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Modelling branchiness of Corsican pine with mixed-effect models (*Pinus nigra* Arnold ssp. *laricio* (Poiret) Maire)

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Abstract – In order to predict the influence of silvicultural practices on knottiness and canopy structure, models were constructed to predict branch characteristics of Corsican Pine (*Pinus nigra* Arnold ssp. *laricio* (Poiret) Maire var. *corsicana*) from usual tree measurements. Thirty-six trees were sampled from a broad range of age, stand density and site index. Mixed models were fitted on branch length and on branch angle after a linearization procedure. A segmented second order polynomial model was chosen for the diameter profile. Nevertheless, this model seemed difficult to be transformed for fitting mixed models, but a global model was however satisfactory. For realistic simulations with these models, we generated simulated correlated residuals of angle and diameter in order to maintain the negative link between angle and diameter of a branch. The mixed model method provides an improvement of the fit by accounting for inter-tree differences and/or intra-tree similarities and also an improvement of the simulation. The possibility to fit mixed-effect non-linear models allows a great number of models. (© Inra/Elsevier, Paris.)

branchiness / *Pinus nigra* ssp. *laricio* / modelling / mixed model / simulation

Résumé – Modélisation de la branchaison du pin laricio à l'aide de modèles à effets mixtes (*Pinus nigra* Arnold ssp. *laricio* (Poiret) Maire). Dans le but final de prévoir l'influence de la sylviculture sur la nodosité et le couvert, des modèles de prédiction des principales caractéristiques des branches à partir des données dendrométriques usuelles ont été construits. Trente-six pins laricio (*Pinus nigra* Arnold ssp. *laricio* (Poiret) Maire var. *corsicana*) ont été décrits. Les modèles

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mixtes ont été ajustés sur les données de longueur de branche et après linéarisation sur les données d'angle de branche. Pour les diamètres, nous avons choisi un modèle polynomial de second ordre segmenté. Cependant, la méthode d'ajustement par la procédure de modèle mixte n'a pas pu être utilisée pour ce modèle complexe d'ajustement. Néanmoins un modèle global satisfaisant pour l'ensemble des arbres a pu être trouvé. Pour une simulation plus réaliste des angles et des diamètres des branches, nous avons généré des résidus corrélés afin de tenir compte de la liaison négative qui existe entre angle et diamètre d'une branche. En conclusion, les modèles mixtes améliorent les ajustements en tenant compte des différences et/ou des similarités inter- et intra-arbre. La possibilité d'ajuster des modèles non linéaires à effets mixtes permet d'augmenter le choix des modèles. À partir de ces modèles les simulations sont améliorées. (© Inra/Elsevier, Paris.)

branchaison / *Pinus nigra* ssp. *laricio* / modélisation / modèle mixte / simulation

1. INTRODUCTION

Both silviculturists and wood scientists need management tools that integrate both growth and wood quality information in order to predict the influence of site quality and silvicultural regime on individual tree growth, on stand yield, on stand structure and on wood quality. Our project consists in setting up interconnected sub-models that range from growth models to saw quality simulators. The quality is defined mainly in terms of wood density, mechanical properties and knottiness. Directly linked with this latter property, the crown is considered to be the most sensitive component of a tree under direct influence of genetics and of surrounding growth conditions [10, 31]. It is considered as a link between the internal structure of the stem, the knottiness and the branch growth [4].

The branching of a tree must be specified in terms of vertical profiles of branch number per annual shoot, status: living or dead, angle and diameter at insertion on the trunk, length, lateral extension and inclination of each whorl branch along the stem. The first four variables are considered as inputs into wood quality simulators. These simulators have a prediction component of knot shape (for instance Leban and Duchanois [14]). This shape is predictable if branch angle and diameter as well as bole radius are available. It has been shown for instance that the more acute is the angle, the more important is the volume of wood affected by the knot. The capacity to predict these branch characteristics is therefore the key to the successful linking of silvicultural regimes and wood product quality [21]. Concerning length, extension and inclination of branch this information is interesting for representation of trees in the stand and of the canopy structure [5]. The branch length is important for the foliage display and thus influence tree growth [24]. The branch growth depends on the apical control of the main stem. It decreases from the top of the tree to the base and from the inside of the tree to the outside [11].

Numerous relationships between stem and branches have been established on other coniferous species, for instance: relationships between diameter at breast height (DBH) and height, and the diameter of the thickest branch of *Pinus sylvestris* or of *Picea abies* [8], relationships between DBH and the diameter of the thickest branch at 70 % of the height (*Picea abies*, [9]), DBH and height and mean branch diameter at the base of the living crown [19]. Mitchell [23] observed that for *Picea glauca* the length of whorl branch at the largest extension of the crown is related with the length between the tree top and the branch insertion. Considering these previous results we planned to predict the vertical profiles of branch characteristics based on the stem attributes (such as DBH, height, etc.). In order to fit these profiles, methods have been proposed [4] but they still need to be improved to clearly distinguish different levels of variability and between-tree variability.

Therefore, the aim of this paper is to propose the use of mixed models which improves both modelling and simulation of the vertical profiles of angle, diameter and length of branch for Corsican pine.

2. MATERIALS AND METHODS

2.1. Structural development of Corsican pine

This study concerns Corsican pine (*Pinus nigra* Arnold ssp. *laricio* (Poiret) Maire var. *corsicana*). It is a fast growing conifer with good wood quality and a straight stem. The stem and the branches are monopodial with a strong apical control. Branch and stem elongation are annual, and each annual shoot constitutes one growth unit (GU). Lateral branching usually occurs 1 year after bud formation (proleptic branching). Branches are located only at the top of each annual growth unit, clustered in whorls. There are no inter-whorl branches.

2.2. Sampling

Twelve plantations of Corsican pine located in the region 'Centre' (France) were selected in order to investigate a broad range of age, individual growing space and site index (*table I*). We tried to select only trees from the variety *corsicana*. Artificially pruned plantations and unhealthy plantations were avoided. In each plantation, a 0.3-ha plot was installed. Girth at breast height of all trees was measured in order to select three trees of different social status: one dominated (from the lower girth class), one medium (with a girth near the mean girth) and one dominant (from the higher girth class). Trees with very serious crown defects and with forked stems were excluded. Thirty-six trees were felled and measured in 1995. Data describing crown size and development were collected, based on the analysis of all the branches directly inserted on the main stem, the primary branches.

Table I. Attributes of the 12 sample stands.

Stand	Mean age[a] (years)	Current density (ha^{-1})	Dominant Height (m) (at age in year)
BO	19	500	9.2 (18)
RG	23	2060	13.0 (21)
LL	23	790	12.5 (21)
EC	25	530	11.8 (22)
SP	25	2190	10.6 (22)
IN	25	790	11.0 (22)
RI	40	520	22.0 (40)
SR	52	380	25.0 (45)
LB	54	400	26.0 (54)
CN	61	200	28.0 (61)
MT	69	290	29.0 (69)
GZ	71	200	30.0 (71)

[a] Age since the plantation.

2.3. Variables

Two kinds of variables were used: branch descriptors and whole tree descriptors (*table II*). The latter were the standard tree measurements, crown heights and combination of variables: diameter at breast height (DBH) (in cm, measured to the nearest 5 mm); total height (TH) of the stem (in m, to the nearest 5 cm); height to the lowest living branch (HLLB) (in m, to the nearest 5 cm); height to the lowest living whorl (HLLW) (in m, to the nearest 5 cm) where at least three quarters of branches were living; crown length 1 (CL): CL = TH – HLLB (in m); crown length 2 (HLLWA): HLLWA = TH – HLLW (in m); length between the lowest living whorl and the lowest living branch (DIFF) (in m); crown ratio 1 (CR): CR = (TH – HLLW)/TH; crown ratio 3 (CR3): CR3 = (TH – HLLB)/TH; crown ratio 2 (CR2): CR2 = (CR + CR3)/2; based on the bud-scale scars and whorl, each annual elongation or growth unit (GU) was identified by its rank recorded from the tree top: GU = 1 is the youngest growth unit elongated in year *y*, GU = 2 is the growth unit elongated in *y* – 1, etc.; length of each annual growth unit

Table II. Summary statistics on sample tree and branch characteristics.

Variable	Meaning	Unit	Mean	SD[a]	Min	Max
DBH	Diameter at breast height	cm	25.53	11.99	8.00	53.00
TH	Total height	m	18.67	8.05	7.68	33.00
A	Age	years	40.89	18.96	20.00	71.00
HLLB	Height to the lowest living branch	m	9.55	6.49	1.51	20.11
HLLW	Height to the lowest living whorl	m	11.00	7.22	1.62	23.02
CL	Length between the apex and HLLB	m	9.11	2.35	4.66	14.72
HLLWA	Length between the apex and HLLW	m	7.66	1.57	4.28	10.21
DIFF	Length between HLLW and HLLB	m	1.45	1.19	0.00	4.74
CR	Crown ratio		0.47	0.17	0.25	0.84
CR3	Crown ratio		0.54	0.17	0.31	0.84
BD	Branch diameter at stem insertion	mm	21.13	12.52	2.00	107.00
BA	Branch angle at stem insertion	grad	84.72	17.45	15.00	145.00
BL	Branch length	cm	173.99	108.77	0.00	721.00

[a] SD = standard deviation.

(GUlength) measured between two successive whorls (in cm, to the nearest 5 cm); distance from the apex (DFA): absolute distance from each whorl (top of the growth unit) to the top of the stem (in m, to the nearest 5 cm); age (A) of the tree based on the number of whorls and checked by counting the annual rings on the stump section after felling (in years).

For each branch, we measured: branch diameter over bark (BD) (in mm, to the nearest mm, at a distance from the bole that was approximately equal to one branch diameter, on the horizontal axis; dead and living branches are measured); branch insertion angle (BA) (in grad, to the nearest 5 grad) between the axis of the branch and the axis of the main stem (dead and living branches are measured); branch length (BL) (in cm, to the nearest 1 cm): distance between the top of the branch and its branch insertion (living branches are measured).

2.4. Statistical analysis

The variables to be predicted are BL, BA and BD, as functions of DFA, GU and/or GUlength and also whole tree descriptors. The analyses were carried out following three main steps.

2.4.1. First step: establishment of a global fixed-effect model

First, we modelled the variation of each variable along each stem with individual equations (one per tree) [22] as:

$$Y_{i,j} = f(X_{i,j}\,;\,\theta_i) + \varepsilon_{i,j} \qquad (1)$$

where Y_{ij} represents for example the branch angle, X_{ij} the independent variable (i.e. the predictors), i denotes the ith tree, j the jth annual growth unit, θ_i the model parameters specific to the ith tree and $\varepsilon_{i,j}$ the within-tree residual variation.

Then, linear regressions were carried out in order to analyse the variability of the parameters θ_i in relation to the whole tree descriptors:

$$\theta_{ik} = g_k(\mathrm{DBH}_i,\ \mathrm{TH}_i,\ \mathrm{Age}_i,\ \mathrm{TH}_i/\mathrm{DBH}_i,\ \mathrm{HLLB}_i,\ \mathrm{HLLW}_i, \mathrm{CR}_i, \mathrm{DIFF}_i, \mathrm{CL}_i, \psi_k) + \eta_{ik} \qquad (2)$$

where θ_{ik} denotes the kth parameter in the vector θ_i, ψ_k denotes the global parameters common to all sampled trees and η_{ik} is a random error representing unexplained between-tree variations. It may happen that some parameters θ_{ik} do not have any clear relationship with the whole tree descriptors; in this case, equation (2) above simply becomes: $\theta_{ik} = \mu_k + \eta_{ik}$ where μ_k is the mean of θ_{ik} over the trees.

Finally, we transformed the individual models into a global model by progressively replacing the θ_i parameters in (1) by their predictions (2). We obtained fixed-effect models of the following form:

$$Y_{i,j} = f(X_{i,j}\,;\,\theta(\mathrm{DBH}_i,\ \mathrm{TH}_i,\ \mathrm{Age}_i,\ \mathrm{TH}_i/\mathrm{D}_i,\ \mathrm{HLLB}_i,\ \mathrm{HLLW}_i,\ \mathrm{DIFF}_i,\ \mathrm{CR}_i,\ \mathrm{CL}_i,\ \psi)) + \varepsilon'_{i,j}$$

In such models, the unexplained between-tree variations η_{ik} in (2) are neglected.

2.4.2. *Second step: linearization of the global model, if necessary*

In order to change the global models into mixed models, we had to transform the non-linear models into linear ones. Several methods have been proposed to fit non-linear mixed models (Lindstrom and Bates [16]; Wolfinger [32]; and others: see Gregoire and Schabenberger [7]). One of the simplest due to Beal and Sheiner [2] and used by Gregoire and Schabenberger [7] is to approximate the marginal distribution of the response vector by expanding the global model in a first-order Taylor series; it was adopted in the present study.

2.4.3. *Third step: fitting of mixed linear model*

In this step, we improved the linear fixed-effect model by taking into account the variability between trees due to the mixed model.

The mixed linear model (with both fixed and random effects) is a generalization of the standard linear model; the generalization being that it is possible to analyse data with several sources of variation and especially within- and between-tree variations. For a detailed description of the theory, refer to Laird and Ware [13] and Diggle et al. [6].

Suppose for example that a variable Y_{ij} (for instance branch length) is linearly linked to others variables X_{ij} within each tree:

$$Y_{ij} = \theta_i X_{ij} + \varepsilon'_{ij}$$

where ε'_{ij} is the within-tree unexplained variation and θ_i is the vector of parameters, specific of the ith tree. Suppose that θ_i varies from tree to tree independently at random, so that, when looking at different trees, one can write:

$$\theta_i = \theta + \delta_i$$

where θ is the mean of θ_i over the trees and δ_i is the ith tree individual deviation from θ, with mean zero and variance–covariance matrix B.

Returning to Y_{ij}, this yields:

$$Y_{ij} = \theta X_{ij} + \delta_i X_{ij} + \varepsilon_{ij}$$
$$(1) \quad + \quad (2) \quad + \quad (3)$$

where (1) is explained variation (fixed effects), (2) is the between-tree random deviation (tree effects), and (3) is the within-tree residual variation.

In general, the tree vector parameters θ_i may also be a linear function of tree variables, and some parameters in θ_i may have no random variation. The general mixed-effect model is then:

$$Y_{ij} = \theta X_{ij} + b_i Z_{ij} + \varepsilon_{ij} \qquad (3)$$

where θ is a fixed-effect parameter vector, X_{ij} is the fixed-effect variables, b_i is the vector of (tree) random effects, Z_{ij} is the vector of variables associated with the random effects, ε_{ij} is the residual within-tree random variation. Furthermore b_i and ε_{ij} are supposed normally distributed, independently of each others:

$$b_i \sim N(0, B)$$
$$\varepsilon_{ij} \sim N(0, \sigma^2)$$
$$\text{and } \mathrm{Cov}(b_i\,, \varepsilon_{ij}) = 0$$

where B is the variance–covariance matrix of random effects and σ^2 the within-tree residual variance.

The unknown parameters (fixed-effect parameter θ, variances and covariances of random effects and residual variance σ^2) are estimated using restricted maximum likelihood [13].

One of the criteria to measure the goodness of fit is the Akaike information criterion (AIC) which permits us to compare models with the same fixed effects but different variance structure. AIC is computed as: $\mathrm{AIC} = \hat{l} + 2\,p$

where $\hat{l}$ is twice the negative log-likelihood evaluated at the maximum likelihood estimates (or restricted maximum likelihood estimates) and p is the number of estimated parameters.

A procedure was designed especially for fitting mixed linear model in SAS/STAT. This function called PROC MIXED has been available in release 6.07 [17, 28].

2.5. Generation of values from normal distribution with mean 0 and given variance–covariance matrix

After improving each model and its fitting with our data, the last stage was to include them in a growth simulator. With the characteristics of simulated trees given by the growth simulator, our equations permit us to simulate their branchiness. For each equation constructed with mixed model procedure, or in order to take into account the correlation between residuals of different models, we had to generate values of parameters (for example, $\gamma 1$, $\gamma 2$) from normal distribution with mean 0 and given variance–covariance matrix V:

$$V = \begin{vmatrix} \text{var 1} & \text{cov 12} \\ \text{cov 12} & \text{var 2} \end{vmatrix}$$

We first generated a random vector g from a normal distribution with mean 0 and identity variance–covariance matrix, using the SAS function Normal [28]. g is then transformed to a $N(0,V)$ by multiplying it by a lower triangular matrix L such that $LL^t = V$ (Cholevski decomposition of V).

3. RESULTS

For diameter and angle, dead and living branches were taken into account in the fit of individual profiles. In fact for each tree, the scatter of diameter and angle data is continuous at the level where the two kinds of branches overlap. Only living branches were taken into account for branch length. For all the following analyses, we removed branches with a particularly acute angle (ramicorn branches) (i.e. a total of seven branches in sampled trees) and branches with a diameter of less than half of the maximum diameter per whorl (*figure 1*). In term of knottiness, the influence of these thin branches can be neglected.

3.1. Branch length

3.1.1. Construction of a linear mixed model

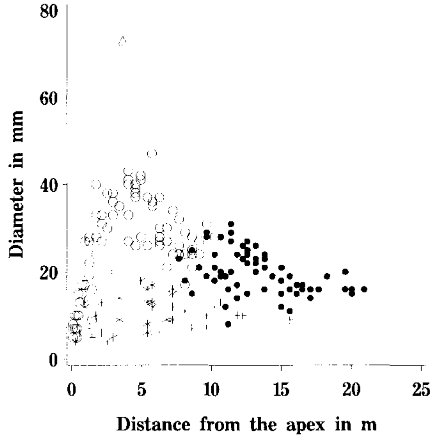


Figure 1. Example of the diameter values for one tree from stand CN. Symbols: living branches in circles and stars, dead branches in dots and pluses. We removed branches in stars and plus symbols and also the ramicorn branch (triangle symbols). The tree top corresponds to DFA = 0.

First, for each tree, we fitted individual linear models with the distance from the apex (DFA) as the independent variable:

$$BL_{ij} = a_{1i}\,DFA_{ij} + a_{2i}\,DFA_{ij}^2$$

where a_{1i} and a_{2i} are the individual parameters for each tree. The R-square ranged between 0.93 and 0.99 and the residual standard deviation ranged between 20 and 55 cm depending on trees. Then, we analysed the variability of the parameters a_{1i} and a_{2i} in relation to the whole tree descriptors. DBH had a linear relationship with a_{1i} ($R^2 = 0.30$). Other tree descriptors, such as crown variables, did not show any relationship with the individuals parameters. This led to the following global model with DFA, DFA^2 and DFA.DBH as independent variables (fitted to 1782 branches):

$$BL_{ij} = a_0 + a_1\,DFA_{ij} + a_2\,DFA_{ij}2 + a_3\,DFA_{ij}.DBH_i$$

The R-square was equal to 0.835 and the residual standard deviation was equal to 43 cm. This fixed-effect model has been improved by taking into account the variability between trees due to the mixed linear model. This was carried out here by adding a random tree component to some or all parameters a_0, a_1, a_2, a_3. Among several attempts of different random effect combinations, we chose the model with the highest AIC, which included random effects for the intercept, DFA, DFA^2:

$$\begin{aligned} \mathrm{BL}_{ij} = A_0 + A_1\,\mathrm{DFA}_{ij} + A_2\,\mathrm{DFA}_{ij}^2 \\ + A_3\,\mathrm{DFA}_{ij}.\mathrm{DBH}_i + \alpha_{0i} + \alpha_{1i}\,\mathrm{DFA}_{ij} \\ + \alpha_{2i}\,\mathrm{DFA}_{ij}^2 + \varepsilon_{ij} \qquad (4) \end{aligned}$$

Parameter estimates of fixed effects (A_0, A_1, A_2, A_3), variances/covariances of random effects (α_{0i}, α_{1i}, α_{2i}) are provided in *table III*. The standard deviation was only 34.3 cm. *Figure 2a* shows how the mixed linear model fits the data for one tree.

3.1.2. *Simulation of branch length profile*

The estimates of the covariance parameters allowed us to simulate different profiles of trees. For each tree, the values of α_{0i}, α_{1i} and α_{2i} were generated from a trivariate normal distribution with mean 0 and variance–covariance matrix given by the fit of model (4). Then for each branch in a tree, a random residual was simulated from a normal distribution with mean zero and variance equal to the residual variance of the model (4). *Figure 2b* shows an example of a simulated branch length profile from growth characteristics (DFA, DBH, number of branches per whorl).

3.2. Branch angle and diameter

3.2.1. *The branch angle model: a non-linear mixed model*

To predict the vertical trend of angle for both dead and living branches, we used the number of annual growth units counted downwards from the top of the stem (variable GU) as independent variable. According to Meredieu and Colin [22], we fitted the following non-linear individual model:

Table III. Analysis of fixed parameter estimates and variances/covariances of random effects for prediction of branch length (model 4).

Fixed parameter	Estimate	Std error	DDF	T	Pr>ITI
A_0	10.12	4.20	35	2.41	0.0212
A_1	37.72	2.72	34	13.87	0.0001
A_2	–4.68	0.24	35	–19.50	0.0001
A_3	1.09	0.07	1674	16.12	0.0001

Variances/covariances of random effects	Estimate	Std error
var α_0	354.51	156.04
cov (α_1,α_0)	–111.62	72.46
var α_1	137.96	46.04
cov (α_2,α_0)	0.23	5.83
cov (α_2,α_1)	–10.49	4.08
var α_2	1.21	0.44

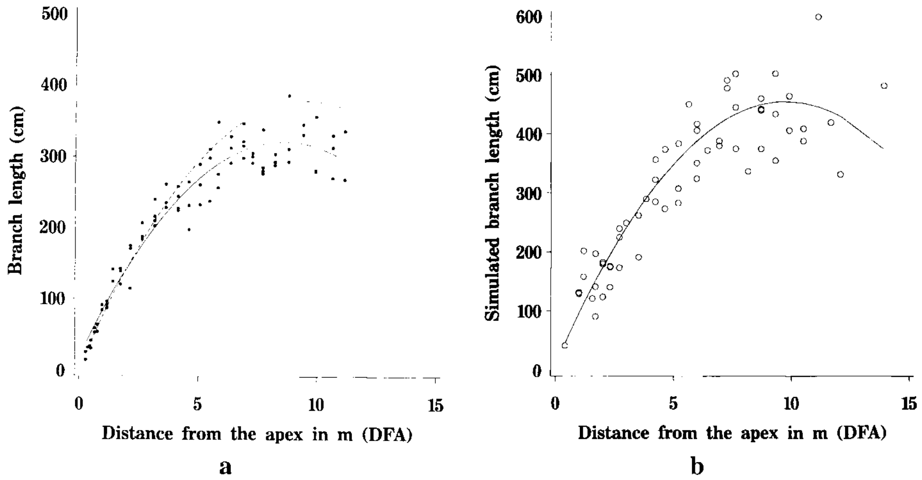


Figure 2. a Fit (standard line) of branch length (in cm) versus the distance from the apex (DFA) of a sample tree. Dotted line represents the profile predicted from the fixed-effects version of the model (4); solid line represents the profile predicted from the mixed-effects model (4). The tree top corresponds to DFA = 0. **b** Simulated branch length profile. The standard line is the mean predicted values with mixed effect model. The tree top corresponds to DFA = 0.

$$\mathrm{BA}_{ij} = b_{1i} + c\left(1 - \exp(-b_{2i}\,\mathrm{GU}_{ij})\right) \quad (5)$$

where b_{1i} and b_{2i} are parameters constrained to be positive, and c is a constant ($c = 51$).

We did not obtain good relationships between individual parameters and global tree characteristics. Nevertheless, it was important to characterize both inter-individual and intra-individual variations adequately in order to permit valid simulations. For this reason, we adopted the following mixed-effect model:

$$\begin{aligned}\mathrm{BA}_{ij} &= (B_1 + \beta_{1i})\\ &+ c\left(1 - \exp(-B_2 + \beta_{2i})\,\mathrm{GU}_{ij}\right) + \varepsilon_{ij} \quad (6)\end{aligned}$$

To fit this non-linear mixed model we approximated the marginal distribution of the response vector by expanding our model (6) in a first-order Taylor series. A first-order Taylor expansion of our model, around guessed values b_{10} and b_{20} (obtained by fitting the fixed-effect version of model (6)), gave the following approximate linear model (7):

$$\begin{aligned}\mathrm{BA}_{ij} &= b_1 + c\,(1 - \exp(-b_2\,\mathrm{GU}_{ij}))\\ &+ \left|\frac{\partial \mathrm{BA}}{\partial b_1}\right|_{b_{10},\,b_{20}} (B_1 + \beta_{1i} - b_{10})\\ &+ \left|\frac{\partial \mathrm{BA}}{\partial b_2}\right|_{b_{10},\,b_{20}} (B_2 + \beta_2 - b_{20}) + \varepsilon_{ij} \quad (7)\end{aligned}$$

where the derivative expressions mean the partial derivative with respect to the indicated parameter, evaluated at the guessed values. We have:

$$\frac{\partial \mathrm{BA}}{\partial b_1} = 1 \qquad \frac{\partial \mathrm{BA}}{\partial b_2} = c\,\mathrm{GU}_{ij}\exp(-b_{20}\,\mathrm{GU}_{ij})$$

Defining $v_{1ij} = c\left(1 - \exp(-b_{20}\,\mathrm{GU}_{ij})\right)$; $v_{2ij} = c\,\mathrm{GU}_{ij}\exp\left(-b_{20}\,\mathrm{GU}_{ij}\right)$

and rearranging, this yields:

$$\begin{aligned}\mathrm{BA}_{ij} + b_{20}\,v_2 - v_1 &= B_1 + \beta_{1i}\\ &+ v_2\,B_2 + v_2\,\beta_{2i} + \varepsilon_{ij} \quad (8)\end{aligned}$$

Model (8) is a linear mixed model where the non-linear response has been replaced by an approximated linear model.

The approximation is better if the guessed values b_{10} and b_{20} are chosen near the true unknown values b_1 and b_2. We used estimates obtained by fitting the fixed-effect version of model (6). Then we estimated the parameters of the new linear mixed-effect model. New estimates were obtained. If necessary we repeated this step with the updated estimates as guessed values until the change in the likelihood was insignificant.

The fixed effect version of (8) was fitted to benchmark the anticipated improvement offered by the inclusion of the random parameters in the model. When (8) was fitted with only fixed effects, AIC = –17003 and when it was fitted with random and fixed effects, AIC = –16535. For this latter model $\sigma^2 = 118.2$ and all the parameters were clearly significant (*table IV*). The branch angle profile predicted by this model is shown by a solid line in *figure 3* and the deficiencies of the fixed-effect version of the model become apparent.

3.2.2. *Construction of the branch diameter model: a fixed-effect model*

According to Colin and Houllier [3] we chose for the diameter profile a segmented second order polynomial model with a joint value ξ which is the location of the estimated thickest branch:

$$\mathrm{BD}_{ij} = d0 + d1\ \mathrm{DFA}_{ij} - d2\ \mathrm{DFA}_{ij}^2 \quad \text{if } \mathrm{DFA}_{ij} < \xi$$

$$\mathrm{BD}_{ij} = d0 + d1\ \xi + d2\ \xi^2 - d3\ (\mathrm{DFA}_{ij} - \xi)^{d4} \quad \text{if } \mathrm{DFA}_{ij} \geq \xi$$

where $d0$, $d1$, $d2$, $d3$ and $d4$ are positive constrained parameters and $\xi = -d1 / (2\ d2)$.

This model was fitted independently for each tree [22]. Then we tried to construct a single global model. First, $d4$ was fixed at 1. This parameter was therefore transformed into a constant in further analyses. Then, we analysed the variability of the parameters ξ, $d1$ and $d3$ in relation to the whole tree descriptors. Among various combinations of whole-tree descriptors, the best fits were given by:

$$\xi = s\ \mathrm{HLLWA}_i$$
(statistic of fit: R-square = 0.55) (9)

$$d1 = d1_0 + d1_1\ \mathrm{DBH}_i$$
(statistic of fit: R-square = 0.76) (10)

$$d3 = d3_0 + d3_1\ \mathrm{CR2}_i + d3_2\ \mathrm{CR2}_i^2$$
(statistic of fit: R-square = 0.79) (11)

Consequently, we deduced from ξ and $d1$ one relation for $d2$. We formed a global model (12) which was estimated for all trees.

Table IV. Analysis of fixed parameter estimates and variances/covariances of random effects for prediction of branch angle (model 8).

Fixed parameter	Estimate	Std error	DDF	T	Pr>ITI
B_1	44.575	1.46	35	30.64	0.0001
B_2	0.098	0.01	35	6.59	0.0001
Variances/covariances of random effects	Estimate	Std error			
var β_1	63.11	18.24			
cov (β_1,β_2)	–0.47	0.17			
var β_2	0.007	0.002			

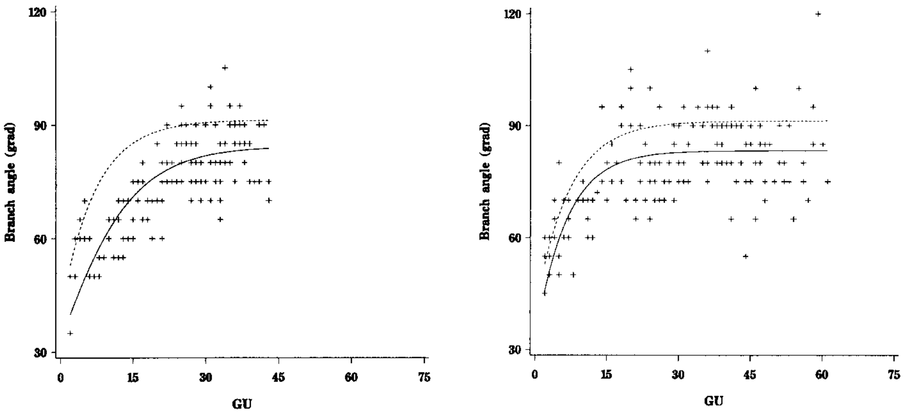


Figure 3. Fit of the branch angle profile of two sample trees. Dotted line represents the profile predicted from the fixed-effect version of the model (8); solid line represents the profile predicted from the mixed-effect model (8). The tree top corresponds to GU = 1.

$$\mathrm{BD}_{ij} = d0 + d1\ \mathrm{DFA}_{ij} + d2\ \mathrm{DFA}_{ij}^2 \quad \text{if } \mathrm{DFA}_{ij} < \xi \qquad (12)$$

$$\mathrm{BD}_{ij} = d0 + d1\ \xi + d2\ \xi^2 + d3\ (\mathrm{DFA}_{ij} - \xi) \quad \text{if } \mathrm{DFA}_{ij} \geq \xi$$

$$\text{where } \xi = s\ \mathrm{HLLWA}_i$$

$$d1 = d1_0 + d1_1\ \mathrm{DBH}_i$$

$$d2 = -d1 / (2\ \xi)$$

$$d3 = d3_0 + d3_1\ \mathrm{CR2}_i + d3_2\ \mathrm{CR2}_i^2$$

The parameter values and their standard errors were estimated as follows in *table V* (statistics of fit for 4 303 observations on 36 trees: root mean square error (RMSE) = 6.5 mm). *Figure 4* shows how the model fits the data for two trees.

If the linearization of this complex model was also possible using the same method as for branch angle, the mixed model introduced numerous fixed and random effects which could not be dealt with classical statistical package (SAS statistical package).

3.2.3. Joint simulation of branch length and branch angle profiles

To simulate diameter and angle profiles along a tree stem in a realistic fashion, we had to take into account the link between diameter and angle within a tree: globally, the thickest branches had an acute angle whereas the thinner branches had an open angle. Although a part of this link is taken into account in the models above through the common or linked variables of each model, it remains a relationship between the unexplained within-tree variations of diameter and angle (*figure 5*).

Formally, for a branch j in a tree i, we have to simulate the branch angle BA_{ij} and the branch diameter BD_{ij} according to:

$$\mathrm{BA}_{ij} = f_{\mathrm{A}}(\mathrm{GU}_{ij}, B_{\mathrm{A}}, \beta_i) + \varepsilon_{\mathrm{A}ij}$$

$$\mathrm{BD}_{ij} = f_{\mathrm{D}}(\mathrm{DFA}_{ij}, d_{\mathrm{D}}) + \varepsilon_{\mathrm{D}ij}$$

where f_{A} is the angle model (8), f_{D} the diameter model, B_{A} and d_{D} the fixed-effect parameters for angle and diameter, respectively, β_i is the vector of random tree effects for angle (to be generated from a bivariate normal distribution with variance–covariance matrix as given in *table IV*, and $\varepsilon_{\mathrm{A}ij}$ and $\varepsilon_{\mathrm{D}ij}$ are the correlated within-tree random variations of angle and diameter, jointly distributed as a bivari-

Table V. Parameter estimates for prediction of branch diameter (model 12).

Parameter	Estimate	Asymptotic standard error	Asymptotic 95% confidence interval	
			Lower	Upper
$d0$	7.509	0.498	6.533	8.486
$d1_0$	3.657	0.232	3.203	4.112
$d1_1$	0.202	0.005	0.193	0.211
$d3_0$	-7.164	0.237	-7.629	-6.698
$d3_1$	27.362	1.004	25.394	29.331
$d3_2$	-30.082	0.998	-32.038	-28.127
s	0.655	0.008	0.639	0.671

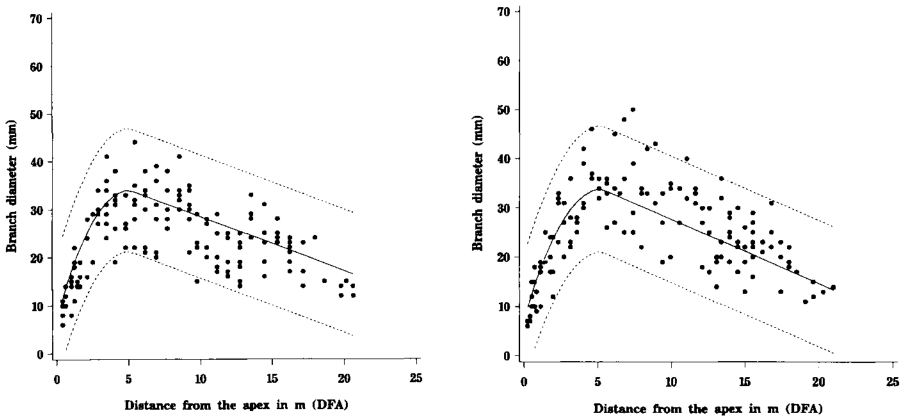


Figure 4. Fit (standard line) of the diameter (in mm, plus) profile versus the distance from the apex (DFA) for two example trees (model 12). Dotted lines are the 95 % confidence interval limits. The tree top corresponds to DFA = 0.

ate normal distribution with mean 0 and variance–covariance matrix:

$$V_\varepsilon = \begin{vmatrix} \operatorname{var}(\varepsilon_{\mathrm{A}ij}) & \rho\left(\operatorname{var}(\varepsilon_{\mathrm{A}ij})\operatorname{var}(\varepsilon_{\mathrm{D}ij})\right)^{0.5} \\ \rho\left(\operatorname{var}(\varepsilon_{\mathrm{A}ij})\operatorname{var}(\varepsilon_{\mathrm{D}ij})\right)^{0.5} & \operatorname{var}(\varepsilon_{\mathrm{D}ij}) \end{vmatrix}$$

The fit of the angle and diameter models provides estimates for var($\varepsilon_{\mathrm{A}ij}$) and var($\varepsilon_{\mathrm{D}ij}$) (*tables IV* and *V*), but does not for the correlation ρ between $\varepsilon_{\mathrm{A}ij}$ and $\varepsilon_{\mathrm{D}ij}$. This would have required the joint fit of the diameter and angle models, which is possible in principle, but lead to a too complicated computation problem. Instead, we have estimated ρ by the observed correlation between the residuals of the indi-

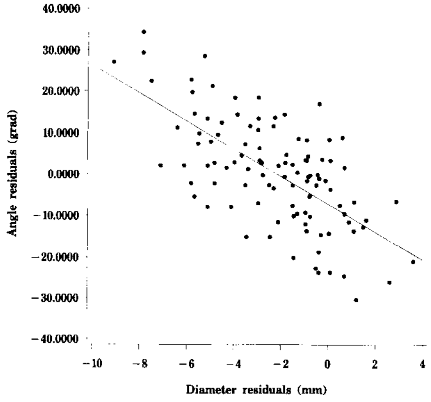


Figure 5. Residuals behaviour from the branch angle and diameter models for one tree.

vidual models of angle and diameter (*figure 5*: for example for this tree, $\hat{\rho} = 0.66$). *Figure 6a* shows an example of simulated values of branch diameter and angle along a tree stem; *figure 6b* illustrates the within-tree correlation obtained between simulated diameters and angles.

4. DISCUSSION

4.1. Statistical methods

This paper gives information on how to use mixed models on branch length and branch angle and how to generate variability around the mean profiles of diameter and angle by taking the correlation of the residuals into account.

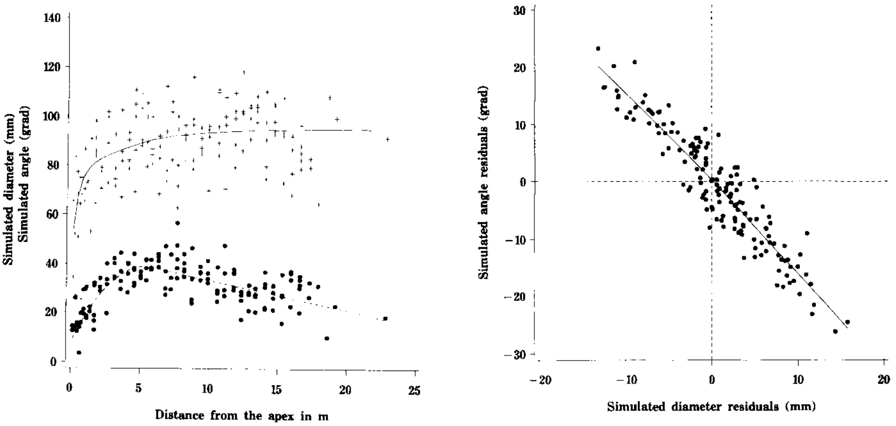
4.1.1. The proposed mixed models

Compared to other studies, the proposed models present an improvement concerning the statistical description of the variability.

When we analysed individual models of branch characteristics, we noted a data structure. The mixed models allow analysis of data with several sources of variation. Like the traditional linear model we can analyse the mean variability of sample trees, but we can also share the residual variability in a between-tree variation and an unexplained individual variation. This method leads us to decrease the residual variability of the traditional linear model. This method can have a great interest in forestry research where the between-tree variation for a variable is sometimes larger than the variation between populations.

Indeed in our model of branch length we had a better estimation of the fixed effect due to the association of the tree characteristics and an estimation of the variability inside the sampled trees.

We did not use the joint generalized least-squares method (as explained by Meredieu and Colin [22]) which permitted the estimation of a system of independent equations of branch diameter and branch angle with correlated random errors. But, we improved the model of branch angle



a

b

Figure 6a. Simulated branch and angle profiles for one tree. Symbols: branch diameter in dots, branch angle in pluses. The lines are the mean predicted values with mixed effect model for branch angle (8) and with global model for branch diameter (12). The tree top corresponds to DFA = 0. **b** Simulated residuals behaviour from the branch angle and diameter models for one tree.

with a mixed model as well as the branch diameter model. For this latter we found a global model. Furthermore, when we simulated a tree we took into account the correlation between the residuals of the two models.

The possibility to fit mixed-effect nonlinear models allows a great number of models. Nevertheless, for complex models such as the segmented second order polynomial model, the linearization was possible, but the capacity of the statistical package did not allow the fitting of this type of model with too numerous variables.

4.1.2. The simulation of tree branchiness

Mixed models also have a great power for simulation: the fixed effect model gives the mean tendency, the random effect model with the variance–covariance matrix gives several possible tendencies within the population. We just have to generate a vector of x positions of mean 0 and given variance–covariance matrix of random effect. We made one drawing of a value per tree and then one drawing of a value for each branch in the variance–covariance matrix of within-branch error.

We did not use a system of equations for fitting both angle and diameter but we took into account the residual correlation in the simulation. This method permits us to improve the characteristics of simulated trees used in a wood quality simulator. The branch characteristics are now compatible thus the biggest branch of a whorl has one of the smallest angles.

4.2. Methodological aspects

4.2.1. Choice of static model

The choice of static allometric models is due to several reasons: we need equations with which the outputs of a distance-independent growth model were able to give us detailed information about branchiness. The role of the branch equations is to provide information first about branchiness for technical pruning management and second about knottiness at different simulation steps (thinning or clear cutting) for logging operations and for grading standing or felled trees. Furthermore our goal is to provide a management tool which permits to give information on yield and wood quality with the minimum information usually measured by forest managers. Lastly, our model could be used to predict the external shape of the crown with the branch length model.

4.2.2. Choice of tree descriptors

The choice of tree descriptors was limited by the tree attributes usually provided by growth simulators such as tree age (A), tree height (TH), past height growth curve, past height annual increments curve, DBH, past radial growth curve, height to the lowest living whorl (HLLW), height to the lowest living whorl branch (HLLB), and their combinations such as different crown ratios, etc. For a given growth unit we have: its identification number GU and the distance to the apex of its upper limit (DFA).

We did not use stand variables such as local density, basal area, stand density or social status. We chose allometric relations between bole dimensions and crown dimensions. Silvicultural effects are taken into account through the growth models which give the characteristics of trees and through the values of variables reflecting the past growth conditions.

The mean vertical profile of length can be obtained, based on information on DFA and DBH. This result is similar to the conclusions of Mitchell [23] and Kozlowski [11] concerning the relation between branch length and its insertion level from the apex. At the same distance from the apex, the increase of tree size (DBH) induce the increase in branch length. Like Kramer [12] we showed that the branch lifespan becomes longer as the tree ages because in the equation the increase in DFA implies an increase in tree age.

The mean vertical profile of diameter, model introduced by Colin and Houllier [4], can be obtained based on information on DFA, DBH, CR2 and HLLWA. This model is consistent with other results: Schöpf [29], Maguire et al. [20] and Uusvaara [30] observed that the branch size is linked to crown shape (CR2, HLLWA) and to stem size (DBH). Nevertheless it is known that branch diameter is under environmental control (for instance spacing) [1]. CR2 and HLLWA could give indications on silvicultural management.

It was impossible to obtain such relations between usual tree measurements and branch angle profile. Nevertheless, there is an effect of tree age on the insertion angle of the branches. GU gives information on the position of the branch in the crown: first, in the upper crown, angle is linked with the apical control and branches are oriented towards the light. Second, due to the mechanical pressure of the stem wood at the insertion point and due to the branch weight the angle becomes larger. We did not observe any effect of silvicultural management through tree variables but there is a random effect between trees. This global result has however to be considered according to the genetic origin of the trees. It is known that branch angle is under stronger genetic control [30]. Comparative studies between Corsican pine varieties (corsicana and calabrica) showed different angle patterns [25]. Comparative studies on different provenances are needed to remove the genetic effects from the random parameters of our model. It can be interesting to distinguish the variability between trees into a provenance variability and a real between-tree variability.

4.2.3. Sampling design and statistical models

Our sampling design had several levels of variability: between-stand (site, age, silvicultural and genetics effects), within-stand (social status effects), within-tree (i.e. between-whorl including age, climat and varying-over-time tree to tree competition effects) and within-whorl variability (within-branch competition and position effects [15]). Our results have taken into account the within-tree and a between-tree variability. With the information of residual variability it is possible to include the within-whorl variability. Our sampling describes a great variability needed by the final objective of the study: the prediction of branchiness characteristics of simulated trees from a growth model.

To check if social status, age or fertility had an effect, we used the random-effect solution vector of the branch length model and the branch angle model. With box-plots, we were able to verify the non-effects of these sampling variables. So, these effects were taken into account through the tree characteristics used in these mixed models. Nevertheless, we could not check the between-stand variability. Only three trees per stand were studied, and these trees had different social status. There are possibilities for improving the description of this variability due to silvicultural management by increasing the sampling on some stands.

We chose trees without crown defects. The occurrence of ramicorn branches were not be studied here. We know that it depends partially on the genetic origin, the site conditions and tree age [26, 27]. It can be interesting to study this phenomenon more intensively in order to take this aspect into account by stochastic simulation at the stand scale.

The branches analysed for their angle and diameter are only branches with a relatively large diameter (i.e. branches exhibiting a diameter higher than half of the maximum diameter per whorl). The removed branches have a low impact on wood quality. These thin branches have a short lifespan, are located at the base of the whorl and self-pruned after a short time. This kind of branch represented from 2 to 20 % of all branches. Further studies on the removed branches should have been carried out in order to explain further biological aspects. In the branch length model, we only studied living branches which give the crown shape.

4.3. Evaluation of this type of model

Although the crown morphology results from dynamic functional processes which include genetics, site conditions, stage of development of the tree, local density of the stand, social status of the tree, our models do not need information about the stand but only current tree characteristics. So, for evaluation, we do not need to know the site quality nor the past silvicultural management to choose sample trees. Conversely to growth models which need trees belonging to stands with past information, our branch models are easy to evaluate with new data.

Mixed model interest for evaluation is to allow us to check both if the mean tendency is the same for the new sample (same fixed effects) and if the range of variation of new sample trees is well explained with the variance–covariance matrix of random effects.

4.4. Vertical profile of knot size and shape

Branch diameter and angle at a given height give access to the size of the knot at the radial external limit of the bole. To obtain the entire knot shape inside the bole, we use a stem taper equation to obtain the bole radius at each level. The information on branch angle, bole radius and distance from the apex may give indication on the curvature of the pith of the knot and with the branch diameter on the ovality of the knot inside the bole. Then, it will be possible to describe the envelope of the knot. Furthermore, we modelled the proportion of living branch per whorl [22], so we are able to give information on the delineation between tight and loose black knot zones [18].

This work will finally lead to statistical relationships between branching traits, knot shape and also knot volume. The set of branch models and the set of knot models will be then combined. We will then be able to link tree attributes to knottiness features, and also growth conditions to knottiness and crown structure.

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