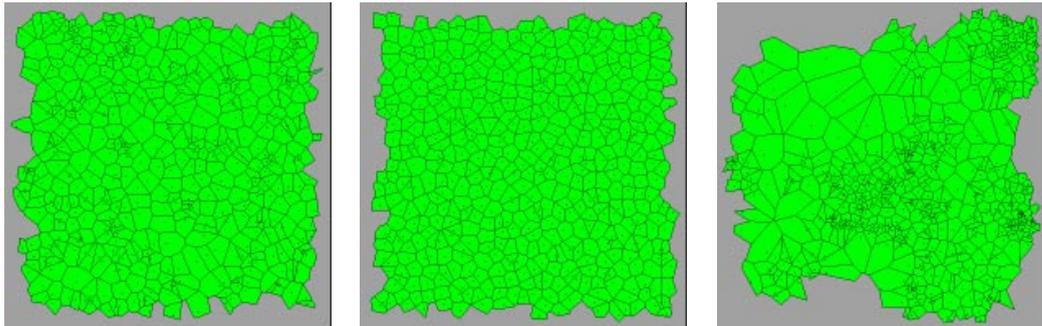


Figure 1 : Voronoi tessellation where polygons containing small hatched circles are marginals.

in the sampling window until the tessellation is complete. The injection of a new generator point modifies local contiguities. Such an algorithm uses lists of generator points and vertices, and is computationally efficient (resolution time in $O(n)$).

Certain polygons, called marginal, are partially determined by sampling window boundaries. Such marginal polygons are not representative of the population and should be excluded from any analysis. To select marginal polygons, we use the algorithm proposed by Kenkel et al. (1989a).

To use Voronoi tessellation for spatiotemporal models, some generator points are inserted and others are suppressed from the tessellation through time steps, according to rules for recruitment (arrival of saplings in the stand)



(a) Random Regular Aggregative

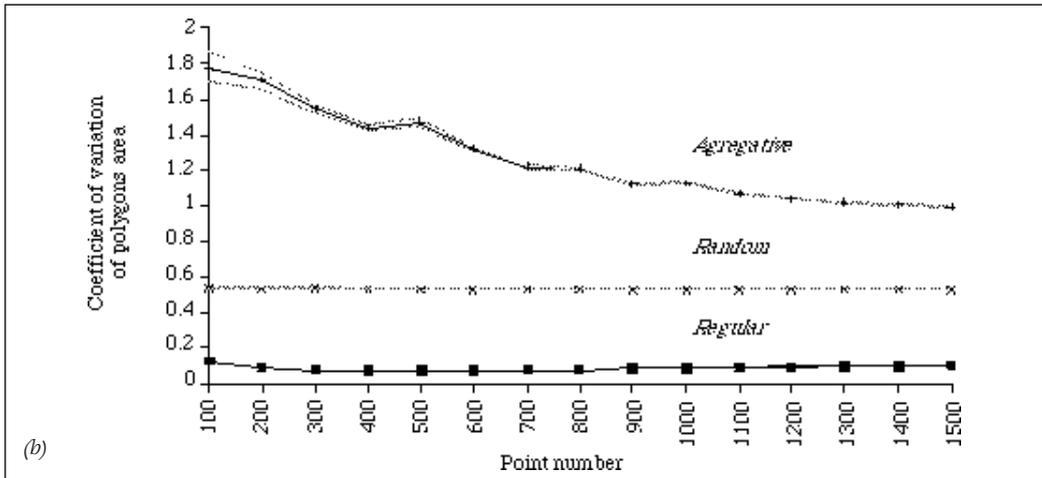


Figure 2 : (a) Voronoi tessellation constructed with 618 points determined from three different point processes. (b) Coefficient of variation of polygon area with respect to the number of points, to detect the spatial pattern. Curves are bounded by confidence intervals obtained from Monte Carlo simulations of aggregative (Neyman-Scott), random (Poisson) and regular (randomized periodic) point processes.



and mortality (removal of trees). Thus, insertion and suppression of points will induce local modifications in the simulated forest stand spatial patterns. However, recruit number and tree mortality are functions of the total population size. Thus, while the population size dynamics is managed at a global level, the changes in spatial pattern through time arise from local events. Furthermore, plants can change their internal state (such as age or diameter) according to a growth model. In this article, age is incremented at each time step but the growth process is not included.

A preliminary analysis of Voronoi polygon properties led us to prefer the coefficient of variation of polygon area (CV) as the most simple and efficient variable for describing the spatial pattern of generator points (Fig. 2) (see also Vincent et al. 1976, Upton & Fingleton 1985, Hutchings & Discombe 1986, Lorz 1990, Marcelpoil & Usson 1992).

2.2. Random recruitment hypothesis

A first model has been conceived for analysing the behaviour of Voronoi polygons used in spatiotemporal models. At the initial time, a Voronoi diagram is constructed with

618 points corresponding to the mean density of trees (with a dbh(*) >10cm) observed on 1 ha at the Paracou experimental site (Schmitt & Bariteau 1990) in French Guiana (5°15'N, 52°55'W) between 1984 and 1994 (Fig. 3). The initial points are randomly distributed following a Poisson point process, in accordance with the spatial pattern of trees observed on field data. At each step, r individuals are recruited and m trees are removed, such as :

$$N(t+1) = N(t) + r - m,$$

with $r = \text{Bin}(R, N(t))$ and $m = \text{Bin}(M, N(t))$

where Bin(n, p) refers to the binomial distribution with n, the number of trials and p, the success probability. The symbol R represents the recruitment rate, M, the mortality rate and N(t), the population size at time t. The coordinates of the recruits are determined from a Poisson point process and each individual has the same probability of being eliminated. As trees are recruited at dbh = 10 cm, one time step equals the necessary time to reach such a diameter i.e. approximately 10 years.

(*) dbh = diameter at breast height is the more common measure of tree size.

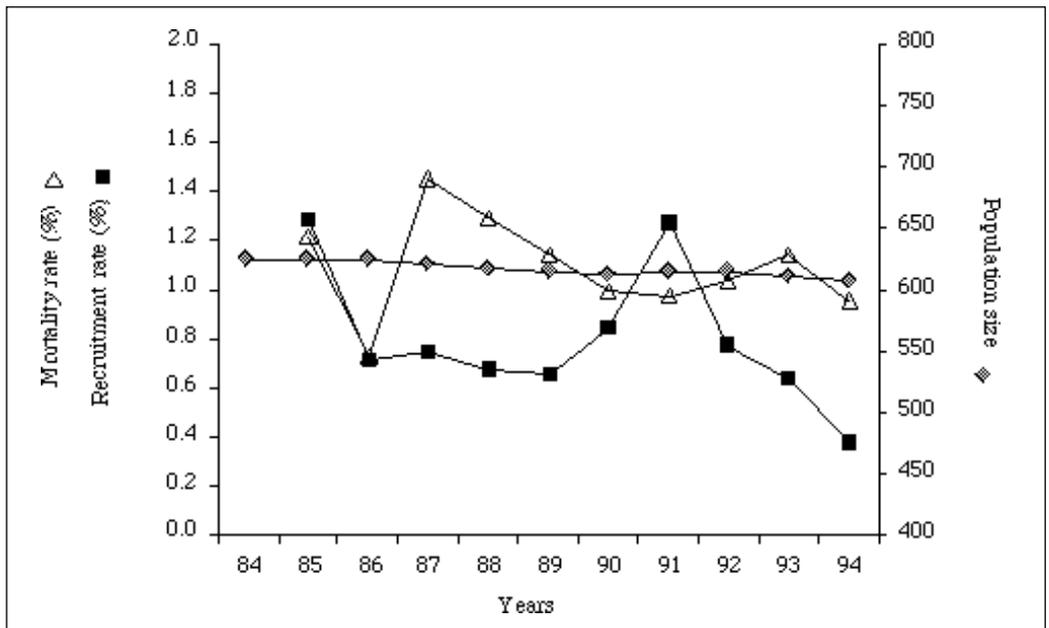


Figure 3 : General characteristics of the forest dynamics at Paracou experimental site (French Guiana) between 1984 and 1994. Recruitment and mortality rates are expressed in % of the population size.



During, the simulation procedure, we test several values for R and M, including the extreme ones observed on the Paracou site. The simulations are realized for different initial spatial patterns : complete spatial randomness (Poisson point process), Neyman-Scott aggregative process (see Stoyan et al. 1995 for a review) and "muddled" periodic spatial pattern. For each set of parameters, 30 simulations are performed in order to obtain statistically valid results. The output variables i.e. population size, age and CV, are observed on 200 time steps.

2.3. Results

The system is obviously sustainable when M approaches R but a small difference between the values of R and M lead to a fast deviation from equilibrium (Fig. 4).

On Paracou station, we observed the rates $R = 0.89\% N/\text{year}$ and $M = 1.05\% N/\text{year}$. When the model runs with these values, the population dynamics is unsteady and the simulated forest stand perishes after 122.3 steps, i.e. 1223 years.

However, this result is founded on the unlikely hypothesis

of persistence of the values of R and M over several centuries. As the population size dynamics seems sensitive to small differences between recruitment and mortality rates, the next model will be based on the hypothesis of a steady state of the forest stand, such that $M = R = \text{Bin}(p, N(t))$, where represents both recruitment and mortality rates.

The age distribution of the trees becomes stable between 25 and 50 steps depending on the values of R and M (Fig. 5).

Whether the initial point process is random, aggregative or regular, the spatial pattern becomes random after 20 time steps (Fig. 6). This phenomenon follows from the random choices of the coordinates of recruits and the identity of trees to suppress.

3. Gap effects on forest stand spatial patterns

3.1. Canopy gap modelling

On average, 1% of the forest canopy is annually opened by treefalls and branchfalls. In these canopy gaps (Brokaw 1982)

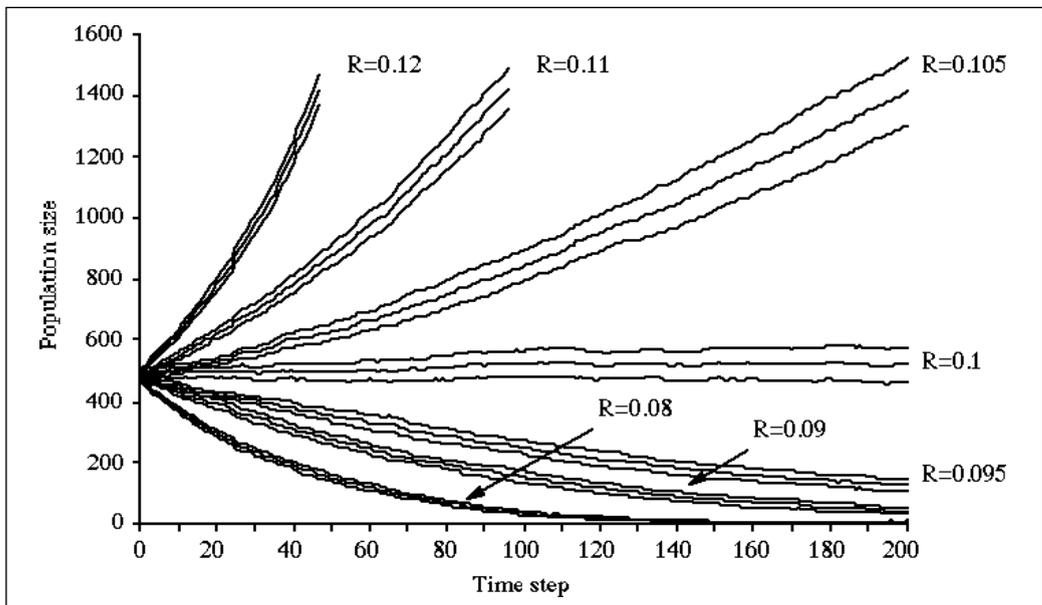


Figure 4 : Influence of the difference between recruitment and mortality rate on the population size dynamics. R represents the recruitment rate (%/step i.e. %/10 years). M, the mortality rate, equals 0.1 N/step. Curves are bounded by confidence intervals obtained with 30 simulations.

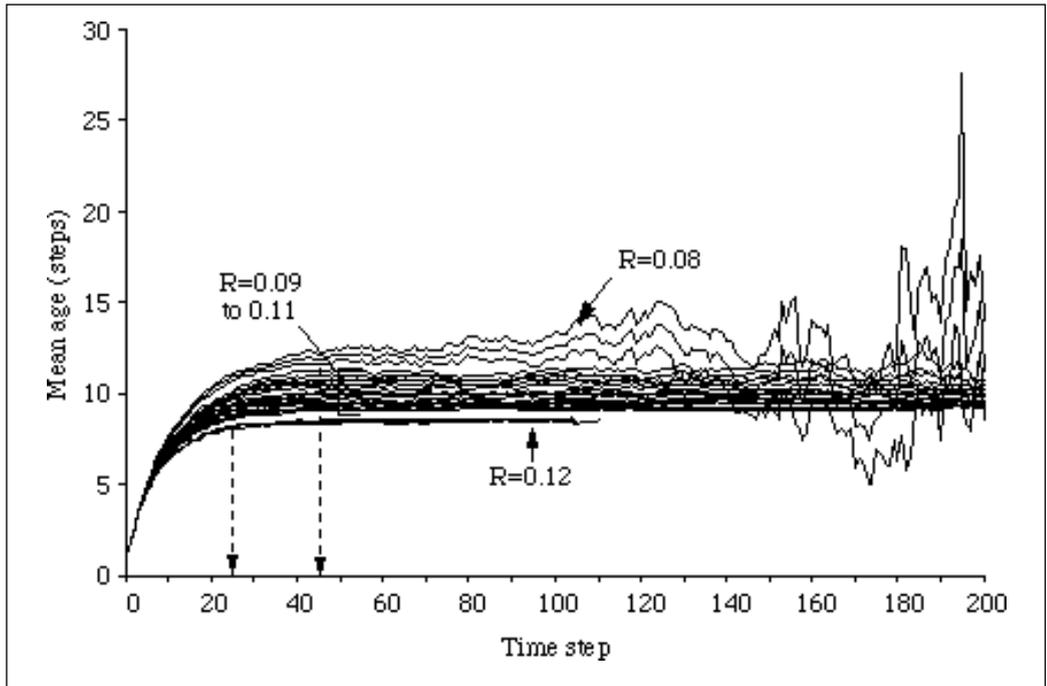


Figure 5 : Influence of the difference between R and M on the mean age of the forest stand, with M equals 0.1 N. Curves are bounded by confidence intervals obtained with 30 simulations.

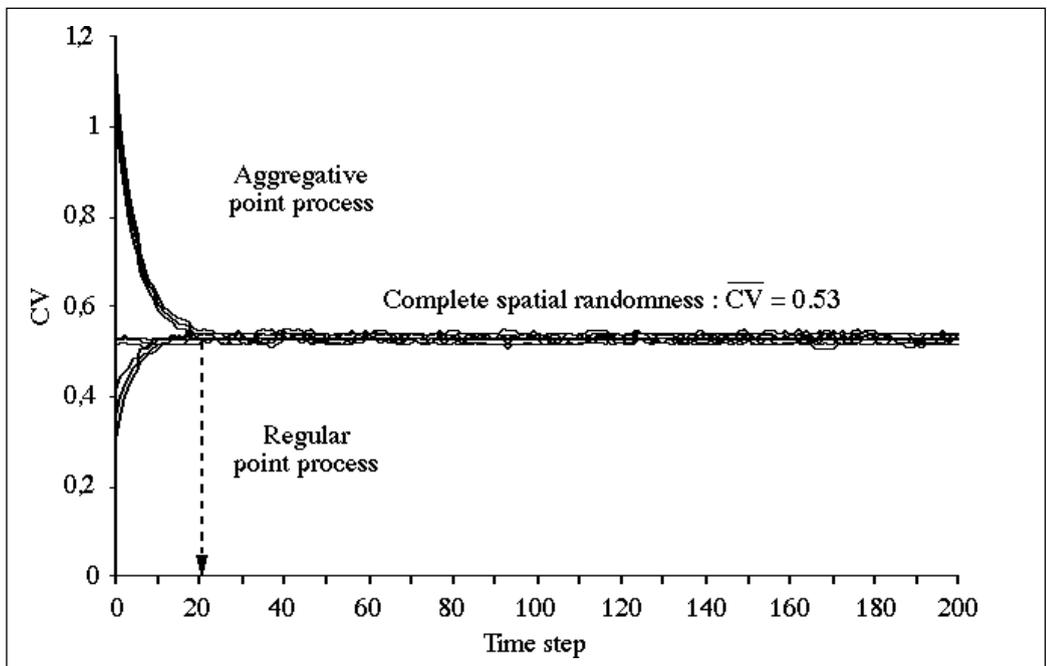


Figure 6 : Coefficient of variation of polygon areas (CV) during simulations of a forest stand dynamics with Voronoi models initialized with different spatial patterns of trees. Curves are bounded by confidence intervals obtained with 30 simulations.



new patches of vegetation start to grow which later will form the forest canopy. Gaps in the canopy increase light levels and modify other characteristics of the environment (Denslow 1987, Brown 1993) sufficiently to influence the dynamics of the tree population (Pickett & White 1985, Platt & Strong 1989, Van der Meer 1995). Numerous seedlings establish themselves in these openings, inducing a clumped spatial pattern (Armesto et al. 1986).

Our aim is to estimate the aggregation intensity obtained in a simulated forest stand where canopy gaps appear. Consequences of different opening rate, gap area distribution and initial spatial stand pattern on the forest dynamics are analysed with regards to the age, population size and CV changes through time.

To include the canopy opening process in the Voronoi model, we determine at each time step, a total opened area, $tg(t)$, such as :

$$tg(t) = \text{Norm}(mg, vg) \times A,$$

where Norm refers to the normal law, mg , the mean open-

ing rate, vg , the variance of opening rate and A , the total area of the study plot. The total opened area is spread over several gaps whose areas, $sg(i)$, verify $\sum sg(i) = tg(t)$.

Values of $sg(i)$ are samples of a Gamma law fitted on the size distribution of field observed gaps (Fig. 7).

Openings are assumed circular and their centers are randomly located in the plot. Trees located in gaps are eliminated (gap mortality process) and the openings are immediately filled by recruits. The number of recruits, r , is proportional to the gap area, as the recruitment density approaches stand density. While all recruits appear in gaps, only 52% of trees die through canopy openings; the rest (48%) are dead standing trees (Durrieu de Madron 1993). Hence, the population dynamics is expressed as :

$$N(t+1) = N(t) + r - (Mg + Mds),$$

with $Mg \sim \{sg(i)\}$, $Mds = (0.48/0.52) Mg$ and $r = \sum_i (N(t)/A) sg(i)$,

where Mg , the number of fallen trees during opening of the canopy, depends on the size of the gap and Mds , repre-

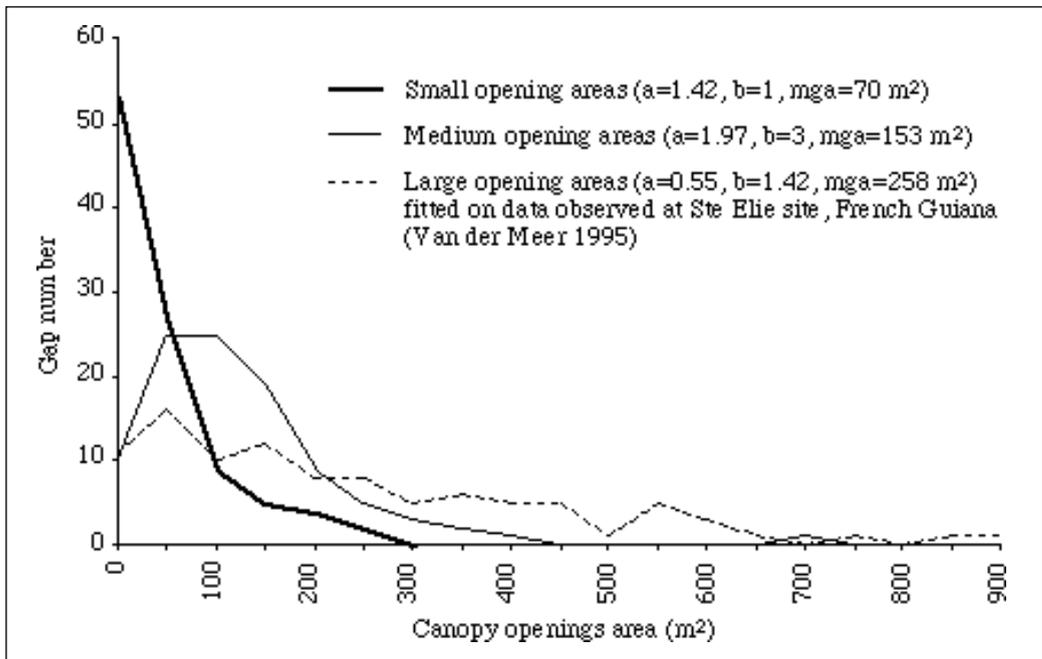


Figure 7 : Gamma laws fitted on observed gap distributions in French Guiana (Van der Meer 1995) or generated artificially. The parameters a and b represent respectively the scale and shape parameters of the Gamma law. With respect to the mean value of a Gamma law, mga is the expected mean gap area $mga = (100 b/a)$.



sents dead standing trees.

The combination of three values of tg , three couples a, b and three initial spatial patterns allow us to simulate various disturbance modes of the neotropical rain forest (Table 1). As previously, 30 simulations are realized on 200 steps for each set of parameters. The observed output variables are population size and CV, polygon area and tree age distributions, plus some information on gap characteristics (number of gaps, mean and variance of their areas).

3.2. Results

Changes in opening rate and Gamma function parameters (a and b) imply variations in the gap numbers (Table 2). Gap number increases with tg but the mean gap area remains equal to 159.2 m^2 ($SD = 6.8$). Thus, turnover rate(*) increases and, consequently, mean age decreases because the total opened area of the forest stand increases with tg (Fig. 8a). The necessary time to reach a stationary mean age (the "transient regimen") decreases as tg increases (Fig. 8a).

Though the gap number decreases when the mean area of the simulated gap increases (Table 2), the age distribution of the forest stand remains unchanged because the total opened area is the same however it is split into individual gaps (Fig. 8b).

The coefficient of variation of polygon areas varies accord-

ing to the opening rate but also to the gap area distribution. The box plots of CV illustrate these differences (Fig. 9). We conclude that gap dynamics plays an important role in generating a tendency to aggregation in the spatial pattern of the forest stands.

Finally, we analyse the effect of the initial spatial pattern of trees on changes in CV with time, when the opening rate equals 10 %/step and the gap area distribution corresponds to an intermediate case ($a=1.97, b=3.00$). The transient regimen is shorter than the observed one in the reference model, and the CV mean is higher (0.75) (Fig. 10). Thus, the introduction of the canopy opening mechanisms seems to enhance the aggregativity of the forest stand.

4. Discussion and perspectives

The study of tropical forest dynamics is based on the analysis of three closely linked elements : first, the population size influenced by recruitment and mortality mechanisms and secondly, the diameter distribution or basal area which depends on the growth processes. The last element is the spatial distribution of the forest stand. Usually, we accept the following sequence :

clumped juveniles -> random adults -> regular old adults

(*) Turnover rate = number of years it takes to cover a unit area of forest with gaps, using the average area annually affected by gaps (Van der Meer 1995).

Table 1 : Simulated gaps features

Initial spatial point pattern	tg (%/step)	a	b
Poisson point process	5	1.42	1.00
"Muddled" periodic point process	10	1.97	3.00
Neyman-Scott point process	20	0.55	1.42

Table 2 : Gap numbers obtained from different opening rates or gap area distributions

Opening rate (%/step)	Mean gap number (SD)	Gamma parameters (a, b)	Mean gap area (SD) (m^2)	Mean gap number (SD)
for $mga=159.2$		for $tg=10$		
5	3.9 (0.19)	(1.42, 1.00)	75.5 (4.3)	15.1 (0.75)
10	7.2(0.31)	(1.97, 3.00)	159.2 (6.8)	7.2 (0.31)
20	13.8 (0.69)	(0.55, 1.42)	298.0 (20.2)	4.8 (0.34)



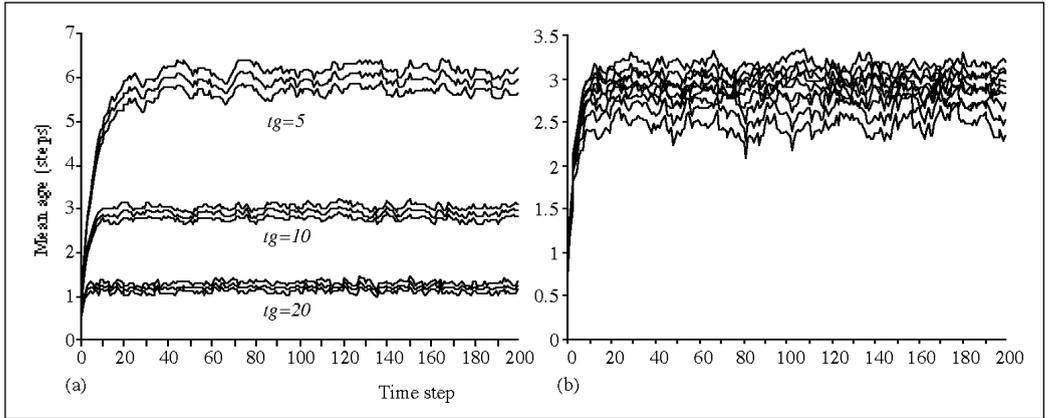


Figure 8 : Mean age of simulated forest stands. Curves are bounded by confidence intervals obtained with 30 simulations. (a) Effect of the opening rate when the mean gap area (mga) equals the typical value of 159.2 m². (b) Effect of the gap area distribution when the opening rate (tg) equals 10%/step.

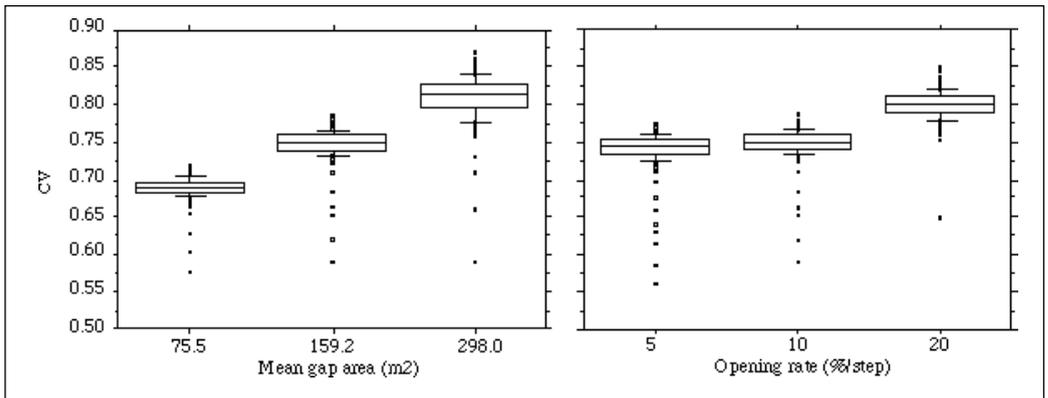


Figure 9 : The coefficient of variation of polygon areas as functions of (a) opening rate and (b) gap area distribution.

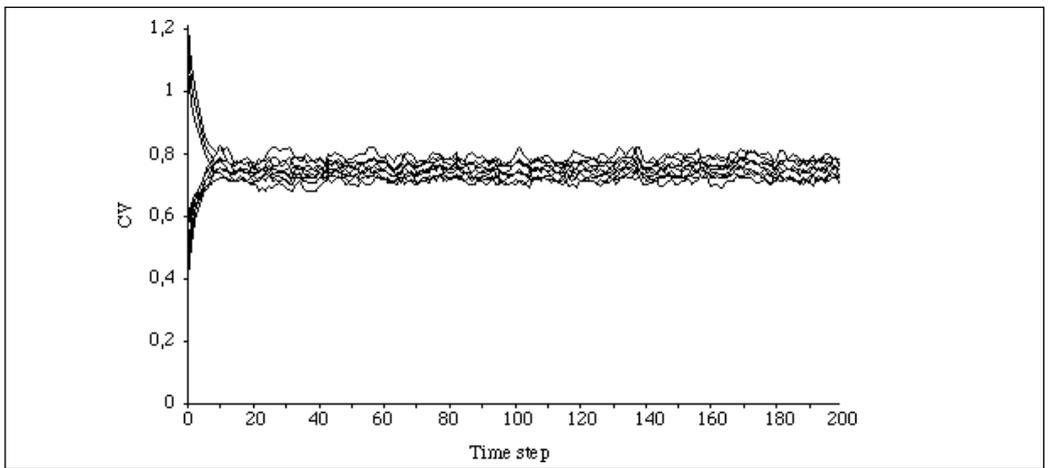


Figure 10 : CV dynamics when the opening rate equals 10%/step and the disturbance mode corresponds to an intermediate case ($a=1.97$, $b=3.00$). Curves are bounded by confidence intervals obtained with 30 simulations.



to describe the changes in the spatial patterns of a forest plot with time (Kenkel 1988, Gavrikov & Stoyan 1995). This sequence results from a massive recruitment of seedlings which induce the formation of aggregates in zones favourable to sapling establishment. The high density characterizing these zones then triggers a self-thinning process in the plot due to the competitive interactions for resources. So, as time advances, we observe a repulsion phenomenon between individuals, leading to a regular distribution of the forest stand.

This theoretical scenario is not always verified and the underlying mechanisms are not always known. Typically, in the above time sequence, gap influence is not considered. The studies realized on French Guiana forests suggest the intervention of at least four factors in the spatial structuration of the forest stand : competition between individual trees, seed dispersal, soil features and canopy openings.

As canopy openings are propitious zones for recruitment, we test the hypothesis of an increased aggregation intensity in disturbed forest. The results give an average $CV=0.75$ in disturbed simulated forests vs. 0.53 in undisturbed ones, leading us to conclude on an aggregative effect of canopy openings. In addition, the aggregation rate increases with opening rate. The same trends appears when the mean gap area increases from 75.5 m^2 ($SD = 4.3$) to 298.0 m^2 ($SD = 20.2$). Though these results were expected, the observed values of CV for the plots of primary forest in Paracou station remain near random at 0.53 while the mean opening rate equals 1% per ha and per year.

Obviously, it is unrealistic to consider canopy gaps as the unique factor managing the spatial pattern changes in neotropical forests. Consequently, inclusion of the competitive interactions will be the next step in the development of our Voronoi model of forest dynamics. Competition could provoke a self-thinning process to counterbalance the aggregative effect of gaps. The individual based and spatially explicit models applied to forest dynamics study use various expressions of competition in their growth submodel. Several authors suggest using the area of Voronoi polygons as a competition index. However,

Kenkel et al. (1989) and Welden et al. (1990), exploring this form of competition index on forest stands explain less than 30% of the growth variation of studied trees. Indeed, one drawback of this approach is ignoring individual tree size, since the polygon area depends solely on the positions of neighbouring points.

To conclude, the model presented in this article introduces a new way to study the forest dynamics with spatiotemporal models (Czàran & Bartha 1992). Voronoi diagrams offer the opportunity to analyse simultaneously the spatial pattern of the forest stand and the local competition pressure occurring between trees. An example of such a Voronoi forest model led us to highlight the determinant role of gaps in generating an aggregative spatial pattern of trees. To analyse the effect of interindividual competition on spatial pattern and diameter distribution, in further work we will introduce a growth process in our model with a competition index that considers both polygon area, size of the corresponding tree and size of its neighbours.

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