THE SILVICULTURAL EXPERIMENTAL PLOTS OF PARACOU IN FRENCH GUIANA: EXAMPLE OF USE AND LIMITS OF THE AVAILABLE DATA FOR DEVELOPPING INDIVIDUAL GROWTH MODELS

Sylvie Gourlet-Fleury
Avner Bar-Hen
Nicolas Fauvet

CIRAD-forêt, Campus International de Baillarguet
Montpellier, France.

ABSTRACT

Long-term monitoring of the rainforest dynamics, according to various kinds of disturbance, has been undertaken in French Guiana since 1984, on the Paracou site, 50 km north-west from the spatial center of Kourou. The great amount of detailed and spatialised data gathered on twelve plots, 9 ha each, and dealing with more than 46 000 trees, allowed us to build models of forest dynamics. One of them is an individual-based spatially explicit model, the development of which led us to describe as precisely as possible the different components of the dynamics : growth, mortality and ingrowth, at an individual scale, before including them inside a simulator. The object of the paper is to present the results obtained with the growth component. It has been developped using the " potential x modifier " philosophy, but adapted to take into account the rainforest conditions. It presently predicts the mean annual diameter growth of trees, according to their diameter, local environment described through competition indexes, and species they belong to. Trials to take into account pedological and topographical information remained unsuccessful due to the lack of accuracy of the available data. Problems encountered and remaining to improve this model are discussed.

INTRODUCTION Since the beginning of the 1970's, the forest department of CIRAD (ex " CTFT") settled or took part to the settlement of large size experimental plots in natural and/or disturbed tropical moist forests around the world, in order to gather data and elaborate knowledge about their dynamics and functioning (Maître, 1990, Favrichon *et al.*, 1998). The Paracou experimental design, located in the north-eastern part of the amazonian region in French Guiana, is the last but one of them. Installed in 1984, it is particularly interesting because it made profit from the successes, failures and inadequacies of the preceding experiments and the following issues, for example, were particularly addressed:

- delimitation and survey of big surfaces (more than 1 ha), to take into account the biological and physical heterogeneity of the environment,
- delimitation of plots in previously undisturbed stands and repeated survey before any silvicultural treatment, so that each plot can be its own control,
- survey of all trees more than 10 cm dbh, whatever the species (potentially commercial or not) they belong to,
- following of all identifiable types of mortality, natural or consecutive to silvicultural treatments. For natural mortality, three categories are concerned: standing death, primary windthrow, secondary windthrow,
- coupling with a systematic survey of regeneration.

Since 1984, a lot of informations have been collected which are definitely useful to the lowland evergreen rainforests managers, notably for the definition of felling cycles in the management units

of the coastal part of French Guiana. Results from Paracou helped to imagine " ideal " silvicultural scenarios, which are currently tested in real scale in managed forests (Gourlet-Fleury, 1992a).

In 1993, in addition to this costly field experimentation, CIRAD-forêt started a modelling program in order to: (*i*) make profit from the huge amount of data gathered on the experimental plots, were they demographical or physical, to describe and predict the growth of stands according to various silvicultural scenarios; (*ii*) thus identify gaps in our knowledge and modify consequently the current surveys; (*iii*) try, through the synthesis of current knowledge and the analysis of the model functioning, to better understand the underlying mechanisms of tropical rain forest dynamics. Up today, a density-dependent matrix model was built by Favrichon (1995, 1998), as well as a first version of a single-tree, distance dependent model (Gourlet-Fleury, 1997, 1999) implemented in a simulator called SELVA (Caruso, 1994). Another approach, derived from the gap models, is still under completion (see Vanclay, 1994, for more details on forest dynamics models).

In this paper, we will focus on the single-tree model and more precisely on the possible improvement of its growth component. In a previous work (Gourlet-Fleury, 1997, Gourlet-Fleury and Houllier, 1999) we put forward a model linking diameter growth increment with diameter at the beginning of the growth period, competition indices rendering the local environmental pressure, and taking into accout species information. Here, our specific objectives will be:

- to study and discuss the remaining plot effect on the residuals of the growth model,
- to examine the physical data allowable on those plots (dealing with soil on some of the plots, and topography on all of them) and their potential ability to improve the efficiency of the growth model,
- to discuss, in the light of the growth model behaviour, some of the main weaknesses of the Paracou design.

MATERIALS

Paracou was settled in 1984 in a previously undisturbed forest area of the coast, about 50 km WNW from Kourou, near Sinnamary. 12 plots, 9 ha each, were delimited on a globally homogeneous substrate qualified as " Sols à drainage principalement superficiel " (soils with mainly superficial drainage), which represent the most commonly encountered soil conditions in the area (Boulet et Brunet, 1983). Those soils are developped on schists (" Série de Bonidoro ") and mainly consist of clay and sandy-clay.

On each plot, all trees more than 10 cm of dbh are localized by their cartesian coordinates inside a core of 6.25 ha (the core is surrounded by a buffer zone 25 m wide), and their girth (gbh) is measured each year since 1984. Recruitment and mortality are monitored as well. The trees have been botanically identified when possible: 200 so-called species (*ie* several appellations contain more than one species) are distinguished. The identification by means of Herbarium collection is still ongoing. Physical information allowable on the stands are:

- data from soil profiles sampled in the 3 control plots (Barthès, 1991). 6 variables were examined (see table 1): depth of usefull soil (" drainage "), hydromorphy at the top of the soil profile (" hydromorphy "), presence of layers with coarse sand (" coarse sand "), presence of layers with ferruginous nodules (" nodules "), pH of water (" pH ") and carbon content (" carbon ") between 5 and 20 cm of depth;
- topography, by the way of a digital elevation model, elaborated for the 12 plots from 5 meters contour lines.

Between 1986 and 1988, 3 types of silvicultural treatments were applied on 9 of the plots (each treatment repeated 3 times), the last 3 remaining control plots (T0). The treatments were the following: (T1) traditional selective felling of commercial species, representing about 10 trees more than 50 to 60 cm dbh per hectare; (T2) selective felling plus thinning by poison-girdling of all non-commercial species (NCS) more than 40 cm dbh; (T3) selective felling plus logging of NCS between 40 and 50 cm dbh (for fuel wood), followed by poison-girdling of all NCS more than 50 cm dbh (Schmitt, 1989). Table 2 summarizes for each treatment the evolution of the number of trees and the total basal area between 1984 and 1994.

To adjust the components of the single-tree / distance dependent model, we focused on 8 of the 12 plots (2 plots per treatement), in order to keep an independent data set for a validation work. In each plot, to calculate diameter increment, we considered trees as far as: (*i*) they did not present any measurement anomaly and (*ii*) they were located more than 30 m from the border line, to authorize the calculation of competition indices. This left us with 10 745 trees and 173 species (or so-called). We worked on a three-years time step basis.

Table 1: *Soil variables and notations used in the analysis. The classes are described according to Barthès (1991).*

Variables	Classes	Notations
Drainage	Bottomland, greyish sandy profile, moistened to humid from bottom to top	*drain1*
	Moistened profile with a depth more than 100 cm	*drain2*
	Moistened profile with a depth between 80 and 100 cm	*drain3*
	Moistened profile with a depth between 60 and 80 cm	*drain4*
	Moistened profile with a depth less than 60 cm	*drain5*
Hydromorphy	No trace	*hydro0*
	Clear signs at the top of the profile	*hydro1*
	No sandy layers	*sable0*
Coarse sand	Presence of a layer with coarse sand, thickness more than 30 cm	*sable1*
PH (water between 5 and 20 cm of depth)	$pH \leq 4.6$	*pH1*
	$4.6 \leq pH < 5$	*pH2*
	$pH \geq 5$	*pH3*
Carbon (carbon content between 5 and 20 cm of depth)	Content < 1%	*carbo1*
	Content between 1 and 3 %	*carbo2*
	Content ≥ 3%	*carbo3*
Nodules	No trace	*nod0*
	Presence of a layer with ferruginous nodules, thickness more than 30 cm	*nod1*

Table 2: *Number of trees more than 10 cm dbh (N) and total basal area per hectare (G) for each treatment (3 plots per treatment) at the Paracou site. Timber felling took place from Oct. 1986 to May 1987, and thinning from Dec. 1987 to Jan. 1988. After Prothery (1995).*

Years	Control plots		Treatment 1		Treatment 2		Treatment 3	
	N	G (m^2)	N	G (m^2)	N	G (m^2)	N	G (m^2)
1984	625	30.9	603	30.6	623	31.9	628	32.1
1985	626	30.9	606	30.7	626	32.0	626	32.0
1986	626	31.0	606	30.7	626	32.1	625	32.1
1987	622	30.8	512	25.0	523	25.5	442	21.3
1988	618	30.7	506	24.9	496	20.4	425	17.6
1989	615	30.7	508	25.0	488	19.3	423	17.1
1990	614	30.7	509	25.1	489	19.2	431	17.2
1991	616	30.8	521	25.4	504	19.4	449	17.3
1992	614	30.9	530	25.6	513	19.7	470	17.7
1993	611	30.9	533	25.8	525	20.1	487	18.1
1994	607	30.9	531	25.9	527	20.3	490	18.5

METHODS

The growth model consists of 15 submodels, each one fitted to a particular group of species. It was built according to the " potential x modifier " philosophy (see, for example, Monserud, 1975, Hahn and Leary, 1979, Leary and Holdaway, 1979, Shugart, 1984, Fairweather, 1988, Parresol, 1995, Murphy and Shelton, 1996 and, for a more systematic review, Gourlet-Fleury, 1997): in this class of model, growth is considered to be the product of " potential growth ", the maximum possible growth when there is no competition, and a " modifier component ", usually a function of more or less empirical competition indices (Dreyfus, 1988, Biging and Dobbertin, 1992, 1995, Gourlet-Fleury, 1992b, 1998) which represent the environmental pressure on the tree. The calibration was done by ordinary least square regression after log-transformation of the dependent variable, diameter increment.

A one-way analysis of variance (ANOVA) was used to study the plot effect on residuals (hypothesis of ANOVA were checked). In order to explain this plot effect, we investigated the informations brought by soil and topographical data (namely altitude and slope, extracted from the digital elevation model), taking into account the fact that the only way to extrapolate pedological information (availability restricted to control plots) was to rely on topographical ones.

First, we studied the relationships between soil variables (all discrete). The association was tested by means of the Pearson chi--square test of independence for a pairwise study of the variables. Since they do not have the same number of classes, the tests do not have the same number of degrees of freedom. Therefore it is not possible to compare directly the Pearson chi--square values obtained for the different variables. For this purpose, the coefficient phi is a better statistic (see Bishop *et al.*, 1975). It varies between 0 and 1 and any test is associated with this coefficient. A value near zero indicates a weak association and a value near 1 indicates a strong association. A

multiple correspondance analysis (MCA, Lebart *et al.*, 1984) was performed to precise the nature of the associations.

To quantify the relationships between topographical and pedological variables, while taking into account the relationships between altitude and slope, we performed a multivariate analysis of variance where those variables were the response variables and the soil variables were the factors.

We finally realized a canonical correlation analysis. Given two sets of variables X and Y (here, the topographical and soil variables respectively), this type of analysis find linear combinations of X and Y (called the canonical variables) such that the correlation between the two sets of variables is maximized. Canonical correlation analysis has certain maximal properties similar to those of multiple correspondance analysis. However, whereas MCA considers interrelationships within a set of variables, the focus of canonical correlation is on the relationship between the two groups of variables. Simple and multiple correlation are special cases of canonical correlation in which one or both sets contain a single variable (see Mardia *et al.*, 1979). This analysis provided us with canonical variables and we studied the interest of the first of them to improve our growth model.

All computations were performed by using procedures of SAS (SAS, 1990).

RESULTS

The growth model

The 15 submodels use the following expressions:

$$Log(\Delta D + 0.287) = Log(potential) + Log(modifier) + \varepsilon,$$

with, in all cases,

$Log(potential) = Log(a) + Log(D) + Log[Log(K) - Log(D)]$ that is to say the Gompertz model and, according to the species groups:

- $Log(modifier) = bNBD^{1/2} + c\Delta NBD + d\Delta NBD^2 + e$ [6]
- $Log(modifier) = bNBD^{1/2} + c\Delta NBD + d\Delta NBT^2 + e$ [7]
- $Log(modifier) = bLog(NBD + 1) + c\Delta NBD + d\Delta NBT^2 + e$ [8]
- $Log(modifier) = bNBD + c\Delta NBD + d\Delta NBD^2 + e$ [9]
- $Log(modifier) = c\Delta NBD + d\Delta NBD^2 + e$ [10]
- $Log(modifier) = c\Delta NBD + d\Delta NBT^2 + e$ [11]
- $Log(modifier) = c\Delta NBD + e.$ [12]

D is the diameter at breast height (cm) in 1988, immediatly after the completion of silvicultural treatments, D*D* the annual diameter increment of the tree, smoothed over the period 1988-1991 (cm/yr). *NBD*, D*NBD* and D*NBT* are competition indices:

- *NBD* (resp. *NBT*) is the total number of neighbours with a dbh greater than or equal to the subject one in 1988 (resp. total number of neighbours ≥ 10 cm of dbh) and located less than 30 m from it;

- D*NBD (resp.* D*NBT)* is the variation of the *NBD* (resp. *NBT*) index during the 3 years period preceding the current period of growth, *ie* from 1985 to 1988: negative values of ΔNBD render a decreasing environmental pressure on the subject tree, either because it grew faster than its neighbours or because death — natural, logging or poison-girdling — occured; positive values, on the contrary, result from a better growth of the neighbours and render an increase in competition. D*NBD* is particularly efficient in rendering the effect of silvicultural treatments.

a and *K* (cm) are the parameters of the Gompertz model: *a* is the inverse of a time constant and *K* is the maximum value *D* can reach. *b*, *c* and *d* are the other regression parameters. Their values, all significantly differing from zero, are shown on table 3. Details about the species grouping and the method followed to build the submodels will be found in Gourlet-Fleury (1997, p.119-133).

The global efficiency of the growth model can be roughly characterized by the pseudo-R^2:

$pseudo - R^2 = 1 - \left[{}^{SSR}/_{CSS}\right] = 0.42$ with *SSR* (sum of squared residuals) = 995 and *CSS* (centered sum of squares) = 1715. Residual distributions are norl (Shapiro-Wilk tests) for all but two species groups (g1.2 and g3.1). However, the deviation was not judged sufficiently important to invalidate the following analysis.

Table 3: *Values of the parameters of the 15 submodels (the line titled " sub-model fitted " refers to equations given in the main text). The 15 species groups are allocated among 5 super-groups corresponding to size criteria and susceptibility to social position. Inside each of them, species groups are characterized by an increasing mean of diameter growth. Note that group g1.3 gathers non identified species belonging mainly to Chrysobalanaceae (" gaulettes "). NB. See Gourlet-Fleury (1997, p.119-133) for more details .*

Table 3(a) Super-group 1: small size species with no obvious susceptibility to social position.

Species group	Group g1.1	Group g1.2	Group g1.3	Group g1.4
Mean diameter increment on the control plots (cm/yr)	0.05	0.05	0.11	0.07
Typical species	*Catostemma fragrans* Bentham Bombacaceae	*Iryanthera sagotiana* (Bentham) Warburg Myristicaceae	—	*Sloanea cf. guianensis* (Aublet) Bentham Elaeagnaceae
Sub-model fitted	[6]	[6]	[6]	[6]
Parameters	Estimate *(s)*	Estimate *(s)*	Estimate *(s)*	Estimate *(s)*
a'[a]	-4.29 *(0.04)*	-4.28 *(0.05)*	-4.39 *(0.06)*	-4.29 *(0.05)*
K (cm)	71.68 *(3.88)*	77.13 *(6.07)*	93.81 *(7.59)*	87.27 *(7.62)*
b ($*10^{-3}$)	0.00	0.00	0.00	0.00
c ($*10^{-3}$)	-9.97 *(0.84)*	-12.66 *(1.02)*	-15.70 *(1.37)*	-11.40 *(0.89)*
d ($*10^{-3}$)	-0.050 *(0.009)*	-0.070 *(0.011)*	-0.053 *(0.014)*	-0.053 *(0.010)*

[a]: see bottom of table 4(d).

Table 3(b): *Super-group 2: average to big size species showing no obvious susceptibility to social position.*

Species group	Group g2.1	Group g2.2	Group g2.3	Group g2.4
Mean diameter increment on the control plots (cm/yr)	0.06	0.09	0.12	0.17
Typical species	*Bocoa prouacensis* Aublet Caesalpinia-ceae	*Lecythis poiteauii* Berg Lecythidaceae	*Licania cf. micrantha* Miq Chrysobala-naceae	*Eperua falcata* Aublet Caesalpinia-ceae
Sub-model fitted	[6]	[5]	[5]	[5]
Parameters	Estimate *(s)*	Estimate *(s)*	Estimate *(s)*	Estimate *(s)*
a'[a]	-4.38 *(0.06)*	-4.52 *(0.03)*	-4.45 *(0.03)*	-4.50 *(0.05)*
K (cm)	81.66 *(5.40)*	94.21 *(2.76)*	96.78 *(2.26)*	112.85 *(4.57)*
b ($*10^{-3}$)	0.00	0.00	0.00	0.00
c ($*10^{-3}$)	-13.72 *(1.84)*	-22.47 *(1.55)*	-20.91 *(1.62)*	-30.64 *(2.76)*
D ($*10^{-3}$)	-0.044 *(0.014)*	-0.174 *(0.027)*	-0.153 *(0.029)*	-0.278 *(0.045)*

[a]: see bottom of table 4(d).

Table 3(c): *Super-group 3: large size species with obvious susceptibility to social position. Super-group 4: average to large size species with obvious susceptibility to social position.*

Species group	Group g3.1	Group g3.2	Group g4.1	Group g4.2
Mean diameter increment on the control plots (cm/yr)	0.27	0.50	0.16	0.31
Typical species	*Qualea rosea* Aublet Vochysiaceae	*Sclerolobium melinonii* Harms Caesalpinia-ceae	*Recordoxylon speciosum* (R, Ben) Norm. et Marq Caesalpinia-ceae	*Symphonia globulifera* Linnaeus f. Clusiaceae
Sub-model fitted	[4]	[7]	[1]	[1]
Parameters	Estimate *(s)*	Estimate *(s)*	Estimate *(s)*	Estimate *(s)*
a'[a]	-4.38 *(0.08)*	-4.36 *(0.28)*	-3.73 *(0.15)*	-4.05 *(0.17)*
K (cm)	131.53 *(8.80)*	196.34 *(83.99)*	69.98 *(4.60)*	99.71 *(12.65)*
b ($*10^{-3}$)	-1.19 *(0.47)*	0.00	-47.25 *(10.45)*	-27.28 *(10.49)*
c ($*10^{-3}$)	-28.82 *(3.22)*	-19.03 *(4.32)*	-24.15 *(2.72)*	-29.89 *(2.60)*
d ($*10^{-3}$)	-0.257 *(0.056)*	0.00	-0.125 *(0.044)*	-0.192 *(0.042)*

[a]: see bottom of table 4(d).

Table 3(d): *Super-group 5 : small size species with obvious to great susceptibility to social position.*

Species group	Group g5.1	Group g5.2	Group g5.3
Mean diameter increment on the control plots (cm/yr)	0.09	0.18	0.25
Typical species	*Drypetes variabilis* Uittien Euphorbiaceae	*Couepia cf. caryophylloïdes* R, Ben Chrysobalanaceae	*Inga cayennensis* Sagot ex Bentham Mimosaceae
Sub-model fitted	[3]	[3]	[2]
Parameters	Estimation *(s)*	Estimation *(s)*	Estimation *(s)*
a'[a]	-2.96 *(0.28)*	-3.14 *(0.16)*	-3.76 *(0.35)*
K (cm)	56.62 *(4.39)*	74.70 *(3.70)*	94.83 *(29.04)*
b ($*10^{-3}$)	-234.94 *(48.31)*	-223.95 *(30.02)*	-47.73 *(18.58)*
c ($*10^{-3}$)	-17.33 *(1.18)*	-17.72 *(1.16)*	-21.93 *(1.88)*
d ($*10^{-3}$)	-0.069 *(0.014)*	-0.055 *(0.011)*	-0.107 *(0.021)*

[a] The constant e in the modifier components cannot be estimated separately from the parameter a of the Gompertz model (potential component). The parameter estimated then is a'=Log(a)+e.

Soil and landfacets effects

A significative plot effect remains on the residuals and a Bonferroni test (multiple comparison of means) separates three groups (table 4): (*i*) plot 10 (treatment 2), with diameter increments definitely underestimated by the growth model, (*ii*) plots 1 and 6 (control plots) with only a slight underestimate and (*iii*) plots 4, 5, 7, 9, 12 (all treatments) where diameter increments are slightly overestimated. This plot effect is not due to a treatment effect, as was confirmed by a hierarchical analysis of variance " Plot (Treatment) " of the residuals (Gourlet-Fleury, 1997, appendix 6, table a11). Among the remaining factors which can play a part, physical ones are worth being investigated: as a matter of fact, table 3 shows that, before the implementation of silvicultural treatments, mean increments were highest on the control plots than on the others despite similar densities of trees more than 10 cm dbh. This could be due to site effects, at least for the group of plots with negative residual means.

Table 5 shows the relationships between the 6 soil variables collected on plot 1 and 6. All the chi-square tests are significant at the 0.1 % level, indicating redundancy information among them. The phi coefficient ranges from 0.1 to 0.7 for all but three pairs, and show that " drainage ", " hydromorphy ", " coarse sand " and " carbon " are well linked together, " drainage " being associated to " nodules " as well. As can be seen on the two first factorial axes of the MCA (fig.1) for the best described classes, signs of hydromorphy, bottomlands, presence of sandy layers, low carbon content and absence of ferruginous nodules are linked. There is evidence, from Barthès maps and explanations, that those variables are more or less dependent from the toposequence. This can be quickly checked on fig.1, where we projected (as an additional variable) on the first factorial plan the classes of a variable defined from " altitude " and " slope " as follows: bottomlands (altitude ≤ 5 m and slope ≤ 5°), hillsides (slope > 5°, whatever the altitude) and summits (altitude > 5 m and slope = 0).

Table 4: *Ranking of the plots (resp. of the silvicultural treatments) by decreasing values of the growth model residuals (last column). A Bonferroni test (multiple comparison of means) allows a distinction between three groups of plots, according to the mean values of this variable: they are respectively represented with italic, normal and bold type in the last column. (A total of 10745 trees are concerned by the study).*

Plot (treatment)	Number of trees studied	Mean (standard deviation) diameter increment before treatment: 1984-1986 (cm/yr)	Mean (standard deviation[a]) diameter increment after treatment: 1988-1991 (cm/yr)	Mean (standard deviation) of the residuals (Log(cm))
10 (T_2)	1177	0.117 (0.439)	0.325 (0.090)	*0.100 (0.336)*
1 (T_0)	1596	0.217 (0.599)	0.142 (0.033)	0.021 (0.280)
6 (T_0)	1561	0.267 (0.790)	0.127 (0.029)	0.013 (0.279)
12 (T_3)	1250	0.159 (0.543)	0.252 (0.052)	**-0.017 (0.298)**
9 (T_1)	1344	0.121 (0.384)	0.202 (0.046)	**-0.018 (0.303)**
5 (T_2)	1449	0.124 (0.419)	0.232 (0.064)	**-0.023 (0.311)**
7 (T_1)	1376	0.157 (0.539)	0.188 (0.042)	**-0.027 (0.289)**
4 (T_3)	992	0.143 (0.499)	0.282 (0.065)	**-0.038 (0.333)**
Treatment				
T_2	3157	0.242 (0.700)	0.274 (0.078)	0.032 (0.329)
T_0	2626	0.139 (0.469)	0.135 (0.031)	0.017 (0.279)
T_1	2720	0.121 (0.428)	0.195 (0.044)	-0.023 (0.296)
T_3	2242	0.152 (0.524)	0.266 (0.058)	-0.026 (0.314)

[a] NB. In this column, diameter increment is equal to the slope of a straight line fitted to 4 consecutive measures of diameter, resp. in 1988, 1989, 1990 and 1991. In the previous column, diameter increment is calculated as an arithmetic mean of two values (increment between 1984 and 1985, and increment between 1985 and 1986). Hence, standard deviations are not comparable between the two columns.

Table 5: *Relationships between the different categorical soil variables, as tested by chi-square tests and measured by the phi coefficient: in bold type in the table (Bishop et al., 1975). The analysis are realized on 3157 trees located on the control plots 1 and 6.*

Chi-square (df) **Phi coef-ficient**	Drainage	Hydromor-phy	Coarse sand	pH	Carbon	Nodules
Drainage	-					
Hydromor-phy	1044 (4) **0.575**	-				
Coarse sand	1523 (4) **0.695**	1042 (1) **0.574**	-			
pH	286 (8) **0.301**	394 (2) **0.353**	41 (2) **0.114**	-		
Carbon	1212 (8) **0.620**	541 (2) **0.414**	563 (2) **0.422**	257 (4) **0.285**	-	
Nodules	1032 (4) **0.572**	124 (1) -0.198[a]	49 (1) -0.124[a]	147 (2) **0.216**	164 (2) **0.228**	-

[a] It has to be noted that for 2X2 table, SAS is using a formula which allows negative values.

The class " bottomlands " is by far the best represented on the plan, and strongly linked with the class *drain1* of " drainage " and the corresponding classes of " hydropmorphy ", " coarse sand " and " carbon ". The class " hillsides " is also well represented but in a more neutral position given the great heterogeneity of the soil profiles encountered in that position. The class " summits " is not well represented. Those observations are enforced by the results of the MANOVA (table 6), which show a strong effect of all the pedological variables on the topographic ones except for " hydromorphy " and " coarse sand " which are redundant with " drainage " and are then the less informative.

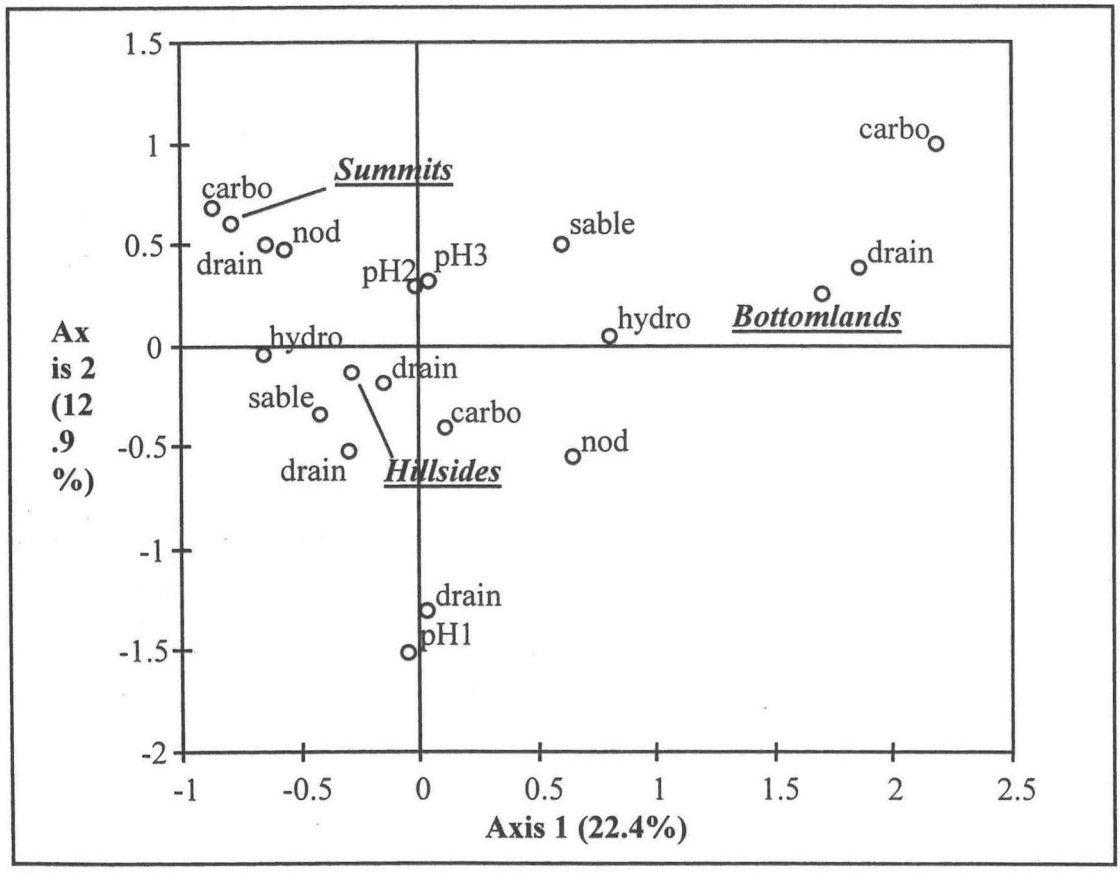


Figure 1: *Projection of the classes of each soil variable (see table 1) on the first factorial plan of a multiple correspondance analysis. The topographical variable (with 3 classes) is treated as an additional variable. This analysis was performed using the three control plots (5182 trees used).*

Table 6: *Results of a MANOVA on the topographical and pedological variables.*

	Wilk's □	F	num. df	den. df	P
Drainage	0.97	11.43	8	6210	<0.0001
pH	0.98	18.12	4	6210	<0.0001
Carbon	0.99	7.14	4	6210	<0.0001
Nodules	0.99	22.71	2	3105	<0.0001
Coarse sand	≈ 1	0.41	2	3105	0.66

Building of a synthetic topographical variable

The landfacets are interesting mainly because they can be calculated on all the plots, and it can be checked that they have a significative effect on diameter increment as well as on the growth model residuals (table 7. F=9.64, df=2, P<0.001 for the residuals). However, the classes " hillsides " and " summits " are pedologically heterogeneous and we decided to look for a more optimal use of the overall information brought by the soil variables, while using the fact that " altitude " and " slope " are continuous variables. This is why we performed the canonical correlation analysis.

It appears from it that the correlation is not very high between " altitude " and " slope " (r = 0.21). The first canonical variable, which equation is:

$$var1 = 0.82 * altitude + 0.43 * slope,$$

is from far the most important and explain 92% of the correlation between the topographical variables and the pedological ones. The equation of the second canonical variable is: $var2 = -0.61 * altitude + 0.93 * slope$. Its contribution is well smaller than the first one, but the effect is still significant. Var1 mostly represents the toposequence, with minimum values obtained in bottomlands and maximum values on the top of the hillsides (see fig.2), while var2 characterizes the hillsides. The canonical redundancy analysis shows that var1 is a good overall predictor of the pedological variables with an explained proportion of variance of 42%. Var2 does not strongly improve the model.

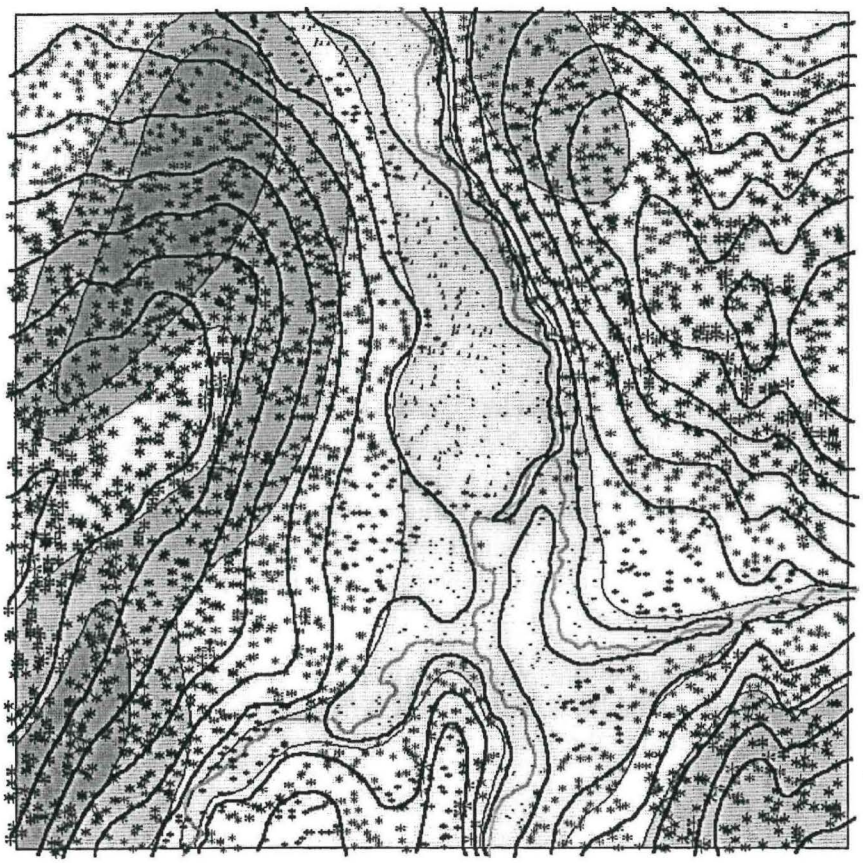
The residuals of the growth model are plotted against var1 on figure 3. It can be seen that the correlation between the two variables is weak, but it differs significantly from zero (r = -0.08). A simple linear model can be fitted to those data:

$$\varepsilon = a_1 * var1 + a_2 + \varepsilon_t$$

with ε: residuals of the growth model, ε_t residuals of the linear model (*ie* residuals of the growth model once the topographical variable has been taken into account) and coefficients a_1 and a_2 significantly differing from zero (table 8). The resulting *SSR* (989), compared to that initially obtained with the growth model (995: see above) shows that the potential improvement with topography is negligible: it is finally quite comparable to the improvement that can be obtained by directly using a plot factor (*SSR* = 979, but with 7 more parameters instead of 2).

DISCUSSION AND PERSPECTIVES

Information available in the data base of Paracou allowed us to build an individual, spatialised tree growth model which we developped following several steps. The first step consisted in linking diameter increment with diameter of the tree at the beginning of the growth period, and competition indices describing the environment. This resulted in a model working whatever the species, which pseudo-R^2 was equal to 0.23 (Gourlet-Fleury, 1997, p.109). A definite improvement came from the building and taking into account of 15 species groups, defined according to size, mean growth and susceptibility to social position. They allowed to almost double the efficiency of the model.



Values of the first canonical variable

* 28 * 14 · 2.8

Classes of the variable "drainage"

drain 1 drain 2 drain 3 drain 4

Figure 2: *Map of plot 6, showing the different classes of the variable " drainage ", the 5 m contour lines and the synthetic topographical variable (ie the first canonical variable) obtained through the canonical correlation analysis.*

Table 8: *Results of the fitting of a simple linear model linking the residuals of the growth model to the first canonical variable (10745 trees used for the analysis).*

Source	df	Sum of squares	Mean square	F
Model	1	6.15	6.15	66.75 (P<0.001)
Error	10743	989.15	0.09	
C. total	10744	995.29		
		Parameter estimates		
	df	Estimate	Standard error	
Var1 (a1)	1	-0.0037	0.00046	
Intercept (a2)	1	0.056	0.0073	

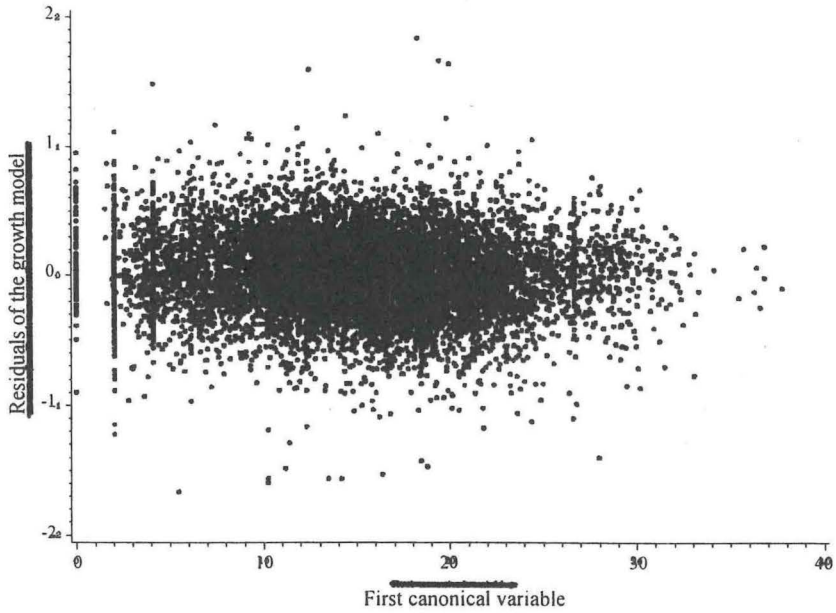


Figure 3: *Link between the residuals of the growth model and the synthetic topographical variable built with the canonical correspondance analysis (10745 trees used).*

Among the soil variables available on the control plots, three deal with the hydrological functioning of the soils (" drainage ", " hydromorphy " and " coarse sand "). Now, it is well known that availability of water along the year is a very important factor which can be critical for a lot of species in those stands; it has an influence on spatial and structural patterns as well as on the overall dynamics (see Barthès, 1990, for a synthesis on the subject in the Guianan forests, and Collinet, 1997), especially growth: trees grow faster in bottomlands. This is well verified at Paracou: see table 7, especially the results obtained with residuals as they allow to get free from such confusing effects as size (trees tend to be smaller in badly drained soils), environment (density tends to be higher in bottomlands) and possibly species. If other soil variables seem to have an effect on growth, like for example " Nodules " (on the control plots, the absence of ferruginous nodules goes with higher increments), this is mainly due to a confusing effect of bottomlands (where nodules are absent). The variable pH does not really bring a useful information and the pattern of its variations on the plots is confused (Barthès, 1991). As far as " carbon " is concerned, the information brought is redundant with " altitude " but in a quite surprising way: contents are smaller in the bottomlands, medium on the hillsides and higher on the summits when the inverse situation would be expected (Ferry, *pers. comm.*). Increments being higher in the bottomlands, a negative link with the carbon content appears.

Those analysis show that the real important information to take into account is the presence of a bottomland, and this makes the potential interest of the topographical variables altitude and slope. The first canonical variable built is strongly linked to " altitude " and reveals to be negatively correlated with the residuals of the growth model: for low values of var1, increment observations tend to be underestimated by the model, while for high values of var1, they tend to be overestimated. This is coherent with what was precedently said. However, the link between var1 and the residuals is too loose to bring any significative improvement to the prediction of growth, and does not prove more efficient than a mere " plot factor ".

In fact, the sampling design made by Barthès to analyse the pedological cover (29 , 39 and 59 soil profiles realized resp. on plot 1, 6 and 11) was very loose, while the author recognized himself (Barthès, 1988) that very contrasted local situations could be encountered on the plots, with important changes occuring on a few meters (eg. changes in soil depth, presence of sand pockets ...). A recently and precise study of the bottomlands on one of the control plots led Ferry to completely reconsider the limits of the very important class " *drain1* " of the variable " drainage ", and to question the real interest of variables like carbon content (Ferry, *pers. comm.*). Important progresses must be made in this field at Paracou.

Table 7: *Effect of landfacets on diameter increment, as measured on the trees of our calibration data set (10745 trees are taken into account).*

Landfacets	Number of trees	Mean annual diameter increment		Residuals of the growth model	
		Mean (cm)	Variance (cm^2)	Mean (Log(cm))	Variance ($(Log(cm))^2$)
Bottomlands	751	0.224	0.066	0.040	0.104
Hillsides	9225	0.212	0.054	0.001	0.091
Summits	769	0.192	0.049	-0.028	0.098

Nevertheless, the plot effect remaining on the residuals of our growth model cannot be entirely attributed to topographical and physical effects, as proven by the opposite behaviour of plot 4 and 10. On those plots, mean diameter increments and densities were similar before the treatments, increments being slightly more important on plot 4 (see table 4). The silvicultural treatment applied to plot 4 was particularly heavy (T3), with resulting increments smaller than those observed on plot 10 less heavily touched (T2), a phenomena that the growth model failed to predict. Among the possible explanations, a physiological stress due to a severely modified micro-environment could be put forward (as shown by Colin, 1989, with *Goupia glabra*), but remains to be proved.

We focused here more specifically on plot effects to lighten the information still lacking at Paracou. But other problems remain to be solved, which could lead to significantly increase the efficiency of our model. Botanical determination is one of them, as the relevance of our species groups greatly depend on it. At least as important is the problem of the measurement of large trees. In our calibration data set, those trees are under-represented, because they frequently are buttressed or warped and diameter increments are not reliable. This causes the *K* parameters of the growth models to be estimated with a low accuracy, with important consequences when they are implemented in a simulator of forest dynamics. Our trials (Caruso, 1994, Gourlet-Fleury, 1997, 1999 — to be published —) showed that the *K* parameters play an important part in the under- or over- accumulation of large trees in simulated stands and hence on basal area and global as well as local competition, thus finally on the general behaviour of the system. A method to correctly estimate the dbh of those individuals, and to re-introduce them in the data set, is currently under study.

We finally can mention that other sources of informations also are quite usefull for modelling the growth. Thanks to the availability of now long time series, we could calculate and introduce autocorrelation between successive predicted increments, leading to a definite improvement of the simulator behaviour. There also is a possibility to take climate effects into account, as we could show, for example, a link between peaks in annual rainfalls and high diameter increments two years after. This could be interesting for the simulation of long term scenarios.

ACKNOWLEDGMENTS

People that work at Paracou, or with the Paracou data base are indebted to Laurent Schmitt and Pascal Petronelli, as well as to the many persons who settled the design and are currently ensuring the surveys. We are grateful to Guillaume Cornu for precious help in data transfers and processing.

REFERENCES

Barthès B. (1988). Où pousse cet arbre ? Premiers résultats à l'étude des relations sol-végétation en forêt de Paracou (Guyane). Cas du Wapa et du Gonfolo. Rap. ORSTOM / CTFT. 33 p.

Barthès B. (1990). Etude des relations sol-plante : le cas de la forêt primaire sur socle en Guyane française. Article préparé pour l'Atelier sur l'Aménagement et la Conservation de l'Ecosystème Forestier Tropical Humide MAB/UNESCO - MAB/France - IUFRO - FAO, Cayenne, 12-16 mars 1990 (résumé publié dans les actes).

Barthès B. (1991). Caractérisation pédologique de parcelles du dispositif "Forêt Naturelle" du C.T.F.T. à Paracou (Sinnamary, Guyane). Rapport interne ORSTOM / CTFT,14 p.

Biging G.S. and Dobbertin M. (1992). A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *Forest Science* 38(3) : 695-720.

Biging G.S. and Dobbertin M. (1995). Evaluation of competition indices in individual-tree growth models. *Forest Science* 41(2) : 360-377.

Bishop Y.M.M., S.E. Fienberg and P.W. Holland (1975). Discrete Multivariate Analysis: Theory and practice. Cambridge, MA: The MIT Press.

Boulet R. et Brunet D. (1983). Prospection pédologique en vue de l'implantation des blocs de l'opération CTFT " Forêt Naturelle ". Rapport ORSTOM, 7 p.

Caruso D. (1994). Modélisation d'une forêt tropicale par une approche multi-agents (étude préliminaire). Mémoire du DEA IARFA, LAFORIA, Université Paris VI. 15 p.

Colin F. (1989). Ecophysiologie en forêt équatoriale. Contribution à la connaissance de Goupia glabra. Mémoire de stage de 1ère année de l'ENGREF. INRA/ENGREF, 37 p. + ann.

Collinet F. (1997). Essai de regroupements des principales essences structurantes d'une forêt dense humide d'après l'analyse de leur répartition spatiale (Forêt de Paracou - Guyane). Thèse de doctorat de l'Université Claude Bernard Lyon I / ENGREF. 203 p. + ann.

Dreyfus P. (1988). Compétition et croissance dans de jeunes peuplements résineux. Aspects biologiques, écologiques et sylvicoles. Thèse d'écologie forestière - Université de Droit, d'Economie et des Sciences d'Aix-Marseille - Faculté des Sciences et Techniques de Saint-Jérôme.

Fairweather S.E. (1988). Development of an individual tree growth model for Pennsylvania. *Forest Growth Modelling and Prediction* - USDA Forest Service, General Technical Report NC-120 : 61-67.

Favrichon, V. (1995). Modèle matriciel déterministe en temps discret - Application à l'étude de la dynamique d'un peuplement forestier tropical humide (Guyane française). Thèse de doctorat de l'Université Claude Bernard Lyon I / CIRAD, 252 p. + ann.

Favrichon, V. (1998). Modeling the dynamics and species composition of a tropical mixed-species uneven-aged natural forest : effects of alternative cutting regimes. *Forest Science*, 44(1), 113-124.

Favrichon V., Gourlet-Fleury S., Bar-Hen A. et Dessard H. (1998). Parcelles permanentes de recherche en forêt dense tropicale humide. Eléments pour une méthodologie d'analyse des données. Coopération française / CIRAD / CIFOR. Série FORAFRI, document n°14. 67 p.

Gourlet-Fleury S. (1992a). Simulation d'éclaircies sur le dispositif sylvicole de Paracou (Guyane française) : recherche de méthodes d'intervention en forêt, après exploitation. Mémoire technique du DEA

d'Analyse et de Modélisation des Systèmes Biologiques - I.A.S.B.S.E. - Université Claude Bernard, Lyon I, 34 p. + ann.

Gourlet-Fleury S. (1992b). Indices de compétition : les possibilités d'application à la gestion en forêt dense tropicale humide. Mémoire bibliographique du DEA d'Analyse et de Modélisation des Systèmes Biologiques, I.A.S.B.S.E., Université Claude Bernard, LYON I, 30 p. + ann.

Gourlet-Fleury S. (1997). Modélisation individuelle spatialement explicite de la dynamique d'un peuplement de forêt dense tropicale humide (dispositif de Paracou - Guyane française). Thèse de doctorat de l'Université Claude Bernard Lyon I / CIRAD, 274 p. + ann.

Gourlet-Fleury S. (1998). Indices de compétition en forêt dense tropicale humide : étude de cas sur le dispositif sylvicole expérimental de Paracou (Guyane française). *Annales des Sciences Forestières*, 55(6), 623-654.

Gourlet-Fleury S. (1999). Individual-based spatially explicit modelling of forest stands in French Guiana. Proceedings of the international conference: *Data Management and Modelling Using Remote Sensing and GIS for Tropical Forest Land Inventory*. Jakarta, Indonesia, October 26-29, 1998. 25 p. *To be published.*

Gourlet-Fleury S. and Houllier F. (1999). Modelling diameter increment in a lowland evergreen rain forest in French Guiana. *Submitted.*

Hahn J.T. and Leary R.A. (1979). Potential diameter growth functions. In: *A generalized forest growth projection system applied to the Lake States Region.* USDA Forest Service - General Technical Report NC 49 : 22-26.

Leary R.A. and Holdaway M.R. (1979). Modifier function. In : *A generalized forest growth projection system applied to the Lake States Region.* USDA Forest Service - General Technical Report NC 49 : 22-26.

Lebart L., Morineau A. and Warwick K. M. (1984). Multivariate descriptive statistical analysis: correspondence analysis and related techniques for large matrices. Wiley, NY, UK.

Maître H.-F. (1990). Recherche sur la dynamique des peuplements arborés en vue de définir une sylviculture de conservation et production durable. In: " Conservation de la forêt dense en Afrique Centrale et de l'Ouest ", World Bank Environment Paper, 1: 146-158.

Mardia K. V., Kent J. T. and Bibby J. M. (1979). Multivariate analysis. Academic Press, New York, London.

Monserud R.A. (1975). Methodology for simulating Wisconsin northern hardwood stand dynamics. PhD Thesis, University of Wisconsin-Madison. 156 p.

Murphy P.A. et Shelton M.G. (1996). An individual-tree basal area growth model for loblolly pine stands. *Canadian Journal of Forest Research* 26 : 327-331.

Parresol B.R. (1995). Basal area growth for 15 tropical tree species in Puerto Rico. *Forest Ecology and Management* 73: 211-219.

Prothéry N. (1995). Recherches sylvicoles sur les peuplements naturels en forêt dense guyanaise - Présentation de quelques résultats d'ensemble 11 ans après la mise en place du dispositif. Rapport interne CIRAD-Forêt, 42 p. + ann.

SAS Institute Inc. (1990). SAS/STAT User's Guide, Release 6.03. Edition Cary, NC: SAS Institute Inc.

Schmitt L. (1989). Etude des peuplements naturels en forêt dense guyanaise. Compte-rendu de mise en application des traitements sylvicoles sur le dispositif de PARACOU. Rapport interne, C.T.F.T., 51 p.

Shugart H.H. (1984). A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models. Springer-Verlag New-York. 278 p.

Vanclay J.K. (1994). Modelling Forest Growth and Yield - Applications to Mixed Tropical Forests. CAB International, Wallingford (UK), 280 p.

CIRAD is a French scientific organisation specialized in development-oriented agricultural research for the tropics and subtropics (Centre for International Cooperation in Agricultural Research for Development).