchell, 1988; Väisänen *et al*, 1989) and by the conception of a software, called SIMQUA, that simulates the quality of any board sawn in a tree whose stem (*ie* global size, taper curve and ring width pattern) and branches (*ie* number, location, insertion angle of each nodal or internodal branch) are *a priori* known (Leban and Duchanois, 1990).

This software has to be fed with fairly detailed information about branchiness; presently these data have to be measured directly. Of course, this situation does not meet the requirements of operational applications and there is a strong need for predicting crown and branchiness characteristics from usual whole-tree measurements (*ie* total age, diameter at breast height, total height, etc).

The present study was initiated in this context with the specific aim of developing a new method for assessing the quality of wood resources on a regional scale. More precisely the idea was to use jointly the database of the French National Forest Survey (NFS) and Simqua in order to im-

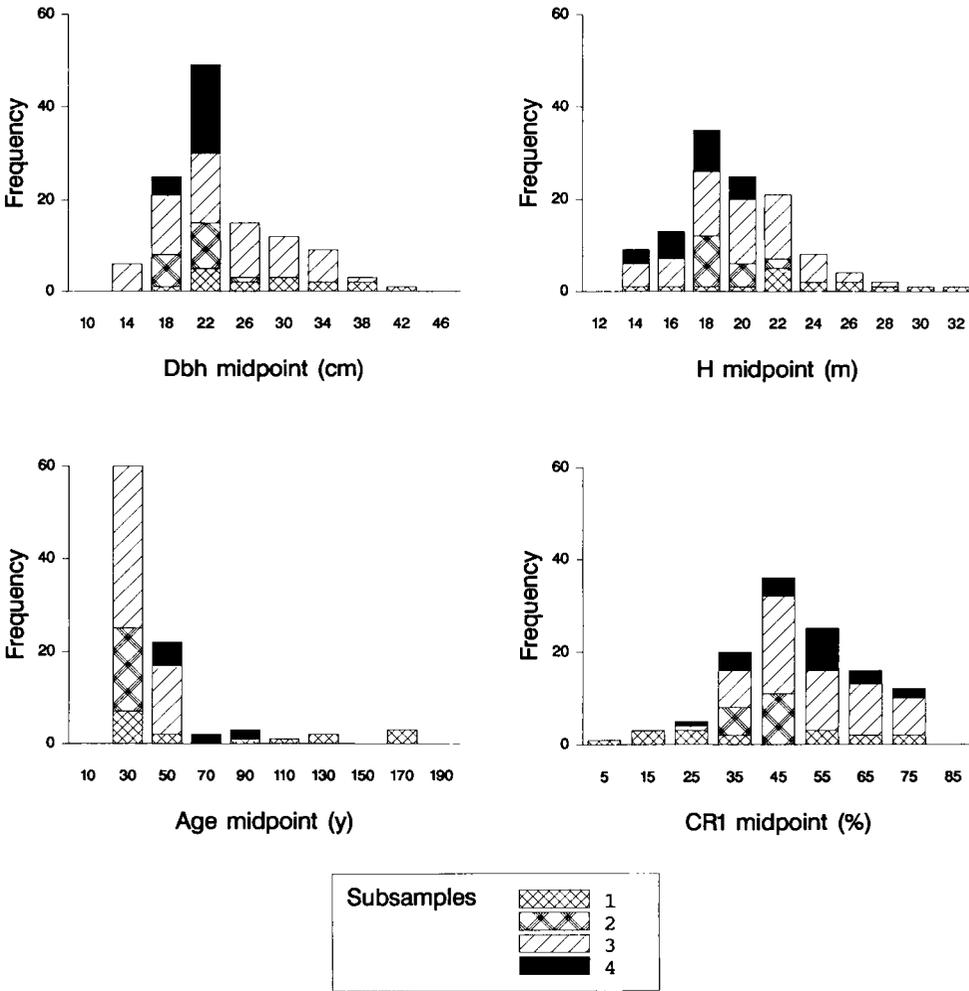
prove the evaluation of the various wood products of Norway spruce in France. Since no branchiness data are collected by the NFS, the following question arose: is it possible, merely with usual tree measurements, to predict the branchiness parameters which constitute the input of SIMQUA?

In order to answer this question, a detailed description of a small sample of Norway spruce was made and we focused on mid-size trees with a diameter at breast height (DBH) that ranged between 15–35 cm (Colin and Houllier, 1991). A latter paper presented results for the maximal nodal branch size. Our objectives here are to complete it: i) by exploring the relationships between usual whole-tree measurements and other branchiness characteristics; and ii) by displaying preliminary models. This paper deals mainly with whorl branches. Although small internodal branches do play some role in wood quality assessment, it was considered that quality is mostly determined by the characteristics of the largest branches. Moreover, from a more scientific point of view, the study of small branches leads to some technical difficulties (*eg* death and self-pruning) that were beyond the scope of this first approach.

## MATERIALS AND METHODS

### *Data collection*

The study area has been described in Colin and Houllier (*op cit*). Four subsamples called S<sub>1</sub>, S<sub>2</sub>, S<sub>3</sub> and S<sub>4</sub> were collected. The number of trees amounted to 12 for S<sub>1</sub>, 18 for S<sub>2</sub>, 63 for S<sub>3</sub> and 24 for S<sub>4</sub>. Figure 1 provides the frequency distribution of sampled trees for various characteristics: total height, DBH, age and crown ratio (see below). These distributions are not balanced for two reasons: the study was focused on mid-size trees which were relatively young (20–60 yr); the successive subsamples were carried out with different objectives (*eg* the 18 trees in S<sub>2</sub>



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

came from the same even-aged stand and were sampled for studying within-stand variability).

For three subsamples ( $S_1$ ,  $S_2$  and  $S_4$ ) measurements were taken after felling, whereas  $S_3$  trees were described by climbing them. The latter operation was primarily intended to validate limb-size distribution models (Colin and Houllier, *op cit*). The trees belonging to subsamples  $S_1$  to  $S_3$  were already described in Colin and Houllier

(*op cit*). The trees of subsample  $S_4$  came from forests managed by the ONF (l'Office National des Forêts) and were located in the Vosges mountains (northeastern France). Branchiness was described by measuring the diameter (to the nearest 2 mm) and length (to the nearest 2 cm) of the branches whose diameter was > 5 mm, and the number of whorls per 1-meter-length-unit. The following whole-tree descriptors

were measured: the diameter at breast height (to the nearest 5 mm), the total height (to the nearest 10 cm), the age at the stump (to the nearest 1 to 5 yr, depending on age), the height to the first live branch, the height to the first dead branch and the height to the base of the live crown (to the nearest 10 cm) which was defined by the first whorl where at least tree-quarters of branches were still living (modified from Curtis and Reukema, 1970; Maguire and Hann, 1987; Kramer, 1988).

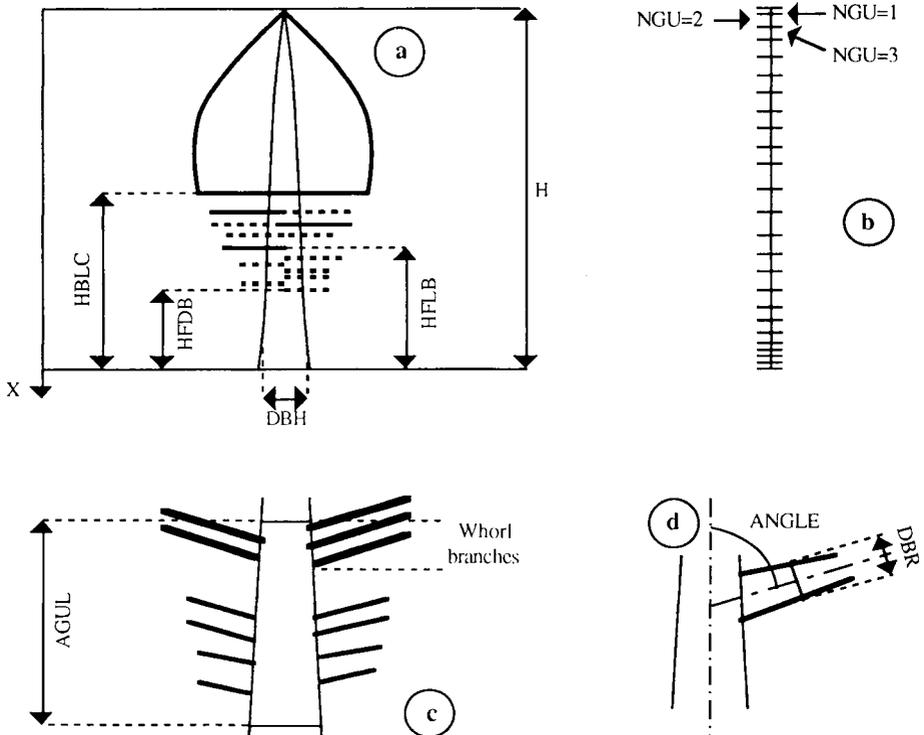
### Variables

Two kinds of data were used: 'branch descriptors' and 'whole-tree descriptors'. The latter were the usual tree measurements and different crown heights and crown ratios (fig 2a):

*AGE* = total age of the tree (in yr); *DBH* = diameter of the stem at breast height (in cm); *H* = total height of the stem (in m); *H/DBH* = ratio between *H* and *DBH* (in cm/cm); *HFLB* = height to the first live branch (in m); *HFDB* = height to the first dead branch (in m); *HBLC* = height to the base of the live crown as previously defined (in m); *CR* =  $100 (H - HBLC/H)$  (in %); *CR*<sub>3</sub> =  $100 (H - HFLB/H)$  (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 (figs 2b,c):

*X* = absolute distance from the upper bud scale scars of the annual shoot to the top of the stem (in m); *RX* =  $100 (X/H)$  = relative distance from the upper bud scale scars of the annual shoot to the top of the stem (in %); *NGU* = No of the growth unit counted downward from the top of



**Fig 2.** Definitions of crown heights (fig 2a), of annual growth unit number (fig 2b), of the annual growth unit (fig 2c) and of the insertion angle and the branch diameter (fig 2d).

the stem;  $DBR$  = diameter of the branch (in cm);  $ANGLE$  = external insertion angle of the branch with the stem (in degrees);  $DBR_{MAX}$  = diameter of the thickest branch for an annual shoot (in cm);  $DBRAVE$  = mean diameter of whorl branches for an annual shoot (in cm);  $NTOT$  = total No of observed branches (dead or living) for an annual shoot;  $NW$  = total No of observed whorl branches (dead or living) for an annual shoot;  $N_{10}$  = total No (for an annual shoot) of branches (dead or living) whose diameter is  $\geq 10$  mm;  $N_{05}$  = total number (for an annual shoot) of branches (dead or living) whose diameter is  $\geq 5$  mm.

### Statistical analysis

The data were analysed using the SAS Statistical Package (version SAS 6.03) on a Compaq 386/25 computer with an 8 Megabytes extended memory.

During statistical analysis, trees with erroneous field data or many missing data were removed. Linear and nonlinear regression methods (Tomassone *et al.*, 1983) were extensively used. First, linear regressions were carried out in order to select the best combinations of independent variables by using adjusted  $R$ -square criterion ( $R_{adj}^2$ ). Nonlinear regressions were then used to establish most of the final models. The proposed equations were chosen as compromises between i) the search for a good fit as measured by adjustment statistics and by a visual analysis of residuals and ii) the parsimony and the robustness of the model (*ie* we tried to avoid a too great number of parameters). The following results include parameter estimates, their standard error, and their 95% confidence interval, root mean squared error ( $RMSE$ ) or weighted mean squared error ( $WMSE$ ), adjusted  $R$ -square ( $R_{adj}^2 = 1 - [(n-1) / (n-p)] (1 - R^2)$ ), global  $F$ -test, weighting expressions (when weighted least squares were used) and a graphic display of residuals. For nonlinear models, these statistics have only asymptotic properties (Seber and Wild, 1989).

Generalized linear models (Dobson, 1983) were introduced when the dispersion of the data did not look like a normal distribution around a general trend and when the random error seemed to be multiplicative rather than additive. These models were fitted by maximizing the like-

lihood of the observations. The choice of the model, which includes both the equation of the deterministic trend and the probability distribution of the random error (*eg* normal, lognormal, Weibull) was based on the value of the likelihood and on  $\chi^2$  statistics for testing the individual significance of variables and covariates (SAS, 1988).

### Other methodological aspects

The problem we deal with is quite different from those considered by Mitchell (1975), Väisänen *et al* (*op cit*) or Ottorini (1991), whose main aim was to stimulate branchiness as the result of the dynamic functional processes that link stand density and tree-to-tree competition to crown development and to stem growth. Our objective here is more descriptive and static, since we address the problem of predicting crown and branchiness characteristics from usual whole-tree measurements for trees that already exist and that are described by usual inventory data (*ie* the past silviculture of the stands as well as the site quality and the genetic origins are mostly unknown).

However, the search for good predictors of crown morphology is not independent from our knowledge on the processes that influence crown development. The most important factors are the genetic origin and the site, the stage of development of the tree as measured by its age, its size (*ie*  $H$  or  $DBH$ ) or its growth rate (*ie* length of the annual shoot), as well as the local density of the stand and the social status of the tree, which both depend on silviculture. These factors interact and simultaneously affect stem size and crown development. For example, genetic origin, site and silvicultural conditions have a strong influence on the global vigour of the tree.

As a consequence, when selecting the usual whole-stem descriptors that have good allometric relationships with crown and branch characteristics and when proposing models, the difficulty that we face is that the usual stem descriptors are correlated and that it is not possible to directly assess the underlying causes of the relationships that we observe. However, by using  $AGE$ ,  $H$  and  $DBH$  and their various combinations, especially  $H/DBH$ , it is often possible to roughly separate site, genetic and silvicultural effects.

## RESULTS

### Global description of the crown

The dependent variables were height to the first dead branch (*HFDB*), height to the first living branch (*HFLB*), height to the base of the living crown (*HBLC*) and crown ratio (*CR*) (fig 2a).

The tested independent variables were total height (*H*), total age (*AGE*), diameter at breast height (*DBH* in cm) and various combinations of these variables, such as:  $1/H$ ,  $H^2$ ,  $H/DBH$ , etc.

### Crown ratio (*CR*)

For the 117 trees, the best individual predictors were *AGE*, *DBH/H* and  $AGE^2$  ( $R_{adj}^2 = 0.21$ ). A more detailed analysis indicated that the best fit of *CR* using *AGE* was obtained with the expression  $\exp(-\alpha AGE^\beta) + \delta$  where  $\alpha$ ,  $\beta$  and  $\delta$  are parameters, the best value for  $\beta$  being nearly 1.5. It was then established that  $H/DBH$  and  $H^2$  also had to be included in the regression equation so that we finally obtained:

$$CR (\%) = 100 (\delta + \exp(-\alpha AGE^{1.5}) + \beta H/DBH + \gamma H^2) \quad [1]$$

$WMSE = 84.6$ ; residuals vs predicted values are presented in figure 3a and parameter estimates are provided in table I.

In order to take into account the fact that the data set includes both data for isolated trees and data for trees belonging to the same stand (17 trees in the same stand for  $S_2$ , 7–8 trees per stand for  $S_3$ ), the weight of each tree was inversely proportional to the number of trees belonging to the same stand. This weighting procedure led to a good fit especially for the data collected on old, isolated trees.

### Height to the base of the living crown (*HBLC*)

Since  $HBLC = H (1 - 0.01 CR)$  eq (1) was used to predict *HBLC*, the weighting expression being the product of the previous one by  $1/H^2$ .

$$HBLC = H (1 - \delta - \exp(-\alpha AGE^{1.5}) - \beta H/DBH - \gamma H^2) \quad [2]$$

### Height to the first living branch (*HFLB*)

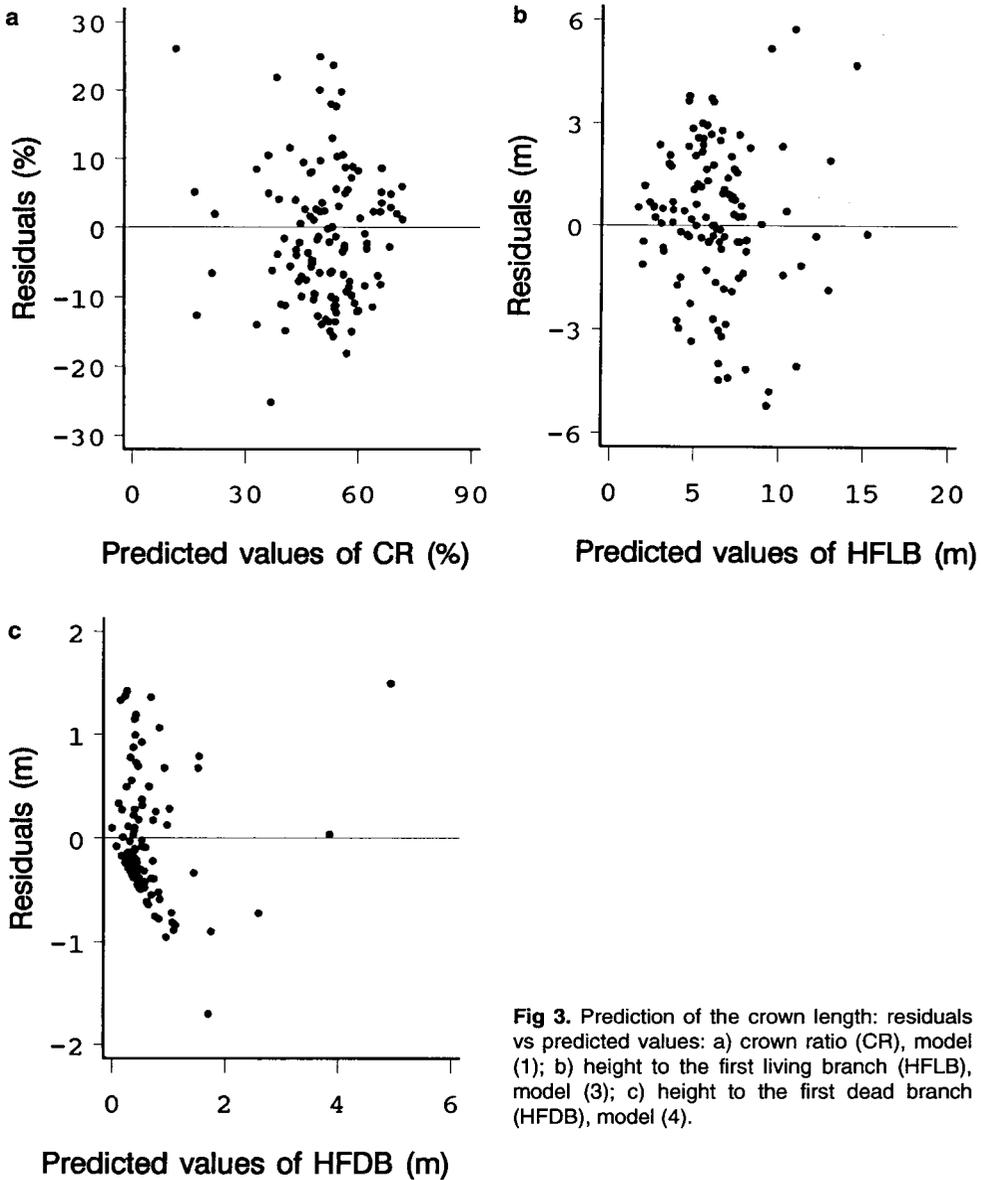
For the same trees, we used the same method (equation and weighting expression) as for *HBLC*. We finally obtained:

$$HFLB = H (1 - \delta' - \exp(-\alpha' AGE^{1.5}) - \beta' H/DBH - \gamma' H^2) \quad [3]$$

$WMSE = 85 \cdot 10^{-4}$ ; parameter estimates are given in table II and residuals are presented in figure 3b.

**Table I.** Parameter estimates for the prediction of crown ratio, *CR* (eq [1]).

Parameter	Estimate	Asymptotic standard error	Asymptotic 95% confidence interval	
			Lower	Upper
$\alpha$	$2.2412 \cdot 10^{-4}$	$0.0442 \cdot 10^{-3}$	$1.3661 \cdot 10^{-4}$	$3.1163 \cdot 10^{-4}$
$\beta$	$-5.4098 \cdot 10^{-3}$	$0.6571 \cdot 10^{-3}$	$-6.7116 \cdot 10^{-3}$	$-4.1080 \cdot 10^{-3}$
$\gamma$	$-2.3791 \cdot 10^{-4}$	$0.7565 \cdot 10^{-4}$	$-3.8779 \cdot 10^{-4}$	$-0.8802 \cdot 10^{-4}$
$\delta$	$1.3273 \cdot 10^{-1}$	$0.6142 \cdot 10^{-1}$	$1.1041 \cdot 10^{-1}$	$2.5441 \cdot 10^{-1}$



**Fig 3.** Prediction of the crown length: residuals vs predicted values: a) crown ratio (CR), model (1); b) height to the first living branch (HFLB), model (3); c) height to the first dead branch (HFDB), model (4).

#### Height to the first dead branch (HFDB)

The statistical analysis was carried out on 96 trees (pruned trees were removed). The previous form of the model was first tested

but the best results were obtained with a linear model including *H.AGE*, *H/DBH* and *DBH.AGE*; as previously, the weighting expression took into account the number of sample trees in each stand.

**Table II.** Parameter estimates for the prediction of height to the first live branch, *HFLB* (eq [3]).

Parameter	Estimate	Asymptotic standard error	Asymptotic 95% confidence interval	
			Lower	Upper
$\alpha'$	$0.9380 \cdot 10^{-4}$	$0.3518 \cdot 10^{-4}$	$0.2410 \cdot 10^{-4}$	$1.6350 \cdot 10^{-4}$
$\beta'$	$-5.6288 \cdot 10^{-3}$	$0.7000 \cdot 10^{-3}$	$-7.0157 \cdot 10^{-3}$	$-4.2419 \cdot 10^{-3}$
$\gamma'$	$-2.2063 \cdot 10^{-4}$	$0.7021 \cdot 10^{-4}$	$-3.7955 \cdot 10^{-4}$	$-0.6172 \cdot 10^{-4}$
$\delta'$	$2.8455 \cdot 10^{-1}$	$0.6532 \cdot 10^{-1}$	$1.5514 \cdot 10^{-1}$	$4.1397 \cdot 10^{-1}$

$$HFDB = \alpha'' H/DBH + \beta'' H AGE + \gamma'' DBH AGE + \delta'' \quad [4]$$

WMSE = 0.59; parameter estimates are given in table III and residuals are presented in figure 3c.

#### Vertical trend of nodal limb size

##### Diameter of the thickest branch per tree

Ramicorn branches with a diameter > 5 cm were removed and trees with evident expressions of ramicorn, due to frost and/or to forest decline damages were not considered. However, ramicorn branches with a smaller diameter were taken into account, since it was difficult to recognize them. In order to predict the maximum branch diameter per tree (*MAXD*) we test-

ed the following independent variables: *DBH*, *AGE*, *H*, *H/DBH*. For a total number of trees of 117, the best individual predictor was *DBH* ( $R_{adj}^2 = 0.59$ ). No additional independent variable could improve the model so that we finally obtained:

$$MAXD = \alpha + \beta DBH \quad [5]$$

RMSE = 0.1412 *DBH*; weighting expression =  $DBH^{-2}$ ; parameter estimates are given in table IV; the model is illustrated in figure 4).

##### Vertical trend of maximal branch diameter (*DBRMAX*)

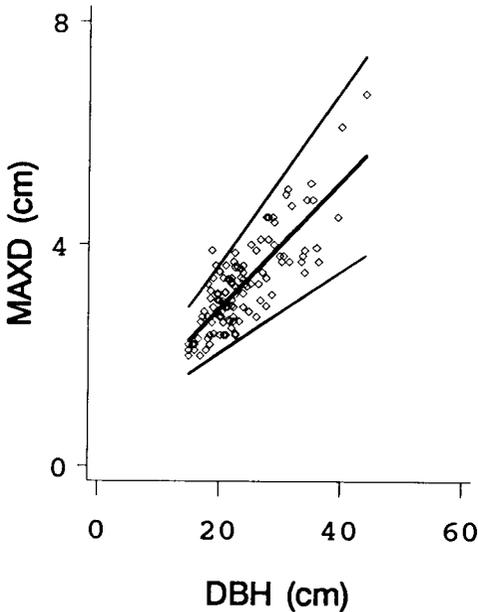
The construction of the model predicting the maximum branch diameter per growth unit is explained in Colin and Houllier (*op*

**Table III.** Parameter estimates for the prediction of height to the first dead branch, *HFDB* (eq [4]).

Parameter	Estimate	Standard error	T for H0 (param = 0)	Prob >  T
$\alpha''$	$5.380 \cdot 10^{-2}$	$0.7264 \cdot 10^{-2}$	-7.101	< 0.0001
$\beta''$	$-4.7200 \cdot 10^{-3}$	$0.7074 \cdot 10^{-3}$	-6.730	< 0.0001
$\gamma''$	$4.0410 \cdot 10^{-3}$	$0.5355 \cdot 10^{-3}$	7.463	< 0.0001
$\delta''$	-4.1738	0.5978	7.270	< 0.0001

**Table IV.** Parameter estimates of the model predicting the diameter of the thickest branch per tree, *MAXD* (eq [5]).

Parameter	Estimate	Standard	T for H0	Prob >  T
$\alpha$	$5.624 \cdot 10^{-1}$	$1.908 \cdot 10^{-1}$	2.948	0.0039
$\beta$	$1.142 \cdot 10^{-1}$	$8.766 \cdot 10^{-3}$	13.185	< 0.0001

**Fig 4.** Prediction of the maximum value of branch diameter per tree (actual and predicted values and 95% confidence interval limits).

*cit*): there is no distinction between dead and living branches; the independent variables are the relative depth into the crown (*RX*), the standard whole-tree measurements *H*, *DBH*, *H/DBH* and the global crown descriptors *HFLB* and *CR<sub>3</sub>*; the model is a segmented second order polynomial model with a join point  $\xi$  corre-

sponding to the position of the estimated thickest branch; the model was improved by adding an intercept term,  $\lambda$ :

$$DBRMAX = \lambda + \alpha RX + \beta RX^2 \quad \text{if } RX < \xi \quad [6.1]$$

$$DBRMAX = \lambda + \alpha \xi + \beta \xi^2 + \gamma (RX - \xi)^2 \quad \text{if } RX \geq \xi$$

where  $\lambda$ ,  $\alpha$ ,  $\beta$ ,  $\gamma$  and  $\xi$  are parameters:  $\lambda > 0$  and

$$\xi = b_1 CR_3 + b_2 H \quad [6.2]$$

$$\alpha = b_3 CR_3 + b_4 H/DBH + b_5 HFLB \quad [6.3]$$

$$\gamma = b_6 + b_7 CR_3 + b_8 DBH \quad [6.4]$$

$$\beta = -(\alpha / 2 \xi) \quad [6.5]$$

The model was fitted to 90 trees using nonlinear ordinary least squares (*RMSE* = 0.48 cm; parameter estimates are given in table V). Figure 5 illustrates the sensitivity of *DBRMAX* to usual whole-tree descriptors by showing three groups of simulations for various combinations of *DBH*, *H* and *CR<sub>3</sub>*.

#### **Vertical trend of average whorl branch diameter (*DBRAVE*)**

Model [6] was adapted to predict the vertical trend of the average whorl branch diameter (*DBRAVE*). This variable could be calculated for 29 trees. For these trees, the model became:

**Table V.** Parameter estimates of the model predicting maximum branch diameter per growth unit, *DBRMAX* (eq [6.1]–[6.5]).

Parameter	Estimate	Asymptotic standard error
$\lambda$	$8.189 \cdot 10^{-1}$	$5.209 \cdot 10^{-2}$
b1	$6.079 \cdot 10^{-1}$	$1.419 \cdot 10^{-2}$
b2	$-1.515 \cdot 10^{-1}$	$3.812 \cdot 10^{-3}$
b3	$1.854 \cdot 10^{-3}$	$5.365 \cdot 10^{-5}$
b4	$-1.429 \cdot 10^{-3}$	$5.055 \cdot 10^{-5}$
b5	$1.703 \cdot 10^{-2}$	$5.826 \cdot 10^{-4}$
b6	$8.277 \cdot 10^{-4}$	$5.475 \cdot 10^{-5}$
b7	$-1.402 \cdot 10^{-5}$	$8.050 \cdot 10^{-7}$
b8	$-1.897 \cdot 10^{-5}$	$1.661 \cdot 10^{-6}$

$$DBRAVE = \lambda' + \alpha' RX + \beta' RX^2 \quad [7.1]$$

if  $RX < \xi'$

$$DBRAVE = \lambda' + \alpha' \xi' + \beta' \xi'^2 + \gamma' (RX - \xi')^2$$

if  $RX \geq \xi'$

where  $\lambda'$ ,  $\alpha'$ ,  $\beta'$ ,  $\gamma'$  and  $\xi'$  are parameters:  $\lambda' > 0$  and

$$\xi' = b_0' + b_1' CR_3 + b_2' H \quad [7.2]$$

$$\alpha' = b_3' CR_3 + b_4' H/DBH + b_5' HFLB \quad [7.3]$$

$$\gamma' = b_6' + b_7' CR_3 + b_8' DBH \quad [7.4]$$

$$\beta' = -(\alpha' / 2 \xi') \quad [7.5]$$

The model was fitted to 29 trees using nonlinear ordinary least squares ( $RMSE = 0.33$  cm; parameter estimates are given in table VI; a comparison with *DBRMAX* model is illustrated in figure 6).

### Insertion angle (ANGLE)

For predicting the vertical trend of *ANGLE* for dead and living whorl branches along the stem, 2 different independent variables were tested: the number of the annual growth unit counted downward from the top of the stem (*NGU*) and the depth into the crown (*X*).

Figure 7 illustrates the relationship between *ANGLE* and *X* for  $S_1$  and  $S_2$  subsamples. Three groups of trees can be seen in this figure: i)  $S_1$  trees for which  $AGE > 60$  yr: their *ANGLE* values appear to be larger than the average trend; ii)  $S_1$  trees for which  $AGE \leq 60$  yr have intermediate *ANGLE* values; iii)  $S_2$  trees ( $AGE = 34$  yr) exhibit the lowest angles, as illustrated for two individuals.

When replacing *X* by *NGU* as the independent variable, the structure of the data looks better: figure 8 illustrates the good superposition of the tree above-defined groups of trees. We therefore chose *NGU* as the predictor and fitted the following nonlinear model:

$$ANGLE = \vartheta_1 + \vartheta_2 (1 - \exp(-\vartheta_3 NGU))^{1/3} \quad [8]$$

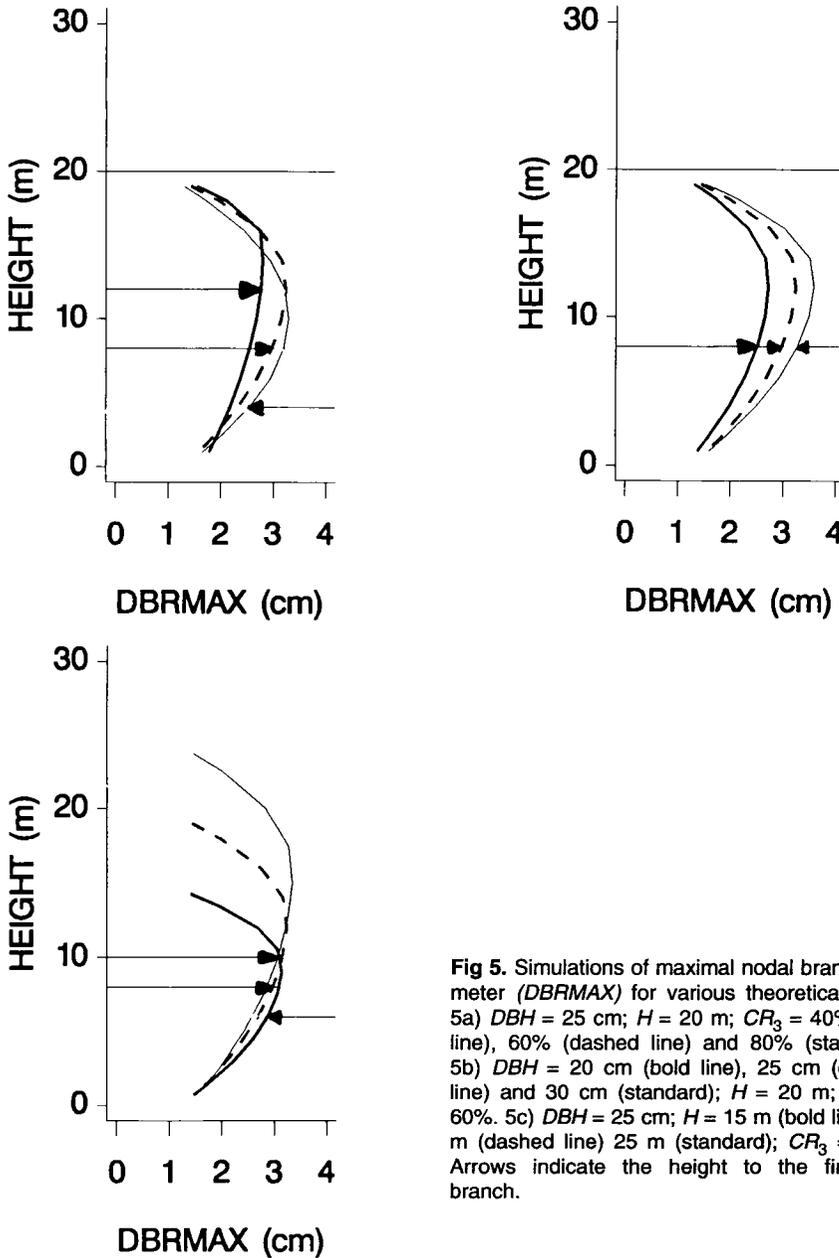
where  $\vartheta_1 + \vartheta_2$  is the maximum angle (ie the plateau value).

$WMSE = 136.319$ ; weighting expression =  $\exp(0.04 NGU)$ ; parameter estimates are given in table VII; data and fitted curve are given in figure 8.

However, when considering separately the 2 subsamples  $S_1$  and  $S_2$ , it appeared that some differences remained. Two separate models, one for each subsample, were therefore fitted and it turned out that they were significantly different (table VIII). Since a detailed analysis of the variability would have required more data than available, it was not possible to elucidate the reasons of this discrepancy (ie site, genetic or silvicultura effect).

### Numbers of branches per growth unit (NTOT, NW, $N_{10}$ and $N_{05}$ )

Figure 9 shows the vertical trend of the numbers of branches for two different trees (respectively 38 and 175 years old). Four variables corresponding to different groups



**Fig 5.** Simulations of maximal nodal branch diameter (*DBRMAX*) for various theoretical trees. 5a) *DBH* = 25 cm; *H* = 20 m;  $CR_3$  = 40% (bold line), 60% (dashed line) and 80% (standard). 5b) *DBH* = 20 cm (bold line), 25 cm (dashed line) and 30 cm (standard); *H* = 20 m;  $CR_3$  = 60%. 5c) *DBH* = 25 cm; *H* = 15 m (bold line), 20 m (dashed line) 25 m (standard);  $CR_3$  = 60%. Arrows indicate the height to the first live branch.

of branches were studied: all branches (*NTOT*), whorl branches (*NW*), and the thickest branches ( $N_{05}$  and  $N_{10}$ ). *NW* and

$N_{10}$  are very similar and are fairly stable along the stem; the mean values of *NW* and  $N_{10}$  are clearly lower for the older

**Table VI.** Parameter estimates of the model predicting average whorl branch diameter per growth unit, *DBRAVE* (eq [7.1–7.5]).

<i>Parameter</i>	<i>Estimate</i>	<i>Asymptotic standard error</i>
$\lambda'$	$5.4744 \cdot 10^{-1}$	$4.8357 \cdot 10^{-2}$
$b_0'$	5.6780	2.8026
$b_1'$	$5.4934 \cdot 10^{-1}$	$3.2989 \cdot 10^{-2}$
$b_2'$	$-3.8122 \cdot 10^{-1}$	$8.9643 \cdot 10^{-2}$
$b_3'$	$1.3676 \cdot 10^{-4}$	$1.0626 \cdot 10^{-4}$
$b_4'$	$-8.5021 \cdot 10^{-4}$	$1.0558 \cdot 10^{-4}$
$b_5'$	$1.3482 \cdot 10^{-4}$	$7.7554 \cdot 10^{-6}$
$b_6'$	$7.6535 \cdot 10^{-4}$	$1.2120 \cdot 10^{-4}$
$b_7'$	$-1.0405 \cdot 10^{-5}$	$1.1887 \cdot 10^{-6}$
$b_8'$	$-1.8927 \cdot 10^{-5}$	$3.4150 \cdot 10^{-6}$

**Table VII.** Parameter estimates of the global model predicting the vertical trend of the insertion angle of branches, *ANGLE* (eq [8]).

<i>Parameter</i>	<i>Estimate</i>	<i>Asymptotic standard error</i>
$\vartheta_1$	2.4392 10	3.3043
$\vartheta_2$	7.9298 10	2.3854
$\vartheta_3$	$3.1842 \cdot 10^{-2}$	$5.3910 \cdot 10^{-3}$

slow-growing-trees; the general trend of *NTOT* is not easy to determine, whereas  $N_{05}$  is clearly decreasing downward the stem; there are high frequency fluctuations (probably due to annual climatic variations) around the general vertical trend.

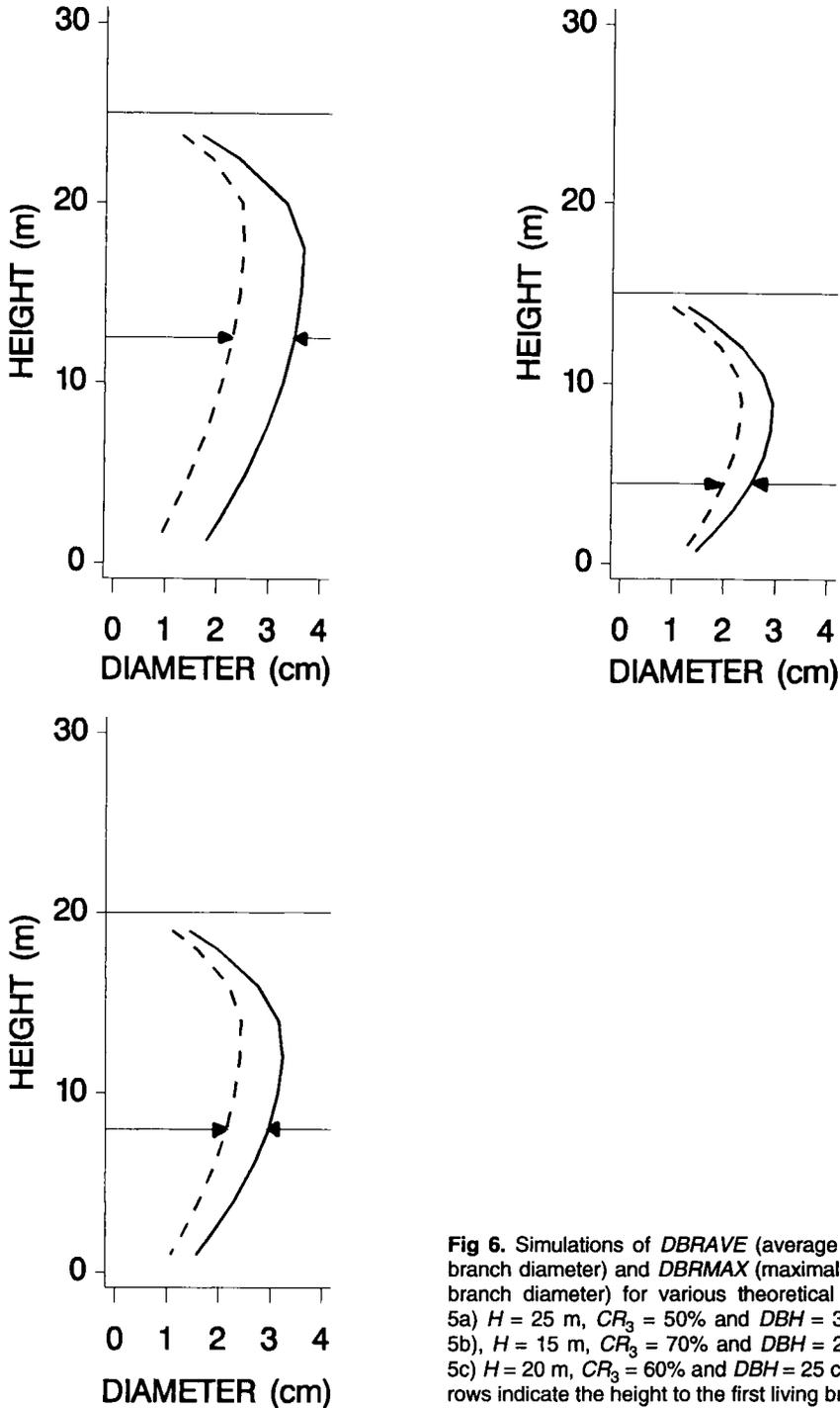
Some branch studies (Cannell, 1974; Cannell and Bowler, 1978; Remphrey and Powell, 1984; Maguire *et al.*, 1990) have shown that there is a good relationship between the length of the annual growth unit (*AGUL*) and its number of branches so that *AGUL* can be used as an independent

variable in predicting the number of branches. In all these studies, linear or nonlinear regressions were carried out and the distribution of the random error was assumed to be normal. However, de Reffye's team seldom observed normal distributions when modelling growth and ramification by counting the number of internodes ('stem units') and axillary buds occurring on annual growth units (de Reffye *et al.*, 1991; Caraglio *et al.*, 1990). The statistical models of branch numbers should therefore be based on other probability distribution functions.

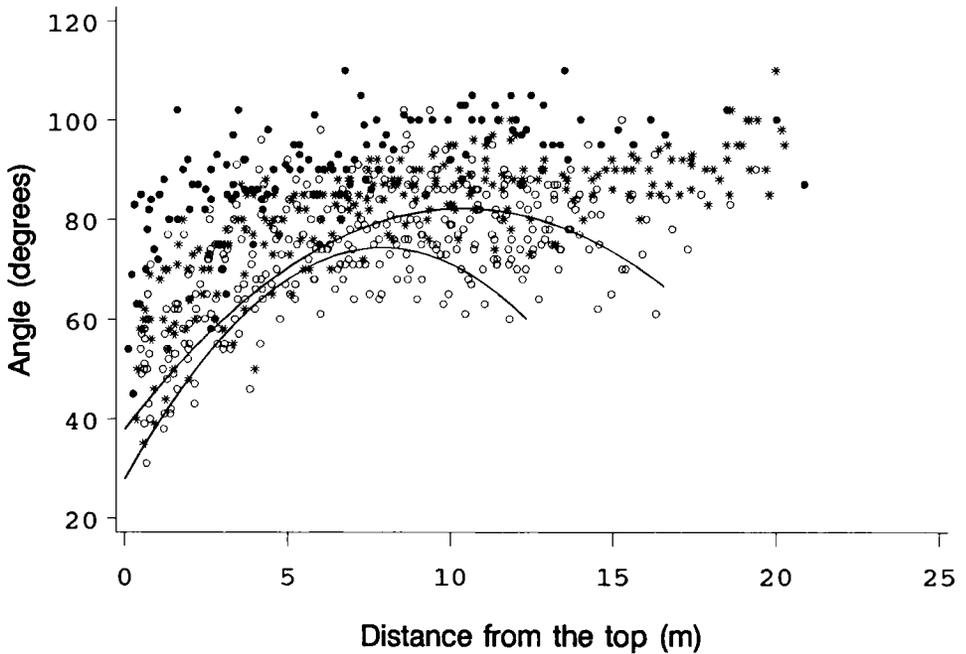
These results are confirmed here. There is a statistical relationship between *AGUL* and the number of branches and although the stage of development is not the same for younger and older trees, this relationship does not seem to be influenced by tree age (fig 10a). Young trees (*ie*  $AGE < 60$  yr) for which the height growth is still linear have longer growth units than older slow-growing trees (there are four such trees in the data set with  $AGE = 90, 102, 175$  and  $180$  yr) which have nearly reached their maximum height, but the trend of the relationship is the same. This figure also shows that the dispersion of the number of branches increases with increasing values of *AGUL*.

Figure 10b shows the frequency distribution of  $N_{10}$  for the annual growth units studied for both old and young trees ( $AGE > 60$  yr vs  $AGE \leq 60$  yr). The average values of  $N_{10}$  are different because of the difference of the length of the annual growth units, but the distributions have a similar shape (they are left-skewed). A single model was therefore elaborated, assuming that *AGUL* synthesizes the effect of age and climate on branch numbers.

Since the dispersion is neither normal nor additive but multiplicative, different generalized linear models were tested so that we finally obtained:



**Fig 6.** Simulations of *DBRAVE* (average nodal branch diameter) and *DBRMAX* (maximal nodal branch diameter) for various theoretical trees. 5a)  $H = 25$  m,  $CR_3 = 50\%$  and  $DBH = 30$  cm. 5b),  $H = 15$  m,  $CR_3 = 70\%$  and  $DBH = 20$  cm. 5c)  $H = 20$  m,  $CR_3 = 60\%$  and  $DBH = 25$  cm. Arrows indicate the height to the first living branch.



**Fig 7.** Actual data of angle (in °) vs distance from the top (X) for old trees (age > 60 yr) of subsample S<sub>1</sub> (symbol: dot), for young trees (age ≤ 60 yr) of subsample S<sub>1</sub> (symbol: star) and for trees of subsample S<sub>2</sub> (symbol: circle). The two solid curves are parabolas adjusted to two S<sub>2</sub> trees.

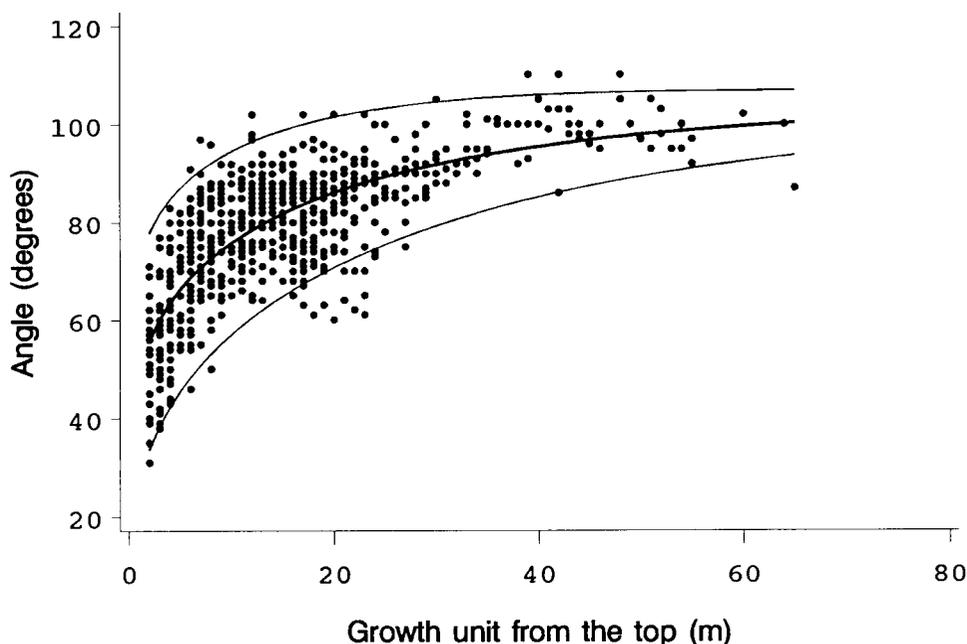
**Table VIII.** Parameter estimates for the separate models predicting the vertical trend of the insertion angle of branches, *ANGLE*, for subsamples S<sub>1</sub> and S<sub>2</sub> (eq [8]). (Comparison to the global model: *F*-statistic = 32.5 with 3 and 681 df).

Parameter	S <sub>1</sub> subsample estimate ± as st error	S <sub>2</sub> subsample estimate ± as st error
ø1	1.9660 10 ± 4.6644	0.0000 *
ø2	8.0745 10 ± 4.0076	8.1992 10 ± 12.3577
ø3	4.8911 10 <sup>-2</sup> ± 6.7297 10 <sup>-3</sup>	1.5702 10 <sup>-1</sup> ± 3.8386 10 <sup>-2</sup>

\* ø1 was bounded to be positive; st error: standard error.

$\text{Ln}(N) = \alpha \text{Ln}(AGUL) + \beta \gamma \text{NGU} + \varepsilon$ , with distribution of  $\varepsilon = \text{normal law } N(0, \sigma)$  [9.1]  
 or  $N = AGUL^\alpha \exp(\beta) \exp(\gamma \text{NGU}) \cdot \varepsilon'$  with distribution of  $\varepsilon' = \text{lognormal law } LN(0, \sigma)$  [9.2]

Figure 11 illustrates a simulation for  $N_{10}$ . Each group of three curves (for instance the curves in standard line) correspond to the 5th, 50th and 95th quantiles and de-



**Fig 8.** Fit of angle (in °) vs number of the annual growth unit (actual and predicted values and 95% confidence interval limits).

scribe the modelled dispersion of  $N_{10}$  for a given value of  $NGU$ . Two values of  $NGU$  are proposed:  $NGU = 15$  (standard line) and  $NGU = 30$  (dashed line). The values of the parameters are given in table IX, while examples of average numbers for two values of  $AGUL$  (0.5 and 1 m) are given in table X. The same method was applied to  $NW$ ,  $N_{05}$  and  $NTOT$ . The results are given in tables IX and X.

#### **Whorl branch location**

The distance from upper scale scars to the first whorl branch was never great: maximum value was approximately 10 cm. The distribution of the relative length of the part of the stem supporting whorl branches

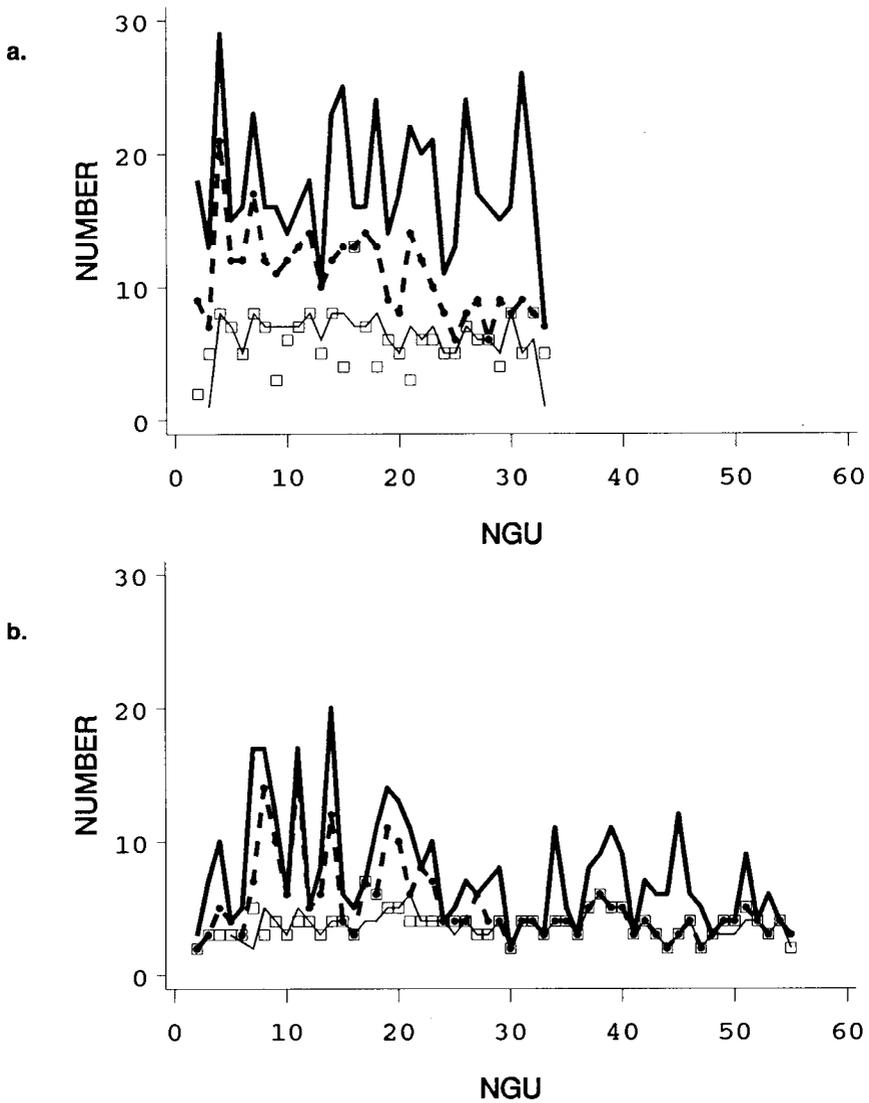
(single or double whorl in case of lammas shoots) is illustrated in figure 12. The main characteristics of these distributions are provided in table XI.

## **DISCUSSION**

### ***Methodological aspects***

#### **Dynamic vs static points of view**

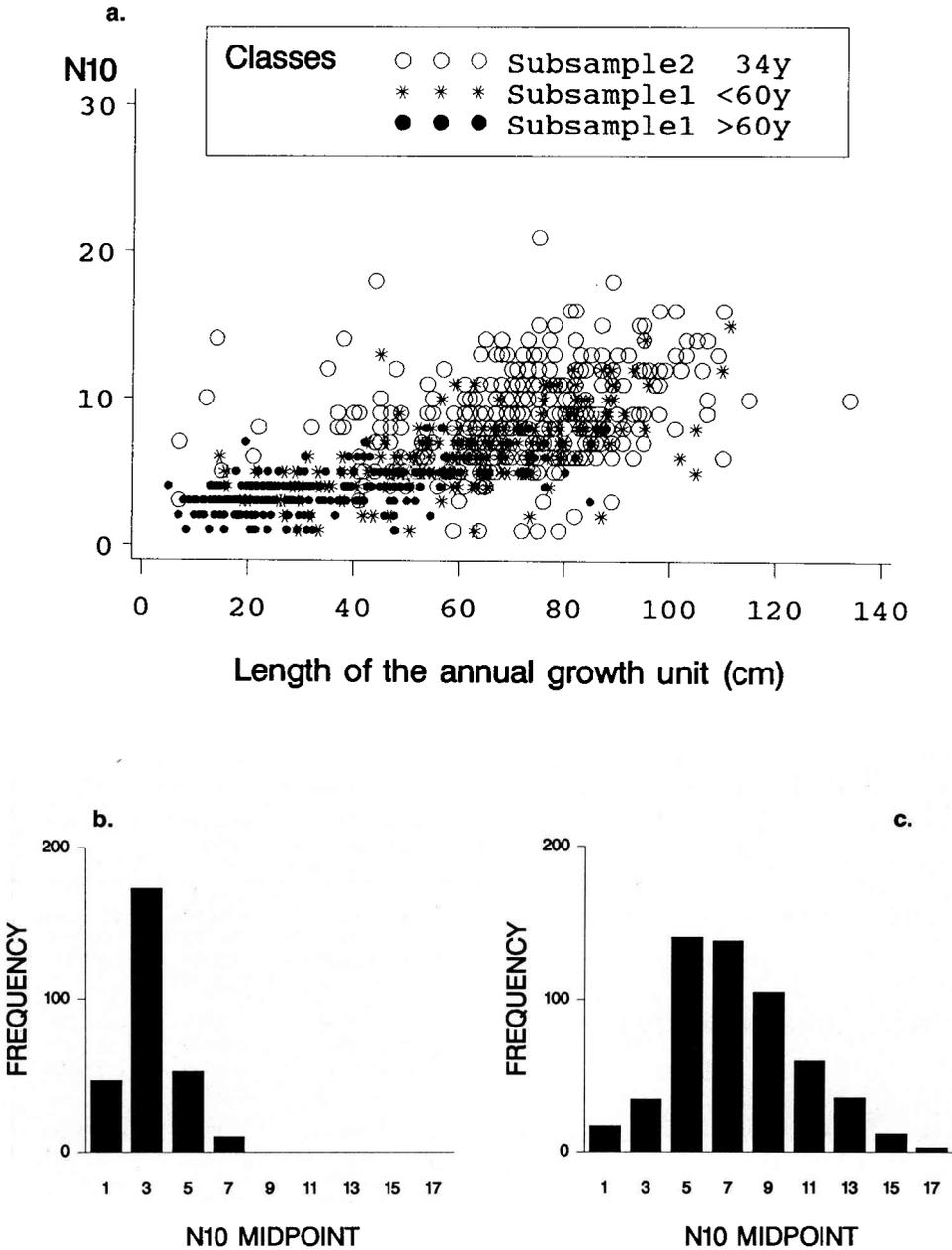
As already stated our approach does not directly address the dynamic processes which determine the relationships between stem, crown and branch characteristics. Our models must be considered as static allometric models that enable the predic-



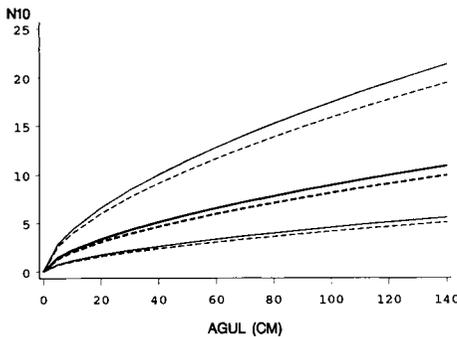
**Fig 9.** Vertical trend of branch numbers per annual growth unit: total number,  $NTOT$  (bold curve), branches of diameter  $\geq 0.5$  cm,  $N_{0.5}$  (dashed curve), branches of diameter  $\geq 1$  cm,  $N_{1.0}$  (standard curve) and whorl branches  $NW$  (squares): 9a) example of a young tree (AGE = 38 yr); 9b) example of an old tree (AGE = 175 yr).

tion of branchiness from usual stem measurements. However, we checked that these models are dynamically compatible.

As an example, we used data provided by yield tables (Décourt, 1972) for predicting branch diameter at different ages along the



**Fig 10.** Modelling of  $N_{10}$  (number of branches with a diameter  $\geq 1$  cm) for subsamples  $S_1$  and  $S_2$ . a) Actual data of  $N_{10}$  vs length of the annual growth unit of old  $S_1$  trees ( $AGE > 60$  yr), of young  $S_1$  trees ( $AGE \leq 60$  yr) and of  $S_2$  trees. 10b) Frequency distribution of  $N_{10}$  for trees of  $AGE > 60$  yrs and c) for younger trees.



**Fig 11.** Predicted number of branches  $N_{10}$  (5th, 50th and 95th quantiles) vs length of the annual growth unit (AGUL, in cm) for  $NGU = 15$  (standard lines) and for  $NGU = 30$  (dashed lines).

stem (fig 13) of the mean dominant tree. These simulations show; 1) that superposition of the curves is consistent with growth processes (*i.e.* the curves do not cross

each other and are nearly the same for the lower part of the stem where dead and declining branches are located); and 2) that the maximum branch diameter increases when trees get older.

A comparison with tree architecture studies leads to the same kind of remark. For example, the aim of Caraglio *et al* (*op cit*) or de Reffye *et al* (*op cit*) is to stimulate tree architecture by using botanical and statistical knowledge on the dynamic behaviour of apical meristems. The aim of the present study was quite different, since the current number of branches at a point of time and at a level in the tree had to be assessed from usual whole-tree descriptors and average relationships (including the usual height-over-age growth curves). Therefore, whereas other authors would consider that the length of the annual growth unit is functionally determined by the number of internodes or axillary buds

**Table IX.** Estimated parameters for the general linear models used for predicting the number of branches:  $NTOT$ ,  $N_{05}$ ,  $N_{10}$  and  $NW$ . Error ( $\epsilon'$ ) was supposed to be lognormal with  $\sigma$  = scale parameter (eq [9]).

Numbers	Model Log (likelihood)	Parameter estimates	Standard error	$Pr > \chi^2$
$NTOT$	$N = AGUL^\alpha \cdot \exp(\beta) \cdot \exp(\gamma \cdot NGU) \cdot \epsilon'$ -393.501	$\alpha = 0.7391$	0.0216	< 0.0001
		$\beta = 0.1857$	0.0910	0.0412
		$\gamma = -0.0201$	0.0008	< 0.0001
		$\sigma = 0.5137$	0.0093	
$N_{05}$	$N = AGUL^\alpha \cdot \exp(\beta) \cdot \exp(\gamma \cdot NGU) \cdot \epsilon'$ -345.809	$\alpha = 0.7286$	0.0211	< 0.0001
		$\beta = -0.3290$	0.0892	0.0002
		$\gamma = -0.0159$	0.0008	< 0.0001
		$\sigma = 0.3643$	0.0089	
$N_{10}$	$N = AGUL^\alpha \cdot \exp(\beta) \cdot \exp(\gamma \cdot NGU) \cdot \epsilon'$ -417.443	$\alpha = 0.6037$	0.0277	< 0.0001
		$\beta = -0.5006$	0.1194	< 0.0001
		$\gamma = -0.0063$	0.0009	< 0.0001
		$\sigma = 0.4085$	0.0102	
$NW$	$N = AGUL^\alpha \cdot \exp(\beta) \cdot \exp(\gamma \cdot NGU) \cdot \epsilon'$ -375.124	$\alpha = 0.4634$	0.0215	< 0.0001
		$\beta = -0.0195$	0.0905	0.8299
		$\gamma = -0.0057$	0.0008	< 0.0001
		$\sigma = 0.3768$	0.0109	

**Table X.** Simulation of the 50th quantile for the number of branches per annual growth unit. ( $NTOT$  = total number,  $N_{0.5}$  = branches with diameter  $\geq 0.5$  cm,  $N_{1.0}$  = branches with diameter  $\geq 1$  cm,  $NW$  = whorl branches) for 2 values of the length of annual growth unit ( $AGUL = 0.5$  and  $1$  m) and for 2 values of the number of the growth unit ( $NGU = 15$  and  $30$ ).

No of branches		AGUL = 0.50 m	AGUL = 1.0 m
$NTOT$	NGU = 15	16.0	26.8
	NGU = 30	11.9	19.8
$N_{0.5}$	NGU = 15	9.8	16.2
	NGU = 30	7.7	12.8
$N_{1.0}$	NGU = 15	5.8	8.9
	NGU = 30	5.3	8.1
$NW$	NGU = 15	5.5	7.6
	NGU = 30	5.1	7.0

(eg Kremer *et al*, 1990, or Guyon, 1986 for pines) we predicted the numbers of branches by using  $AGUL$  as the main independent variable.

Another important point concerns the distinction between living and dead branches. Our models provide a description of the different zones in the crown but they do not provide any information about the status of a particular branch.

## Variability

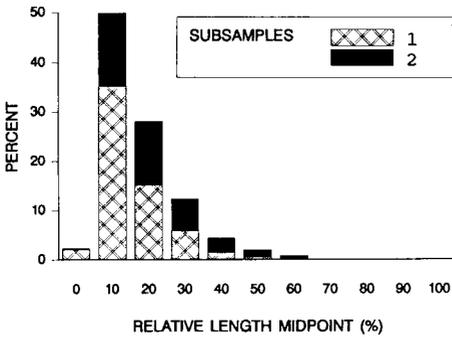
Since the final objective of the study is to predict crown and branchiness characteristics from forest inventory data at a regional scale, we had to deal with several levels of variability: between-stands (including age, site, silvicultural and genetic effects), within-stands (including genetic and tree-to-tree competition effects) and within-tree variability (including age, climatic and varying-over-time tree-to-tree competition effects). Our results will therefore be compared to four groups of studies: within-tree, within-stand, between-stands and extensive forest inventory surveys.

## Sampling design and statistical models

Most statistical difficulties that appear in this study are due to the fact that our sampling design could not be used to model the effects of all the factors that determine branchiness and in particular to explore in detail the different levels of variability that have been listed. As an example, let us consider the case of branch insertion angle. Since only one branch was sampled in each whorl (it was subjectively chosen as being 'representative' of the other branches in the whorl) and since eq [8] is a global model adjusted on all sample trees, within-whorl variability, between-growth unit variability and between-tree variability cannot be clearly distinguished in figures 7 and 8.

**Table XI.** Main characteristics of the distribution of the relative length of the whorl.

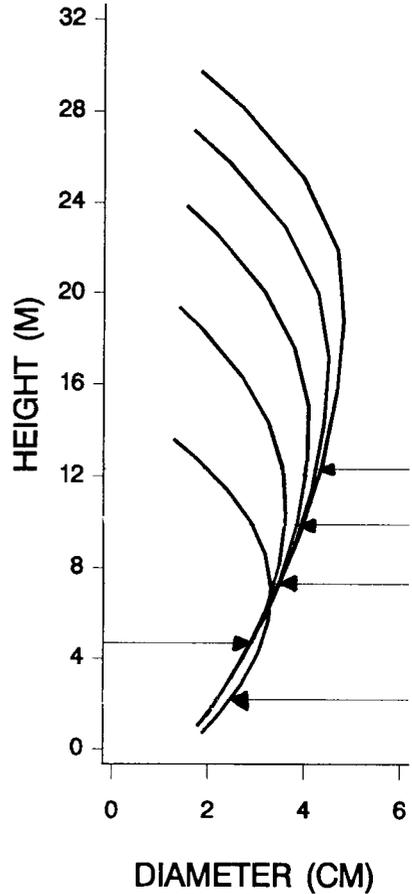
Samples	No of whorls	Minimum	Maximum	Mean	SD
S1	465	0.16	80.47	15.13	8.96
S2	285	4.41	63.3	21.7	12.3



**Fig 12.** Frequency distribution of the relative length of the whorl within annual growth unit (AGU) for subsamples  $S_1$  and  $S_2$ .

Our sampling design has two drawbacks. First, the choice of a sample representative of the resource for a fixed size-range (except for subsample  $S_2$ ) leads i) to a design that is not balanced according to stand characteristics (eg only few old stands were sampled); and ii) to equations that cannot be extrapolated to the whole life of a stand or a tree (eg the effect of age on crown recession is not precisely described for early stages so that eq [1-4] cannot be extrapolated to young ages). Second, the number of trees varies from 1-18 per stand, so that weighting functions had to be modified in order to give the same weight to the different stands.

There are at least two possibilities for improving the description of the variability. Firstly, a better statistical approach in the context of such a sampling design would be to use random-effect linear or nonlinear models (ie the model parameters are assumed to be randomly distributed among a tree or stand population; see Lappi, 1991, for an application in another domain); this was not carried out because our main goal was to model the global trends and relationships and because fitting such models



**Fig 13.** Simulation of the maximum diameter of branch per whorl along the stem for different ages and sizes of a mean dominant tree, according to Décourt's yield tables (1972) and to second yield class. Arrows indicate the successive heights to the first living branch.

requires specialized software that is rarely available. Secondly, it is possible to initiate specific studies in order to obtain more precise information about the effect of the different factors; such studies are presently being carried out for genetic and silvicultu-

ral (*ie* stand density and social status) aspects.

### **Different parts of the crown**

The comparison to other studies is possible for the height to the first dead branch and the height to the first live branch whose definitions are always the same, whereas care must be taken when analyzing crown ratio and height to live crown since in most cases their definition are somewhat different from ours.

### **Within-stand studies**

Burger (1936, 1939a,b) found a high correlation between *DBH* and the different heights of crown within a stand. The situation changes according to the stage of development of the stand. For young stands (*ie* before 40 yr), where competition is high, *HBLC* is lower for suppressed and overtopped trees than for the others. When the stands get older, *HBLC* becomes nearly the same for all trees. This fact was confirmed by Delvaux (1979).

Studying the slow self-pruning process for *Picea abies*, Köster (1934) observed that a branch-free part began to appear on the trunk when trees were about 85 yr old; when trees were 105 yr old the length of this part was only 1.5 m. Therefore, *HFDB* depends on tree age after at least 80 years.

### **Between-stand studies**

For *Picea abies* even-aged stands where the same forest management had been applied, Kramer (1962) established a close relationship between the average total height and the average height to the live crown base. By using this relationship and the mean height growth curve correspond-

ing to a given site index, he could picture that the trends of *HBLC* and *CR* according to *AGE*: *CR* approximately followed an exponentially decreasing function. Eversole (1955), Curtis and Reukema (1970), Kramer and Smith (1985; in Kramer, 1988) demonstrated the effect of initial density on *HBLC* and *CR* for trees of the same age. The latter authors further showed that this effect may actually be predicted from the size of the trees, *ie* two trees with the same *DBH*, one suppressed in a first stand (low density), the other dominant in a second stand (high density), have about the same *HBLC* and *CR*. Consequently, for a given age, tree size measurements are pertinent independent variables for predicting crown characteristics.

### **Forest inventory studies**

The main studies that we refer to concern Lithuanian and Finnish Norway spruce resources (Arlauskas and Tyabera, 1986; Hakkila *et al*, 1971, Hakkila *et al*, 1972). The number as well as the main characteristics of the sampled trees are not the same: 2 306 trees in Lithuania (*DBH* range: 7–35 cm; *AGE* range: 60–120 yr), and 1 864 trees in northern and southern Finland (*DBH* range: 5–35 cm, average *AGE* = 105 yr with *AGE* standard error = 55 yr).

Finnish spruce had a crown ratio of approximately 75–80%, with nearly no difference between north and south. Such *CR* values seem to correspond to widely spaced trees, but they may also be due to an effect of the high latitude (Kuuluvainen and Pukkala, 1991). The following correlations were found:  $r = -0.38$  with  $H/DBH$ , 0.29 with *DBH*, 0.10 with *AGE* and 0.06 with *H*. Lithuanian trees were more contrasted, with a *CR* ranging from 55–80%. In this case, *CR* was related to the independent variables *DBH*, *AGE*,  $AGE^2$ ,

$DBH.AGE$ ,  $DBH.AGE^2$ , but no information was given about residual standard error or coefficient of determination, and height measurements had not been carried out.

Concerning height to the base of live crown and height to the first live branch, Hakkila *et al* (*op cit*) established that the height to the base of green branches increases when  $DBH$  and total height increase but that it becomes nearly constant with a maximum value of about 4–5 m (*ie* when  $DBH$  increases from 20–35 cm,  $HFLB$  varies from 3.5 m to 4.5 m). This value is smaller than our values, but this might be due to the fact that the trees are smaller. For Arlauskas and Tyabera (*op cit*), the independent variables were again  $AGE$ ,  $AGE^2$ ,  $DBH.AGE$ ,  $DBH.AGE^2$ . The height to the base of the green branches ranged from 7–11 m.

In Lithuania, the height to the first dead branch ranged from 2–5 m. The authors emphasized that natural pruning was less intensive than branch death, and noticed that natural pruning did not seem to be influenced by site conditions (soil and climate). In Finland, Hakkila *et al* (*op cit*) noticed a value of approximately 1 m for  $HFDB$ . These data and our results confirm the fact that natural pruning is not efficient for Norway spruce. Our non-pruned trees have almost all their dead branches (most of them are younger than the Finnish and Lithuanian sample trees).

### The models

Although the list of the best predictors that we found is somewhat different from those provided by the above-mentioned authors, it must be stated that this list is strongly influenced by the sampling design and that crown development and recession are controlled by several factors that are not directly assessed through global tree characteristics. For instance, Hakkila (*op cit*)

considered that variations in  $CR$  are caused fundamentally by genetic factors and stand density in the different ages of tree. It can therefore be explained only fairly inadequately by means of the tree characteristics. Some specific site conditions (*eg* slope, exposition, elevation) may also play a role in crown dynamics.

Our results are therefore consistent with previous studies and confirm that crown recession is an age-dependent phenomenon that is regulated by stand density and by individual tree social status. More precisely it depends on: i) the stage of development of the tree which is indirectly measured by age, total height and  $DBH$  and which is affected by site conditions; ii) the past and current density of the stand (Delvaux, *op cit*, Bryndum, 1974); iii) the social status of the tree within the stand (Delvaux, *op cit*).

Equations [1–3] provide a means for integrating these factors: the effect of age is modelled by an exponentially decreasing function that is consistent with Kramer's observations (1962); the term with  $H/DBH$  is a correction to the general age-trend that accounts for both the current social status of the tree and the past density of the surrounding stand;  $H^2$  term accounts for a size effect whose interpretation is less clear. The structure of our model is also fairly similar to that of Dyer and Burkardt (1987) for *Pinus taeda*.

Since crown importance and location determine both annual increment of wood along the stem and the status of the knots (intergrown or encased knot), it is interesting to determine whether the dynamics of crown recession can be investigated with our data. Figure 1 illustrates that our sampling design is not suitable for exploring this question. In fact, a complementary sampling should be achieved, including trees of various ages (especially young and old trees) within stands of various densities.

## Branch diameters

### Thickest branch in a tree

Hakkila (*op cit*) sampled 245 trees coming from 49 stands located in all parts in Finland. He noticed that the greater part of the variation (of branch size distribution) is associated with characteristics that illustrate the tree size. After testing various variables (*ie* AGE, H, DBH, stem volume, dry weight, CR, H/DBH, branch class) he built a model for predicting the diameter of the thickest branch:

$$MAXD \text{ (mm)} = 15.9 + 0.978 \text{ DBH} - 7.45 \text{ H/DBH} \text{ (} R = 0.81; \text{ RMSE} = 3.8 \text{ mm)}.$$

Hakkila's equation is similar to eq [5] except that H/DBH was not found to be significant in our sample. For Scots pine at pole stage (DBH range: 3–17 cm), Kellomäki and Väisänen (1986) also found a good relationship between diameter of the thickest branch and DBH.

These results confirm that tree size (*ie* DBH) is the most efficient predictor of MAXD and that stand density and social status of the tree (as synthesized by H/DBH) play some additional role in predicting.

### Vertical trend of branch diameter

Few vertical profiles of branch diameter have appeared in the literature. Schöpf (1954) on *Pinus sylvestris* between 18 and 64 yr compared crown structure, internal structure of the stem and vertical trend of branch diameter. He observed i) that branch diameter increases from the top of the tree to a point that is near to the level of maximum lateral extension of the crown; and ii) that it then decreases towards the base of the tree. The size of the branches is therefore linked to crown shape and to

tree size (DBH). Uusvaara (1985, 1991) noticed the same vertical trends in *Pinus sylvestris* in Finland. Maguire *et al* (*op cit*) modelled this trend in young *Pseudotsuga menziesii*; since the seedlings had a CR of nearly 100%, their model concerned the upper part of the curve (*ie* from the top to the level of maximum lateral extension). The situation was similar in Abetz's study (1970) on *Pinus sylvestris* in Germany.

The decreasing part of the vertical trend has been investigated in particular by Bernhart (1960), Merkel (1967) and Kramer *et al* (1971) on *Picea abies* and Dietrich (1973) on *Abies alba*. Merkel demonstrated the effect of stand density which changes with time. Due to successive silvicultural practices the remaining trees, *ie* dominant and codominant trees, get more and more growth space. Kramer (1962) showed that the lifespan of the branches becomes longer when the tree gets older so that the maximum branch diameter also increases.

The model introduced by Colin and Houllier (*op cit*) was slightly improved and extended to average branch diameter. This model is consistent with the above-cited result: the vertical trend is modelled according to the distance to the top of the tree with additional terms that are related to tree size (*ie* H, DBH), to crown descriptors (*ie* CR<sub>3</sub>, HFLB) and to tree social status (*ie* H/DBH, CR<sub>3</sub>) (for other comments on this aspect, see Colin and Houllier, *op cit*).

### Insertion angle of branches

Figures 7 and 8 show that there is a global effect of tree height growth rate on the insertion angle of the branches. For the same total height, trees that grow quickly have less growth units and the insertion angles are statistically lower (*ie* angles are

more acute). Possible reasons for this result might be the following: firstly, for the same initial stand density fast-growing trees face a more intensive competition when they are young: this might lead to acute angles because branches are oriented toward upper light (Jarret, 1978; for *Pseudotsuga menziesii*): we could neither reject nor validate this hypothesis because information about past stand density was lacking for most stands. Secondly, since all sample trees are about the same size, older trees are those which come from poorer sites that are often located at a high elevation: these trees are therefore submitted to heavy weights of snow and intercepted rainfalls during most of the year.

From our results it therefore appears that for mid-size spruces the merchantable part of the stem (*ie* from tree bottom to 70% of total height or between 30–100% of relative depth into crown) supports whorl branches with angles ranging approximately from 70° (for fast-growing trees and/or for trees from stands where initial density was high) to 100° (for slow-growing trees and/or for trees which grew in conditions where the loads on branches are high). Due to knot inclination inside the bole, the volume of wood disturbed by knots is greater in the first case.

This global result has to be shaded according to the genetic origin of the trees. For instance, the fact that  $S_2$  trees – which all come from the same stand and hence from the same provenance – have more acute insertion angles might be due to their genetic origin. Comparative studies of different provenances and descendances are under way in order to confirm the magnitude of genetic effects on the parameters of our model. Similarly the occurrence of ramicorn branches – which were not studied here – is partially dependent on the genetic origin; it also depends on site conditions and tree age, and we indeed observed that trees growing at a high ele-

vation in Vosges mountains often have ramicorn branches. The frequency of this phenomenon should be more intensively studied in the future.

However, since genetic origin is unknown when using National Forest Survey data, it is not possible to take this aspect into account when extrapolating our models (except by stochastic simulation).

### **Number of branches**

Compared to other studies, the proposed models present an improvement concerning the statistical description of the variability (random errors were not assumed to be normal). Nevertheless, the general trends that were fitted are similar to those modelled by Maguire *et al* (*op cit*), by Cannell (*op cit*) and by Remphrey and Powell (*op cit*). It appears that the number of branches per annual growth unit increases when the length of the growth unit increases, but that the slope of this trend decreases progressively from the top to the bottom of the stem (fig 11).

The analysis of annual climatic effect was not within the scope of this study. The previous year's climate influences the number of stem units of the annual shoot as well as its length (Cannell and Bowler, *op cit*; Kremer *et al*, *op cit*; Guyon, *op cit*) and hence the number of axillary buds and potential branches; the climate of the following spring then influences organogenesis (Powell, 1982); so that the final number of branches presents a strong variability even if the length of the annual growth unit has been taken into account.

On figure 9 we observe a decreasing trend for  $N_{0.5}$ . This is probably due to the fact that internodal branches have a short lifespan and fall after a certain time. On the other hand, the branches with a diameter < 0.5 cm include branches developed from

'proventive' buds (Edelin, 1977); this phenomenon leads to a regular replacement of very small branches that have a very short lifespan and provides an explanation for the stability of *NTOT* and for the introduction of *NGU* when modelling  $N_{05}$ . This aspect must be further investigated in future studies, but this will require dynamic analysis (*ie* repeated observation of the same trees).

Concerning site effects, the role of growth conditions is important since the length of the annual shoot has a strong influence on the number of branches.

Cannell (*op cit*) observed slightly different numbers of lateral buds per leader length unit between the different provenances which he investigated. This might be due to inherent differences in branch-needle numbers ratio (Cannell and Bowler, *op cit*). At this stage of branchiness knowledge, and before extending current results to the whole resource in a given region it is therefore essential to compare the main provenances that are used in this region and to check whether there is an effect on the parameters of our models.

On the other hand, Pollard and Logan (1979) observed that the primordium initiation is variable when conditions of sunlight exposure are contrasted: for instance, a reduction of light intensity from 20 000 to 3 400 lux leads to a reduction of primordium initiation of 40–46% depending on provenances. Hence, silviculture might have some influence on branch numbers: low stand density and regular thinnings could lead to an increase of the number of branches per annual shoot length unit.

#### ***Whorl branch location and diameter distribution inside the whorl***

The location of whorl branches is determined overall by upper scale scars position. Knowing the height growth curve al-

lows a rough prediction of whorl position. In fact, whorl branches are attached to the stem in an area that represents about 20% of annual shoot length.

Similarly, Maguire *et al* (*op cit*) observed that approximately 24% of the total number of branches (likely whorl branches) on young Douglas fir trees are located in the first percentage of the relative depth in an annual shoot. Our distribution seems to be slightly more spaced, especially for  $S_2$  trees.

#### ***Extrapolation to other species***

Our approach may be extrapolated to other regions for the same species by extending our samples and calibrating our models. It is also likely that it may be adapted to other coniferous species such as Douglas fir, Sitka spruce, larches and pines with relatively strong apical control; and more broadly, to tree species having close architectural models (according to the definition of Hallé and Oldeman, 1970).

#### **CONCLUSION**

We emphasize: i) that our purpose was not to look for functional relationships: in the context of this study this would have been hopeless, since annual stem and crown development are dynamically linked so that their present status is only the visible result of the accumulation of annual processes; ii) that this study constitutes an exploratory statistical analysis, that addresses the following question: can usual tree measurements be used as predictors of branchiness characteristics?; iii) that the model equations are temporary, since prediction could change slightly if more trees were sampled and especially if the range of sampled trees were extended to smaller, larger, younger or older trees.

These models provide a comprehensive and consistent framework for predicting crown length and branchiness characteristics from usual tree measurements as those available from either local management or regional resource inventories. As a first step, crown length may be estimated from age, height and DBH data (eq [1–4]); the evaluation of the height to the first dead branch is less interesting because natural pruning is a very slow process for Norway spruce, and the model does not take artificial pruning into account. As a second step, the size of whorl branches may be predicted at any point along the stem (eq [5–7]). Third, if a height growth curve model is available (from preliminary studies), it is possible to reconstruct how the tree grew and to estimate the length of the annual shoots, the location of the whorls, the number of branches (eq [9]) and their insertion angle (eq [8]). Since information about residual variability is available, it is possible to make stochastic simulations rather than purely deterministic predictions.

However, as stated in the discussion, some aspects must still be investigated and these models do not account for all factors that may determine stem branchiness and knottiness in a bole. As an example, further specific studies should be carried out in order to investigate more precisely the influence of genetics and of tree social status in a modelling context. Also, information concerning small internodal branches are partial and have not been considered in detail here. Moreover, the present status of the knots that are entirely included inside the wood (in the lowest part of the stem) cannot be assessed from our models.

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