Individual-based spatially explicit modelling of forest stands in French Guiana

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Introduction

Unlike most dense evergreen tropical forests all around the world, rainforest in French Guiana (located in South America between 2° and 6° of latitude north) which covers about 90% of the 8.5 millions ha of the department, has not suffered, till now, heavy pressure. The low density of the population, mainly concentrated along the coast and the Maroni river, with a high level of life, and high costs of logging excluding French Guiana from the international timber market, indirectly contribute to its relative quietness.

Logging occurs in forests managed for wood production by the National Forest Office (ONF). They cover about 600 000 ha inside a 2 million ha area spreading from one border (Brazil) to the other (Suriname) along the coast. Theoretically, those managed forests should furnish round wood to the local market, on a long-term basis, thus preventing roads and logging trails from extending further and further inside the remaining virgin forest. Today, no more than 4 to 5 trees are logged per hectare (about 10 000 hectares logged each year, for 50 000 to 70 000 m^3 of round wood) and felling cycles are of 40 years which seems quite reasonable. However, due to uncertainty about wood demand in the future (inhabitants were 33000 in 1961 and 131000 in 1996), ONF would like to do, after the logging operations, complementary liberation of valuable trees to stimulate their growth and shorten felling cycles.

In this context, a lot of questions raise about the silvicultural rules to apply and the way the stands will evolve after such treatments, as far as their structure and floristic diversity are concerned. A way to partly answer those questions, in the more or less long run, is to elaborate models of forest dynamics (see Vanclay, 1994, 1995, for a review) by using the great amount of data already gathered on experimental plots settled in the department.

In 1995, Favrichon (1995, 1998) built for French Guiana a first size class model based on the use of Usher matrices (Vanclay, 1994), well adapted to the simulation of simple stand

management patterns. Besides, we decided to build a distance dependent / single tree model (Munro, 1974) : (*i*) to take into account the uniqueness of individuals, primarily reacting to their immediate neighborhood — which may be particularly variable in such an heterogeneous system as moist tropical forest — ; (*ii*) because a lot of questions asked by foresters as well as researchers from various fields deal with single trees ; individual-based models can thus be an interesting integration tool, making dialogue and cooperation easier ; (*iii*) because ONF is testing tree-oriented liberation, rather than systematic thinnings and this cannot be simulated by matrix models ; and finally (*iv*) because it may be important to take into account spatial patterns of species, mainly the most exploited ones, to explore the consequences of logging.

In a first phase, statistical models (based on regression) of growth, mortality and recruitment have been calibrated for trees located inside a stand, without taking species into account. A simulator, called SELVA, has been computed in the object-oriented language SmallTalk80 to operate those models at the tree level (Caruso, 1994, Gourlet-Fleury, 1997) and allow for the study of dynamics behaviour, in the presence or absence of disturbance. We focus, in this text, on some aspects of this first phase. In a second phase, the growth model has been improved by taking species effects into account: this will make part of the conclusion, as well as the ungoing work to improve the global model.

Materials and methods

We used the data from the silvicultural experimental plots of Paracou, settled in 1984 near Sinnamary, about 50 km north-west of Kourou (Schmitt, 1984, 1985, 1989). There, 12 plots, 9 hectares each, were delimited in a previously untouched forest. All trees more than 10 cm dbh were located inside a 6.25 ha square inside each plot (leaving a 25 m wide buffer zone around) and their circumference has been yearly measured since 1984. This represents, today, a data bank of almost 50 000 trees.

Between 1986 and 1988, three types of silvicultural treatment, repeated three times, have been applied to 9 of the plots, the last 3 being control plots. They were : (*i*) selective felling of about 10 valuable trees more than 50 to 60 cm dbh, per hectare (treatment 1) ; (*ii*) same selective felling as previously (10 trees/ha), followed by systematic poison-girdling of non commercial trees more than 40 cm dbh (30 trees/ha) (treatment 2) ; (*iii*) same selective felling as previously

(10 trees/ha), plus systematic felling of unvaluable trees to make fuelwood (15 trees/ha), followed by systematic poison-girdling (10 trees/ha more). These different treatments, corresponding to a growing intensity of perturbation, are rendered at the tree level by very contrasted local environments.

Six individual models were calibrated, using data from eight of the plots (2 plots per treatment): a growth model, four models of death and an ingrowth model. We chose to work with a 3-year time step, to smooth year to year variations in the dependent variables, and three periods of time were considered: (*i*) 1985-1988, used to characterize the intensity of treatment; (*ii*) 1988-1991, used to calculate the dependent variables and (*iii*) 1991-1994, used to evaluate the temporal autocorrelation in growth.

Ordinary least square regression after log-transformation of the dependent variable was used to calibrate the growth model, which follows the « *potential* x *modifier* » philosophy (Botkin *et al.*, 1972 and most of the subsequent gap models, Ek and Monserud, 1974, Monserud, 1975, Hahn and Leary, 1979, Leary and Holdaway, 1979, Belcher *et al.*, 1982, Martin and Ek, 1984, Murphy and Shelton, 1996 ...). In those models, actual growth is the product of « potential growth », the maximum possible growth when there is no competition, by a « modifier component », usually a function of more or less empirical competition indices (Dreyfus, 1988, Biging and Dobbertin, 1992, 1995, Gourlet-Fleury, 1992, 1998) which represent the environmental pressure on the tree.

For mortality, with binomial dependent variables, we used logistic regression as in Monserud, (1976), Wan Razali (1986), Vanclay (1991), Hasenauer (1994) or Ong and Kleine (1996). A logistic model was also used for describing ingrowth.

Results

The growth model

Instead of fitting separately the two components of the « *potential* x *modifier* » model as usually done, we directly fitted our model to a unique data set of 10745 trees (see also Parresol, 1995 or Murphy and Shelton, 1996). The final expression is the following:

$$Log(\Delta D + 0,287) = a' + \left[Log(m) + Log(D) + \left(1 + \frac{1}{m}\right) Log[Log(K) - Log(D)] \right]$$

$$+ \left[b\sqrt{NBD} + c\Delta NBD + d\Delta NBD^2 \right] + \varepsilon \qquad\qquad [1]$$

with $Log(potential) = Log(a) + Log(m) + Log(D) + \left(1 + \frac{1}{m}\right) Log[Log(K) - Log(D)]$,

$$Log(modifier) = \left[b\sqrt{NBD} + c\Delta NBD + d\Delta NBD^2 + e \right]$$

and $a' = Log(a) + e$. The potential component is the Korf model (Zeide, 1993) and a, m, K are

its parameters, K representing the asymptotic maximum size of a tree. D is the dbh (cm) in

1988, ΔD the mean annual diameter growth between 1988 and 1991 (cm/yr), NBD the total

number of neighbours with a dbh greater than or equal to the subject one in 1988, and located

less than 30 m from it. ΔNBD is the variation of the NBD 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. NBD and ΔNBD are the two competition indices evaluated as the most efficient

ones to describe growth when all species are pooled (Gourlet-Fleury, 1997, 1998). a', b, c, d,

m and K are regression parameters.

Results of the fitting are given in table 1. The domain of variation of the growth model is

illustrated on fig. 1 and the behaviour of the modifier component on fig.2.

As the model was fitted in one step, the potential and modifier component lost their initial

meaning. Potential growth, here, can be seen as the growth of a tree in a « neutral

environment », ie which would neither stimulate nor refrain its development. According to the

values taken by NBD and ΔNBD, the modifier can be greater or lesser than 1 (see fig.2) thus

increasing or decreasing potential growth (the equality to one fit the neutral situation. See fig.1).

It must also be noticed that the abnormally high estimate of K is due to the shifting forward of

the values of ΔD, with the use of the constant « 0.287 » to take negative data into account. It

can be verified on fig.1 that the final model doesn't predict any positive growth, whatever the value of the modifier, after D has reached 210 cm. Note also that the low precision associated with the estimate of K is due to a very little number of big trees in our data set.

Even if a lot remains to be done to improve the quantitative efficiency of the model (particularly through the introduction of species and site effects as we will see later), model [1] still exhibits interesting qualitative behaviour:

- the modifier always decreases when *NBD* increases: individual growth tends to decrease in crowded environments;

- the relation between the modifier and Δ*NBD* is a second order polynomial. For high values of Δ*NBD*, growth logically decreases. When Δ*NBD* decreases, as it occurs with silvicultural treatments for example, the modifier first increases and so does the growth, but only to a certain point: if too many neighbours disappear, the growth is refrained. This is consistent with what can be observed at Paracou in treatment 3 (there is no significative difference in growth between treatment 2 and 3) or along the recently open roads (rapid death of trees on the border lines).

The analysis of residuals shows that:

- the treatment effect on growth has been taken into account correctly, through the use of the index Δ*NBD*;

- three more or less important effects remain: (*i*) a strong species effect, which led us, in a second phase, to build groups of species; (*ii*) a plot effect we tried to eliminate through the introduction of topographic variables; (*iii*) a temporal autocorrelation, assessed through the study of two consecutive periods; this effect was implemented in the simulator as part of the stochastic component of the individual growth.

The mortality models

Following the work done on the subject by Durrieu de Madron (1993) at Paracou, we described four mortality phenomenons: standing death, primary windthrow (initial fall of a tree), secondary windthrow (fall of trees due to a primary windthrow) and complex windthrow (fall

of unsteady trees on the border of previously created gaps). The two last models were built empirically (see Gourlet-Fleury, 1997).

A lot of independent variables were tested for inclusion into the two first models. Standing death, which can occur consequently to age and/or competition pressure and/or illness, clearly depends on past growth and the model used in the simulator is the following:

$$p(MSP = 1) = 1 - \frac{e^{(a\Delta D_{past}+b)}}{1 + e^{(a\Delta D_{past}+b)}} \tag{2}$$

with $p(MSP = 1)$ probability, for a tree, to die standing and ΔD_{past} mean diameter growth during the previous 3 years period (1985 to 1988). (a, b) are regression parameters. Results of the fitting are given in table 2 and the model is illustrated on fig.3. Growth can be linked to vigor and the less a tree grows, the greater its probability of dying.

Primary windthrow was first found to depend on past growth and on local density. Once included in the simulator with the other models, observed dysfunctions led us to replace past growth by diameter, the model finally being:

$$p(CHA1 = 1) = 1 - \frac{e^{(-0.01D+0.182STT+2.884)}}{1 + e^{(-0.01D+0.182STT+2.884)}} \tag{3}$$

with $p(CHA1 = 1)$: probability, for a tree, to fall the first at a given time and STT: cumulated basal area of trees more than 10 cm dbh, located less than 30 m from the tree examined. The behaviour of the model is illustrated on fig.4. It can be seen that : (i) the probability of falling is greater in places were STT has low values, that is to say either that the stand is locally « empty », or that it is made of a lot of small trees. The first case occurs, for instance, when a gap is present in the immediate neighbourhood: trees on the border lines are desequilibrated and this results in a greater probability of windthrow. The second case can be encountered in some parts of the plots, such as in the bottomlands, where the soil conditions favour windthrows and prevent from the presence of big trees. (ii) The bigger a tree, the greater its probability to fall. This is not seeable from our data, but was introduced to limit, in a first approach, the tendency of big trees to accumulate in our simulated stands.

Secondary windthrow was modelled very simply, using Durrieu de Madron (1993) observations. Each time a tree falls, it creates damages to its neighbours. The mean number of trees broken by a primary windthrow according to its diameter is given in table 3.

Finally, the model of complex windthrow was introduced to reinforce the desequilibrium effect occuring near recently opened gaps (less than 3 years ago). Its expression is:

$$p(CHAC = 1) = 1 - \frac{e^{(0.182STT+2.884)}}{1 + e^{(0.182STT+2.884)}} \quad [4]$$

with $p(CHAC = 1)$: probability to fall. This is systematically calculated for all the neighbours of a primary windthrow as soon as its diameter is bigger than 40 cm.

The ingrowth model

Ingrowth (above a diameter limit of 10 cm) is modelled on 100 m^2 quadrats (10 m x 10 m). At Paracou, the maximum number of new trees which appeared on such quadrats during the period 1988-1991 is 5, and the treatments have a significative effect on this number.

We used a logistic model to relate ingrowth to local density (after having tried various independent variables) in the following expressions:

$$P(R \le i) = \frac{e^{(a_i + b_i ST_{dtot})}}{1 + e^{(a_i + b_i ST_{dtot})}} \quad \text{for } i=0 \text{ to } 4$$

and $P(R \le 5) = 1$ [5]

with i: number of recruits on a quadrat and ST_{dtot}: basal area cumulated on the quadrat and its 8 adjacent neighbours. (a_i, b_i) are regression parameters. The results of the fitting appear in table 4 and the model is illustrated on fig.5. Logically, the probability of recruiting one or more new trees in the stand increases with the decrease of ST_{dtot} values.

Integration into the simulator

The simulator SELVA was developed according to the multi-agent system philosophy (Ferber, 1995), in collaboration with the LAFORIA' laboratory of the Paris VI university (Caruso, 1994). It operates trees and quadrats (10 m x 10 m) as agents able to analyse their environment

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and to act according to rules given by the above regression models. The initial environment and conditions are given by one of the Paracou plots.

SELVA is characterized by a friendly interface, allowing the user to (*i*) explore the environment of simulation (list of trees and quadrats, location, characteristics, neighbours of each tree, ...); (*ii*) follow on maps and graphics the evolution of the stand and each of the trees, (*iii*) realize logging and other silvicultural operations with all types of rules (systematic, based on critical diameters or tree-oriented). A full description of SELVA can be found in Gourlet-Fleury (1997).

Main simulation results

Simulations were performed to evaluate the ability of the whole model: (*i*) to reproduce the behaviour of an undisturbed plot and (*ii*) to ensure a go back of a stand to an equilibrium state, after a more or less severe disturbance. Criteria to assess this ability come from the analysis performed on data collected on the control plots of Paracou, assuming that those plots are themselves in an equilibrium state (no human disturbance historically known, basal area slightly fluctuating around a mean of 31 m^2/ha since 1984).

Fig.6 shows the evolution of one of the control plots of Paracou over a 200 cycles (600 years) run. Predicted basal area as well as the total number of living trees, dead trees (standing or windthrows) and ingrowth fluctuate around a stable mean which can be compared to the observed ones (see table 5). It can be seen that:

- 'the predicted total number of trees alive is slightly smaller than on real plots, while the total basal area is more important. This is explained by the maintenance, on the simulated plot, of a greater number of big trees than expected (see below);

- the predicted mortality is slightly higher than the observed one (8 /ha /yr against 6.7 /ha /yr) and this mainly comes from the primary and complex windthrows components. Those particular models have been built and modified empirically on the basis of the first simulation results, and still need to be improved. Nevertheless, it can be seen that the total number of windthrows almost exactly compensate for the number of standing dead trees, which is consistent with what is observed on the control plots;

- the predicted ingrowth is also higher than expected (8 /ha /yr against 5.9 /ha /yr), but it compensates for the total number of dead trees which is consistent with the steady state hypothesis.

The predicted mean individual growth is higher than expected on a control plot (0.166 cm /yr versus 0.126 cm /yr).

We compare, on fig.7, the initial and predicted distribution of trees by diameter classes at the end of simulations of various lengths. Three signs of dysfunction can be observed:

- a tendency for trees to accumulate in the first size class, due to a high rate of ingrowth coupled with a slow upgrowth to the second diameter class;

- a tendency for the second diameter class to loose trees;

- a tendency for trees to accumulate in the last diameter class (there is a stabilisation of the predicted number of trees more than 70 cm of dbh, at values between 9 and 15 instead of an observed mean of 5 in the control plots. This stabilisation occurs around the 20th cycle).

Predicted and observed distribution by diameter classes significantly differ from each other ($\chi^2 \geq \chi^2_{(12,0.05)}$) from cycle 6 on, that is to say after 18 years.

Fig.8 shows how the spatial structure of the stand evolves during the simulation, this being rendered by the distribution of two of the competition indices used respectively in the growth model (*NBD*) and in the primary windthrow model (*STT*). The distribution of *NBD* remains quite stable and that shows that the spatial pattern of trees is globally kept by the model, even in the long term. However, the distribution of *STT* exhibits a trend towards high values, rendering the tendency for big trees to accumulate in the stand.

The consequences on simulated stands, of three types of increasingly high disturbance, have been studied with SELVA. With this aim in view, we started with the initial conditions of plots having undergone respectively treatment 1 (plot 9), treatment 2 (plot 8) and total cut of the existing biomass (« empty » plot). Results are presented on fig.9. They show that whatever the disturbance, the model allows the restoration of a stand the characteristics of which are the same as the simulated undisturbed one. The return to a steady state occurs after a peak in

number and basal area, due to the massive « arrival » of young trees after the disturbance. The more intense the disturbance, the more important the values of the peak as well as the delay before the return to equilibrium.

Discussion and perspectives

The coupling of the independently calibrated models of growth, mortality and recruitment inside the simulator resulted in a globally good qualitative behaviour:

- correct interactions are observed between the different components. When basal area decreases, ingrowth increases and, after a few years, feed the last diameter classes which make basal area increase again and slow down ingrowth. The increase of ingrowth comes with an increase in mortality: (*i*) standing death due to competition / low growth in the small diameter classes; (*ii*) windthrows due to low basal area in all classes. Those phenomenons limit the accumulation of small trees in the first diameter class even if they don't totally prevent it;

- the simulator ensures the return of disturbed stands to an initial steady state;

- observed spatial patterns in control plots are globally maintained by the simulator even after long runs.

Quantitatively speaking, things are not so satisfying. Among dysfunctions that remain to be solved, we will discuss the two most important.

The first problem is revealed by the behaviour of the diameter class distribution during the simulation. Two mechanisms interact to explain the depletion and inflation of respectively the intermediate and last classes: (*i*) the growth model has been calibrated without taking species into account. Then, each individual, according to the growth model [1], is susceptible to reach big sizes (up to 210 cm, see fig.1) when in reality only some species can. This results in an irrealistic number of trees with a dbh more than 70 cm, which in turn maintains a high basal area on the simulated plots. (*ii*) The mortality models don't play an efficient role to limitate this phenomenon and especially the primary windthrow one: we realized that there was a conflict between the sensitivity of this model to high basal area (which prevents from windthrow) and to diameter (high diameter favours windthrow).

The second problem appears when comparing the results illustrated on fig.9 to results obtained by Favrichon (1995) at Paracou with its matrix model, or found otherwise in the litterature. It seems clear that the delay at which the peak in number of trees and basal area appears, and the delay before returning to equilibrium, are too long when using SELVA. Starting from an « empty » plot, the peak in number should appear around 30 to 50 years and the equilibrium state around 100-120 years, the behaviour of basal area or total biomass being moved forward 80 to 100 years (Shugart, 1984, Bossel and Krieger, 1991, Favrichon, 1995, Williams, 1996) (compare with fig.9). Even faster are the evolutions reproduced by KIAMBRAM (Shugart *et al.*, 1980) or CAFOGROM in the forest of Tapajos in Brazil (Alder, 1994, 1995). The main trouble comes from the coupling between mortality and ingrowth models, which is not tight enough. The link is made through the means of basal area (STT for model [3], ST_{dtot} for model [5]) and none of the models are sensitive enough to this variable. After an even light disturbance, ingrowth should increase rapidly which is not the case as it can be seen on fig.6. Moreover, we observed at Paracou that the effect of a disturbance may be long-lasting and largely exceeds the time step of 3 years, which the present ingrowth model does not account for. As a consequence, re-adjustments on disturbed plots are, for the moment, too slow.

The second phase, in the development of SELVA, is ongoing. It consists on introducing species effects in order to be able to study the evolution of floristic composition of the stands after disturbance, as well as the evolution of their size and spatial structure. A first work has been done as far as the growth model is concerned: 15 species groups have been built, and specific growth submodels calibrated, leading to a noticeable improvement in the efficiency of growth predictions (pseudo-R^2=0.416, instead of 0.230 obtained through model [1] — see table 1 —) (Gourlet-Fleury, 1997). We also tried to take topographic effects into account (top of hills / slopes / bottomlands), but this resulted only in slight improvment of predictions for three of the species groups.

The main trouble, with species effects, is encountered in modelling ingrowth. If it is possible to quantify the phenomenon per species group, prediction of the localisation of « new individuals » in the stand is not immediate (there is no direct link between a potential mother tree and young trees appearing above 10 cm of dbh) and necessitates a minimum of quantified

knowledge about specific regeneration processes. Two directions are presently explored to progress on this subject: (*i*) synthesis of ecological knowledge about the main species of Paracou, with the objective of building soundly based « regeneration groups » and corresponding models; (*ii*) species-oriented regeneration surveys which would give us missing quantified elements such as mean number of young plants produced by a mother tree and mean distance between these plants and the mother (Ribbens *et al.*, 1994).

Despite the evident remaining weaknesses of our model, we can already say that:

- logged over stands, even if lightly disturbed, take a long time to reconstitute their living stock;

- if logging has to be followed by a silvicultural treatment, that delay will greatly increase. Then, shortening the felling cycle will inevitably lead to a modification of the stand structure and consequently its floristic composition.

Those first results are encouraging and we currently work on their improvement.

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Acknowledgments

Table 1. Results of the fitting of model [1] to a data set of 10745 trees. 8 plots (2 plots per treatment) were taken into account.

Parameters	Estimate	Asymptotic standard error
a' (Log(a)+e)	-6.77	0.67
m	0.514	0.119
K (cm)	693	298
b ($*10^{-3}$)	-31.71	4.89
c ($*10^{-3}$)	-18.41	0.59
d ($*10^{-3}$)	-0.13	0.01
SSR[a]	1323	
$\hat{\sigma}^{2}$[b]	0.123	
Pseudo-R^{2}[c]	0.229	

[a] Sum of squared residuals

[b] Estimate of residual variance (SSR/df)

$$ ^{c}\ 1 - \left(\frac{SSR}{\sum (y_i - \bar{y})^2} \right) $$

Table 2. Results of the fitting of model [2] to a data set made of 11109 trees alive and 209 trees dead standing between 1988 and 1991. 8 of the 12 plots of Paracou were used. The analysis was realised with the PROC LOGISTIC of the SAS software (SAS Institute Inc., 1989).

	Mean model	Complete model	χ_1^2 [a]	P ($> \chi_1^2$)
-2 Log (likelihood)	2082.695	1986.273	96.423	0.0001

Analysis of goodness-of-fit estimators

Explicative variable	Parameter estimate	Standard error	Wald statistic	P ($> \chi_1^2$)
Constant	3.420	0.082	1761.785	0.0001
ΔD	4.957	0.592	70.112	0.0001

Model efficiency

|			
t [b]	2321781		
Concordant pairs	66.9%	Somers' D	0.397
Discordant pairs	27.2%	Goodman-Kruskal's Gamma	0.422
Tied pairs	5.9%	Kendall's Tau-a	0.014

[a] Test of the H_0 hypothesis: all coefficients included in the model but the constant, are null.

[b] Number of pairs with a value differing from the observed variable: (0,1) or (1,0).

Table 3. Damages (number of trees killed) due to a primary windthrow according to its diameter at breast height. Data observed at Paracou and final rules used in SELVA.

Diameter class of the primary windthrow	Mean number of trees killed (= secondary windtrows) by a primary windthrow	
	Observed (Durrieu de Madron, 1993)	Rule used in SELVA
10-20 cm	0.08	0
20-30 cm	0.12	0
30-40 cm	0.29	0
40-50 cm	2.78	3
50-60 cm	3.67	4
60-70 cm	3.33	4
≥ 70 cm	4.86	4

Table 4. Results of the fitting of model [5] to ingrowth data on quadrats of 10mx10m. The data set was made of 8*529 quadrats on which 0, 1, 2, 3, 4 or 5 new trees more than 10 cm dbh appeared between 1988 and 1991. 8 of the 12 plots of Paracou were used. The analysis was realised with the PROC LOGISTIC of the SAS software (SAS Institute Inc., 1989).

	Mean model	Complete model	$\chi_3^{2\,a}$	$P\,(>\chi_3^2)$
-2 Log (likelihood)	6379.176	6225.439	153.737	0.0001

Analysis of goodness-of-fit estimators

Explicative variable	Parameter estimate	Standard error	Wald statistic	$P\,(>\chi_1^2)$
Constant 1 (a_0)	-0.364	0.117	9.768	0.0018
Constant 2 (a_1)	1.456	0.126	133.458	0.0001
Constant 3 (a_2)	3.184	0.183	304.146	0.0001
Constant 4 (a_3)	4.540	0.308	216.800	0.0001
Constant 5 (a_4)	5.642	0.512	121.356	0.0001
St_{dtot} (b)	0.665	0.056	142.150	0.0001

Model efficiency

$t^{\,b}$	3719203		
Concordant pairs	61,4%	Somers' D	0,235
Discordant pairs	37,9%	Goodman-Kruskal's Gamma	0,237
Tied pairs	0,7%	Kendall's Tau-a	0,098

[a] Test of the H_0 hypothesis: all coefficients included in the model but the constant, are null.

[b] Number of pairs with a value differing from the observed variable: (0,1) or (1,0).

Table 5. Mean values of some characteristics of stand strcuture and dynamics, respectively observed on control plots and predicted with SELVA. Note that initial conditions of the simulation are given by a real plot.

	Observed (mean value 1984/1994)	Predicted (mean value over a 600 years run)
Number of trees		
Alive (/ha)	576	566
Dead (all types, /ha /yr)	6,67	8,02
Dead standing (/ha /yr)	3,28	3,69
Windthrows (all types, /ha /yr)	3,39	4,33
Ingrowth (/ha /yr)	5,89	8,00
Total basal area (m2/ha)	30,9	32,7
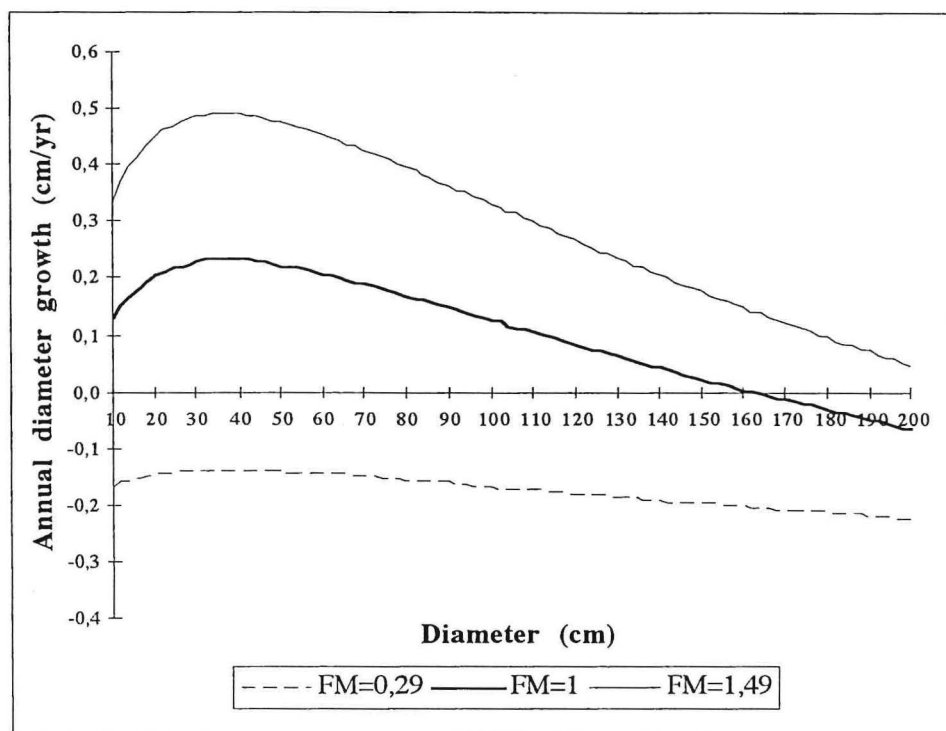
Fig.1. Domain of variation of model [1]. FM is the value taken by the modifier component (0.29: minimum, 1.49: maximum, according to the values taken by *NBD* et Δ*NBD* in our calibration data set). FM=1 indicates the neutral situation. Note that the decimal comma has been used on this graph.
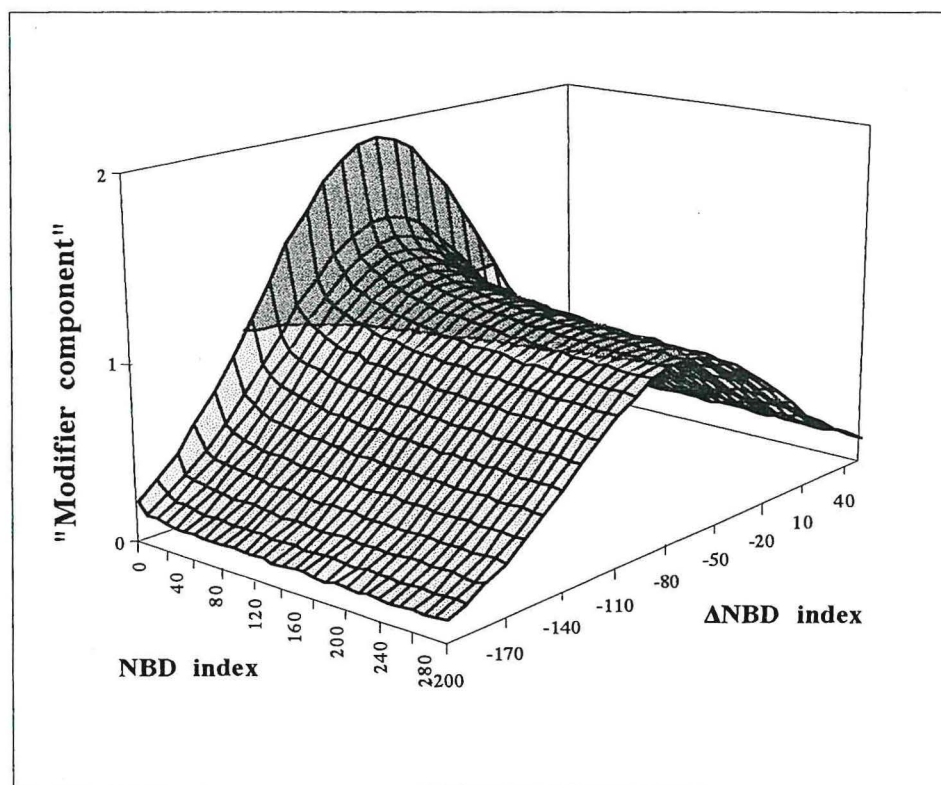
Fig.2. Behaviour of the modifier component (model [1]) according to the values simultaneously taken by the indices *NBD* and Δ*NBD*.
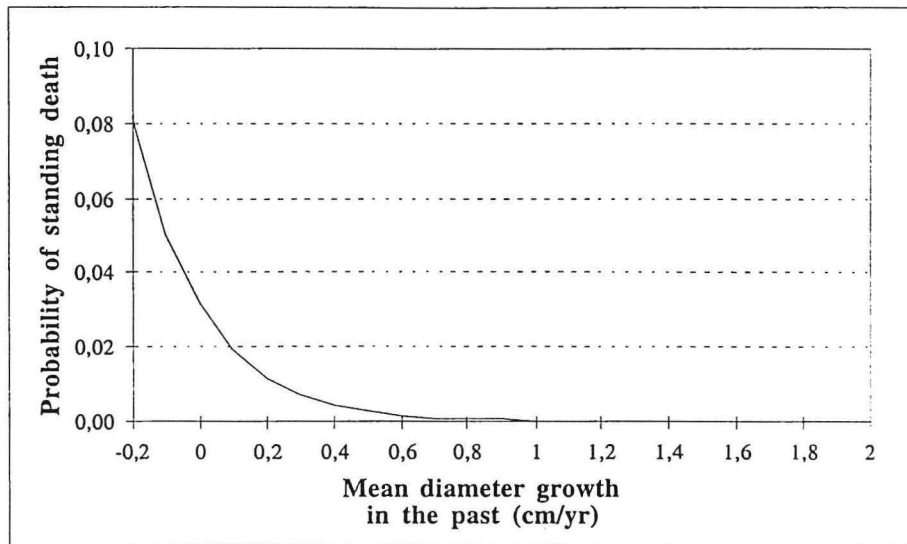
Fig.3. Behaviour of model [2]. The probability, for a tree, to die while standing (competition, old age) increases when past diameter growth decreases. Note that the decimal comma has been used on this graph.
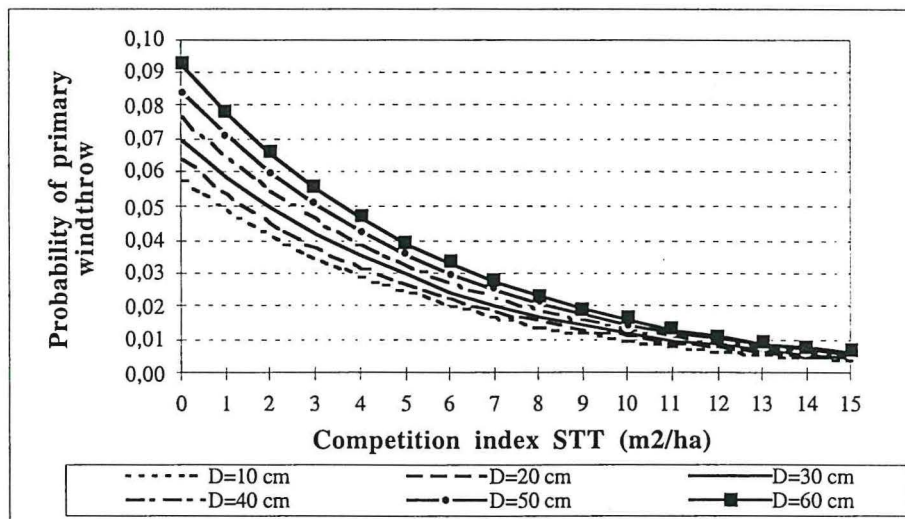
Fig.4. Behaviour of model [3]. The probability for a tree to fall as a primaty windthrow depends on (*i*) local density expressed by the way of STT: the probability of windthrow increases when density decreases; (*ii*) diameter of the tree: big trees are more susceptible to fall than small trees (this last effect has been artificially introduced). Note that the decimal comma has been used on this graph.
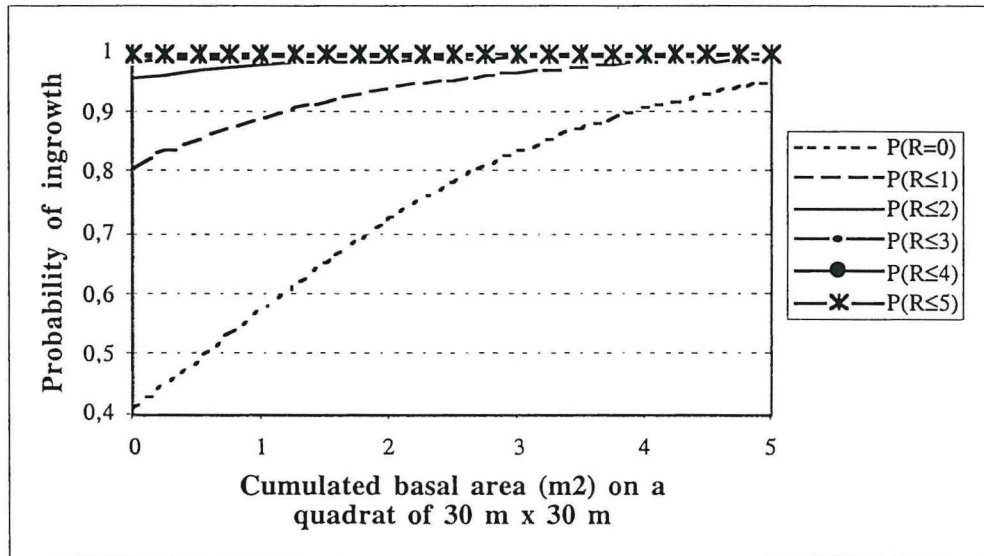
Fig.5. Behaviour of model [5]. The probability for a quadrat of 10 m x 10 m to recruit 0, 1, 2, 3, 4 or 5 new trees more than 10 cm dbh depends on available place in the stand. This is expressed by the mean of the ST_{dtot} index, cumulated total basal area on the quadrat and its 8 neighbours. Note that the decimal comma has been used on this graph.
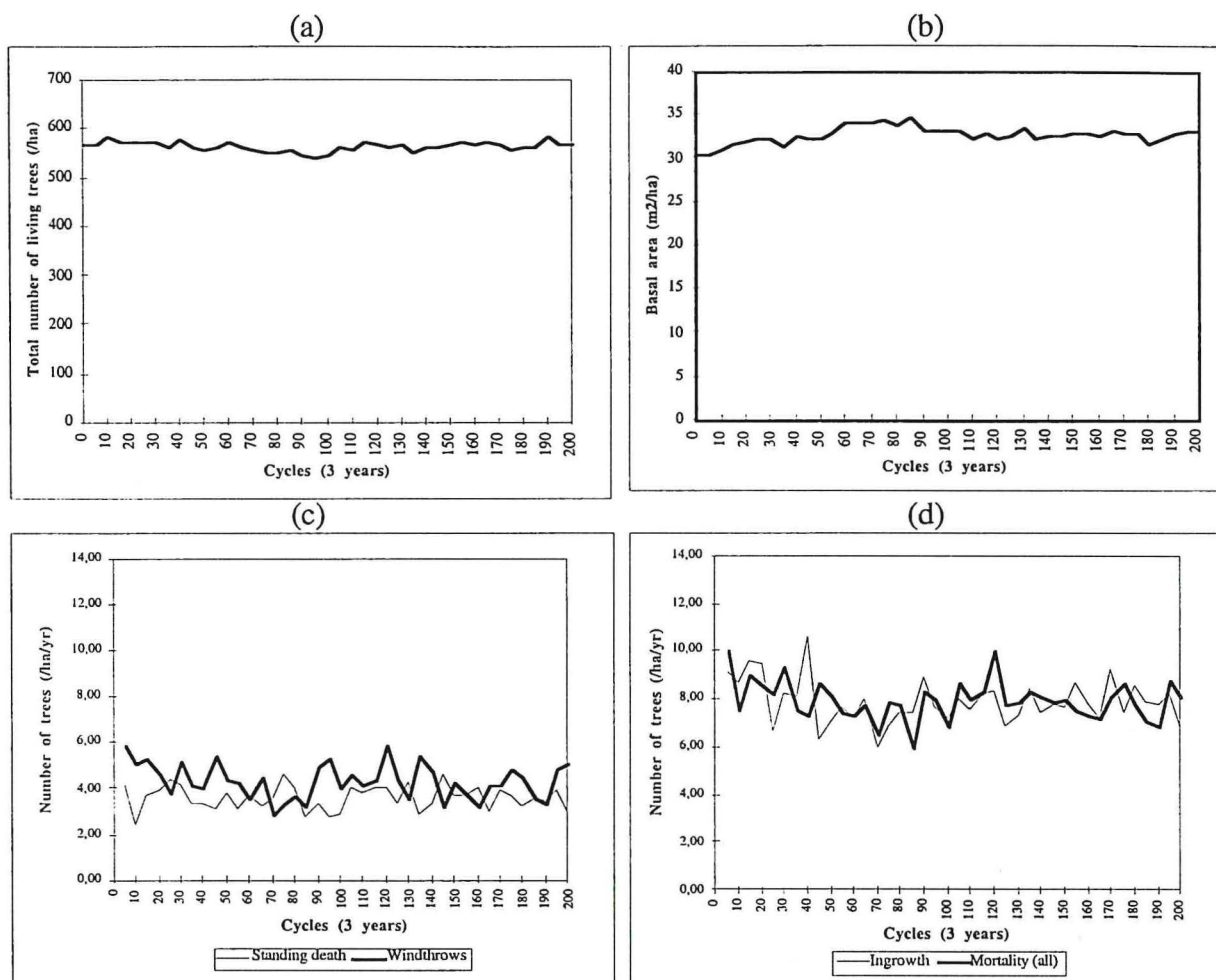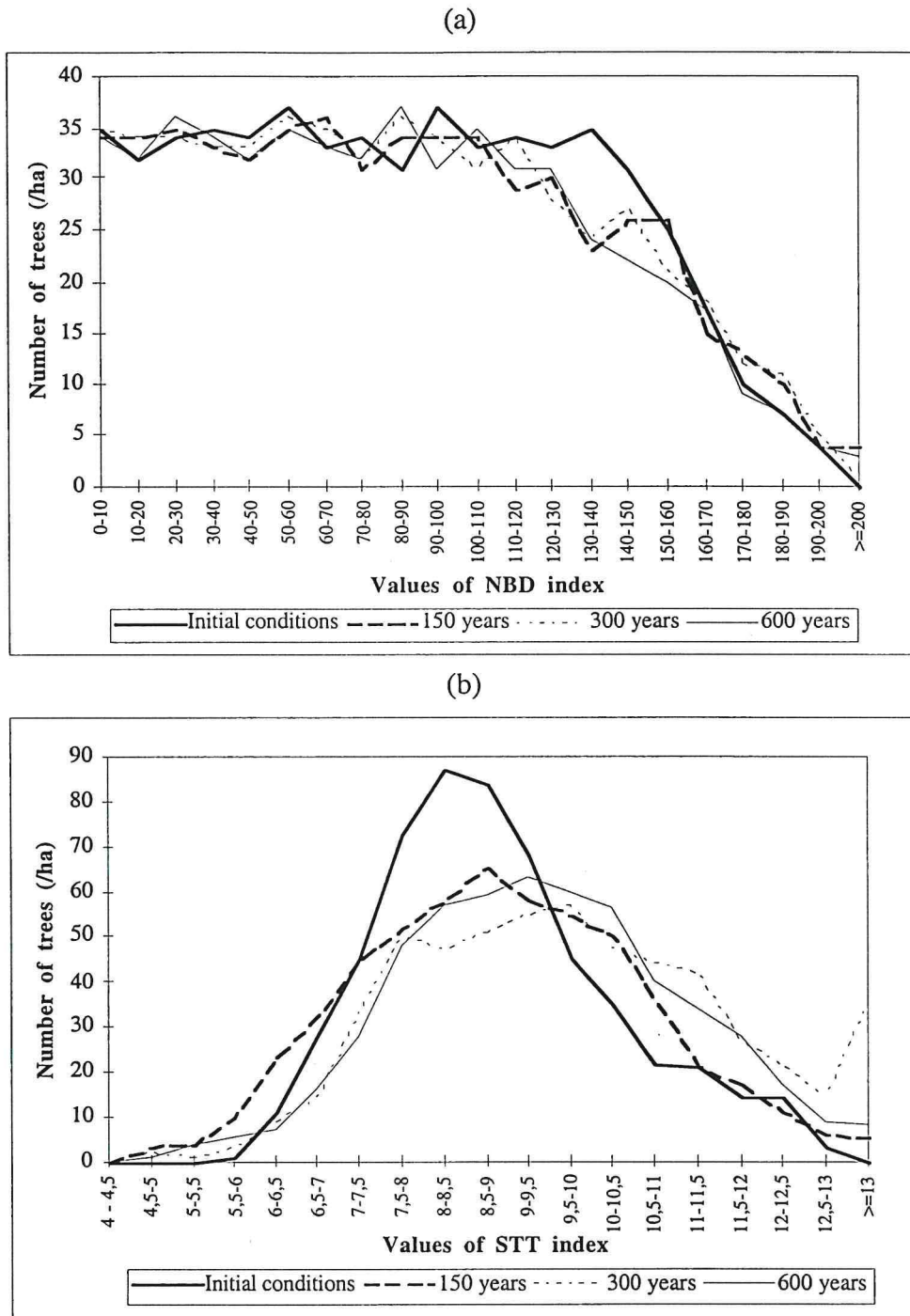
Fig.6. Behaviour of a simulated stand along a 200 cycles run (initial conditions given by one of the control plots of Paracou), in the absence of any disturbance. (a) Total number of living trees more than 10 cm dbh, per ha. (b) Total basal area (m2/ha). (c) Dispatching of annual mortality between standing death and windthrows. (d) Comparison between ingrowth and global mortality. Note that the decimal comma has been used on this graph.
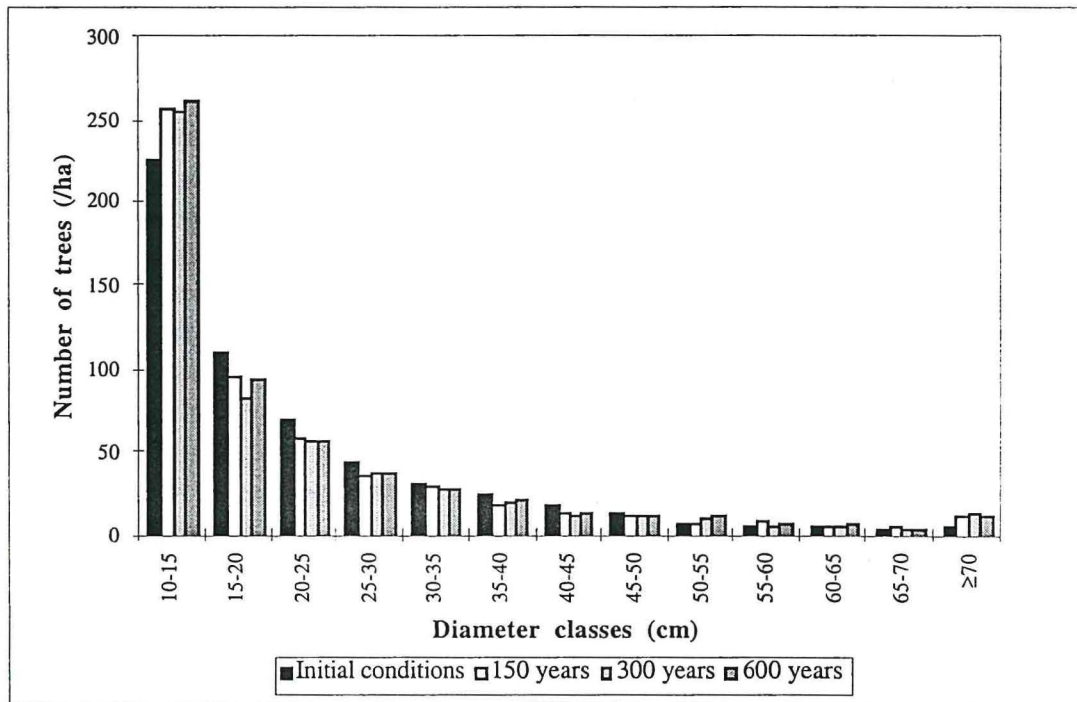
Fig.7. Evolution of the diameter classes distribution of an undisturbed stand along a 200 cycles run (initial conditions given by one of the control plots of Paracou).

(a)

(b)

Fig.8. Evolution of the spatial pattern of an undisturbed stand along a 200 cycles run (initial conditions given by one of the control plots of Paracou). (a) Distribution of the NBD index (cf. model [1]. (b) Distribution of the STT index (cf. model [3]). Note that the decimal comma has been used on this graph.
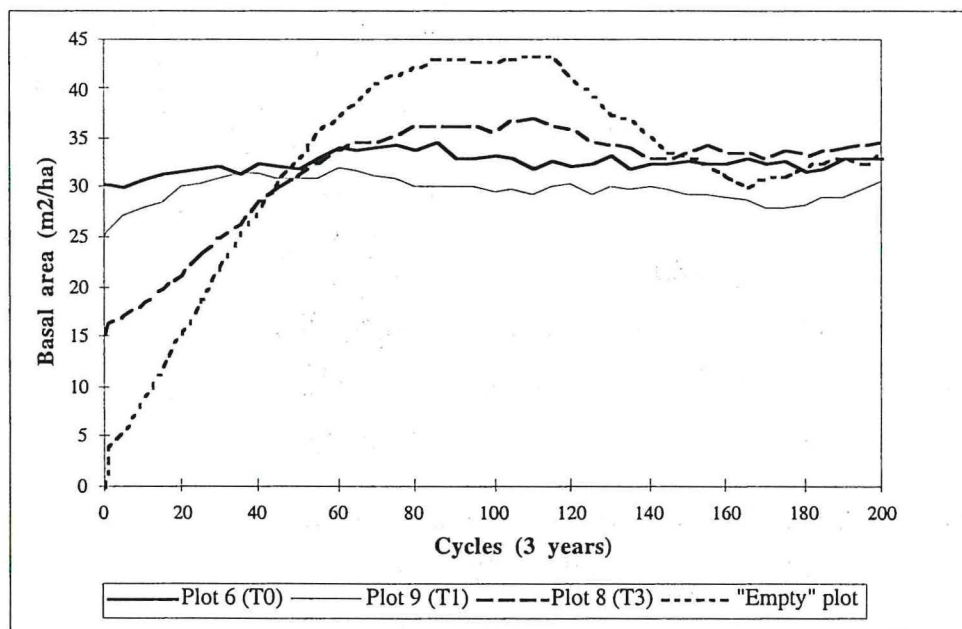
(a)
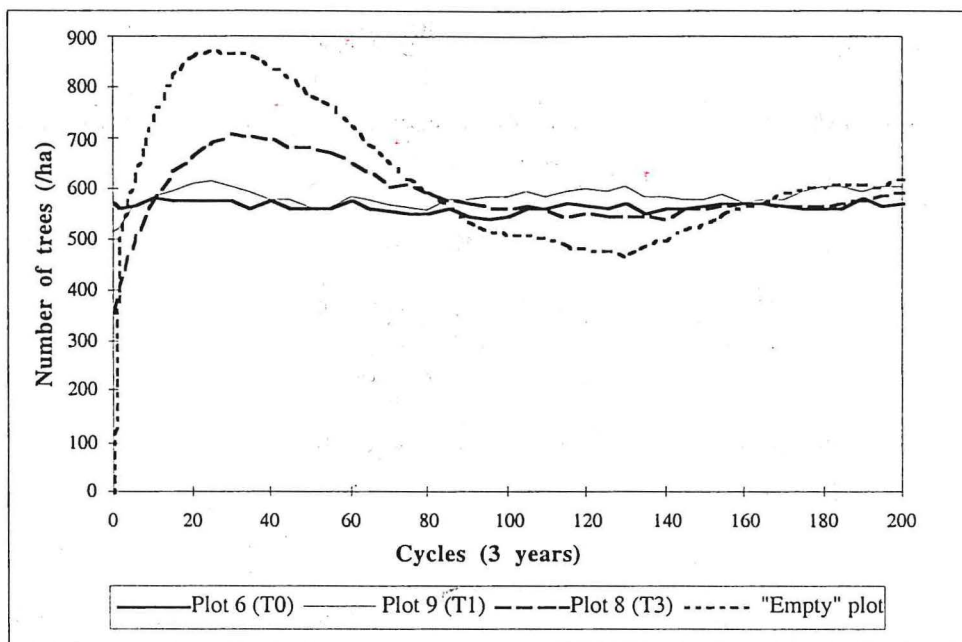
(b)

Fig.9. Compared evolution of two of the global stand variables, according to the plot which gave the initial conditions for the simulation. (a) Total number of trees more than 10 cm dbh, per hectare. (b) Cumulated basal area (m2/ha).