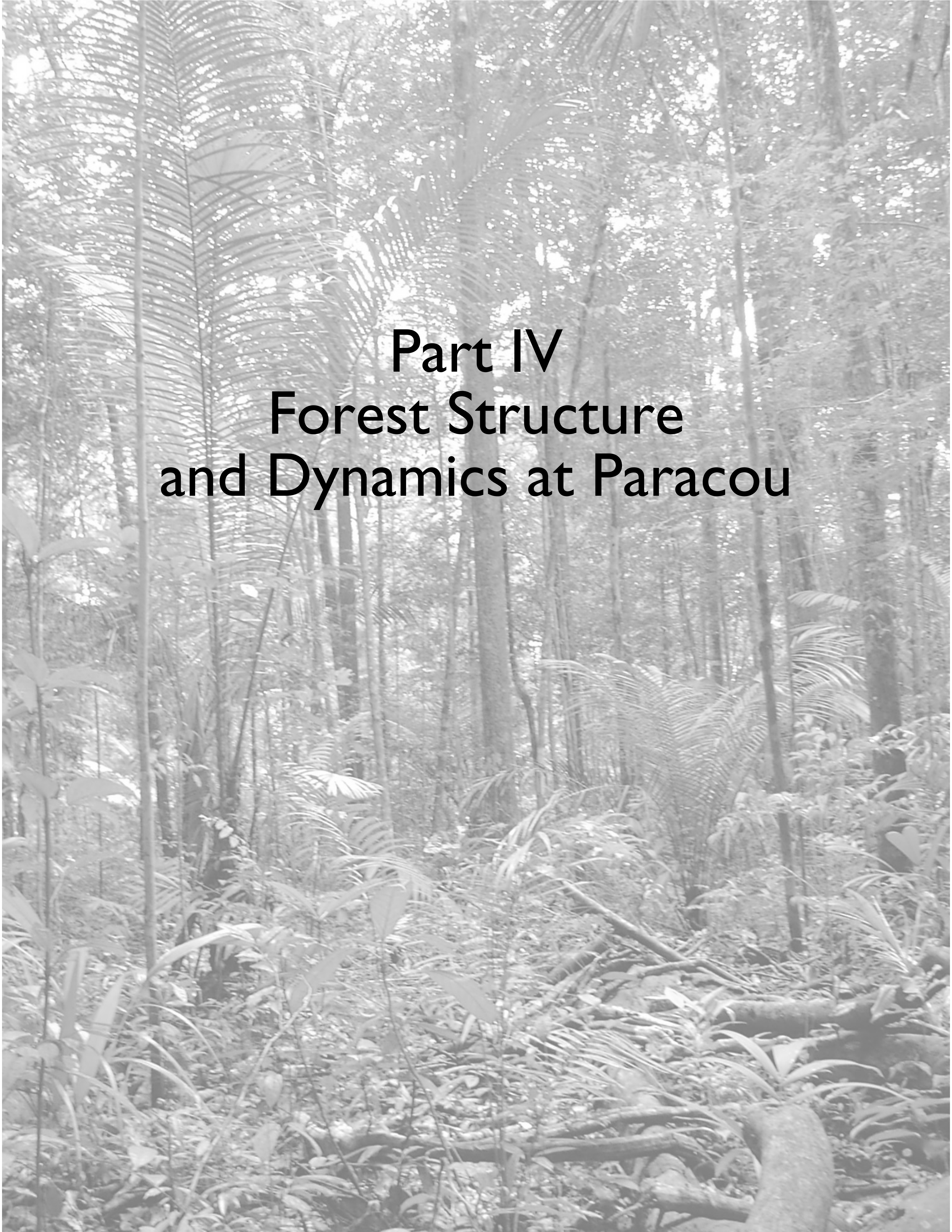


Part IV
Forest Structure and Dynamics at Paracou

Ecology and Management of a Neotropical Rainforest

Forest Structure and Dynamics at Paracou

Sylvie Gourlet-Fleury

Permanent sample plots in tropical forests have been designed and settled to fulfil a variety of objectives: (1) to gather data on the growth and dynamics of forest stands so as to provide managers with essential information on their recovery potential; (2) to collect demographic data on individual tree species, including the rarest ones, in order to provide long-term information on floristic composition and its evolution; (3) to provide a reference to which the evolution of stands inside managed forests can be compared in the future.

The first objective is essentially practical and answers are needed quickly: plots settled within this framework are usually of restricted size (1 ha or less) and can be multiplied inside the same area according to forest types or management alternatives. Such plots have been settled in several parts of the tropical world, mainly in Africa and Asia, following standardised protocols. The second and third objectives, even if relevant to forest managers, are more concerned with research questions such as the identification of the main processes determining the apparition and maintenance of biodiversity. The plots needed to explore such questions are necessarily large, several tens of hectares, such as those established since 1975 in Costa Rica, Panama and elsewhere within the network now coordinated by the Center for Tropical Forest Science.

The Paracou experimental plots were designed wihin a dual context described in the introduction to this book. First, the design had to answer clear applied questions from the National Forest Office (ONF) in French Guiana. Second, CIRAD had gained experience in permanent sample plots in Africa and had learned several lessons, among which the importance of treatment repetitions and the necessity of working on large plots in order to take into account the great local heterogeneity of the forest. As a result, the Paracou plots are of large size and the 12 older ones represent 75 ha of fully mapped forest (trees ≥10 cm DBH), to be compared to the 50 ha covered by the plots of Barro Colorado in Panama or Pasoh in Malaysia (trees greater than 1 cm DBH). The size of the area surveyed allowed a progressive shift in the questions posed and the studies undertaken on the Paracou site, as illustrated by the various subjects treated throughout this book, from questions about the best silvicultural rules to apply in order to quickly recover timber stocks, to a variety of questions about the functioning of forest ecosystems.

Part IV illustrates, in some ways, several steps of the shift in the concerns of the scientific community who have been working at Paracou since the origin of the project. It contains six articles, arranged according to an "ecological" logic: after characterising spatial patterns of several species in Chapter 1, we have a look at the effects of some factors which potentially determine the early success of regeneration in Chapter 2. In Chapter 3, we synthesise the knowledge gained from systematic inventories of regeneration so as to characterise the ecological behaviour of well-represented species. In Chapter 4, we discuss the factors influencing tree growth and, in Chapter 5, we examine systematicly the effects of the silvicultural treatments on the evolution of the main stand parameters. Finally, in Chapter 6, we discuss the several dynamics models built using the Paracou data base in order to predict the future of the stands.

Following a more "historical" logic, Chapter 5 aims at providing the forest managers with practical answers to the questions that motivated the design of Paracou. Chapter 4 focuses on one of the dynamics components of particular interest to foresters – growth – and proposes prediction models. Chapter 6 compares the several dynamics models built to date to simulate the mid- and long-term evolution of the Paracou stands under various disturbance regimes and discusses the limits of these approaches for forest management. One of the limitations which has arisen in predicting the future is the still considerable lack of knowledge on regeneration processes: the first attempts at following juveniles according to a systematic sampling design are related in Chapter 3, with all the limits linked to the protocols adopted. Profiting from this experience, several studies recently started on a limited set of species, with completely mapped populations and in situ experiments, in order to gain better insight into the determinants of the early settlement of new trees in the stands and the spatial and temporal dynamics of these populations in a disturbed or undisturbed context. One example of such studies is given in Chapter 2. Finally, investigations such as those related in Chapter 1 are expected to provide us with keys to extrapolate ecological behaviour and, to some extent, population dynamics from the observed spatial patterns.

Ecology and Management of a Neotropical Rainforest

Chapter 1

Spatial patterns of the most abundant tree species

Hélène Dessard, Nicolas Picard, Raphaël Pélissier, Frédérique Collinet-Vautier

Abstract – The spatial patterns of the most abundant tree species on the Paracou experimental plots were all characterised using the same standard method based on the point process theory. Due to the local heterogeneity of environmental conditions, we analysed each species-plot combination independently. They were classified into three types of process (random, regular or aggregated) at different spatial scales. Most species exhibited aggregated patterns and the others showed various spatial structures, depending on the plot. In some cases, this variability could be explained by soil conditions, and in others cases the structures are so complex that we could only suggest possible explanations. These results are then discussed in the light of results previously obtained in other studies conducted on the same species using different methods. We conclude with some methodological proposals.

Keywords: Point processes, Spatial pattern, Heterogeneity, Summary functions, Tropical rainforest

1. Introduction

Tree spatial patterns result from interactions between individuals (competition, commensalism, etc.) and between individuals and their environment (Legay and Debouzie, 1985) which include biotic (pollinators, pathogens and herbivores) and abiotic factors (such as geology, topography and climate). Studying tree spatial patterns may thus provide good prospects of determining the biological processes that drive forest dynamics. The task, however, is difficult, as it involves inferring causes from effects: similar spatial patterns may result from the action or interaction of different factors that sometimes cannot be identified or disentangled without additional information.

There are many methods to study spatial patterns (Cressie, 1991; Dale, 1999), and a number have been tried at Paracou: quadrat methods (Durrieu, 1989), point-to-tree and tree-to-tree distance methods (Picard, 1996), estimation of first (Dessard, 1996) or second-order (Collinet, 1997) moments of point processes, spectral analysis (Kanaan, 2000) and geostatistics (Bariteau, 1992). Our objective in this chapter is mainly to summarise these results in a consistent way by applying a set of standard methods based on the point process theory. Indeed, as trees at Paracou are located in (x, y) co-ordinates within the experimental plots, which thus can be assimilated to points in a plane, the point process theory is a suitable mathematical framework for analysing observed tree spatial patterns. In general terms, the spatial pattern of trees in a forest stand can be considered as a realisation of a marked point process where the marks are individual values of a (qualitative or quantitative) tree variable (Penttinen et al., 1992). We focused here on a qualitative mark, the species name, which has as many modalities as the taxons identified in the stand. We thus disregarded the other components of the spatial structure, such as tree size or crown position in the canopy. Moreover, we focused on a few species, selected for (i) their abundance in the studied plots and (ii) the reliability of their botanical identifications (see Part I).

An early stage of our analysis of the species spatial patterns was to classify them as random, clustered or regular at the scale of the experimental plots. Randomness is the reference case because the underlying spatial process does not have any structure. It is known to depend on only one first-order parameter: the mean tree density. However, this does not mean that the underlying biological processes are simple, because random patterns may result from independence between trees and between trees and the environment, or from complex interactions, which globally neutralise each other at a given scale. Regular and clustered patterns are more difficult to characterise from only one realisation of the underlying process, the observed point pattern. Nevertheless, consistent inferences can be drawn by combining different second-order summary statistics (Gignoux et al., 1999).

The first part of this chapter describes the methods and the estimation procedures of the first and second-order spatial statistics used to test the observed spatial structures at Paracou. In the second part, we present the results obtained for 15 selected species. We discuss the results in the third section in the light of the results already obtained by previous studies conducted at Paracou.

2. Materials and methods

2.1. The framework of the planar point processes

When a map of all object locations is available and when the characterisation of its spatial pattern is the central question, we can use methods based on the point process theory. A point process is defined as a random mechanism that generates a countable set of points within a given region of space (Stoyan et al., 1995). An observed point pattern is considered to be the result of such a process, for which only one realisation is available.

As we can observe only one realisation of the process, the second-order statistical analysis is possible only if we assume stationarity of the process i.e. that the probabilistic laws of the process are invariant under translation, that is to say that they are identical everywhere in the study area. This assumption is a condition for the existence of summary second-order statistics. The assumption of stationarity also sets the conditions for the ecological interpretation of the spatial pattern in terms of the interactions between points. These interactions might occur independently or depend on the spatial variations of environmental factors, for which we have also to assume stationarity. Moreover, it is assumed that the point process at the origin of the observed spatial structure is isotropic, that is to say, its second-order properties are invariant under rotation. Even if these two conditions are seldom met in nature, summary second-order statistics can detect trends and provide a good starting point for discussions and further analyses based on other frameworks. For a detailed introduction to spatial point processes, see Ripley (1981), Cressie (1991) or Stoyan et al. (1995).

2.2. Summary functions

The first-order properties of a point process are summarised by its local-intensity function $\lambda(x)$, interpreted as the local density of trees at site x, that is to say $\lambda(x) \cdot \mathrm{d}S$ is the probability of finding one tree in the infinitesimal area $\mathrm{d}S$ centred on x (Cressie 1991; Diggle, 1983). For a stationary point process, the local intensity is constant everywhere, so that $\lambda(x) \equiv \lambda$, where λ gives the mean number of trees per unit area.

For a stationary and isotropic point process, Ripley's (1977) K-function summarises the second-order characteristics of the pattern, so that $\lambda K(r)$ gives the mean number of neighbours falling in a disc of radius r centred on any point of the process. As $K(r)$ increases with r^2, a practical choice is the L-function defined as $L(r) = \sqrt{K(r)/\pi}$, where the square-root stabilises the variance (Ripley, 1981). $L(r) = r$ at all distances for a Poisson process becomes greater than r when the pattern tends to be clustered and lower than r when the pattern tends to be regular.

Other functions are also employed to provide more details at short ranges (Diggle, 1983): $G(r)$ is the distribution function of the distance from each point of the pattern to its nearest neighbour. The "empty space function" or "first contact distribution", $F(r)$, is the distribution function of the distance between an arbitrary location and the nearest point of the observed spatial pattern. The arbitrary locations are generally taken at the nodes of a systematic sampling grid covering the area studied. We used a 12.5 m × 12.5 m systematic grid in this paper. Instead of using $F(r)$ and $G(r)$ separately, we used the function $J(r)$ proposed by Van Lieshout and Baddeley (1996), and defined, for $r \geq 0$ and if $F(r) \neq 1$, as:

$$J(r) = \frac{1 - G(r)}{1 - F(r)}$$

For a Poisson process, $J(r) = 1$ at all distances r. For clustered patterns, $J(r)$ has values less than 1 and greater than 1 for regular patterns. The authors demonstrated that "for a very large class of point processes, the function J is constant for values of r larger than the effective range of spatial interaction. Hence J can be used to infer both the range and type of spatial interaction."

Although these functions provide tests of complete spatial randomness (CSR), they reveal different properties of the spatial distribution: $F(r)$ summarises the size of gaps in the patterns, $G(r)$ summarises some interactions between points and $J(r)$ compares the neighbourhood of an arbitrary point of the process with the one of a fixed sampling point. These functions may modulate the results provided by $L(r)$ at short ranges: Gignoux et al. (1999) recalled that $L(r)$ should not be used alone because other functions have different sensitivities to different types of spatial distributions; Diggle (1979) found the following hierarchy of power for samples of size 100: $K(r) > G(r) > F(r)$ against regularity and $F(r) > K(r) > G(r)$ against aggregation; Thönnes et al. (1999) showed that the J-function had a power similar to the higher powers of $G(r)$ and $F(r)$.

2.3. Estimation procedures

Statistical estimations of these summary functions are based on the idea that their expectation is replaced by a spatial average. What appears in the expression of the L-estimator is an edge-effect correction: the domain of observation is usually bounded and only points inside the studied area enter into the estimation procedure, so that the real number of neighbours of some points lying near the border of the plot may be underestimated. The edge-effect correction compensates for this bias. Various edge-effect corrections are available (e.g. Haase, 1995) and we have chosen to use the translation correction of Osher (1983) because of its strength against anisotropy. The theoretical distribution properties of the summary functions then become intractable, so that we used Monte Carlo simulations in order to test the null hypothesis of CSR (Diggle, 1983). This consists in simulating a large number of realisations of a point process corresponding to a Poisson process, and computing the summary functions for each realisation in order to build a confidence interval of the observed values. In this chapter, we used 99 simulations in order to build 95% confidence intervals. The null hypothesis of CSR for the univariate point pattern was simply simulated by taking point co-ordinates in a uniform distribution.

The maximum range at which the pattern can be analysed by the L-function equals half the width of the plot. Beyond this threshold, the counting disc covers the plot almost completely, the variances of the estimators increase dramatically, so that no deductions can be made. Given the plot size at Paracou, the maximum range $r_{\max}$ at which the tree spatial patterns were analysed is thus 125 m. For G- and F-functions, the maximum range is given by the distance at which they reach 1. For the J-function, it is given by the distance at which $F(r)$ reaches 1. It thus depends on the studied pattern, but was always less than $r_{\max}$.

Explicit formulas for the different estimators can be found in Ripley (1981), Cressie (1991), Goulard (1995) or Baddeley and Gill (1997).

2.4. Presentation of the results

The spatial structure appeared more variable between the Paracou plots for a given species than in a given plot from one species to another because of the local heterogeneity of environmental conditions such as soil properties (Barthès, 1991; Sabatier et al., 1997) or light availability (Ferment et al., 2001). We thus assumed that each species-plot combination resulted from particular interactions between a point process and local environmental factors, and tried to classify them independently of each other as random, clustered or regular spatial structures using $L(r)$, $F(r)$, $G(r)$ and $J(r)$.

Of course, the type of pattern depends on the scale at which it is observed. As $L(r)$ tests for randomness at multiple spatial scales, we used this function to describe the broad-scale pattern. We supplied some details at smaller scales from the J-, G- and F-functions. We systematically specified the range of distances (m) at which regularity or clustering was detected by one of the summary functions. In many cases, however, the spatial distribution of trees was restricted to one part of the plot, producing a clustered pattern at the large scale. According to Pélissier et al. (2001), this may indicate a non-stationary process: the probabilistic laws of the process vary from place to place such that the observed pattern displays some heterogeneity. One typical form of heterogeneity is the variation of the local density, so that "a dense part of the study area could be interpreted as a cluster approaching the size of the study area. This cluster could not be considered as a repeated structure at the scale of the study region" (Pélissier et al., 2001). In other words, one could not determine, without repetitions and using small domains of observation, whether or not the variations in density were structural: this could just reflect the variability caused by a stationary clustering process, with clusters of a size close to the plot size, or be due to the heterogeneity of exogenous factors, such as the soil properties, for instance. As the comparison between species was the main concern, such patterns were classified as clustered in patches. From an ecological point of view, this conclusion is, however, not fully satisfactory and probably hides the true nature of the species spatial structure. We thus systematically specified the within-patch properties using $G(r)$.

In some other cases, the divergence of $L(r)$ at the large scale is explained by the geographical location of the plot relative to the area of distribution of the studied population, which can be only partially included within the plot. In such a case, we were not able to conclude about the type of pattern at the plot scale, even when the *G*-function detected significant aggregation. We have thus distinguished two subgroups of clustered populations, according to whether or not the observed *L*-function remained outside the confidence interval of CSR at very large scale.

2.5. Description of the data

Spatial pattern analysis was restricted to 15 selected species or groups of species with at least 20 individuals in each of the 250 m × 250 m plots of Paracou (for a detailed presentation of the site, see Part I). Below this density, the statistical tests may be less powerful (Diggle, 1979) or require some refinement (Gignoux et al., 1999). We used the diameter at breast height larger than 10 cm for all the trees of the 12 older plots (P1, …, P12) in 1984, that is to say before any silvicultural treatment was applied.

The 15 studied species were (the names given in parentheses correspond to the taxonomic categories used in Paracou inventories): *Bocoa prouacensis* (Boco), *Dicorynia guianensis* (Angélique), *Vouacapoua americana* (Wacapou), *Recordoxylon speciosum* (Wacapou guittin), *Manilkara bidentata* (Balata franc), *Chrysophyllum sanguinolentum* (Balata pomme), *Carapa procera* (Carapa), *Goupia glabra* (Goupi), *Sextonia rubra* (Sextonia), *Eperua falcata* (Wapa), *Pradosia cochlearia* (Kimboto), *Qualea rosea* (Gonfolo rose), *Moronobea coccinea* (Moronobea), *Virola michelii* (Virola) and *Eperua grandiflora* (Grandiflora) (see Table 1, in Annex 1, Part I).

3. Results

3.1. Random patterns

Globally random patterns were identified when $L(r)$ took values within the 95% confidence interval of CSR. However, local departures from randomness were detected when $J(r)$, $G(r)$ or $F(r)$ showed local fluctuations towards regularity or clustering at the intermediate scale and for a small range of distances.

The following species-plot combinations exhibited strictly random patterns (all functions stood within 95% confidence intervals): *B. prouacensis* in P5 and P2; *C. procera* in P4, P5 and P9; *Q. rosea* in P4 and P8; *M. bidentata* in P11; *C. sanguinolentum* in P11; *S. rubra* in P1, P3, P4 and P10; *M. coccinea* in P5 and P9; *G. glabra* in P9 and P11; *R. speciosum* in P4, P5, P6, P10, P11 and P12; *P. cochlearia* in P10 and P12 and *V. michelii* in P11.

Species that displayed globally random patterns but local aggregated structures were (characteristic distances of aggregation are given in brackets): *R. speciosum* in P7 (2.5–5) and P9 (24–28); *B. prouacensis* in P6 (13–18), P10 (12–19) and P12 (10–14); *C. procera* in P1 (26–30); *G. glabra* in P1 (26–31) and P7 (10–12); *M. bidentata* in P9 (9–11); *M. coccinea* in P6 (17–22) and P12 (8–19) and *P. cochlearia* in P4 (15–18).

Only one species presented a local regular pattern: *C. procera* in P2 (13–17), P6 (26–27), P10 (12–15), P11 (28–30) and P8 (98–104).

Fig. 1 shows the example of *C. procera* in P1 and P2, where the *L*-function indicated a globally random pattern, but the *G*- and *J*-functions revealed local

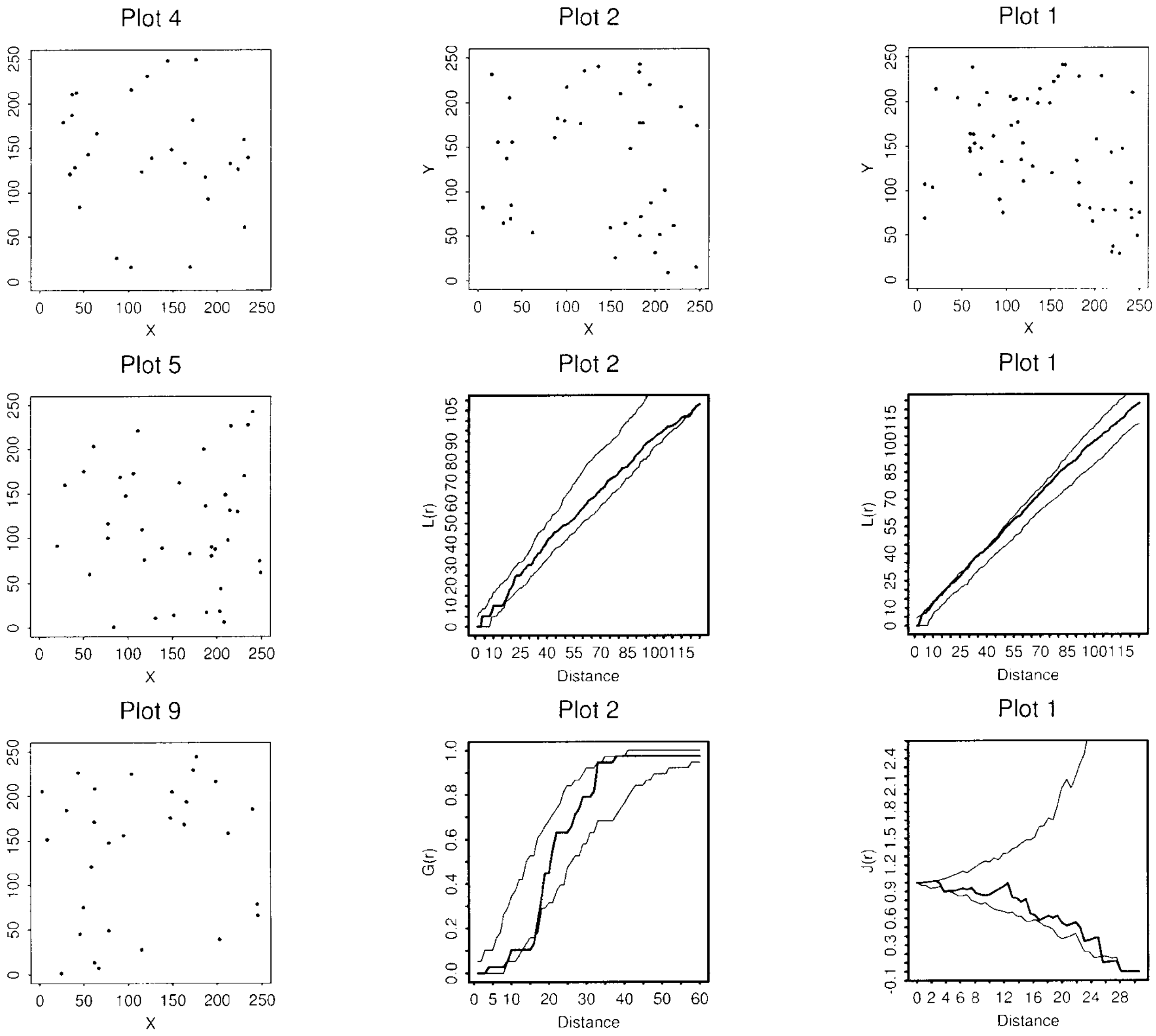


Fig. 1. Random patterns: *C. procera*.

aggregation or regularity. Strictly random patterns of C. *procera* are shown also.

3.2. Regular patterns

Regularity was detected when at least *L*(*r*) or *G*(*r*) stood below the lower limit of the confidence interval of CSR, whereas *J*(*r*) or *F*(*r*) stood above the upper limit. The structure was detected from a threshold distance $r_{\min}$ below which the pattern was recognised as random.

The following species exhibited regularity for a range of distances above $r_{\min}$ and less than the scale of the plot: *B. prouacensis* in P7 (9–30); *P. cochlearia* in P3 (15–30), P5 (3–16; 20–23), P6 (7–39) and *M. coccinea* in P5 (32–46; 77–98).

3.3. Aggregated patterns

Aggregated patterns were detected when *L*(*r*) and/or *J*(*r*) stood above the upper limit of the 95% confidence interval of CSR beyond a threshold distance $r_{\min}$, or when *F*(*r*) stood below the confidence envelope. For a few species-plot associations, *L*(*r*) returned inside the confidence envelope at large distances, defining an aggregated scale that could be detected at the scale of the studied plot. For the other species-plot combinations, aggregated patterns hold up to $r_{\max}$ and

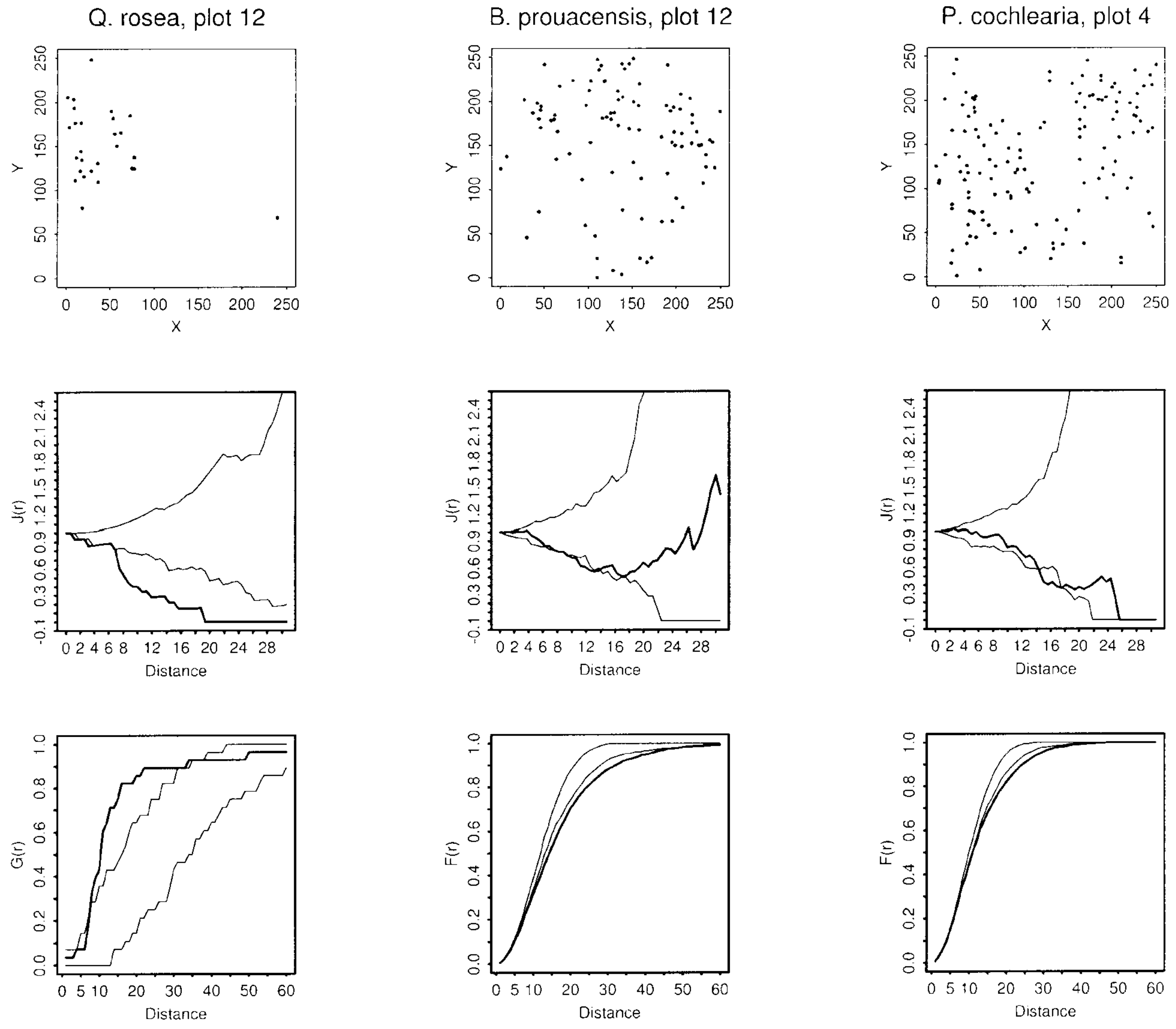


Fig. 2. Complex aggregated patterns.

may indicate a non-stationary process (Pélissier et al., 2001). We have thus distinguished two subgroups whether the observed *L*-function remained inside the confidence interval at very large scale. We described *D. guianensis* separately because of its particular spatial structure.

The following species exhibited a significant deviation towards clustering at $r_{\max} = 125$ m and were considered as clustered in patches (the threshold distance is indicated in brackets): *B. prouacensis* in P11 (14) and P12 (8); *M. coccinea* in P6 (17); *R. speciosum* in P8 (15); *V. americana* in P1 (6) and P10 (16); *Q. rosea* in P1 (8) and P12 (4); *E. grandiflora* in P5 (6), P6 (10) and P9 (7) and *E. falcata* in P9 (6). We assigned *C. procera* to this subgroup in P1 (25) as it showed a slight deviation towards clustering between 4 and 6 m. Some of these patterns are presented in Fig. 2.

A second subgroup is composed of species-plot combinations that presented clustered patterns over a long range of distances on the basis of which they were then recognised as random (the distances at which the pattern is detected are given in brackets): *B. prouacensis* in P5 (5–85) and P6 (12–20); *M. coccinea* in P12 (9–22); *S. rubra* in P1 (46–72); *V. americana* in P5 (7–108); *R. speciosum* in P5 (50–104) and P6 (62–74); *P. cochlearia* in P4 (15–103) and P12 (32–100); *Q. rosea* in P3 (8–19), P7 (10–70) and P11 (38–108);

Table 1
Types of complex clustering patterns: rand.: random, clus.: clustered, reg.: regular. Distances at which significant structures were detected are given in brackets.

Species	*Plot*	*Pattern (range)*
B. prouacensis	P1	rand.(6) reg.(9) rand.(14) clus.(76) rand.
	P3	rand.(26) reg.(45) rand.(60) clus.
	P4	rand.(9) clus.(18) rand.(30) reg.(34) clus.(65) rand.
	P8	rand.(10) clus.(16) rand.(25) reg.(34) clus.
C. procera	P1	rand.(4) clus.(6) rand.(25) clus.(30) clus.
	P3	rand.(17) reg.(23) clus.(67) rand.(74) clus.(115) rand.
	P7	rand.(11) clus.(13) rand.(24) clus.(26) rand.(37) reg.(39) rand.
	P12	rand.(14) clus.(19) rand.(37) reg.(45) clus.(48) rand.
C. sanguinolentum	P7	rand.(12) clus.(14) rand.(23) reg.(33) clus.(86) rand.
	P8	rand.(3) clus.(5) rand.(11) clus.(37) reg.(52) clus.(104) rand.
	P9	rand.(6) clus.(17) rand.(20) clus.(31) rand.(34) reg.(37) rand.(62) clus.(78) rand.
	P10	rand.(8) clus.(46) reg.(50) clus.(109) rand.
G. glabra	P7	rand.(10) clus.(12) rand.(53) clus.(104) rand.
R. speciosum	P1	rand.(4) clus.(14) rand.(22) clus.(25) rand.(50) clus.(62) rand.(76) clus.(80) rand.
P. cochlearia	P7	rand.(7) clus.(26) reg.(42) clus.
	P8	rand.(17) reg.(20) clus.(112) rand.
	P9	rand.(15) clus.(27) reg.(33) clus.(107) rand.
	P10	rand.(29) reg.(31) rand.(39) clus.(58) rand.
	P11	rand.(3) reg.(6) rand.(12) reg.(20) clus.(73) rand.
V. michelii	P10	rand.(26) clus.(34) rand.(43) reg.(45) rand.
V. americana	P3	rand.(8) clus.(22) reg.(36) clus.
	P6	rand.(14) clus.(30) reg.(35) clus.(57) rand.
	P9	rand.(7) reg.(12) clus.(48) rand.
Q. rosea	P2	rand.(12) clus.(22) rand.(42) reg.(44) clus.(107) rand.
E. grandiflora	P11	rand.(7) clus.(22) reg.(30) clus.(54) rand.
	P12	rand.(18) clus.(105) rand.
E. falcata	P5	rand.(3) reg.(6) clus.(115) rand.
	P6	rand.(2) reg.(6) clus.(105) rand.
	P7	Rand.(2) reg.(7) clus.
	P8	rand.(10) clus.(14) rand.(24) reg.(43) clus.

E. grandiflora in P8 (18–74) and P12 (18–105); and *E. falcata* in P3 (5–104), P4 (6–110), P10 (4–111), P11 (5–92) and P12 (6–93).

Two species-plot combinations exhibited a succession of random and aggregated patterns: *G. glabra* in P7 (10,12; 53,104) and *R. speciosum* in P1 (4,14; 22,25; 50,62; 76,80). For these species, the scale of aggregation differed for each species-plot combination, but the conclusion of homogeneous clustering is (almost) without ambiguity.

The other species-plot combinations are recognised as clustered patterns too, but integrated some regularity

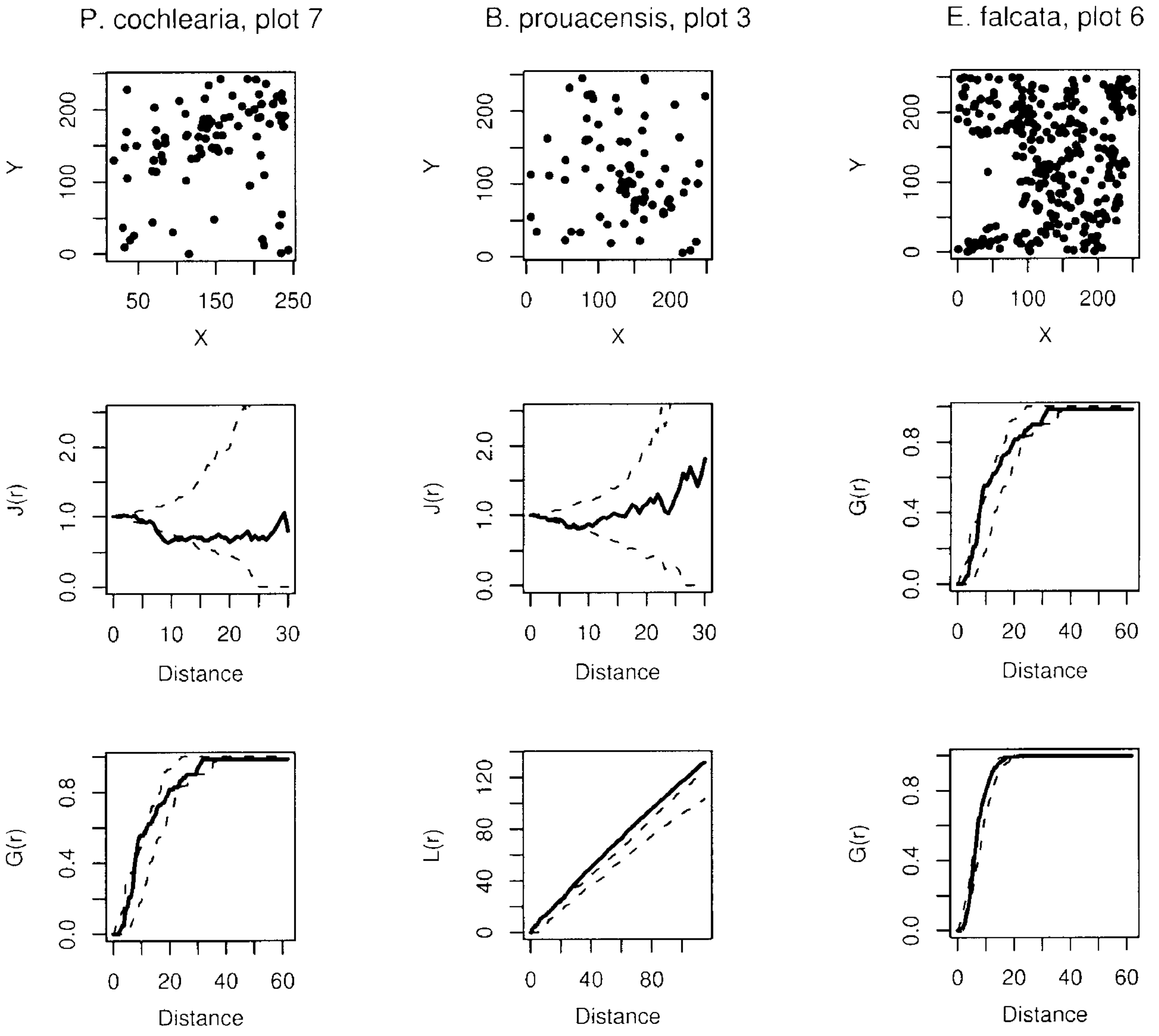


Fig. 3. Complex aggregated patterns.

at various scales and at times some randomness. The results are presented in Table 1 and some patterns are shown in Figs. 3 and 4.

These species-plot combinations can be classified, as above, in two subgroups depending on the detected pattern at r_{max}. Most of these species-plot combinations exhibited randomness at the scale of the plot: *B. prouacensis* in P1 and P4; *C. procera* in P3, P7 and P12; *C. sanguinolentum* in P7, P8, P9 and P10; *P. cochlearia* in P8, P9, P10 and P11; *V. michelii* in P10; *V. americana* in P3, P6 and P9, *Q. rosea* in P2; *E. grandiflora* in P11 and *E. falcata* in P5, P6 and P8. Only a few species-plot combinations showed aggregated patterns at 125 m: *B. prouacensis* in P3 and P8; *P. cochlearia* in P7.

Some aggregated patterns exhibited local regularity. The interpretation of this regularity depends on the scale at which it occurs. At small scale, this regularity is probably caused by competition between trees, as for *E. falcata*. At the larger scale, the regularity appears after clustering was detected, and could be interpreted as small clusters regularly spaced, as for *P. cochlearia* or *E. grandiflora*. The presence of clumps embedded in larger clusters containing some regularly spaced trees may explain the intermediate regularity and aggregation at large scale.

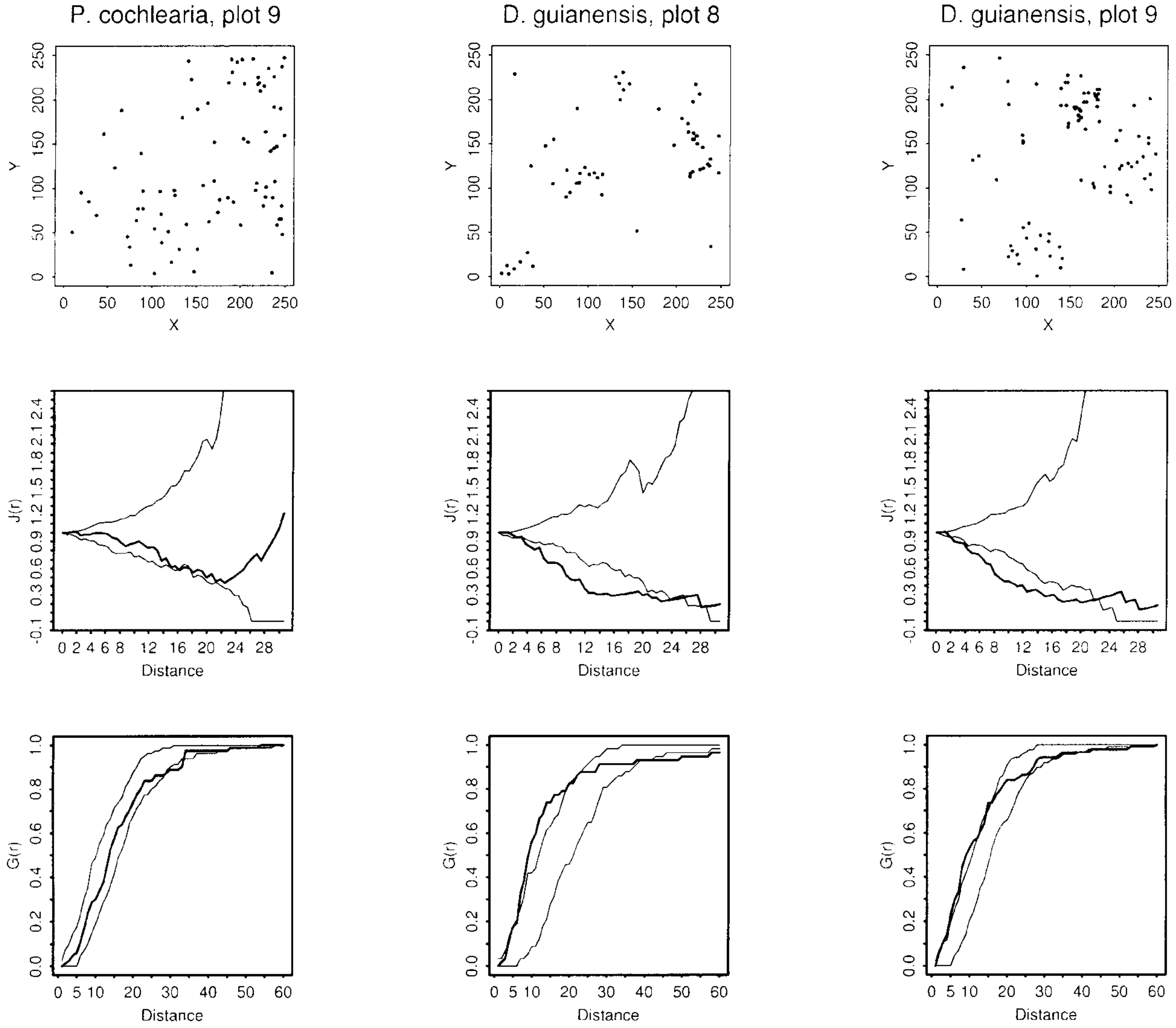


Fig. 4. Complex aggregated patterns.

Compared to other species, *D. guianensis* exhibited a specific pattern (Fig. 4). In all the plots except P6, the spatial structure of *D. guianensis* was characterised by a sharp continuous decrease of *J*(*r*) and by a short distance beyond which *J*(*r*) = *0* as *G*(*r*) quickly reached 1 (except in P2, P5 and P7 where the trees were more spaced than in the other plots), and by *L*-functions above the confidence envelope of CSR for the following ranges: in P1 (10–47), P2 (14–77), P3 (5–53), P4 (5–53), P5 (15–45), P7 (17–74), P8 (7–60), P9 (3–95), P10 (13–94), P11 (3–100) and P12 (4–71). *L*(*r*) stood close to the upper limit of the confidence interval in P6, and without examining *F*(*r*), we could conclude randomness. However, *F*(*r*) showed an aggregation from 8 to 55 m. From the maps in Fig. 4, the maximum distance of aggregation was interpreted as a typical radius (ranging from 47 to 100 m) of punctual clusters. As a matter of fact, the shape of the clusters was not so regular and it was at times be difficult to isolate one cluster from another, as in P6 or P10. Nevertheless, some easily distinguishable clusters contained 6 to 27 trees in areas varying between 625 m^2 and 6,600 m^2. Characterising the spatial distribution of the clusters is not an easy task, but from the four plots P9, P10, P11 and P12 that are almost joined, we inferred that the distance between two clusters was between 70 and

150 m. $G(r)$ showed a slight regularity from 45 to 85 m in P8 and from 45 to 60 m in P9. This was due to some trees located outside of the clusters and separated by a minimal distance of about 45 m. Except for P6, all trees inside the clusters tended to be aggregated within 11 to 30 m, as shown by $G(r)$ being above the upper confidence limit of CSR.

4. Discussion

Despite the variability of the spatial structures detected for a given species from one plot to another, we can now synthesise the dominant characteristics of the spatial patterns of the most abundant species at Paracou. We recall that the patterns were analysed at all scales within a disc of diameter 250 m: a species will thus be characterised by its dominant pattern, both in terms of plot and of scale. In order to make the interpretation easier, we distinguished clumps of trees corresponding to compact groups with less than five trees within a disc of diameter less than 10 m, from clusters of more than five trees within a disc of diameter less than 50 m, and patches for clusters of diameter larger than 50 m. Similar distinctions have been made by Chessel (1978) and Collinet (1997).

R. speciosum, *M. bidentata*, *S. rubra* and *G. glabra* were mainly distributed at random, even though these species tended to be clustered in some plots. Such a tendency to cluster was probably due either to local clumps (more frequent or with trees closer together than expected under randomness (*M. bidentata* or *S. rubra*) or to slight variations in density (*R. speciosum* or *G. glabra*).

M. coccinea, *C. procera*, *P. cochlearia*, *C. sanguinolentum* and *V. michelii* exhibited clustered, regular or random structures depending on the plot considered. It was noted that species density in plots where regularity occurred was always lower than in plots exhibiting clustering. Regularity may thus in some cases be interpreted as a consequence of higher competitive stress in dense plots that could force the species to distribute in a scattered way within the stand (see Part I, Fig. 12(a); P3, P10, P12 are characterised by high basal areas per hectare, whereas P4, P5 and P11 present an high number of stems per hectare). In other cases, we could only invoke the spatial heterogeneity of the resources that were favourable (or unfavourable) to the given species. This kind of argument has been advocated by Collinet (1997) for *C. procera*, with a restriction of the competitive stress due to edaphic factors only: *C. procera* seems to have random or regular distributions outside bottomlands, but tends to appear in clusters within bottomlands. One may also note that *P. cochlearia*, which tends to avoid the bottomlands (Collinet, 1997; Deschère, 1991), exhibited small clumps in most plots at Paracou (P7, P9, P11 and P12). The presence of clumps within patterns that are globally random or regular could result from the seed distribution (seeds are buried by monkeys in small quantities) allowing the seeds to survive and grow in restricted light-gaps or in locally favourable soil conditions.

B. prouacensis exhibited various patterns, from random to regular and clustered. For this species, Collinet (1997) supported a spatial distribution in patches, so that, even if we were not able to prove it, the variable spatial structure at Paracou resulted mainly from local fluctuations of environmental conditions. At present, the characterisation of these conditions is very rough at Paracou, even if some studies (Baraloto, 2001; Ferment et al., 2001) have demonstrated that microhabitats, both within and among plots, were very variable. Among the plots, variability could affect the establishment and survival of young trees, which probably depend on unrecorded exogenous factors whose spatial distribution differs from plot to plot.

D. guianensis is an exemplary case, showing a spatial distribution in punctual clusters having a radius of about 50 m. A research programme is currently focusing on this species in order to better understand its autecology (Gourlet-Fleury, 1999). Indeed, *D. guianensis* is of particular interest because it is the first harvested species in French Guiana and neither its biological traits nor the known environmental factors (Ecofor Annual Report, 2000–2001) can explain its spatial distribution. *D. guianensis* is an heliophilic but shade tolerant, wind-dispersed species (Forget, 1988) and 95% of the seeds fall within a distance of 30 m from the mother tree (Loubry, 1993). These traits are, however, not sufficient to explain the scale of clustering. One could expect an expansion of the clusters as a result of the dynamics of the species and the occurence of favourable conditions like windthrows. However, the mean size of the windthrows is too small with respect to the size of the clusters. The spatial distribution could reflect a meta-population functioning: this kind of structure exists (Messié, 1998) but was not fully satisfactorily confirmed by demographic studies (Chevolot, 2001).

V. americana, *E. falcata*, *E. grandiflora* and *Q. rosea* were distributed in patches larger than the plot size and exhibited clustered structures embedded within large patches. For *V. americana*, Traissac (1998) detected two different levels of clustering, at 20 and 80 m, within sampling windows of about 36 ha. Collinet (1997) assumed the existence of another level of clustering between 120 and 180 m for the same species. At the plot scale (6.25 ha), the spatial structure of *V. americana* appeared heterogeneous (P1, P5 and P10), or showed alternating middle range regularity and clustering (P3, P6 and P9). In P3 and P6, aggregation was detected at a smaller range than was regularity, because some trees were scattered between clusters, as if clusters had formed nuclei around which some trees were distributed according to a decreasing gradient of density. Conversely, regularity appeared at a smaller range than clustering in P9, indicating that the trees were scarcely dispersed within the clusters. In P1, clusters with a radius of about 44 m were detected in the southern part of the plot, as well as in the northern and south-eastern parts in P5. In P10, a straight line at about 150 m from the plot boundary marked the limit of a large patch (Traissac, 1998). These distributions in patches appeared to be caused by the fact that *V. americana* tends to avoid the wettest soils, although it is able to settle in any soil conditions (Forget et al., 1999; Traissac, 1998). *E. falcata* also formed patches larger than the size of plots (Bariteau, 1992; Cabrera-Gaillard and Gignoux, 1990; Gader, 1990). The characteristic size of these patches is still unknown and further studies are needed. However, within-patch clustering was detected in all the plots, from 2 to 8 m, except in P1 and P2 where *E. falcata* is almost absent. Collinet (1997) found smaller clusters with a characteristic radius of about 20 m (P6 and P11), whereas Cabrera-Gaillard and Gignoux (1990) detected another level of clustering at about 100 to 200 m by the Greig-Smith method. The spatial pattern appeared more complex in P5, P6, P7 and P8, because of local variations in density. Some other studies have shown that *E. falcata* tends to avoid the water-saturated bottomlands (Bariteau, 1992; Barthès, 1990; Couteron et al., 2002) and are often found on soils rich in aluminium. This could explain the presence of large surfaces without *E. falcata*. However, it seems that the meso-scale abundance in *E. falcata* could also be related to stand portions where late stages of forest reconstitution after tree falls are frequent (Couteron et al., 2002).

Several authors have noted on the basis of field observations that *E. grandiflora* formed patches in areas deserted by *E. falcata*. As for *V. americana*, the spatial pattern of this species was, however, heterogeneous in most plots. Using the *G*-function, we detected a random within-patch distribution in P12, but small-scale aggregations in P5, P6 and P9. According to observations of harvesters at Paracou (in Deschère, 1990), *Q. rosea* is distributed in patches greater than 1,000 or 2,000 m. In our results, *Q. rosea* appeared clustered at various scales, from 19 to 108 m in P3, P7 and P11. Collinet (1997) found clusters with a characteristic radius of about 80 m, whereas Bariteau (1992) detected two levels of clustering at 85 and 170 m in P1, and 60 and 120 m in P11. Barthès (1988) and Sabatier and Prevost (1990) noted that this species preferred not too hydromorphic and deep quartzly soils.

In summary, most of the studied species, even if water demanding, tend to avoid hydromorphic bottomlands at Paracou (Barthès, 1988; Collinet, 1997), and their colonisation strategies seem quite efficient in favourable soil conditions. Collinet (1997) tried to relate the type of spatial pattern to the mode of seed dissemination. Her only conclusion was that species distributed at random were always endozoochorous.

At plot scale, the prevalent pattern of the studied species was clustering. This prevalence has been recognised by Collinet (1997) at Paracou, and by many studies in other tropical forests (e.g. Batista and Maguire, 1998; Condit et al., 2000; Forman and Hahn, 1980; Legg and Laumonier, 1999; Pélissier, 1998). Of the 110 species-plot associations that we studied, 8.2% showed random patterns, 13.6% presented some regularity at medium range (≤ 50 m), and among those remaining, 78.2% exhibited clustered patterns, 14% punctual clusters, 35% multi-scale clusters and 51% complex clusters. The proportion of regular patterns was higher in our study than in other studies: Forman and Hahn (1980) found 28 clustered species for only one regularly spaced species. The proportion of random patterns was also higher in our study. These discrepancies may be explained by species autecology in that area of the Amazonian forest, by our method of classifying the patterns, or by the fact that other authors did not use statistics powerful enough to detect regularity.

Regularity probably expresses intra-specific competition (distance of seedlings from their parent tree) or inter-specific competition through unexplored processes (emission of harmful substances, root system congestion, etc.). Randomness is more difficult to interpret, because it can reflect either the absence of particular ecological requirements, or the simultaneous action of inhibition and clustering processes that compensate for each other.

From a methodological point of view, the detection of different kinds of clustered patterns was made possible by the use of different test functions. Although each function is not powerful enough to fully characterise the encountered patterns (see results for *B. prouacensis* in Fig. 3 or *P. cochlearia* in Fig. 4), their confrontation still can detect complex patterns reflecting a mixture of different processes acting at different scales.

Estimations of the *G*-, *J*- and *L*-functions, which focus on the second-order properties of the point process only, may be biased when the stationarity and isotropy assumptions are not met, or when the number of points is too small (< 30). Of course this remark also applies to regular patterns. More precise classification of spatial patterns could be obtained from estimations of the third-order moments of point processes (Schladitz and Baddeley, 2000; Stoyan et al., 1995), or from the use of local tests of interactions (Allard et al. 2001; Chadoeuf et al., 2000).

Another limitation of our approach is that we have chosen the stationary analysis framework, whereas the spatial patterns may be characterised quantitatively in two different ways, using different summary statistics. If we consider that trees interact in the homogeneous environment, the relevant tools deal with the second-order properties of the process. If we believe that individuals interact in the heterogeneous environment, suitable descriptors should be based on the first-order properties of the pattern given by the local-intensity function $\lambda(x)$. Reciprocally, the choice of one tool or the other determines the interpretative framework. Of course, these two approaches are simplistic from the ecological point of view, and the user must be aware of the underlying biological framework. However, they can efficiently complement other analyses or observations. A recent method proposed by Baddeley et al. (2000) allows use of an extended version of the *L*-function to characterise non-stationary processes. This kind of analysis could modify or increase the precision of our classification of the spatial patterns, and provide improved understanding of the ecological processes at the origin of the spatial patterns observed at Paracou.

References

Allard D., Brix A., Chadoeuf J., 2001. Testing local independence between two point processes. Biometrics [in press].

Baddeley A.J., Gill R.D., 1997. Kaplan–Meier estimators of interpoint distance distributions for spatial point processes. Ann. Stat. 25, 263–292.

Baddeley A., Møller J., Waagepetersen R., 2000. Non- and semi-parametric estimation of interaction in homogeneous point patterns. Statistica Neerlandica 54, 329–350.

Baraloto C., 2001. Tradeoffs between neotropical tree seedling traits and performance in contrasting environments, PhD thesis, University of Michigan, 302 p.

Bariteau M., 1992. Régénération naturelle de la forêt tropicale humide de Guyane: étude de la répartition spatiale de Qualea rosea Aublet, Eperua falcata Aublet et Symphonia globulifera Linnaeus f. Annales des Sciences Forestières 49, 359–382.

Barthès B., 1988. Où pousse cet arbre? Premiers résultats de l'étude des relations sols-végétations en forêt de Paracou: cas du wapa et du gonfolo. Rapport technique, ORSTOM, 33 p.

Barthès B., 1991. Influence des caractères pédologiques sur la répartition spatiale de deux espèces du genre Eperua (Caesalpiniaceae) en forêt guyanaise. Revue d'Ecologie (Terre et Vie), 46, 303–320.

Batista J.L.F., Maguire D.A., 1998. Modeling the spatial structure of tropical forests. Forest Ecol. Manag. 110, 293–314.

Birnbaum P., 1997. Modalités d'occupation de l'espace par les arbres en forêt guyanaise. Thèse de doctorat, Université Paris 6, 221 p.

Cabrera-Gaillard and Gignoux, 1990. Répartitions spatiales et sylviculture en forêt guyanaise. Rapport technique. CIRAD-Forêt. Kourou.

Chadoeuf J., Brix A., Pierret A., Allard D., 2000. Testing local dependence of spatial structures on images. J. Microsc. (GBR) 200, 32–41.

Chevolot M., 2001. Dynamique spatiale des populations d'Angélique (*Dicorynia guianensis* Amshoff) en forêt littorale guyanaise. Mémoire de DEA Biologie de l'évolution et écologie, Université Montpellier II.

Chessel D., 1978. Description non-paramétrique de la dispersion spatiale des individus d'une espèce. In: Legay J.M., Tomassone R. (Eds.), Biométrie et écologie. Société française de biométrie, Paris, pp. 45–135.

Collinet F., 1997. Essai de regroupements des principales espèces structurantes d'une forêt dense humide d'après l'analyse de leur répartition spatiale. Thèse de doctorat, Université Claude Bernard, Lyon, 301 p.

Condit R., Hubbell S.P., Forster R.B., 1992 . Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. Am. Nat. 140, 261–286.

Condit R., Ashton P.S., Baker P., Bunyavejchewin S., Gunatilleke S., Gunatilleke N., et al., 2000. Spatial patterns in the distribution of tropical tree species. Science 288, 1414–1418.

Couteron P., Pélissier R., Mapaga D., Molino J.-F., Tellier L., 2002. Drawing ecological insights from a managementoriented forest inventory in French Guiana. Forest Ecol. Manag. [in press].

Cressie N., 1991. Statistics for Spatial Data. J.Wiley & Sons, New York, 900 p.

Dale M.R.T., 1999. Spatial Pattern Analysis in Plant Ecology. Cambridge University Press.

Dessard H., 1996. Estimation de l'intensité locale d'un processus ponctuel de Cox: application à l'analyse spatiale d'un inventaire forestier. Thèse de doctorat, Université Montpellier 2, 207 p.

Dessard H., 1999. Analyse de la répartition spatiale de la régénération de *Dicorynia guianensis.* Rapport annuel Ecofor.

Deschère P., 1991. Etude quantitative de la répartition spatiale de quelques espèces forestières commercialisables en Guyane française; cas particulier: *Dicorynia guianensis*. Rapport de stage Engref, Nancy, 44 p.

Diggle P.J., 1979. On parameter estimation and goodness-of-fit testing for spatial patterns. Biometrics 35, 87–102.

Diggle P.J., 1983. Statistical Analysis of Spatial Point Patterns. Academic Press, London.

Durrieu L., 1989. Étude de l'environnement de l'angélique (Dicorynia guianensis) sur le dispositif d'étude des peuplements naturels en forêt dense humide guyanaise. Mémoire de stage de mastère Engref, Kourou, 37 p.

Ferment A., Picard N., Gourlet-Fleury S., 2001. A comparison of five indirect methods for characterizing the light environment in a tropical forest. Ann. Forest Sci. 58, 877–891.

Forget P.M., 1988. Dissémination et régénération naturelle de huit espèces d'arbres en Guyane française. Thèse de 3^{e} cycle, Université Pierre et Marie Curie, Paris, 245 p.

Forget P.M., Mercier F., Collinet F., 1999. Spatial patterns of two rodent-dispersed rain forest trees Carapa procera (Meliaceae) and Vouacapoua americana (Caesalpiniaceae) at Paracou, French Guiana. J. Trop. Ecol. 15, 301–313.

Forman R.T.T., Hahn D.C., 1980. Spatial patterns of trees in a caribbean semievergreen forest. Ecology 61, 1267–1274.

Gader G., 1990. Étude de l'environnement du wapa (Eperua spp.) sur le dispositif de Paracou en forêt dense humide guyanaise. Mémoire de stage Engref, Kourou, 37 p.

Gignoux J., Duby C., Barot S., 1999. Comparing the performances of Diggle's tests of spatial randomness for small samples with and without edge-effect correction: application to ecological data. Biometrics 55, 156–164.

Goulard M., Pages L., Cabanettes A., 1995. Marked points process: using correlation functions to explore a spatial data set. Biomet. J. 37, 837–853.

Gourlet-Fleury S., 1999. Régénération de l'angélique (*Dicorynia guianensis* Amshoff, Caesalpiniaceae) en Guyane française. Project supported by the GIP ECOFOR.

Grandval A., 1993. Mise en évidence d'une structure spatiale du système de décomposition en relation avec la qualité de la litière en forêt guyanaise. Mémoire de DEA d'écologie générale, Université Paris 6, 36 p.

Haase P., 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: introduction and methods of edge correction. J. Veg. Sci. 6, 575–582.

Kanaan M., 2000. Cross-spectral analysis for spatial point-lattice processes, PhD thesis, University of Leicester.

Kokou K., 1992. Contribution à l'étude du déterminisme écologique de la répartition spatiale de l'angélique (Dicorynia guianensis) en forêt dense guyanaise. Mémoire de DEA de géographie des espaces tropicaux, Université Michel de Montaigne, Bordeaux, 83 p.

Legay J.M., Debouzie D., 1985. Une introduction à la biologie des populations. Masson, Paris, 149 p.

Legg C., Laumonier Y., 1999. Spatial and three-dimensional analysis of tree species distribution in forest sample plots, Jambi province, Sumatera, Indonesia. In: Laumonier Y., King B., Legg C., Rennolls K. (Eds.), Data Management and Modelling Using Remote Sensing and GIS for Tropical Forest Land Inventory. Proceedings of the FIMP-INTAG International Conference, October, 26–29, 1998, Jakarta, Indonesia. Rodeo International Publishers, Jakarta, pp. 299–317.

Lescure R., Boulet J.P., 1985. Relationships between soil and vegetation in a tropical rain forest in French Guiana. Biotropica 17, 155–164.

Lotwick H.M., Silverman B.W., 1982. Methods for analysing spatial processes of several types of points. J. Roy. Statist. Soc. B 44, 406–413.

Loubry D., 1993. Les paradoxes de l'Angélique : dissémination et parasitisme des graines avant dispersion chez un arbre anémochore de forêt guyanaise. Revue d'écologie (Terre et Vie) 48, 353–363.

Mercier F., 1997. Analyse et modélisation de la dynamique forestière guyanaise à l'aide de diagrammes de Voronoï. Thèse de doctorat, Université Claude Bernard, Lyon, 181 p.

Messier C., 1998. Structuration spatiale du polymorphisme de l'ADN chloroplastique chez l'Angélique de Guyane, *Dicorynia guianensis* Amshoff. Rapport de DEA de Biologie Forestière, Université Henri Poincaré, Nancy, 21 p.

Moeur M., 1993. Characterising spatial patterns of trees using stem-mapped data. Forest Sci. 39, 756–775.

Osher J., 1983. On estimators for the reduced second moment measure of point processes. Math. Operationsforsch. Statist. Ser. Statistik 14, 63–71.

Pélisser R., 1998. Tree spatial patterns in three contrasting plots of a southern Indian tropical moist evergreen forest. J. Trop. Ecol. 14, 1–16.

Pélissier R., Goreaud F., 2001. A practical approach to the study of spatial structure in simple cases of heterogeneous vegetation. J. Veg. Sci. 12, 99–108.

Penttinen A., Stoyan D., 1989. Statistical analysis for a class of line segment processes. Scand. J. Stat. 16, 153–168.

Penttinen A., Stoyan D., Henttonen H.M., 1992. Marked point processes in forest statistics. Forest Sci. 38, 806–824.

Picard N., 1996. Répartition spatiale des essences forestières. Etude de distances entre espèces basées sur des dissimilarités entre nuages de points. DEA d'Ecologie Générale, Université Paris 6.

Picard N., Bar-Hen A., Franc A., 2001. Spatial pattern induced by asymmetric competition: a modelling approach. Nat. Resour. Model. 14, 147–175.

Ripley B.D., 1977. Modelling spatial patterns (with discussion). J. Roy. Stat. Soc. B 39, 172–212.

Ripley B.D., 1981. Spatial Statistics. Wiley, New York.

Sabatier D., Prevost M.F., 1990. Quelques données sur la composition floristique et la diversité des peuplements forestiers de Guyane française. Bois et Forêts des Tropiques 219, 31–55.

Stoyan D., Stoyan H., 1994. Fractals, Random Shapes and Point Fields. J. Wiley & Sons, New York.

Stoyan D., Kendall W.S., Mecke J., 1995. Stochastic Geometry and Its Applications, 2nd ed. Wiley, Chichester.

Schladitz K., Baddeley A., 2000. A third order point process characteristic. Scand. J. Stat. 27, 657–671.

Thönnes E., van Lieshout M.N.M., 1999. A comparative study on the power of van Lieshout and Baddeley's *J*-Function. ????? 41, 721–734.

Trichon V., Guillemyn D., Fromard F., 1997. Cartographie d'une canopée de forêt tropicale par photographies aériennes numériques et analogiques – Opération Guyane 96, Guyane française, site de Paracou. Compte rendu de mission (18 octobre–7 novembre 1996) et résultats préliminaires. Laboratoire d'Écologie Terrestre, UMR 5552 CNRS/UPS, Toulouse.

Traissac S., 1998. Étude de la dynamique de la répartition spatiale de *Vouacapoua americana* (Aublet) arbre de forêt tropicale guyanaise. Mémoire de DEA, Université Claude Bernard, Lyon.

Van Lieshout M.N.M., Baddeley A.J., 1996. A nonparametric measure of spatial interaction in point patterns. Statistica Neerlandica 50, 344–361.

Van Lieshout M.N.M., Baddeley A.J., 1999. Indices of dependence between types in multivariate point patterns. Scand. J. Statist. 26, 511–532.

Upton G., Fingleton B., 1985. Spatial Data Analysis by Example, vol. 1. J. Wiley & Sons, New York.

Ecology and Management of a Neotropical Rainforest

Chapter 2

Effects of post-logging microhabitats on regeneration from seed: implications for sustainable forest management

Christopher Baraloto, Pierre-Michel Forget

Abstract – We investigate how selective logging might limit regeneration from seed of timber tree species differing in seed size, by changing the types of microhabitats seeds and seedlings experience, both immediately after logging activity and 12 years later. Directly after logging, several microhabitats can be characterized based on significant environmental changes. Skid trails had more open canopy, less litter, and greater soil compaction; sites where trees were cut had open canopy with fluffed soil from accumulation of organic material; and disturbed forest areas were characterized by slight increases in canopy openness. However, 12 years after logging at Paracou, only slight differences persisted among these post-logging microhabitats. Skid trails still received more light than understory sites, but not as much as the actual canopy gaps. Also, no significant differences in any soil characteristics remained between post-logging microhabitats and undisturbed understorey, although skid trail sites tended to have less soil moisture and greater soil compaction.

Accordingly, seedling establishment probabilities in post-logging microhabitats may change over time. In an experiment simulating soil disturbances characteristic of recently logged sites, two large-seeded and a very small-seeded species exhibited little reduction in survival in response to compacted and bare soils, while other small-seeded non-pioneers failed to establish seedlings. In contrast, survivorship from seed along transects throughout the Paracou plots 12 years after logging differed only slightly among post-logging microhabitats. Still, larger-seeded species exhibited a survival advantage across all microhabitats.

As logging also results in a removal of seed sources, these results suggest that small-seeded timber tree species lacking a seed bank may have reduced seedling establishment immediately following logging, especially in microhabitats with soil disturbances. However, if seed sources are ensured and dispersal mutualisms remain intact, then these results predict little long-term effect of logging damage on seedling establishment.

Keywords: Selective logging, Soil, Nutrients, Light, Environment, Tropical tree seedling, Recruitment limitation, Seed size

1. Introduction

Timber tree regeneration has been widely recognized as an important component of many sustainable management plans in tropical forests (Putz, 1994; Sist et al., 1998). However, most logging impact studies have focused on damage to later life history stages to define felling rotations (Gullison and Hardner, 1993; Webb, 1997; White, 1994). As a result, a deficit of information about post-logging seedling recruitment exists (Putz, 1996), especially in the neotropics (Guariguata and Pinard, 1998).

Many factors contribute to the regeneration potential of tropical timber species after logging, including reduction in seed inputs and loss of dispersal or pollination agents (Guariguata and Pinard, 1998; Hammond et al., 1996). Equally important may be the changes in the physical environment into which seeds are dispersed (Nussbaum et al., 1995; Pinard et al., 1996). Although canopy openings and soil disturbance can be limited by implementation of reduced-impact logging methods (Johns et al., 1996; Pinard et al., 2000), the post-logging forest mosaic will still differ from natural forest in several ways. Seeds dispersed into this mosaic immediately after logging have a greater probability of encountering large canopy openings with high light levels and increased soil temperature (Heydon, 1994), areas of compacted soil lacking litter (Guariguata and Dupuy, 1997; Pinard et al., 2000; Woodward, 1996), and other areas with litter accumulation (Nussbaum et al., 1996; Rab, 1994). In this altered physical environment, timber species are not always favored. For example, Tuomela et al. (1996) found that dipterocarp species were poor colonizers of all but the smallest logging gaps in a logged forest of Kalimantan, Indonesia. Even pioneer species may experience limited establishment in disturbed sites immediately after logging (Pinard et al., 1996).

Several authors have duly noted that the regeneration patterns of timber trees after logging may be related to seed and seedling traits, such as dispersal type and seed size (Guariguata and Pinard, 1998; Hammond et al., 1996). For example, species with larger seeds may be maladapted to increases in canopy opening (Foster and Janson, 1985). In contrast, litter depth may limit the establishment of smaller-seeded species (Molofsky and Augspurger, 1992; Vazquez-Yanes and Orozco-Segovia, 1992). At Paracou, seed size among tree species varies across six orders of magnitude (Baraloto, 2001), and the French Guianan timber trees comprise the same breadth of variation (Fig. 1). If response to microhabitats created by logging activity does indeed differ among timber tree species differing in seed size, then managers might devise strategies for logging activity based on this ecological characteristic, among others (Guariguata and Pinard, 1998; Hammond et al., 1996).

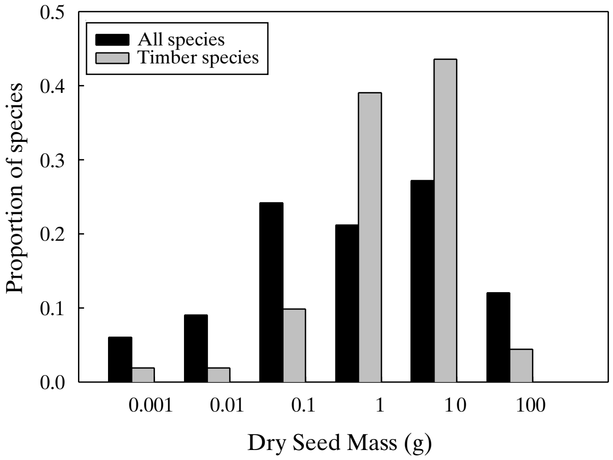


Fig. 1. Frequency distribution of seed size among a large sample of tree species at Paracou, French Guiana (n = 202; see Baraloto, 2001), and the subset of species that are listed by Office National des Forêts as commercially harvested in French Guiana (n = 38).

In this chapter, we investigate how logging affects environmental conditions in the forest, and the consequences of these changes for the regeneration of tree species differing in seed size. We first examine how logging activities affect the microhabitats into which seeds are dispersed, both directly after logging, and after some succession has occurred. We then present results from two experiments investigating the response of timber species differing in seed size to natural and manipulated post-logging microhabitats. Finally, we discuss the degree to which environmental damage as a result of logging might contribute to recruitment limitation of tropical timber trees.

2. Effects of logging on microhabitats

2.1. Immediate effects of logging activity

No baseline environmental measurements are available for the Paracou plots to determine if differences among plots can be attributed to logging activity. Furthermore, no quantified measurements of the environment were made in the logged plots at Paracou until 12 years after logging (Baraloto and Gourlet-Fleury, in review; see below). However, data on the immediate environmental effects of logging damage are available from a study in another French Guianan forest logged in a similar manner to that of Treatment 1 at Paracou (Part I and Baraloto, in review).

In the study, environmental conditions were measured at the same sampling points before and after selective logging, in the Montagnes Tortue National Forest (4°16′ N, 52°20′ W). In August 1998, nine 10 m × 100 m transects were established in primary rain forest scheduled to be logged in September-December, 1998. Transects were established in areas corresponding to a gradient of logging intensity, based on forest inventory data. In addition, a single transect was established as a control in an area not yet scheduled to be logged, within 800 m of the other transects to approximate local soil conditions, but 500 m from any area affected by logging activity (see Baraloto in review for details).

Sampling points were established every 10 m along both sides of the transect (n = 22/transect). At each point, an iron stake was inserted into the ground to facilitate relocation of the point after logging. Sampling was conducted in August 1998 (before logging) and in January 1999 (after logging). Measured environmental variables were selected based on their ease of measurement under varying weather conditions and their established link to plant performance (Whitman et al., 1997). Litter depth was measured to the nearest 0.5 cm as described by Molofsky and Augspurger (1992). Soil compaction was estimated using a pocket penetrometer (Forestry Suppliers, Jackson, MS, USA). Canopy openness was measured using a spherical densiometer (Forest Densiometers, Bartlesville, OK, USA). During post-harvest measurements, each site was classified according to field observations into one of four post-logging microhabitat types:

1. Natural understorey – closed canopy and no evidence of soil or stem damage from logging within 5 m.
2. Disturbed understorey – closed canopy with some stem damage but no evident soil damage within 5 m.
3. Cut tree – site where tree was felled, including the residual canopy and stump.
4. Skid trail – soil disturbance from passage of heavy machinery.

Fig. 2 illustrates the results of the survey. Overall, logging activity resulted in a tenfold increase in canopy openness along skid trails and near felled trees, to more than 30% openness. Even in sites where the forest understorey remained intact (disturbed forest), canopy openness nearly tripled to more than 10% (Fig. 2a).

Some differences in soil measurements can be attributed to the difference in season between the two sampling periods, as indicated by the slight reduction in litter depth in the undisturbed forest sites (Fig. 2b). Still, litter depth was reduced three times more in skid trail areas, often resulting in bare soil. Skid trail sites also were much more compacted after logging. In contrast, cut tree sites actually exhibited a decrease in soil compaction after logging activity, presumably due to soil turning (Fig. 2c).

2.2. Long-term differences in post-logging microhabitats

To determine whether these types of environmental changes persist after logging, we examined the recovery of environmental conditions 12 years after logging in the plots at Paracou. In 1998, we established twelve 10 m × 100 m transects in the Paracou plots, with two transects within each of six plots corresponding to control, Treatment 1, and Treatment 2 (Plots 6, 11; 7, 9; 5, 10; see Part I, and Chapter 5, Part IV, for a detailed description of the plots, treatments, and impacts on the stands). Elsewhere, we present the results from stratified sampling points from this survey (Baraloto and Gourlet-Fleury, in review). Here, we present the results from planting sites also located along these transects, to examine environmental conditions after some succession had occurred.

Planting sites were established along transects according to a random-stratified design. Every 10 m along each transect, 1 m^2 site among the 100 possibilities was chosen using random number tables (120 total planting sites). In March 1998, measures of the physical environment were made at each planting site, as follows. Light energy, expressed as the percentage of photosynthetically active radiation (PAR) transmitted from the canopy (% of full sun), was estimated using the diazo paper method (Friend, 1961). Soil litter depth and soil surface compaction

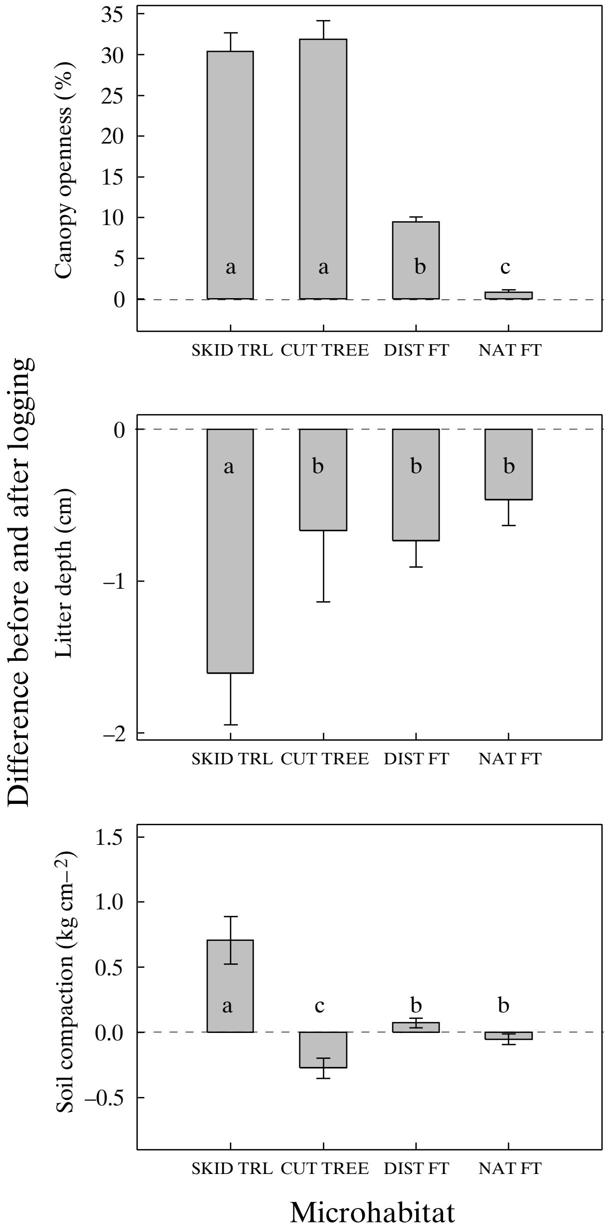


Fig. 2. Differences in environmental conditions at sampling points before and two months after logging occurred, grouped by post-logging microhabitat. Data are the means (SE) of differences for repeated measures at each sampling point, from 220 points along ten transects at Montagnes Tortue, French Guiana. Complete details can be found in Baraloto (in review). Differences among microhabitat types in response to logging activity are indicated by letters, after Tukey's HSD test following one-way analyses of variance on log-transformed data weighted by the sample size within microhabitat types. See text for microhabitat definitions.

were estimated as described in Section 2.1. In addition, a 5 cm diameter soil core of 0–10 cm depth was made, from which gravimetric moisture content was determined after oven-drying to constant mass at 100 °C. A 50 g soil subsample was sieved to 2 mm and transported to the University of Michigan, where soil pH was measured in both distilled water and 0.01 M $CaCl_2$ solution, using a 1:1 ratio with a 5 g subsample. Soil extractable phosphorus was estimated colorimetrically using the orthophosphate procedure on the Alpkem Rapid Flow AutoAnalyzer (OI Analytical, College Station, TX, USA), following extraction of 5 g in 0.1 M $NaHCO_3$ as described in Olsen et al. (1954). Soil organic carbon and nitrogen were determined using a mass spectrophotometer following dry combustion of a 50 mg subsample at 980 °C.

In addition, each planting site was classified according to field observations as follows:

1. Natural understorey – closed canopy and no evidence of soil or stem damage from logging within 5 m.
2. Disturbed understorey – closed canopy with some stem damage but no evident soil damage within 5 m.
3. Canopy gap – open canopy with some direct light reaching the center of the planting site.
4. Stump site – logged stump within 5 m.
5. Skid trail – soil disturbance from passage of heavy machinery.

Planting sites corresponding to different immediate post-logging microhabitats differed only slightly 12 years after logging (Fig. 3). Three groups separated based on light availability, with extremes defined by microhabitats with open canopy and closed canopy, and skid trails exhibiting intermediate light levels, only slightly greater than understorcy sites. Soil disturbances in skid trails persisted only marginally 12 years after logging. While these sites had slightly more compacted soil surfaces and less soil moisture, they did not differ significantly from undisturbed sites (Fig. 3). Furthermore, we found no differences among microhabitats in soil chemical profiles, including extractable phosphorus.

3. Seed size and timber tree response to post-logging microhabitats

3.1. Response to conditions directly after logging: manipulated field experiment

We conducted a field experiment to investigate the response of species differing in seed size to conditions characteristic of post-logging microhabitats. Four soil conditions were established by manipulating litter cover and soil compaction. As light conditions in logged forest also vary tremendously, and light conditions may interact with soil conditions in effects on seed–seedling survival (Molofsky and Augspurger, 1992; Vazquez-Yanes et al., 1990), we located replicates of these treatments along a transect from the center of a medium-sized canopy gap (220 m^2) in primary forest, to completely enclosed understorey. Twelve 1.5 m × 1.5 m plots were established at 5 m intervals along this transect. To permit manipulations of soil disturbances, all soil was removed from each plot to a depth of 40 cm, mixed among all plots, and replaced. Each plot was then divided into four 0.75 m × 0.75 m subplots, each assigned at random to one of four treatments. The "litter + soil turnover" treatment simulated the edges of skid trails where topsoil and litter accumulate; it included replacement of litter to 3 cm depth without compaction of the replaced soil. The "bare + soil" turnover treatment consisted of no further manipulation once soil was replaced. The "compacted soils" were designed to simulate conditions on skid trails; replaced soil in these subplots was compacted to an average 3,0 kg/cm^2 using a mallet and board.

Five seeds of each of the focal species (see Table 1) were planted into caged exclosures (0.6 m × 0.4 m) in each subplot in May 1998. We measured the wet mass of all seeds planted for the two species exhibiting high coefficients of variation in seed mass, *Carapa procera* and *Vouacapoua americana* (Baraloto, 2001). Wet seed mass was standardized to dry seed mass using linear regression equations calculated from at least 50 individuals per species dried to constant mass at 60 °C (Baraloto, unpublished data). For the other species, the mean dry seed mass of at least 30 seeds was determined (see Table 1).

Daily integrated light energy was measured using the diazo paper method (Ferment et al., 2001; Friend, 1961) in each subplot. This measure, calculated as the percent of energy received by a nearby open site (% of full sun), ranged from 19.2% in the gap center to 0.9% in the understorey. Survival data for the 1 year inventory date were analyzed using an analysis of covariance (ANCOVA), with litter and compaction treatments and species as fixed effects and subplot light measures as a covariate.

The effect of soil disturbance treatment differed among species (Table 2). The larger-seeded *C. procera* and *V. americana* exhibited little variability in survival, even in the most extreme soil conditions (Fig. 4). The very small-seeded *Jacaranda copaia* also responded

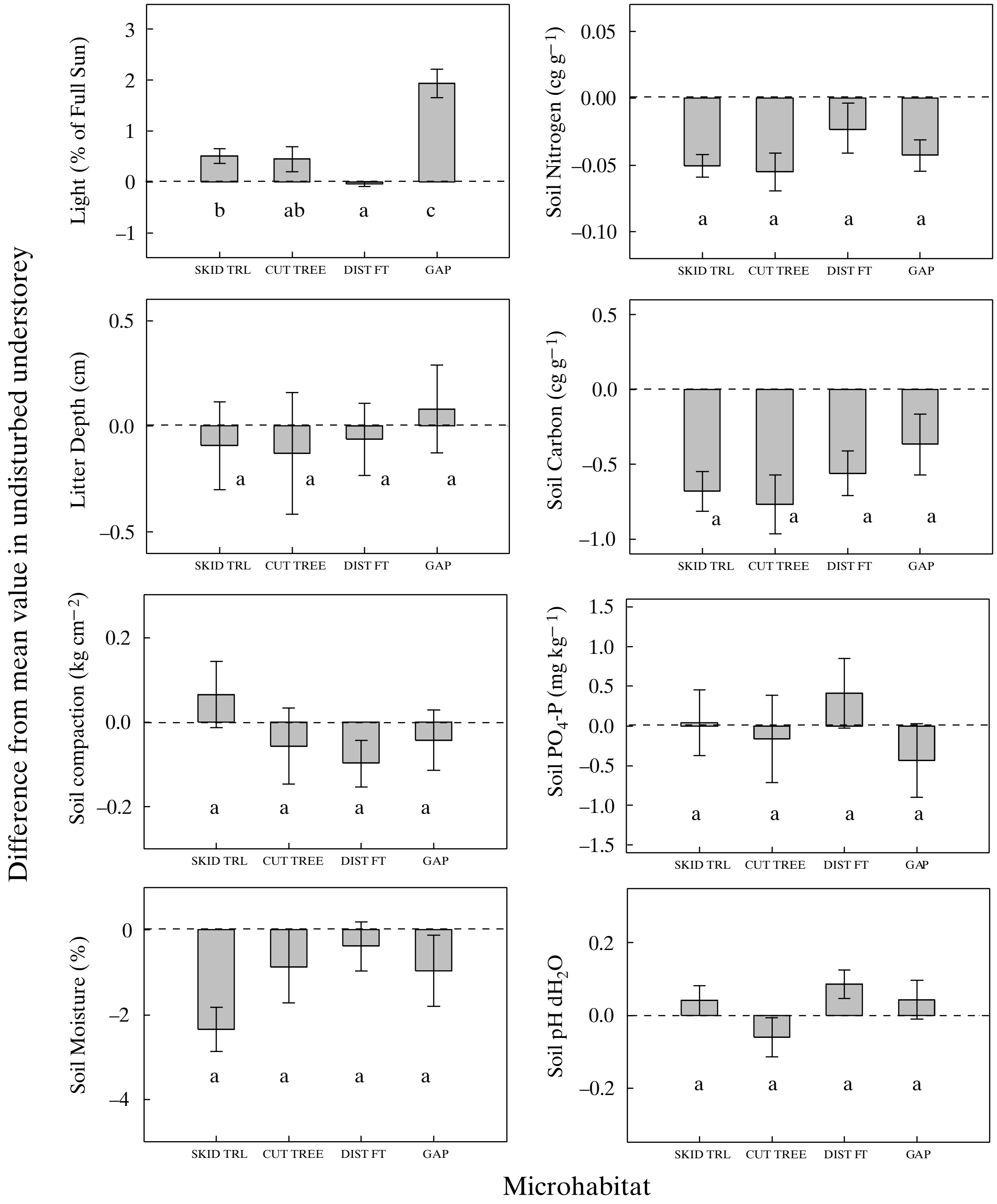


Fig. 3. Differences between environmental conditions among post-logging microhabitats relative to undisturbed understorey sites, twelve years after logging at Paracou. Data are the means (SE) of differences between the value at each sampling point in that microhabitat and the mean value from all undisturbed understorey sites. Complete details can be found in Baraloto and Gourlet-Fleury (in review). Differences among microhabitat types are indicated by letters, after Tukey's HSD test following one-way analyses of variance on log-transformed data weighted by the sample size within microhabitat types. See text for microhabitat definitions.

Table 1
Characteristics of the focal species from the described experiments

Species	*Family*	*Seed Dry Mass (g)*[1]	*Logging Volume (%)*[2]	*Manipulated Experiment*	*Natural Experiment*
Jacaranda copaia	Bignoniaceae	0.028	2	x	
Recordoxylon speciosum	Caesalpiniaceae	0.213	1	x	x
Dicorynia guianensis	Caesalpiniaceae	0.349	38	x	x
Sextonia rubra	Lauraceae	1.18	26		x
Carapa procera	Meliaceae	6.57	4	x	x
Vouacapoua americana	Caesalpiniaceae	12.4	6	x	x
Eperua grandiflora	Caesalpiniaceae	26.7	< 1		x

[1] Mean of at least 30 seeds dried to constant mass, or estimates for seeds planted in the experiments based on species-specific regressions.
[2] Annual percentage of total harvested volume of 60,000 m^3 in 1996, from Perthuisot (1998).

Table 2
Summary of analysis of covariance (ANCOVA) for seed-seedling survival in the manipulated field experiment

Source	*SSE*	*df*	*MSE*	*F*
Species	12.82	4	3.21	16.6***
Litter removal (Bare soil)	0.438	1	0.438	2.26
Soil compaction	0.211	1	0.211	1.09
Species*Litter	0.326	4	0.082	0.422
Species*Compaction	0.898	4	0.225	1.16
Litter*Compaction	0.011	1	0.011	0.058
Species*Litter*Compaction	1.09	4	0.272	1.41
Light (% of full sun)	0.784	1	0.784	4.06
Error	42.3	219	0.193	

Light availability (% of full sun in the visible spectrum; log-transformed) for each subplot was entered into the model as a covariate. Survival data were angularly-transformed for the analysis
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

only slightly to different treatments, though it had the lowest overall survival rate. In contrast, both *Dicorynia guianensis* and *Recordoxylon speciosum* exhibited complete mortality in the bare compacted soil treatment, and highest survival in the litter and soil turnover treatment (Fig. 4). Overall, survival increased with seed mass (Fig. 4), but was not influenced by differences in light availability among the plots (Table 2).

3.2. Response to conditions 12 years after logging: natural field experiment

We also examined seed-seedling survival of species differing in seed size, in recovering post-logging microhabitats in the Paracou plots. In March-April, 1998, a 1 m diameter, 1 m high wire cage exclosure was installed in each planting site described in Section 2.2, to exclude mammalian predators. Six

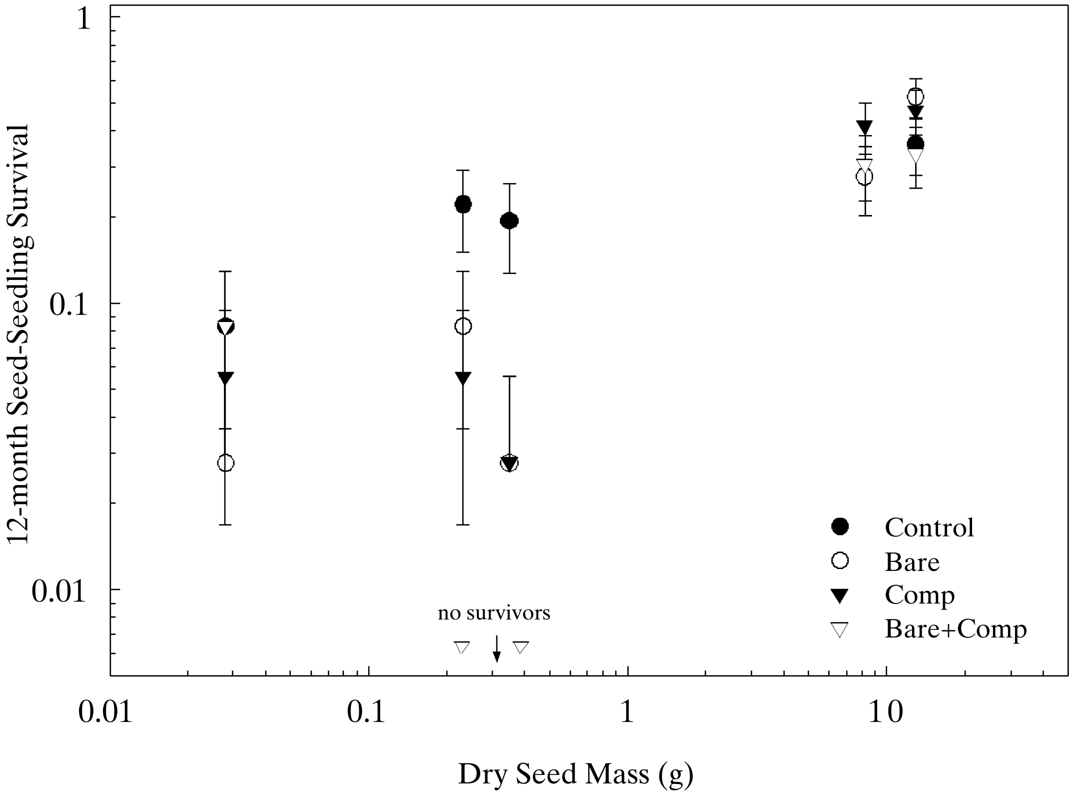


Fig. 4. Relationship between seed size and seed-seedling survival for the four simulated post-logging microhabitats in the manipulated field experiment. Data are the mean (SE) proportion surviving among twelve plots per treatment into which five seeds of each species were planted in May 1998. Bare refers to plots from which all litter was removed; Comp refers to plots where soil was compacted to 3.0 kg cm^{-2}. See Table 1 to cross-reference species with seed size.

Table 3

Summary of two-way analysis of variance (ANOVA) for seed-seedling survival in the natural field experiment

Source	*SSE*	*df*	*MSE*	*F*
Species	97.1	5	19.4	166.1***
Microhabitat	3.81	4	0.952	8.14***
Species*Microhabitat	1.27	20	0.064	0.95
Error	80.65	690	0.117	

Survival data were angularly-transformed for the analysis
*P < 0.05; **P < 0.01; ***P < 0.001

seeds of each of six species (see Table 1) were planted into each cage. We accounted for the effect of seed size in the same way as described in Section 3.1.

All individuals were censused monthly to 4 months from the planting date, and subsequently each 4 months to 1 year. Ungerminated seeds were scored as viable until they exhibited substantial reduction in weight. Missing smaller seeds were assumed to have suffered insect predation. Survival data for the 1 year inventory date were analyzed using a mixed model analysis of variance (ANOVA), with microhabitat as a random effect and species as a fixed effect.

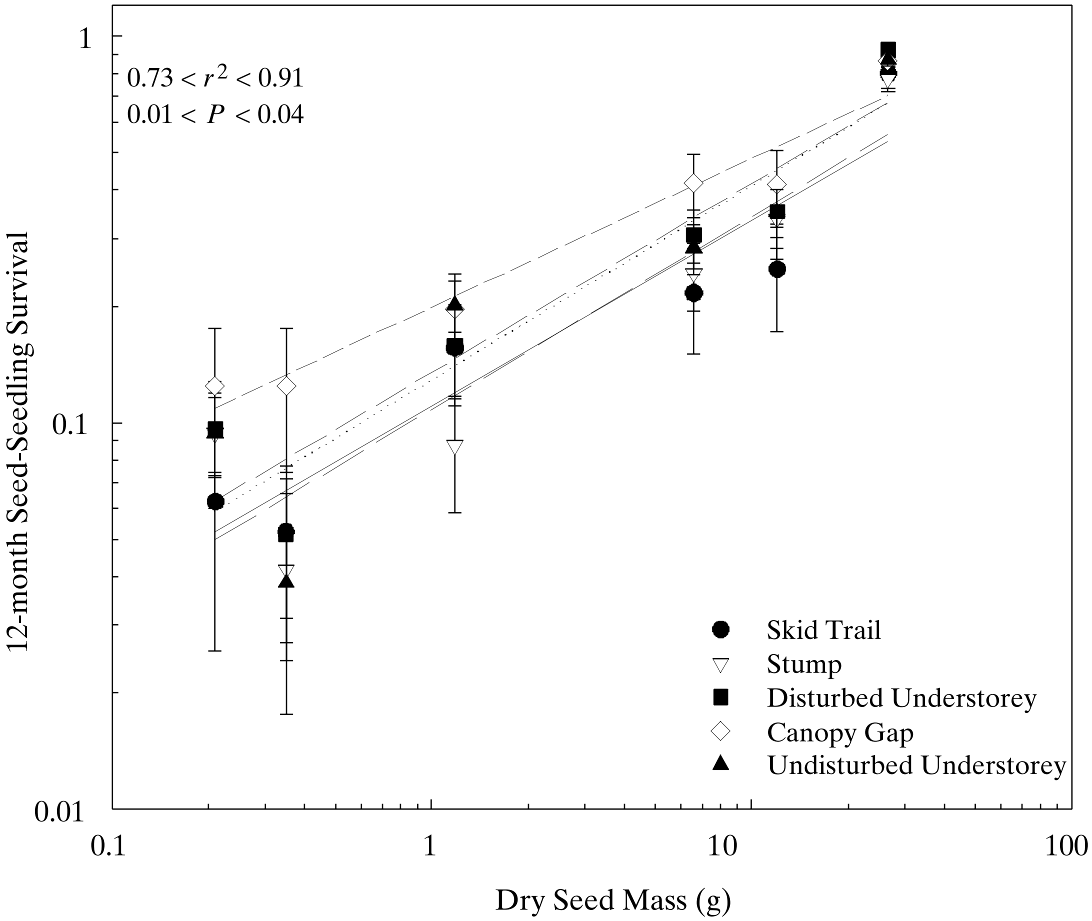


Fig. 5. Relationships between seed size and seed-seedling survival for the five post-logging microhabitat types in the natural field experiment. Data are the mean (SE) proportion surviving among 16 - 39 planting sites per microhabitat type, into which 6 seeds of each species were planted in April-May 1998. See text for microhabitat definitions. See Table 1 to cross-reference species with seed size.

Species differed significantly in 1 year survival rates (Table 3). *Eperua grandiflora* had the highest survival rate, with over 80% of seeds surviving to 1 year. *Dicorynia guianensis* exhibited the lowest survival rate, with less than 7% of seeds surviving to 1 year (see Fig. 5). Overall, a significant positive relationship exists across species between seed dry mass and 1 year seed-seedling survival; larger-seeded species had a higher probability of survival in all microhabitats.

Still, microhabitat did have a significant effect on survival from seed (Table 3). The most marked difference in survival appears to be based on light availability, with open canopy sites having about a 10% survivorship increase relative to closed-canopy sites (larger intercepts in Fig. 5). While the species*microhabitat interaction was not significant (Table 3), the behavior of certain species deviated slightly from global patterns of survival among microhabitats. For example, survival of *D. guianensis* and *C. procera* was more dependent on canopy opening than for the other species. Survival rates in *D. guianensis* were more than three times higher in open canopy areas (13.7%) than in closed canopy microhabitats (4.2%), and those of *C. procera* almost doubled (43.9% vs. 27.6%). In this experiment, little reduction occurred in survival among sites characterized by former soil disturbance; overall, skid trail sites had less than a 3% reduction in survival relative to undisturbed understorey sites.

4. Implications for sustainable forest management

4.1. Changes in environmental conditions in logged forest

Taken together, these results do provide some good news for forest managers. As with many other studies examining the environmental effects of logging (Nussbaum, 1995; Webb, 1997; Whitman et al., 1997), we did find evidence for significant changes in light and soil environments immediately after logging. However, while other studies have found persistent indications of soil physical disturbance more than 20 years after logging (Congdon and Herbohn, 1993), we found only slight differences among some of the most extreme microhabitats at Paracou 12 years after logging (see also Baraloto and Gourlet-Fleury, in review). In this sense, the forest has recovered dramatically. It should be noted that we did not sample among the most intensively logged plots at Paracou, corresponding to treatments where more than 50% of the original basal area was removed by harvesting and poison girdling. These plots are likely to have responded differently given the results of inventories for adult tree mortality and gap formation (Durrieu de Madron, 1994) and sapling diversity (Molino and Sabatier, 2001). However, the sites where we did perform measurements do correspond to the most intensive harvesting done on the most timber-rich sites in French Guiana, where normal timber volume corresponds to less than 10 m^3/ha (compared to over 80 m^3/ha in some of the plots measured here).

4.2. Seedling establishment in post-logging microhabitats

Forest inventories conducted after logging in the Paracou plots have noted that patterns of recruitment for many tree species changed dramatically in response to logging (Montpied, 1995; Molino and Sabatier, 2001; Rankin-de Merona, 1999 and see Chapter 3, Part IV). While many of the changes are likely to have been associated with removal of seed sources and changes in patterns of seed dispersal, the results of the experiment we present here suggest that changes in environmental conditions in the plots directly after logging may also have affected seedling recruitment for some species. In particular, we suggest that the small-seeded species, such as *Dicorynia guianensis* and *Recordoxylon speciosum* would experience difficulties establishing seedlings on completely denuded sites. Both of these species begin development with the emergence of a thick radicle that cannot enter very compacted soils lacking litter (Baraloto, personal observation). That Jesel (1999) actually found higher densities of older seedlings along skid trails than in adjacent understorey plots, however, suggests that at some point immediately after logging, soil turnover along these trails before the runoff caused by subsequent rains may have permitted some seedlings to establish. The high light conditions along these skid trails immediately after logging would have then resulted in increased survival relative to adjacent understory locations, according to the results of the second experiment we present here. That light had no significant effect on seed-seedling survival in the manipulated experiment but did in the natural experiment suggests that extreme soil disturbances may be more limiting to initial seedling establishment in this forest than light, but that light has some influence when soil is less disturbed.

Twelve years after selective logging, the post-logging physical environment even after extreme treatments does not appear to limit seedling recruitment during the initial 12 months of establishment for the species studied here. While differences among microhabitats do exist in terms of both global survival from seed as well as survival for some species, most of this difference appears to be due to light availability (PAR), which at larger spatial scales (hectares) is similar in logged and unlogged forest 12 years after logging (Baraloto and Gourlet-Fleury, in review; Nicotra et al., 1999).

Importantly, we have studied only one of many stages involved in the recruitment of individuals to sub-adult size classes of more than 10 cm DBH. Further transitions from seedlings to saplings may still be affected by the slight differences in microhabitats that persist at Paracou, or by some other factor that we did not measure. For example, while several studies have reported increased seedling growth along skid trails relative to understorey sites during the first year after logging (Fredericksen and Mostacedo, 2000; Whitman et al., 1997), Pinard et al. (2000) found lower woody stem density along skid trails relative to understorey sites in plots logged 4 and 18 years earlier. These authors attributed lower density in part to increased activity of herbivores in these microhabitats.

As Rankin-de Merona (1999) suggests, a more complete understanding of the effects of logging on seedling regeneration at Paracou will require integration of results such as we present here with those from demographic surveys in the plot, using simulation models. Most importantly, we remain uncertain as to whether continued recruitment of seedlings into the seedling bank will be necessary to maintain size class distributions after logging.

4.3. Implications and suggestions for sustainable forest management

We make three suggestions given the results we present here. First, while we found no evidence that logging damage led to long-term changes in conditions for seedling establishment, the long-term implications for population structure of any alterations occurring initially following logging may be important. Furthermore, we do provide evidence that extreme soil disturbances, such as skid trails, have negative effects on the seedling establishment of some species immediately after logging. Reduced-impact logging techniques have been demonstrated to be effective in limiting the surface area converted to skid trails within a logging site without changing harvest volumes: Johns et al. (1996) and Pinard et al. (2000) present evidence that loggers in Brazil can actually save money with prior planning. No effort to plan logging roads or skid trails is currently made in French Guiana, and the implementation of these practices into future management could only favor timber tree regeneration.

Our second suggestion regards the source of seeds in logged forest. One advantage enjoyed by *Dicorynia guianensis* that should not be overlooked is the persistence of a bank of dormant seeds that can remain viable for at least 24 months (Baraloto, unpublished data). For this species, seedlings might establish immediately after logging even in the absence of parent trees. However, especially for other non-dormant smaller-seeded species, such as *Recordoxylon speciosum* and *Sextonia rubra*, that exhibit high early mortality and respond negatively to many post-logging microhabitats, care should be given to ensure ample seed supplies by guarding seed trees. While species with smaller seeds may have greater absolute seed production (Silman, 1996), managers should make prudent estimations of the number of seed trees of these species protected from logging activity to ensure ample regeneration in the post-logging forest mosaic. More information on the seed production potential of timber species, and its temporal variability, will be crucial to the development of these management plans.

Our final point regards the dispersal of these seeds across microhabitats in the logged forest mosaic. While the large-seeded species did perform better across all environments in the experiments we present here, it is important to note that they were placed into these environments at low density by an external dispersal force, the authors. In the forest, many of these species rely on large rodents for seed dispersal out of areas of high-seed density and corresponding low-seedling recruitment (Forget, 1994, 1996, 1997). In many of the logged forests of French Guiana, the density of mammalian communities is altered by hunting soon after logging roads are opened into a new area (Forget et al., 1998). Cascading effects of hunting may alter community-level patterns of seedling establishment. In particular, dispersal limitation, resulting from reduced mammal population densities, might have severe long-term consequences for the population structure of several commercially valuable species.

Acknowledgements

This manuscript was improved after discussion with L. Blanc and S. Gourlet-Fleury and comments from D. Hammond.

We thank CIRAD-Forêt for permission to conduct this research at the Paracou site. P. Petronelli, M. Passou, N. Perthuisot, F. Plancheron, M. Delorme, T. Perot, S. Traissac, D. Duplat, C. Dutech, and I. Nolibos all provided help with field work. Financial support was provided by a fellowship to C. Baraloto from the Helen Olsen Brower Foundation, and SOFT grant (Sols et Forêts Tropicaux No 96042) to Pierre-Michel Forget from the Ministère de l'Environnement in France.

References

Baraloto C., 2001. Tradeoffs between neotropical tree seedling traits and performance in contrasting environments, PhD thesis, University of Michigan, 302 p.

Baraloto C., in review. Timber tree regeneration in French Guiana before and after selective logging of different harvest intensity. Forest Ecol. Manag.

Baraloto C., Gourlet-Fleury S., in review. Environmental recovery twelve years after selective logging in a French Guianan tropical rain forest. Forest Ecol. Manag.

Congdon R.A., Herbohn J.L., 1993. Ecosystem dynamics of disturbed and undisturbed sites in North Queensland wet tropical rain forest 1. Floristic composition, climate and soil chemistry. J. Trop. Ecol. 9, 349–363.

Durrieu de Madron L., 1994. Mortalité des arbres en forêt primaire de Guyane française. Revue d'Ecologie (Terre et Vie) 239, 43–57.

Ferment A., Picard N., Gourlet-Fleury S., Baraloto C., 2001. A comparison of five methods for characterizing the light environment of tropical forest tree seedlings. Ann. Forest Sci. 58, 877–891.

Forget P.-M., 1994. Regeneration pattern of *Vouacapoua americana* (Caesalpiniaceae), a rodent-dispersed tree species in French Guiana. Biotropica 26, 420–426.

Forget P.-M., 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. J. Trop. Ecol. 12, 751–761.

Forget P.-M., 1997. Effect of microhabitat on seed fate and seedling performance in two rodent-dispersed tree species in rainforest in French Guiana. J. Ecol. 85, 693–703.

Forget P.-M., Gourlet-Fleury S., Vannière B., 1998. Exploitation, chasse et régénération naturelle sont-elles compatibles en Guyane française? JATBA 40, 79–101.

Foster S.A., Janson C.H., 1985. The relationship between seed size and establishment conditions in tropical woody plants. Ecology 66, 773–780.

Fredericksen T.S., Mostacedo B., 2000. Regeneration of timber species following selection logging in a Bolivian tropical dry forest. Forest Ecol. Manag. 131, 47–55.

Friend D.T.C., 1961. A simple method of measuring integrated light values in the field. Ecology 42, 577–580.

Guariguata M.R., Dupuy J.M., 1997. Forest regeneration in abandoned logging roads in lowland Costa Rica. Biotropica 29, 15–28.

Guariguata M.R., Pinard M.A., 1998. Ecological knowledge of regeneration from seed in neotropical forest trees: implications for natural forest management. Forest Ecol. Manag. 112, 87–99.

Gullison R.E., Hardner J.J., 1993. The effects of road design and harvest intensity on forest damage caused by selective logging: empirical results and a simulation model from the Bosque Chimanes, Bolivia. Forest Ecol. Manag. 59, 1–14.

Hammond D.S., Gourlet-Fleury S., Van Der Hout P., Ter Steege H., Brown V.K., 1996. A compilation of known Guianan timber trees and the significance of their dispersal mode, seed size and taxonomic affinity to tropical rain forest management. Forest Ecol. Manag. 83, 99–116.

Heydon M.J., 1994. The ecology and management of rain forest ungulates in Sabah, Malaysia: implications of forest disturbance PhD thesis, University of Aberdeen.

Jesel S., 1999. Impact de l'exploitation forestière sur la régénération naturelle de l'angélique (*Dicorynia guianensis* Amshoff, Caesalpiniaceae). DEA, INA-PG.

Johns J.S., Barreto P., Uhl C., 1996. Logging damage during planned and unplanned logging operations in the eastern Amazon. Forest Ecol. Manag. 89, 59–77.

Molino J.-F., Sabatier D., 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. Science 294, 1702-1704.

Molofsky J., Augspurger C.K., 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73, 68–77.

Montpied P., 1995. La régénération naturelle en forêt tropicale humide. Effet des traitements sylvicoles d'intensité variable. Actes du séminaire interne de Silvolab-GUYANE: 51–69.

Nicotra A.B., Chazdon R.L., Iriarte S.V.B., 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. Ecology 80, 1908-1926.

Nussbaum R., Anderson J., Spencer T., 1995. Factors limiting the growth of indigenous tree seedlings planted on degraded rainforest soils in Sabah, Malaysia. Forest Ecol. Manag. 74, 149–159.

Nussbaum R., Anderson J., Spencer T., 1996. Effects of selective logging on soil characteristics and growth of planted dipterocarp seedlings in Sabah. In: Primack, R. Lovejoy, T.E. (Eds.), *Ecology, Conservation, and Management of Southeast Asian Forests*. Yale University Press, New Haven, CT, pp. 105–115.

Nussbaum R.E., 1995. The effect of selective logging on rain forest soil and the implications for recovery, PhD thesis, University of Exeter.

Olsen S.R., Cole C.U., Watanabe F.S., Dean L.A., 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circ. 939, 19.

Pinard M., Howlett B., Davidson D., 1996. Site conditions limit pioneer tree recruitment after logging of dipterocarp forests in Sabah, Malaysia. Biotropica 28, 2–12.

Pinard M.A., Barker M.G., Tay J., 2000. Soil disturbance and post-logging forest recovery on bulldozer paths in Sabah, Malaysia. Forest Ecol. Manag. 132.

Putz F.E., 1994. Approaches to sustainable forest management, CIFOR, Bogor, Indonesia.

Putz F.E., 1996. Research needs and information gaps. In: Viana, V.M. (Ed.), *Certification of forest products: issues and perspectives*. Island Press, pp. 164–178.

Rab M.A., 1994. Changes in physical properties of a soil associated with logging of *Eucalyptus regnans* forest in southeastern Australia. Forest Ecol. Manag. 70, 215–229.

Rankin-de Merona J.M., 1999. Synthesis and evaluation of the results of the INRA inventory studies on the natural regeneration of selected tropical rain forest tree species at the Paracou Silviculture Experiment Station in French Guiana, 1986-1995. CIRAD-Forêt.

Silman M., 1996. Regeneration from seed in a neotropical forest, PhD thesis, Duke University.

Sist P., Dykstra D., Fimberl R., 1998. Reduced-impact logging guidelines for lowland and hill Dipterocarp forests in Indonesia, CIFOR, Bogor, Indonesia.

Tuomela K., Kuusipalo J., Vesa L., Nuryanto K., Sagala A.P.S., Adjers G., 1996. Growth of dipterocarp seedlings in artificial gaps: an experiment in a logged-over rainforest in South Kalimantan, Indonesia. Forest Ecol. Manag. 81, 95–100.

Vazquez-Yanes C., Orozco-Segovia A., 1992. Effects of litter from a tropical rainforest on tree seed germination and establishment under controlled conditions. Tree Physiol. 11, 391–400.

Vazquez-Yanes C., Orozco-Segovia A., Rincon E., Sanchez-Coronado M.D., Huante P., Toledo J.R., et al., 1990. Light beneath the litter in a tropical forest: effect on seed germination. Ecology 71, 1952–1958.

Webb E.L., 1997. Canopy removal and residual stand damage during controlled selective logging in lowland swamp forest of Northeast Costa Rica. Forest Ecol. Manag. 95, 117–129.

White L.J.T., 1994. The effects of commercial mechanised selective logging on a transect in lowland rainforest in the Lope Reserve, Gabon. J. Trop. Ecol. 10, 313–322.

Whitman A.A., Brokaw N.V.L., Hagan J.M., 1997. Forest damage caused by selection logging of mahogany (*Swietenia macrophylla*) in northern Belize. Forest Ecol. Manag. 92, 87–96.

Woodward C.L., 1996. Soil compaction and topsoil removal effects on soil properties and seedling growth in Amazonian Ecuador. Forest Ecol. Manag. 82, 197–209.

Ecology and Management of a Neotropical Rainforest

Chapter 3

Natural regeneration of selected tropical rain forest tree species of French Guiana: established seedlings and saplings during the period 1986–1995

Judy M. Rankin-de Mérona, Pierre Montpied

Abstract – Based on 8 years of natural regeneration inventory data for tagged and untagged individuals, we evaluated the behavior of seedlings and saplings of selected tropical tree species of the coastal rain forest of French Guiana (South America) in undisturbed conditions and under various logging intensities. Marked changes were observed in seedling and sapling abundances, seedling height growth and sapling diameter growth of selected tree species due to the influence of the silvicultural treatments (logging and poison girdling), as well as in initial differences under undisturbed forest conditions between the 23 species studied. These included a number of species of all canopy strata plus emergents and those associated with light gaps. Species reactions to silvicultural treatment range from null to very strong and include all combinations of timing and persistence, from immediate to delayed and ephemeral to sustained. Ecological behavioral profiles based on these data are proposed to describe the temperament of the seedlings and saplings, which are then compared with the behavior of adults of the same species. We conclude that (i) the observed trends in juvenile reactions are not always simple in their relation to, nor proportional to, the silvicultural treatments applied; (ii) no strict relationship exists between adult functional group or juvenile ecological temperament and juvenile trend of a given species for the demographic parameters examined; and (iii) with one exception, none of the species follow the same trend over the three parameters analyzed (seedling height growth, sapling abundance, sapling diameter growth) as a function of treatment intensity. These results are not predictable from data from other sources, including the adults of these species, and imply that direct observation and experimental study of juveniles are obligatory elements in the formulation of management programs for these tropical rain forests.

Key words: Natural regeneration, Rain forest, Forest inventory, Tree seedlings, Saplings, Plant demography, Diameter growth, Recruitment

1. Introduction

The objective of most tropical forest inventories has been to taxonomically characterize the tree component of the community or to determine the stand structure and the potential for economic exploitation of wood. Thus they have generally ignored the juvenile classes, being based on individuals of reproductive or economic size of at least 10 cm diameter at breast height (DBH) or over. However, an increased understanding of how ecological forces acting on the juvenile classes shape the demographic structure and the spatial distribution of the future adult stand (Harper, 1975; cf. Janzen, 1970), the formulation of the concept of the regeneration niche as an important factor influencing community structure (Grubb, 1977) particularly with respect to species-rich tropical forests, and the difficulties encountered in establishing sustained economic management programs for tropical forests (cf. Gomez-Pompa and Burley, 1991) have spurred an increase in the study of the natural regeneration or the juvenile component of the tropical rain forest at the species and the community level over the last 20 years (cf. Augsburg, 1984; Coomes and Grubb, 1998; DeStevens, 1994; Nicotra et al., 1999; Osunkoya et al., 1992, 1993, 1994; Swaine, 1996; Welden et al., 1991). Furthermore, the demand for efficient and realistic models of forest stand behavior has pointed out the need for data on demographic dynamics for all population components including the regeneration (Gourlet-Fleury and Montpied, 1995).

Whereas much important descriptive information can be gathered from static or non-individualized studies, the tremendous reduction in numbers occurring from the seed/seedling class to the established adult tree class (cf. Janzen, 1970; Sarukhan, 1978; Schultz, 1960; Whitmore, 1975, 1990) and the wide variability in individual growth and survival performance within a species (cf. Forget, 1997; Koestel and Rankin-de Mérona, 1998) attest to the necessity of multi-habitat studies of tagged juveniles over time. Only a small number of inventory-based studies that take into account the juvenile classes have been conducted to date in the tropical rain forests of South America (Higuchi et al., 1985; Schultz, 1960; Vieira and Hosokawa, 1989). However, virtually no published studies exist where inventory level information is coupled to observations over time of in situ individually tagged juveniles. In neighboring Panama on Barro Colorado Island, a long-term study of the woody stand >2 cm DBH tagged on a 50 ha inventory plot has begun to produce important results about the juvenile classes in this rain forest community (Hubbell et al., 1999; cf. Welden et al., 1991).

One of the important objectives of regeneration studies has been to characterize the behavior of different ecologically or economically important species under natural and disturbed conditions, such as wood harvesting and silvicultural management. The temperament of a tree species refers to its physiological and ecological potential. Temperament has been variously typified, particularly in relationship to reactions to light and disturbance in the overhead cover and/or soil (“pioneer” vs. “climax”) (cf. Whitmore, 1975) or “light demanding” vs. “shade tolerant” (cf. Canham, 1989). Temperament is generally attributed at the species level, but closer examination throughout the developmental process shows that it may vary with the stature of the individual (Oldeman and van Dijk, 1991).

In this study we use inventory data of tagged and untagged individuals to evaluate the behavior of seedlings and saplings of select tropical tree species across their complete local habitat range in the coastal rain forest of French Guiana. The principal aspects discussed are changes in seedling and sapling abundances, seedling height growth and sapling diameter growth of selected tree species due to the influence of various silvicultural treatments. Based on these results, we establish ecological behavioral profiles describing the temperament of juveniles and compare them with the behavior of adults of the same species.

2. Methods

2.1. The INRA natural regeneration inventory protocol for Paracou

Between 1986 and 1995, the INRA staff of the Station de Recherches Forestières in Kourou, French Guiana conducted five full inventory campaigns and two partial campaigns concerning the natural regeneration of selected tree species of the upland tropical rain forest at the Paracou experimental site, located in the coastal rain forest zone of the French overseas department of Guyane on the northeastern coast of South America. The local forest structure ranged from undisturbed native forest through three levels of silvicultural treatment (logging intensity and poison girdling). Details of the site are discussed in Part I of this book.

2.1.1. Inventory schedule

The inventories were conducted on a 2-year interval, with results for seedlings extending over 6 years from 1986 to 1992 and with individual observations on saplings from 1992 to 1995. A small number of plants were observable over the entire period, from 1986 until the last formal inventory in 1995, or 9 years, having progressed from seedling to sapling in the interval.

2.1.2. Definition of the juvenile classes studied

Only two classes of juveniles are considered in the context of the INRA natural regeneration inventory studies. The seedling class is composed of those smallest plants considered as established and without signs of being recently germinated. The measurement criteria applied are a minimum height of 5 cm and a maximum height of 150 cm. No plants less than 5 cm, regardless of age or physical state (yearling, stunted, broken) are considered. Thus a certain reduction in numbers has already occurred by the time juveniles arrive in the seedling class as defined here, and this reduction may not be the same for all species present on the same plot.

The sapling class is composed of all stems ranging from 150 cm in height to 10 cm in DBH. It is important that the smallest sapling class accurately represents the new arrivals from the largest seedling class, i.e. it should be wide enough with respect to the observation interval to avoid the passage of individuals to the subsequent class before having been detected. Concerning the interval chosen for the present study, results show that a plant not qualifying by height for a given inventory period but qualifying in height by the following inventory period will rarely have attained 2 cm DBH. Thus, those plants greater than 150 cm in height and less than 2 cm DBH faithfully represent the newly arrived plants, or the recruitment for the 2-year observation interval.

2.1.3. Sampling grid and surfaces inventoried

The physical layout of the natural regeneration inventory was established as a function of the adult stand experimental design, based on 12 plots of 6.25 ha each, distributed throughout the forest continuum and subject to various levels of silvicultural treatments as described in Part I in this volume (see also Chapter 5, Part IV, for a detailed description of the impacts of the treatments on the stands). Within this setting, a fixed-point sampling protocol was adopted.

Within each plot, sampling stations in the form of circular subplots were established, centered at the intersections of a 20 m by 20 m grid. Originally, 144 subplots were established per plot. The number of subplots systematically inventoried was reduced to the 64 central subplots in 1992 in response to the increase in subplot radius and changes in the type of data collected.

The subplot radius for sampling varied with the different juveniles classes under study and evolved with the inventory protocol, from a minimum of 1.175 m (1% of surface) to a maximum of 3.717 m (10%). The original protocol used a radius of 1.175 m for the seedling counts and 1.784 m (2.3%) for the sapling counts. In 1992, an assessment of the results to date and a change in protocol to a demographic inventory procedure with individually marked saplings resulted in an increase in the subplot radius to 3.717 m. All data were recorded so as to permit, as needed, a reduction of the subsequent data sets to the pre-1992 precision level.

2.1.4. Species selection

Of the 33 species initially chosen, 12 were selected on the basis of their economic interest for the tropical wood market. The remaining species were chosen on the basis of abundance and the possibility to reliably identify all stages of development. The present discussion is limited to the 23 most abundant botanically recognized species (Table 1). Whereas all species in the list for a given inventory year were included in the abundance data or the diameter measurements, only 12 species were abundant enough to be studied for height growth in the seedling stage.

2.1.5. Data collected

2.1.5.1. Counts and abundance classes

Only abundance class information on inventory subplot occupation by the juveniles of the selected tree species was recorded in 1986. These classes are defined at four levels as: 0 = no plants present, 1 = 1–2 plants

Table 1
Tree species whose seedlings and saplings were the subject of the natural regeneration inventory studies from 1986 to 1995

Botanical name	***Code***	***1986***	***1988***	***1990***	***1992***	***1995***	***Height***
Andira coriacea Pulle	SR	£	+	+	$	$	
Bocoa prouacensis Aubl.	BO	£	+	+	$	$	
Carapa procera A. DC.	CA	£	+	+	$	$	Yes
Dicorynia guianensis Amsh.	AN	£	+	+	$	$	Yes
Eperua falcata Aubl.	EF	+	+	+	$	$	Yes
Eperua grandiflora (Aubl.) Benth.	EG	+	+	+	$	$	Yes
Goupia glabra Aubl.	GI	£	+	+	$	$	Yes
Iryanthera hostmanii (Benth.) Warb.	TH	_	_	+	$	$	
Iryanthera sp.	TO	£	+				
Iryanthera sagotiana (Benth.) Warb.	TO	_	_	+	$	$	
Jacaranda copaia (Aubl.) D. Don	JA	£	+	+	$	$	Yes
Moronobea coccinea Aubl.	MO	£	+	+	$	$	Yes
Sextonia rubra Mez	GR	£	+	+	$	$	Yes
Pradosia cochlearia (Lecomte) Pennington	KI	£	+	+	$	$	
Qualea rosea Aubl.	GO	£	+	+	$	$	Yes
Recordoxylon specisosum (Benoist) Gazel ex Barneby	WG	£	+	+	$	$	
Schefflera decaphylla (Seem.) Harms	SC	£	+	+	$	$	
Sclerolobium melinonii Harms	DA	£	+	+	$	$	
Sterculia sp.	KO	£	+	+	$	$	
Symphonia sp.	SY	£	+	+	$	$	Yes
Symphonia globulifera L. f.	SG				$	$	
Virola michelii Heckel	YA	_	_	+	$	$	Yes
Virola sp.	YA	£	+				
Virola surinamensis (Rolander) Warb.	YS	_	_	+	$	$	Yes
Vouacapoua americana Aubl.	WA	£	+	+	$	$	Yes

£: Abundance class exact counts; +: exact counts; $: exact counts and diameter measurements by 1 cm classes; ≥: two or more botanical species grouped under one common name and later separated; Yes: seedling height growth measured 1986–1992.

Table 1 (*continued*)
Species in alphabetical order by code

Code	*Botanical name*
AN	*Dicorynia guianensis*
BO	*Bocoa prouacensis*
CA	*Carapa procera*
DA	*Sclerolobium melinonii*
EF	*Eperua falcata*
EG	*Eperua grandiflora*
GI	*Groupia glabra*
GO	*Qualea rosea*
GR	*Sextonia rubra*
JA	*Jacaranda copaia*
KI	*Pradosia cochlearia*
KO	*Sterculia* sp.
MO	*Moronobea coccinea*
SC	*Schefflera decaphylla*
SG	*Symphonia globulifera*
SR	*Andira coriacea*
SY	*Symphonia* sp.
TH	*Iryanthera hostmanii*
TO	*Iryanthera* sp., *Iryanthera sagotiana*
WA	*Vouacapoua americana*
WG	*Recordoxylon specisosum*
YA	*Virola* sp., *Virola michelii*
YS	*Virola surinamensis*

present, 2 = 3–9 plants present and 3 = 10 or more plants present. Data for the seedlings are limited to the 1.175 m radius of the subplot and for saplings to 1.784 m.

In 1988, 1990 and 1992 exact counts for both seedlings and saplings replaced estimations by abundance class. Plants counted in one year may not have any relation to those counted in a subsequent year, especially for the seedling class where rapid turnover may be observed. Starting in 1992 through 1993 and 1995, individualized data on saplings were collected following a protocol compatible with the pre-1992 counts.

2.1.5.2. Measurements

Exact height measurements were collected for selected seedlings encountered on the circular subplots. The initial conditions for acceptance into these observation groups were: seedling class status, to be one of the two largest plants in the class and with the best physical build present for that species, and positioned on the subplot closest to the stake marking the subplot center. Only two plants were chosen per species per subplot. In the event of the death of one of the originally tagged plants, that individual was replaced wherever possible.

Starting in 1990, in an effort to increase the number of plants under observation, any plant on the subplot (in 1990 maximum radius = 1.784 m and in 1992 maximum radius = 3.717 m) irrespective of size or form was considered acceptable for inclusion in the permanent seedling height growth group; however the total number of plants per species per subplot was maintained at 2.

The sapling diameter measurement protocol was instituted in 1992, with all saplings of the selected tree species individually numbered, tagged, identified and assigned to 1 cm-wide diameter classes, ranging from 1 to 10 cm, as determined by use of a notched gauge.

2.2. Analytical and statistical treatment of the data sets

The data analyzed in this publication come from one of the several plant data bases found in the Silvolab-Guyane data base management system Arlequin residing on the server kourou.cirad.fr and based at the Campus Agronomique of the Silvolab Research Institutes Group in Kourou, French Guiana. The actual structure of the base, as well as all inventory data from 1986 to 1995, is available on the INRA Natural Regeneration Survey Data CD-ROM, 1998.

All analyses were performed using the SAS Institute Inc. data management and analytic system, version 6.03 (SAS, 1989) on a UNIX operating system.

3. Changes in abundances and growth of the juveniles

3.1. Overall changes in abundances before and after silvicultural treatment (1986–1992)

The increases, decreases and overall changes in the numbers (or abundance class in the case of 1986) of seedlings and saplings of 12 species plus three species pairs were examined at the treatment level from 1986 to 1992. Only those potentially occupiable surfaces within the plots (i.e. sites where individuals of the species were observed at least once), as defined by dispersal distances and observed distributions of the species (Montpied, 1995), were considered.

3.1.1. Abundance changes by 2-year intervals at the local scale

As only abundance classes or counts of seedlings and saplings are available in the four first inventories, changes in numbers from one period to another are interpreted as tendencies rather than absolute demographic changes. Estimates of mortality and in-growth are thus conservative.

Changes in numbers were analyzed at the regeneration subplot level and for 2-year periods between successive inventories. Categorical data analysis was performed using the CATMOD procedure of the SAS/STAT package (SAS Institute Inc.). We investigated the effect of treatments on the mean of the response function, which took the value 1 when the subplot counts increased between two dates, –1 when they decreased and 0 otherwise. The mean response function represents the balance between the loss of individuals and the apparent in-growth. From the results shown in Table 2, species can be classified according to the immediate (1986–1988 period) and delayed (1988–1992) reaction of their seedlings and saplings (Table 3).

Saplings of all but three species (*Bocoa prouacensis*, *Moronobea coccinea* and *Eperua grandiflora*) show a positive delayed reaction to treatments (see Part I for treatments details) vs. control, grading from weak (*Iryanthera spp.* reacts only to treatment level 1, *Schefflera paraensis* to level 3) to strong (*Virola spp.*, *Jacaranda copaia*), whereas only four show an immediate reaction either positive (*Qualea rosea* and *Iryanthera spp.*) or negative (*B. prouacensis* and *Dicorynia guianensis*) regarding sapling counts.

For the seedling class, changes in count patterns are more confusing. Some species show an immediate negative and then a delayed positive reaction (*Sclerolobium melinonii* and *Q. rosea*), some react positively then negatively (*Goupia glabra*), others react always negatively (*M. coccinea*, *Pradosia cochlearia* and *Iryanthera spp.*) or positively (*J. copaia*). This confusion may be due to the fact that a decrease in the number of seedlings on a regeneration subplot combines death with in-growth into the sapling class: *G. glabra* is the most striking species where a lot of seedlings appear immediately after applying treatments and then grow rapidly up to the sapling class, resulting in a strong decrease of seedling numbers in the second period even though few of them die. Nevertheless, this cannot be assessed at the subplot scale because the sampling rate was not the same between seedlings and saplings and therefore, the link between individuals across sampling campaigns cannot be made.

3.1.2. Abundance changes at the level of the silvicultural treatments

To quantitatively assess the behavior of species at the scale of silvicultural treatments, we calculated the cumulative in-growth and mortality of seedlings and saplings over the 6-year periods between 1986 and 1992 at the treatment scale. This was done by summing separately all the positive differences between successive 2-year periods on each subplot, and the negative ones. The lower limit of abundance classes of the first inventory were used for conservative estimates of disappearance and the upper limit for in-growth. The data were converted into mean densities calculated over the potential distribution areas (cf. Montpied, 1995) so as to compare seedling and sapling dynamics. This allowed separation of in-growth into the sapling class from mortality in the accumulated disappearance of seedlings. This procedure yields conservative estimates of initial (1986) and final (1992) densities, mortalities and in-growths for seedlings and saplings for each silvicultural treatment. Under the hypothesis that a seedling cannot reach the sapling class within 2 years after establishment, these estimates may be split into two groups having the same sum, which is an estimate of the total number of individuals involved in the

Table 2

Overall changes in seedling and sapling abundances relative to silvicultural treatment and over three observation intervals through 1992

Species	*Juvenile class*	*Increase–decrease*		
		During 1986–1988	*During 1988–1990*	*During 1990–1992*
Dicorynia guianensis	Seedlings	ns	ns	ns
	Saplings	3 = 1 = 2 < 2 = 0**	0 = 3 < 3 = 1 = 2**	0 = 2 < 2 = 3*
Bocoa prouacensis	Seedlings	1 = 0 < 0 = 3 < 2***	ns	ns
	Saplings	3 = 2 = 1 < 2 = 1 = 0*	ns	ns
Sclerolobium melinonii	Seedlings	1 = 3 < 3 = 0 = 2***	3 < 0 = 2 < 2 = 1***	0 = 2 < 2 = 3 = 1**
	Saplings	ns	0 = 3 < 3 = 2 = 1**	0 = 2 = 1 < 3**
Eperua falcata	Seedlings	ns	3 = 2 < 2 = 1 < 1 = 0**	2 = 0 = 3 < 0 = 3 = 1
	Saplings	ns	0 < 3 = 1 = 2*	ns
Eperua grandiflora	Seedlings	ns	0 = 3 = 2 < 3 = 2 = 1*	2 = 0 = 3 < 3 = 1**
	Saplings	ns	ns	ns
Goupia glabra	Seedlings	0 < 2 = 1 < 3***	3 < 1 = 2 < 0***	1 = 3 < 3 = 2 < 2 = 0***
	Saplings	–	0 < 1 = 2 < 3***	0 = 2 = 1 < 2 = 1 = 3*
Qualea rosea	Seedlings	2 = 1 = 3 < 3 = 0*	0 = 3 < 3 = 1 = 2*	3 = 0 < 0 = 1 = 2**
	Saplings	0 = 1 < 1 = 3 = 2 *	0 < 1 < 3 = 2***	0 = 2 < 2 = 3*
Jacaranda copaia	Seedlings	0 < 1 = 2 < 3 ***	0 = 3 = 1 < 3 = 1 = 2*	ns
	Saplings	–	0 = 1 < 1 = 2 < 2 = 3***	1 = 3 < 3 = 2*
Pradosia cochlearia	Seedlings	3 < 1 = 0 = 2***	3 = 2 < 0 = 1***	3 = 2 < 1 = 0***
	Saplings	ns	0 < 2 = 1 < 3***	0 = 1 = 3 < 3 = 2*
Sterculia sp.	Seedlings	3 < 0 = 2 < 2 = 1***	1 = 2 = 0 < 3**	ns
	Saplings	ns	0 = 3 < 3 = 1 < 1 = 2**	0 = 3 < 3 = 2 < 2 = 1**
Moronobea coccinea	Seedlings	1 = 2 = 3 < 2 = 3 = 0*	3 = 2 = 1 < 0*	ns
	Saplings	ns	ns	ns
Schefflera decaphylla	Seedlings	0 = 2 = 1 < 3***	ns	ns
	Saplings	–	0 = 2 = 1 < 3**	1 = 0 = 2 < 2 = 3*
Symphonia sp.	Seedlings	ns	ns	ns
	Saplings	ns	0 < 3 = 2 = 1***	0 = 1 = 3 < 2**
Iryanthera spp.	Seedlings	3 = 2 < 2 = 1 = 0**	2 = 3 = 1 < 1 = 0*	0 < 3 = 1 = 2***
	Saplings	1 = 0 < 3 = 2 *	ns	0 = 2 = 3 < 1 *
Virola spp.	Seedlings	ns	ns	ns
	Saplings	ns	0 < 2 = 1 = 3 ***	0 = 1 < 3 = 2 ***

Numbers in increase–decrease columns refer to treatment levels. Control: 0; treatment intensities: 1, 2, 3.
Significance levels: *, 0.05; **, 0.01; ***, 0.001.

Table 3
Summary of seedling and sapling abundance changes with silvicultural treatments

Juvenile class	*Reaction*	*Immediate*	*Delayed*
Seedlings	none	AN EF EG SY YA	AN BO SC SY YA
	+ or + +	BO SC | JA GI	JA KO | EG SC GO
	– or – –	DA MO KI TO | GO	EF | MO | TO KI | GI
	+ –	KO	
Saplings	none	DA EF EG GI JA KI KO MO SC SY YA	BO MO EG
	+ or + +	GO TO	TO SC | AN SC EF | GI GO KI KO SY | YA JA
	– or – –	BO | AN	

regeneration processes over the 6-year periods: (i) seedling plus sapling initial density plus seedling in-growth; (ii) seedling and sapling final density plus mortality (Table 4).

A group of three pioneer species (*G. glabra*, *J. copaia* and *S. decaphylla*) stands out from the others: their regeneration densities are very low in 1986, but drastically increase in subsequent years in treated plots. Other species have initial densities that may be very different from one treatment to another. For treatment comparisons, changes in species density were therefore scaled to initial densities except for the three pioneers (Fig. 1)

In an attempt to classify the species, we ordered these along gradients of reactivity of seedlings or saplings to treatments. Seedling reaction was assessed from the total number of individuals involved in regeneration processes relative to initial seedling number, and saplings from the final density relative to initial density (Fig. 2). This representation clearly shows the trade-off between sapling and seedling reactions. This trade-off defines a continuous gradient from negative or weak (*Iryanthera* spp., *M. coccinea* and *E. grandiflora*) to a highly positive reaction to treatment (pioneer species). As the major consequence of silvicultural treatment is canopy opening, this gradient may be interpreted as a light demand gradient, from the low light demanding or high light avoiding species to the high light demanding ones, i.e. pioneers.

A group of four species (*Eperua falcata*, *Q. rosea*, *Sterculia sp.* and *S. melinonii*) departs from this trend: the in-growth of seedlings decreases as the treatment intensity increases while the saplings increase. These are intermediate light demanding species when considering saplings. *Q. rosea* shows a negative reaction immediately after applying treatments and then a positive, though not entirely compensatory, reaction: it may be speculated that its seedlings stay alive several years under closed canopies without growing, but may be sensitive to sudden canopy opening and then may be slowly replaced by new seedlings acclimated to the new environment. The other three species show a negative delayed reaction that may be due to removal of adults and/or an unfavorable environment for germination or seedling establishment.

P. cochlearia shows a particular pattern of seedling in-growth with increase in treatment level 1 but decrease in treatment levels 2 and 3: it is the only species studied whose adults have been poison girdled in the heavier treatment levels.

3.2. Plant growth and demographic trends before and after silvicultural treatment

Only those observations made on tagged and individually numbered plants constitute a true demographic study. We have chosen to limit this discussion of demographic parameters to the most accurately perceived phenomena for this study: seedling height and sapling diameter growth and recruitment into superior size classes.

Table 4

Cumulative estimated in-growth and mortality of seedlings and saplings at the treatment level between 1986 and 1992

Species code	*Treatment level*	*n subplots*	*Initial seedlings*	*Initial saplings*	*In-growth seedlings*	*Total*	*In-growth saplings*	*Dead seedlings*	*Dead saplings*	*Final seedlings*	*Final saplings*
AN	0	159	333	6	333	673	13	509	19	145	0
	1	131	667	18	606	1291	15	671	0	589	31
	2	94	438	0	103	541	53	314	21	173	32
	3	179	511	25	497	1033	34	584	17	393	39
BO	0	192	1602	47	684	2333	97	1661	26	552	94
	1	192	1386	39	1068	2493	132	1742	57	606	89
	2	192	756	31	1416	2203	66	1322	33	796	52
	3	192	1279	47	1116	2442	89	1508	47	805	83
DA	0	191	292	26	2917	3235	10	1956	21	1243	16
	1	192	304	11	1435	1750	47	577	10	1116	47
	2	180	485	6	3265	3756	56	1391	6	2304	56
	3	173	710	25	1899	2635	191	1674	40	741	179
EF	0	108	2617	104	2050	4771	46	2578	46	2027	120
	1	73	2079	131	1408	3618	178	1337	96	1980	205
	2	65	2861	255	549	3665	369	1864	169	1170	462
	3	108	1577	105	509	2191	176	1083	46	840	222
EG	0	144	2781	93	492	3366	63	2194	35	1040	97
	1	99	645	58	161	865	81	478	40	256	91
	2	68	3513	85	1288	4885	74	2705	29	2033	118
	3	90	1751	120	369	2240	167	1293	122	681	144
GI	0	192	36	5	24	65	10	38	16	12	0
	1	192	36	5	961	1002	57	831	16	109	47
	2	192	36	0	997	1033	156	756	21	121	135
	3	192	0	5	1576	1581	391	965	57	219	339
GO	0	128	2440	31	1279	3750	47	1753	16	1926	55
	1	152	813	8	329	1149	66	632	13	445	59
	2	87	954	0	268	1223	310	511	23	402	287
	3	158	1306	23	265	1593	316	850	19	401	323
JA	0	192	48	0	36	84	5	55	0	24	5
	1	192	24	0	145	169	42	30	0	97	42
	2	192	25	0	348	373	78	78	5	217	73
	3	192	12	0	340	352	89	7	16	256	73
KI	0	192	2461	53	3172	5686	68	3509	52	2052	73
	1	192	1953	19	4678	6650	83	3745	31	2801	73
	2	192	5128	91	2488	7708	146	6407	47	1098	156
	3	192	4580	93	2446	7119	208	5984	94	853	188

Table 4 (*continued*)
Cumulative estimated in-growth and mortality of seedlings and saplings at the treatment level between 1986 and 1992

Species code	*Treatment level*	*n subplots*	*Initial seedlings*	*Initial saplings*	*In-growth seedlings*	*Total*	*In-growth saplings*	*Dead seedlings*	*Dead saplings*	*Final seedlings*	*Final saplings*
KO	0	192	146	32	645	823	36	432	31	324	36
	1	192	330	17	1041	1387	151	905	21	315	146
	2	192	290	22	743	1055	177	459	47	398	151
	3	192	150	16	150	317	130	110	52	61	94
MO	0	124	204	24	297	526	65	140	16	297	73
	1	126	144	18	205	367	63	65	16	223	63
	2	119	298	9	128	434	34	218	8	174	34
	3	128	162	39	198	399	39	159	23	162	55
SC	0	192	0	0	12	12	5	7	0	0	5
	1	192	0	0	62	62	26	0	10	36	16
	2	192	0	0	48	48	10	2	0	36	10
	3	192	0	0	266	266	120	48	16	98	104
SY	0	192	1574	36	1213	2822	63	1354	21	1380	68
	1	192	1648	31	1963	3642	130	1994	47	1492	109
	2	192	2166	44	2490	4699	156	2232	26	2280	161
	3	192	1201	6	1579	2785	167	1333	57	1280	115
TO	0	192	421	11	1186	1619	240	636	31	732	219
	1	192	558	34	1285	1877	401	499	52	946	380
	2	192	548	16	1207	1771	208	848	36	700	188
	3	192	453	11	717	1181	146	622	31	402	125
YA	0	192	238	11	132	382	52	140	31	180	31
	1	192	394	11	618	1023	130	434	36	449	104
	2	192	449	17	487	953	266	394	26	277	255
	3	192	515	12	583	1109	281	379	31	439	260

3.2.1. Seedling height growth

A site-wide but limited population protocol was used to examine seedling height growth at Paracou for the period 1986, before logging, through 1992. Ten species were observed throughout the period and two more (*G. glabra*, *J. copaia*) were added in 1990. The data set is extremely heterogeneous in that plants enter and leave the study throughout the total observation period as a result of either natural mortality or the size limit definitions imposed. Nonetheless, important observations on the reactions of seedlings to local conditions may be drawn.

When the raw data for the individual plants regarding the control plots are examined, it is possible to divide the species studied into two groups: those with no growth at the sites in control plots where they establish themselves naturally; and those for which certain individuals may find themselves in situations where they can make visible growth gains during the observation interval. The first group is composed of "quiescent" species (*D. guianensis*, *M. coccinea*, *Sextonia rubra*, *J. copaia* and *E. grandiflora*), while the second group is composed of "*occasionally* well-placed reactives", as overall, only a few individuals ever

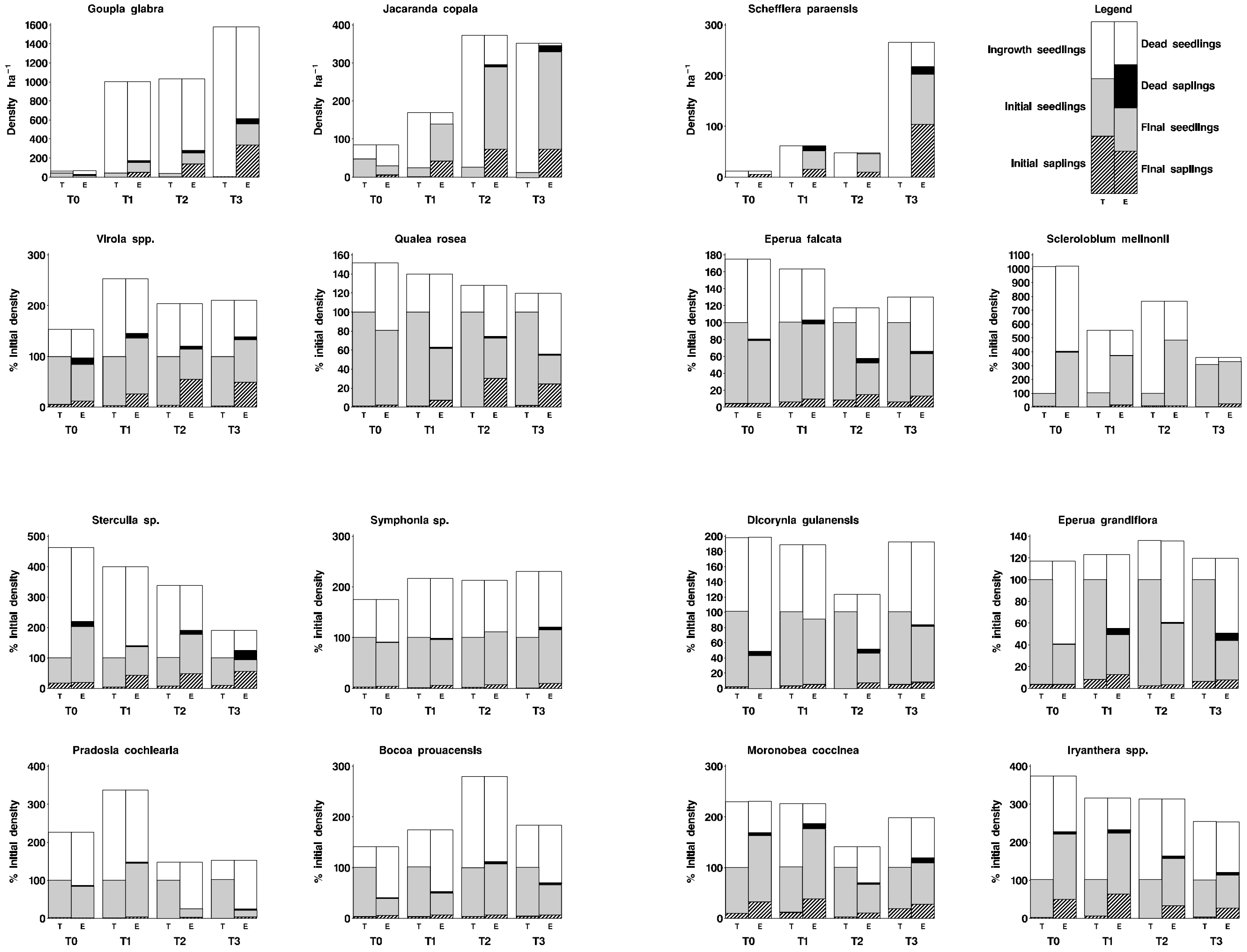


Fig. 1. Changes in estimated seedling and sapling densities inside observed potential distribution areas between 1986 and 1992 and as influenced by silvicultural treatments. NB. *Schefflera paraensis* is now *Schefflera decaphylla*.

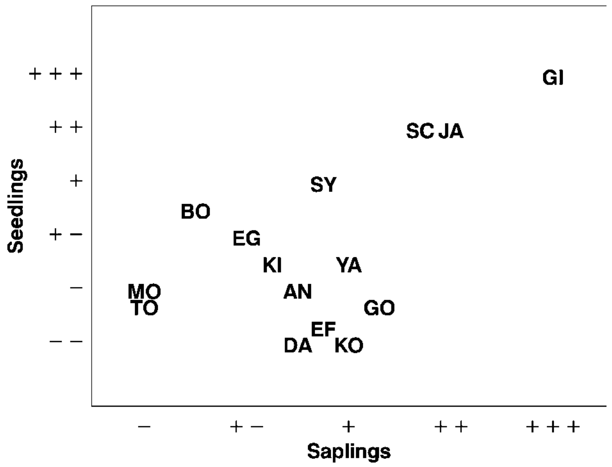


Fig. 2. Species ordered according to silvicultural treatments: final sapling densities (1992) vs. total individuals involved in the regeneration process observed between 1986 and 1992.

encounter the conditions necessary for vigorous growth. When the control plot means for these species are examined by 2-year intervals, such individual progress is undetectable and almost no differences in mean height growth can be observed, with only *M. coccinea* showing a slight gain over all three intervals.

However, when the raw individual data is examined for the treatment plots, all species possess some individuals showing remarkable height growth gains, especially in treatment 3. Notorious quiescent species such as *D. guianensis* and *G. glabra* are effectively capable of height growths of over 200 cm in 2 years. Nonetheless, there are individuals, even in the most extreme treatments, for which no reactions are observed (*E. falcata*, *E. grandiflora*, *J. copaia*, *Symphonia* sp. and *Carapa procera*). Mean height growth is greatest in general for *Q. rosea*, *Virola michelii* and *Virola surinamensis*, followed by *E. grandiflora* and *C. procera* and only in the most extreme treatment conditions.

Non-normal distributions and great variability of the measurements, plus unequal sample sizes, dictate the use of non-parametric tests for the seedling height growth data set. Here the SAS (1989) NPAR1WAY Wilcoxon procedure was used. Table 5 summarizes the results for the 12 species over the four treatments and over intervals of 2, 4 and 6 years spanning the period of silvicultural treatment application. While all combinations of immediate vs. delayed and ephemeral vs. sustained reactions to treatment are observed over the 12 species, the great majority respond immediately and almost half maintain this response over the 6 years of observation. Significant differences in positive height growths are obtained for all but three of 10 species (*C. procera*, *V. surinamensis* and *V. michelii*) for 1986–1988 and all but one species (*V. surinamensis*) in 1988–1990. While *V. surinamensis* apparently reacts vigorously and immediately in height growth, its initially low numbers do not permit statistical demonstration of this response. In 1990–1992 this number dropped to only five of 12 species showing significant differences over treatments. Overall, for the total 6-year observation period, which is also marked by much mortality and recruitment in the study population, six of 10 species show significant increases in height growth with silvicultural treatment. For the two light-loving species, *J. copaia* and *G. glabra*, added in 1990, no differences exist between treatments as they grow well at all treatment levels and are virtually non-existent in undisturbed forest.

More detailed examination of the seedling height growth data permit the identification of several different patterns of response to the different treatment levels applied beyond the general contrast of the control with treatments. The period taken as describing the overall response for a species is that of 1988–1992, so as to include the maximum number of post-exploitation recruited seedlings and to reduce artificial depression of the mean due to the loss of rapidly growing individuals that grow “out” of the study in 6 years. Retaining the concept of an ephemeral vs. a sustained reaction, it is possible to order the species according to their height growth responses to the non-control treatment levels. Table 6 summarizes the observed reactions:

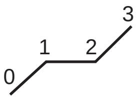
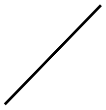
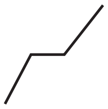
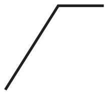
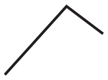
- a monotonic increasing response with treatment level without a “saturation” effect in height growth at treatment level 1 or 2;
- a monotonic increasing response with treatment level with a saturation effect;
- a variety of responses which all show increases for treatment 1 over the control, but for which the differences between the treatments are varied.

Four species, *Symphonia* sp., *V. michelii*, *E. grandiflora* and *M. coccinea*, compose the first treatment response group. These are also all species with sustained reactions over the duration of the entire observation period. They show themselves to be capable of increasing height growth gains through the most severe treatment level.

Table 5
Non-negative seedling height growth and response tendencies over four silvicultural treatments and by inventory interval. Degree of test significance as in Table 2.

Code	*Species*	*Observation dates, intervals, significance levels, df = 3*						*Response type*
		1986–1988 (2 years)	*1988–1990 (2 years)*	*1990–1992 (2 years)*	*1986–1990 (first 4 years)*	*1988–1992 (last 4 years)*	*1986–1992 (all 6 years)*	
AN	*Dicorynia guianensis*	**	***	ns	*	ns	ns	Immediate but ephemeral
GR	*Sextonia rubra*	*	***	ns	*	ns	ns	Immediate but ephemeral
EF	*Eperua falcata*	***	***	***	***	***	**	Immediate and sustained
EG	*Eperua grandiflora*	***	***	***	***	***	**	Immediate and sustained
SY	*Symphonia* sp.	***	***	***	***	***	***	Immediate and sustained
GO	*Qualea rosea*	***	***	***	***	***	***	Immediate and sustained
MO	*Moronobea coccinea*	**	***	***	***	***	ns	Immediate and sustained
YA	*Virola michelii*	* (0.0552)	***	***	***	***	***	Slightly delayed and sustained
YS	*Virola surinamensis*	ns	* (0.0567)	ns	ns	–	–	(statistically) Delayed and ephemeral
CA	*Carapa procera*	ns	***	ns	**	ns	*	Delayed and ephemeral
GI	*Goupia glabra*	–	–	ns	–	–	–	Responsive but non-significant
JA	*Jacaranda copaia*	–	–	ns	–	–	–	Responsive but non-significant

Table 6
Relative seedling height growth trends as a function of silvicultural treatment, 1988-1992.

	Seedling height growth trends over treatments							
	without saturation		*with saturation*		*diverse responses*			
Silvicultural Treatment Level 								
Ephemeral reactions			gr gi	ja	ys			an ca
Sustained reactions	sy ya	eg mo				go	ef	

In the second treatment response group, two species show height growth gain saturation at higher levels of treatment (*S. rubra* and *G. glabra*) and are all also classed as ephemeral response species. For both species, there is no differentiation between treatments 2 and 3. Thus these ephemeral response species have attained their maximum possible height growth response at lower levels of intervention than for the four sustained response species.

In the third treatment response group, four species (*V. surinamensis*, *E. falcata*, *Q. rosea* and *J. copaia*) have in common their reduction in mean height growth at treatment level 3. The ephemeral response species *V. surinamensis* and the sustained response species *E. falcata* are both saturated regarding height growth gains at treatment level 1, while the sustained response species *Q. rosea* and the ephemeral response species *J. copaia* are saturated at level 2.

The remaining two species, the ephemeral response species *D. guianensis* and *C. procera* show responses at treatment levels 1 and 3 which suggest they should be assimilated to behaviors of rapid saturation in height growth gains, compatible with the ephemeral status of the representative species *J. copaia*. However, both have depressed gains at treatment level 2. For *D. guianensis*, this may be due to a local distribution effect due to the under-representation of this species in the subplots of that treatment level, although this requires further confirmation. For *C. procera*, the interpretation is much more difficult as this species depends on terrestrial rodents for dispersal and after germination suffers from herbivory and damping off apparently related to microhabitat (Forget, 1997), all of which may be affected to unknown degrees in turn by silvicultural intervention.

3.2.2. Overall demographic characteristics for saplings 1992–1995

Saplings were not individually studied before 1992 and so it is only from that year that true demographic trends can be extracted. Between 4200 and 5400 stems of 23 species were studied between 1992 and 1995.

Sapling diameter class structure resembles that of adults for the majority of "classic" tropical rain forest examples, that is a negative exponential distribution with some variation in the largest classes. Nine of the 23 species studied have more than 50% of their individuals in the first (the 1 cm) size class. From 1992 to 1995 a noticeable increase in numbers in all classes is observed. The K-S Two Group test shows that these differences are significant and that the greatest deviation is observed for diameter class 2 (= 2 cm) (n in 1992 = 3321, n in 1995 = 4822, Dmax = 0.0559, df = 2, P = < 0.001). Thus emergent differences for saplings after 3 years occur just above the precision level (1 cm lower limit and measurement interval) of the inventory protocol. Close examination of the data reveals that important differences are also found in the larger (8–10 cm) diameter classes (Fig. 3).

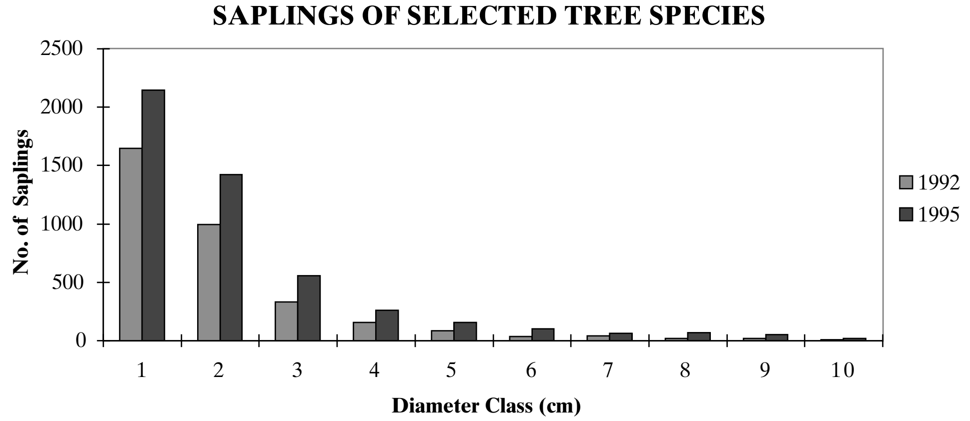


Fig. 3. Number of saplings of 23 selected tree species by diameter class over the inventory plots and for the inventory period 1992–1995.

Examination of trends in abundance by species and by treatment for the same period 1992–1995 distinguish four different responses (Fig. 4): a marked increase with treatment (for 10 species of which three are significant), a weak non-significant and equivalent increase with treatment (two species), an increase for one or two intermediate treatment levels but a relative decrease for the most extreme treatment (six species) and a marked depression in abundance associated with treatment level 1 (four species). *D. guianensis* remains unclassifiable due to problems related to its strongly aggregative distribution pattern and *Vouacapoua americana* is placed in the first group since its low abundance in treatment 3 is apparently due to an uneven distribution pattern.

The saplings in the demographic survey established in 1992 are a subset of those observed in the previous periods 1986–1990, the number of subplots having been reduced to 64 per plot and the radius of each subplot having been increased (see Methods). The overall abundance of these saplings can be equated to the sum of gains and losses for the class as performed for the 1986–1992 data above. The number of significant chi-square tests is reduced here, both because of the decrease in the number of species for which the data meet the test conditions and because several species favored by perturbation have now entered the competition phase which has reduced the initial contrasts in numbers. In general, the temperaments as perceived from global abundance changes are confirmed, with the exception of *E. falcata* and *P. cochlearia* which show the saplings as more reactive to treatment than previously and for which the relationship for *E. falcata* is now significant.

3.2.3. Sapling diameter growth

3.2.3.1. Treatment effects

Over the 1992–1995 (= 3 year) observation period and regardless of silvicultural treatment, more plants (64%) remained effectively static in terms of diameter growth than showed increase. Of those plants showing positive increases, 85% increased by only one 1 cm class in 3 years. Increases were observed up to the 5 cm class but such performances are extremely rare and only 7 of the 23 species studied showed increases over 3 cm (Fig. 5). Eight species showed increases of only 1 cm. No species, however, were observed as having no detectable growth (i.e. all species had at least one plant that changed diameter class over the observation interval).

Given the extremely limited sapling diameter growth responses detectable using 1 cm classes over the 3-year periods, the data was reduced to a binary set of growth vs. no growth responses to test for the effects of silvicultural treatment. These results were then examined for differences using chi-square, where conditions for test application are met, and with Probit analysis (SAS Institute, 1989). Greater incidences of positive growth were observed for four species (*D. guianensis*, *J. copaia*, *Sterculia excelsa*, *S. decaphylla*) regardless of treatment, and approximately equal numbers of “growth” and “no growth” plants for two species (*C. procera* and *Andira coriacea*) (Table 7). Seven of the 23 species meet the conditions for testing (*E. falcata*, *Q. rosea*, *S. excelsa*, *Symphonia* sp., *Iryanthera hostmanii*, *I. sagotiana*, *V. michelii*). Of these,

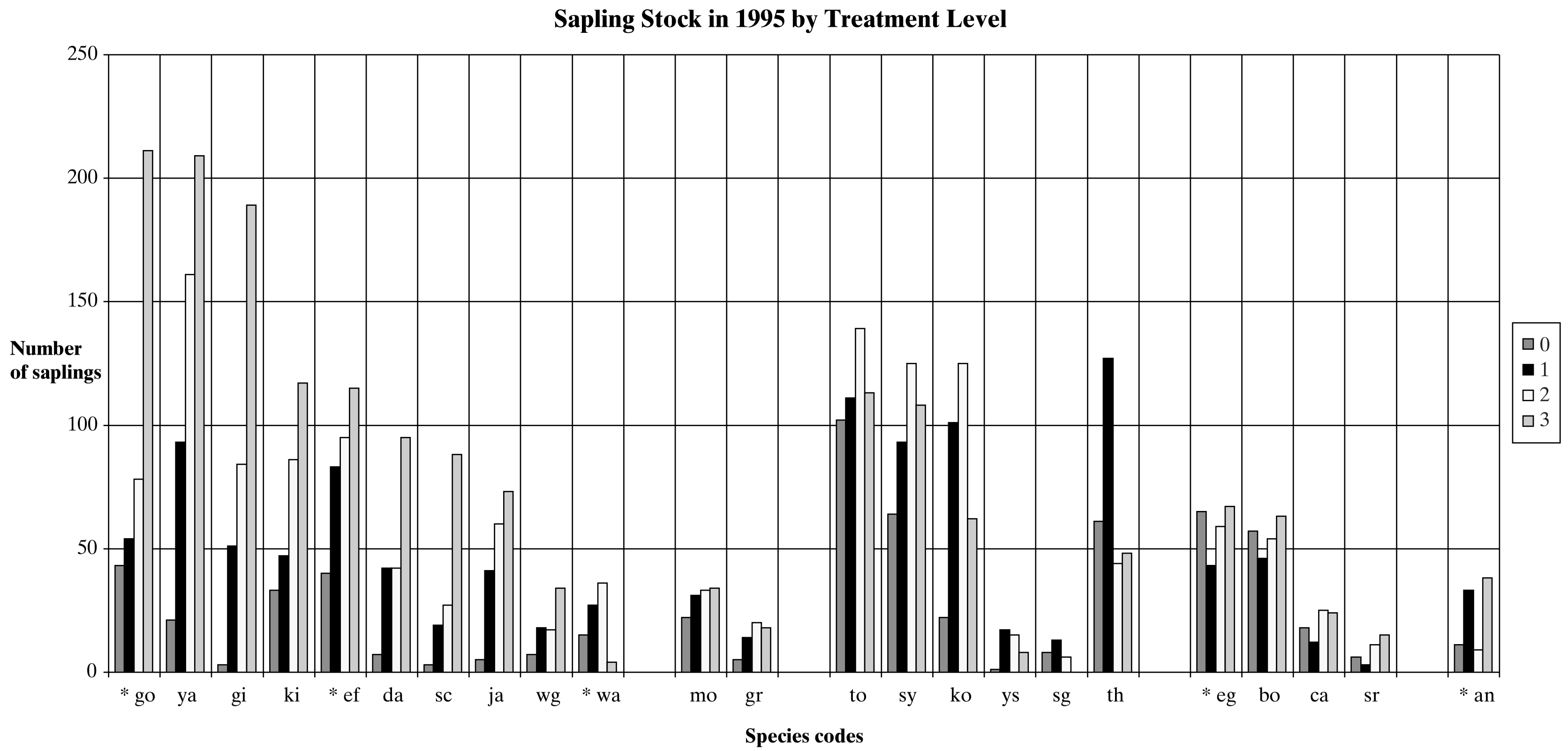


Fig. 4. Changes in sapling stocks from 1992 to 1995 by species by treatment and grouped by response trend (increase, decrease and with respect to which treatment levels). From left to right: general increase: for 10 species, stocks increase with treatment (WA in treatment 3 does not have sufficient density). Similar but non-significant increase with treatment: for two species. Depression for the most severe treatment: for six species stocks increased for treatment 1 or 2 but depressed in treatment 3. Depression for the two most severe treatments: for four species stocks increased in treatment 1 then depressed in treatment 2 and increased again in treatment 3. Specific case of the irregular distribution over small spaces: for Angélique (*Dicorynia guianensis*).

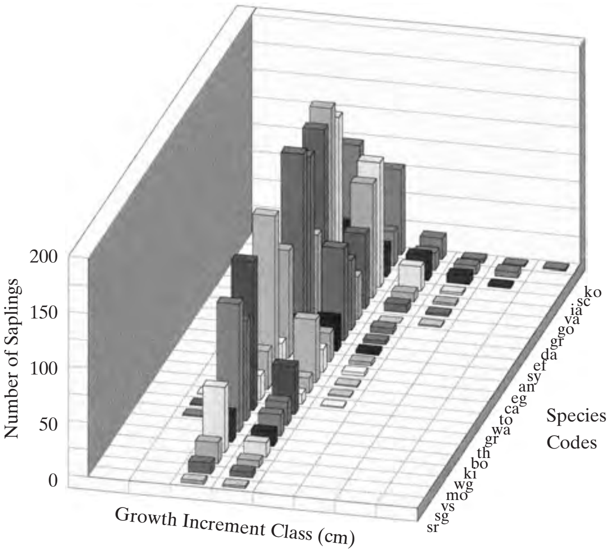


Fig. 5. Sapling diameter increments of 23 tree species by 1 cm diameter classes and by species for all treatments and ordered by decreasing increments as observed in 1995. See also the colour version, p. 311.

S. excelsa is the only species for which the relationship is significant and also the only species for which there are more positive growth plants than no growth plants. Probit analysis for this species permits to further differentiate treatments 2 and 3 as being different from the control, but not for treatment level 1.

The lack of significance for diameter increment is most probably related to the incompatibility of the measurement range (too broad) and the observation period (too short) for the study of this phenomenon. Nonetheless, an examination of the data by treatment reveals emergent trends which will eventually prove significant. By grouping the species by the percent of individuals showing positive growth within each treatment, six growth trends can be detected (Fig. 6):

(1) an equivalent increase for all treatments vs. the control (four species);

(2) a monotonic increase from control to treatment 3 (four species);

(3) greater increases with treatments 1 and/or 2 than with treatment 3 and/or depression with treatment 3 over the other treatments including control (six species);

(4) an increase or not with treatment but a marked depression in treatment 2 (four species);

(5) an increase with treatments plus a marked depression in treatment 1 in general (two species);

(6) a marked decrease in treatments vs. the control, with an important depression in treatment 1 vs. treatment 2 and/or 3 (three species).

Thus for 19 of the 23 species studied, some level of silvicultural treatment does tend to positively, although not significantly, affect stem diameter increment over the 3-year periods. Furthermore, the majority of these 19 species react more favorably or as favorably to a treatment intensity below that of treatment level 3. For three species (*S. decaphylla*, *S. rubra* and *G. glabra*), the effect of any treatment is definitely negative. A non-negligible number of species suggest uneven and varied responses within the three non-control intervention levels. The reason for these results is not immediately evident other than for treatment 3 which can be easily explained as “too destructive”. It remains to be seen if these trends will persist.

4. Discussion of demographic profiles in contrast with species functional groups and other classification systems

Based on the overall abundance changes observed between 1986 and 1992, Montpied (1995) proposed a classification of tree species by their ecological temperaments based on their behavior in the seedling and sapling stages. The composite temperaments range from non-reactive to light plus very shade tolerant to very reactive to light plus shade intolerant. This classification represents an important advance over previous classifications (Oldeman and van Dijk, 1991; cf. Swaine and Whitmore, 1988) in that it does not consider shade tolerance and positive response to sunlight as mutually exclusive. It is also unique in that it considers the juvenile stages and the adult stage as potentially differing in temperament.

Similarly but working with adult trees only, Favrichon (1994) has proposed a functional group classification combining adult canopy level and shade tolerance. This classification is composed of 5 groups: Group 1 = lower canopy strata shade tolerant species, Group 2 = upper canopy strata shade tolerant species, Group 3 = canopy level and emergent semi-shade tolerant species, Group 4 = upper canopy strata heliophilous species, and Group 5 = lower canopy strata heliophilous species.

The demographic data for the seedlings and saplings of the 23 tree species of the present study may be

Table 7
Summary of sapling binary stem diameter growth (positive or zero) by silvicultural treatment, with chi-square and Probit significances. Those species tested met the criteria of cell frequencies greater than 5, more than 10 observations per treatment and no zero cell values.

Code	*Species*	*Growth**			*Chi-square significance*	*Probit significance*
		Positive	*Zero*	*n*		
AN	*Dicorynia guianensis*	32	25	57	–	–
BO	*Bocoa prouacensis*	21	93	114	–	–
CA	*Carapa procera*	25	23	48	–	–
DA	*Sclerolobium melinonii*	40	74	114	–	–
EF	*Eperua falcata*	68	160	228	ns	ns
EG	*Eperua grandiflora*	29	98	127	–	–
GI	*Goupia glabra*	77	164	241	–	–
GO	*Qualea rosea*	114	171	285	ns	ns
GR	*Sextonia rubra*	10	23	33	–	–
JA	*Jacaranda copaia*	59	47	106	–	–
KI	*Pradosia cochlearia*	19	117	136	–	–
KO	*Sterculia excelsa*	102	98	200	ns	$P < 0.001$
MO	*Moronobea coccinea*	13	60	73	–	–
SC	*Schefflera decaphylla*	58	26	84	–	–
SG	*Symphonia globulifera*	5	10	15	–	–
SR	*Andira coriacea*	2	3	5	–	–
SY	*Symphonia* sp.	87	167	254	ns	ns
TH	*Iryanthera hostmanii*	44	137	181	ns	ns
TO	*Iryanthera sagotiana*	59	149	208	ns	ns
WA	*Vouacapoua americana*	15	35	50	–	–
WG	*Recordoxylon specisosum*	13	26	39	–	–
YA	*Virola michelii*	138	154	292	ns	ns
YS	*Virola surinamensis*	6	19	25	–	–

*: Totals over all four treatments.

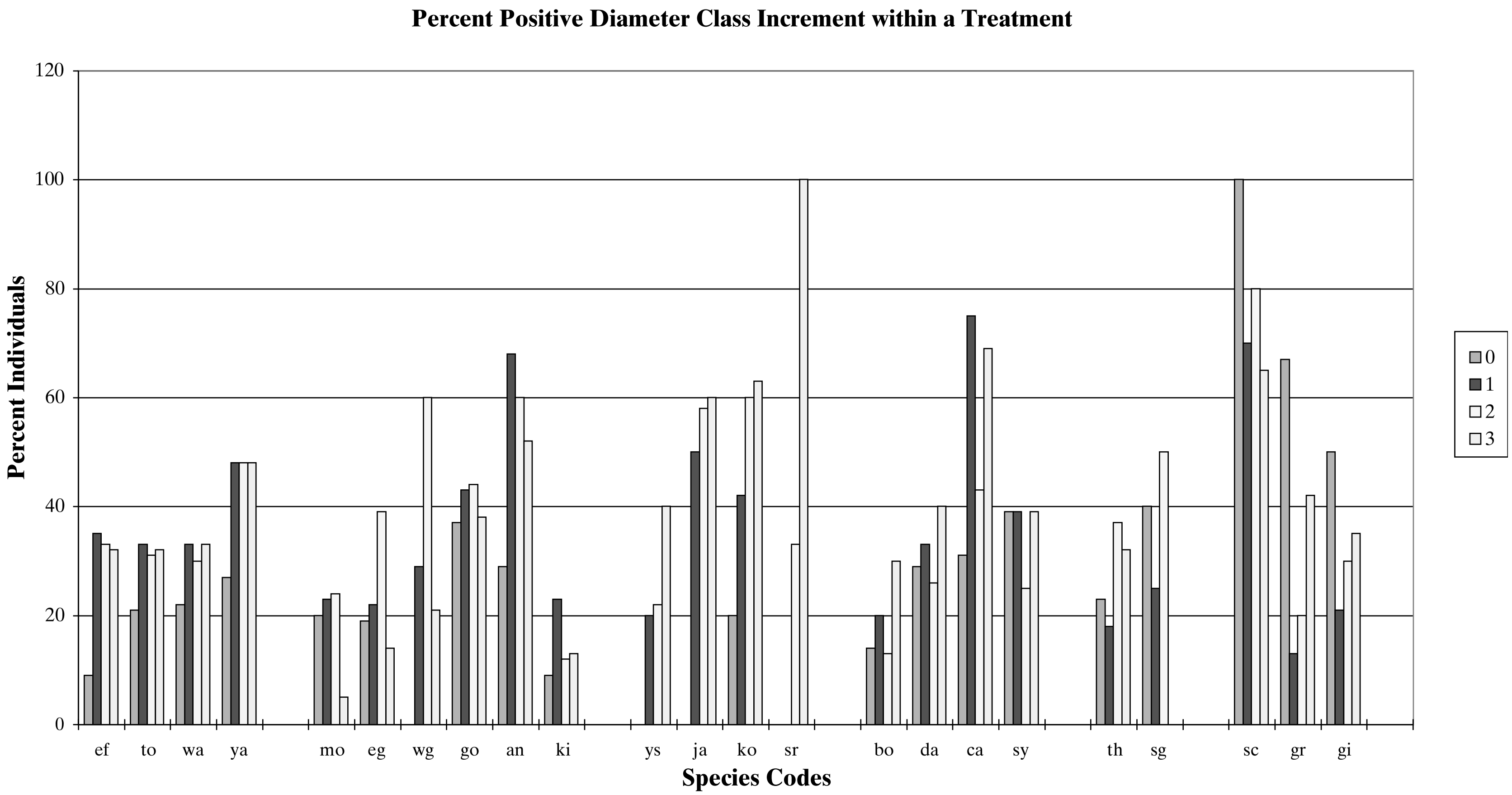


Fig. 6. Percent positive diameter class increment by treatment and by species for the period 1992–1995.

confronted with these different classification systems to determine whether the use of different parameters nonetheless produces similar conclusions about tree species ecological temperaments. To this end we have summarized and contrasted species tendencies by developmental stage and over time for seedling height growth, sapling abundances and sapling diameter growth. The Figs. 7 to 9 depict the general trends observed for the parameter cited, followed by those species exhibiting this trend and their behaviors in the different developmental stages.

In general, the trends presented are not always simple nor proportional to the treatment; much variability in the relation treatment-demographic parameter exists which cannot be simply attributed to distribution patterns, except in one case (*D. guianensis*). Two features are immediately evident:

(1) with one exception (*C. procera*), no species follows the same trend over all three parameters as a function of treatment intensity;

(2) at the treatment level, no strict relationship exists between adult functional group and juvenile trend for the parameters examined.

Thus treatment appears to act differently on the different demographic parameters, and the species responses to treatment are not predictable by adult functional group or juvenile temperament alone. Obviously something important is taking place at the site, which acts above and beyond the basic ecological temperament of a species to produce the different observed trends. For saplings for example, this may be related to height growth rates and ability to resist or recover from breakage, which results in increased survivorship and thus species abundance (Koestel and Rankin-de Merona, 1998).

The synthesis of diverse and sometimes opposing parameters may explain why the adult functional groups of Favrichon (1994) do not correspond to the trends seen for the different parameters concerning juveniles. It is difficult to weight the wide range of characters taken into consideration in the formation of each group and an across-the-board homogenization may hide important variations. It is also true that non-demographic characters (e.g. diameter increments) were used to form the adult functional groups, which have not been considered here. Nonetheless, major emphasis is placed on canopy strata and light requirements and these are not always confirmed in the juveniles with respect to silvicultural treatment. Further confirmation or not of the adult-juvenile relationship for these parameters may be obtained by substitution of the correspondence analyses groups regarding plot microsite conditions for a given period, a more realistic representation of the environment in which the juveniles develop, for the treatment levels, which themselves obviously average great disparities in microsite within the plots.

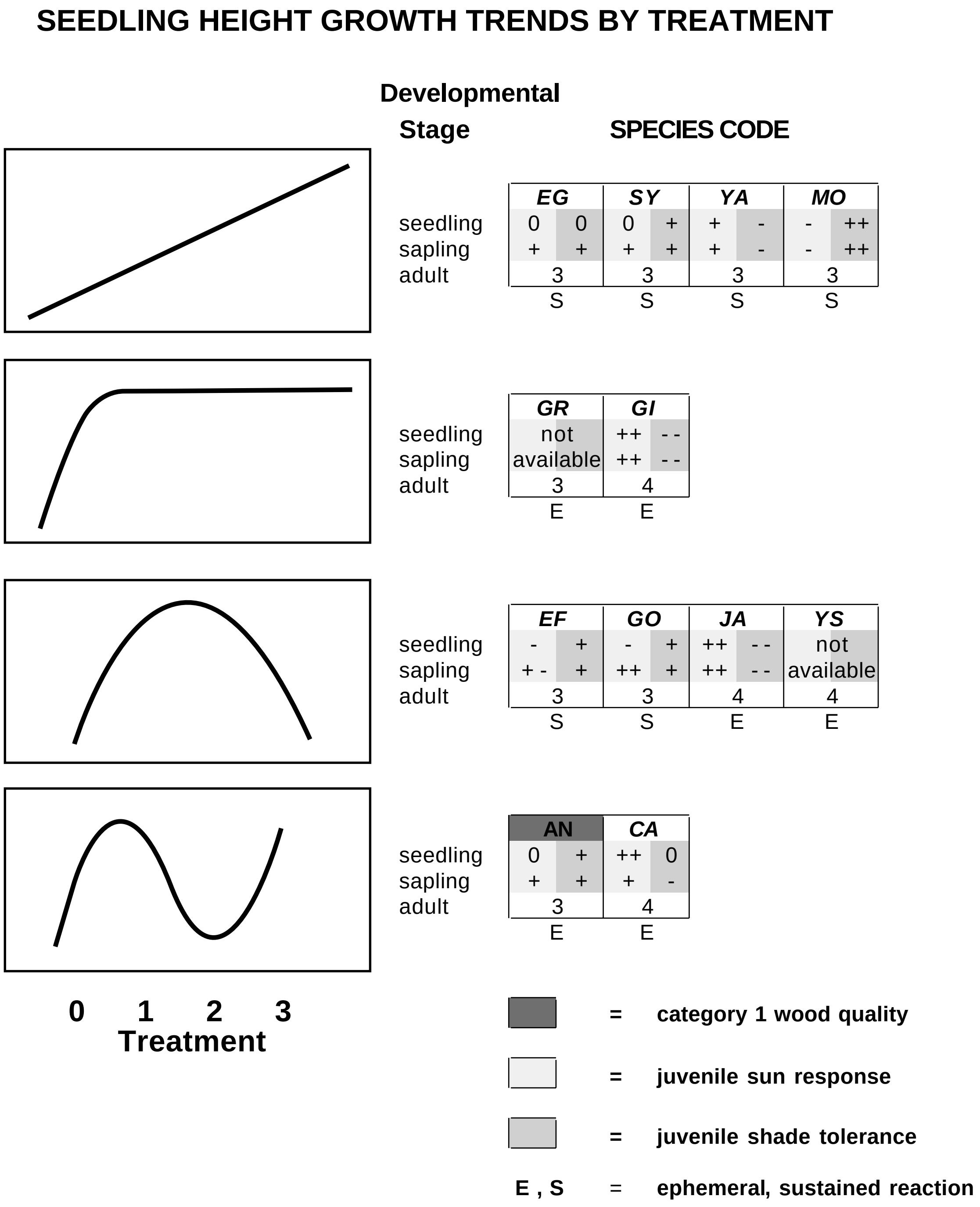
While it is possible to contemplate a further synthesis of these results by correspondence analysis with the objective of forming juvenile demographic behavioral groups, it seems prudent, especially at this early class, to maintain these data separate and in a form which can be directly associated with a parameter to be manipulated. In this form, the data are more directly and unambiguously available for further research efforts or for management application. It also facilitates the incorporation of these data in forest simulation models that can be extremely useful in aiding medium- and long-term management decisions.

5. Conclusions

5.1. Effects of silvicultural treatment on the demography of juveniles 8 years after intervention

In 1990, Schmitt and Bariteau announced that at least a decade would be necessary to see the results of the silvicultural experiment installed at Paracou. Eight years after logging, the natural regeneration inventory has been able to describe the initial trajectories for the demographic parameters for a number of ecologically and economically important tree species as a function of silvicultural treatment and to indicate where extrapolations toward future stand structure may be valid. In some cases, a saturation point has already been reached and it remains to be seen if the trends of the first years will be maintained. In others, it seems that gains will still be made in terms of growth, if not in numbers.

Beyond the specific information gained about the behavior of the juveniles of these species, several important generalizations can be drawn that must influence and inevitably temper the application of these results and the direction of future research in this domain. These are: (i) that no strict relationship exists between adult functional group or juvenile ecological temperament and juvenile trend of a given species for the demographic parameters examined; (ii) that the



Developmental Stage	EG		SY		YA		MO	
seedling	0	0	0	+	+	-	-	++
sapling	+	+	+	+	+	-	-	++
adult	3		3		3		3	
	S		S		S		S	

Developmental Stage	GR		GI	
seedling	not available		++	- -
sapling			++	- -
adult	3		4	
	E		E	

Developmental Stage	EF		GO		JA		YS	
seedling	-	+	-	+	++	- -	not available	
sapling	+ -	+	++	+	++	- -		
adult	3		3		4		4	
	S		S		E		E	

Developmental Stage	AN		CA	
seedling	0	+	++	0
sapling	+	+	+	-
adult	3		4	
	E		E	

▆ = category 1 wood quality

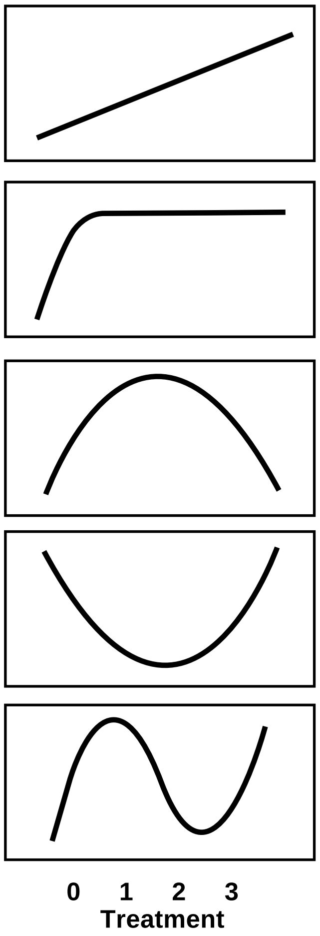
☐ = juvenile sun response

▨ = juvenile shade tolerance

E , S = ephemeral, sustained reaction

Fig. 7. Seedling height growth trends by silvicultural treatment: relative ratings of sun response and shade tolerance are given for seedling and saplings for each species, while numbers for adults correspond to the functional group classifications of Favrichon (1994). Category 1 wood quality species are those of greatest interest for the timber market.

SAPLING ABUNDANCE TRENDS BY TREATMENT



Developmental Stage — **SPECIES CODE**

Developmental Stage	*KI*		*WA*		*WG*		*EF*		*YA*		*GO*		*DA*		*JA*		*GI*		*SC*	
seedling	-	+	not available		not available		-	+	+	-	-	+	+ -	0	++	- -	++	- -	++	- -
sapling	+	+					+ -	+	+	-	++	+	++	+	++	- -	++	- -	++	- -
adult	2		2		3		3		3		3		4		4		4		4	

Developmental Stage	*MO*		*GR*	
seedling	-	++	not available	
sapling	-	++		
adult	3		3	

Developmental Stage	*TO*		*TH*		*SY*		*SG*		*KO*		*YS*	
seedling	-	+	-	+	0	+	not available		-	-	not available	
sapling	+	+	-	+	+	+			+	-		
adult	1		1		3		4		4		4	

Developmental Stage	*BO*		*SR*		*EG*		*CA*	
seedling	-	++	not available		0	0	++	0
sapling	0	+			+	+	+	-
adult	1		3		3		4	

Developmental Stage	*AN*	
seedling	0	+
sapling	+	+
adult	3	

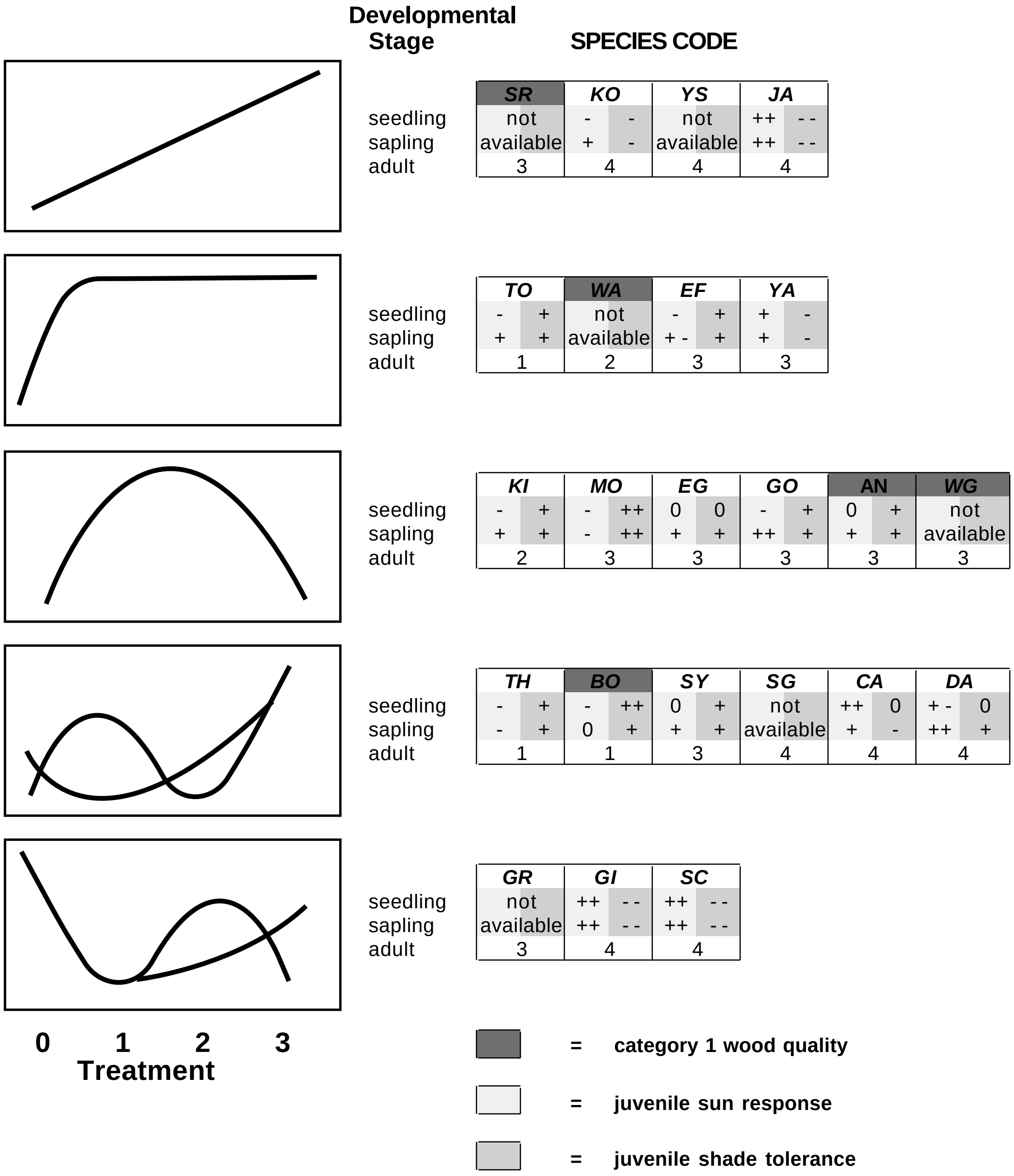
■ = **category 1 wood quality**

□ = **juvenile sun response**

▒ = **juvenile shade tolerance**

Fig. 8. Sapling abundance trends by silvicultural treatment: relative ratings of sun response and shade tolerance are given for seedling and saplings for each species, while numbers for adults correspond to the functional group classifications of Favrichon (1994). Category 1 wood quality species are those of greatest interest for the timber market.

SAPLING DIAMETER GROWTH TRENDS BY TREATMENT



SPECIES CODE

Developmental Stage	SR	KO	YS	JA
seedling	not available	- -	not available	++ - -
sapling		+ -		++ - -
adult	3	4	4	4

Developmental Stage	TO	WA	EF	YA
seedling	- +	not available	- +	+ -
sapling	+ +		+ - +	+ -
adult	1	2	3	3

Developmental Stage	KI	MO	EG	GO	AN	WG
seedling	- +	- ++	0 0	- +	0 +	not available
sapling	+ +	- ++	+ +	++ +	+ +	
adult	2	3	3	3	3	3

Developmental Stage	TH	BO	SY	SG	CA	DA
seedling	- +	- ++	0 +	not available	++ 0	+ - 0
sapling	- +	0 +	+ +		+ -	++ +
adult	1	1	3	4	4	4

Developmental Stage	GR	GI	SC
seedling	not available	++ - -	++ - -
sapling		++ - -	++ - -
adult	3	4	4

■ = **category 1 wood quality**

□ = **juvenile sun response**

▨ = **juvenile shade tolerance**

Fig. 9. Sapling diameter growth trends by silvicultural treatment: relative ratings of sun response and shade tolerance are given for seedling and saplings for each species, while numbers for adults correspond to the functional group classifications of Favrichon (1994). Category 1 wood quality species are those of greatest interest for the timber market.

observed trends are not always simple in their relation to nor proportional to the silvicultural treatments applied; and (iii) that with one exception, no species follows the same trend over all three parameters as a function of treatment intensity. These results are not predictable from data from other sources, including the adults of these species themselves. In short, there are no easy answers and no simple solutions to the understanding, the modeling and eventually the management of the natural regeneration of this and certainly other tropical rain forests, making direct investigation at the species and developmental class an unavoidable requirement.

The process of natural regeneration is a long one and the period necessary for the transition from seedling or sapling to young tree, as defined here, exceeds the period of time elapsed since the beginning of this study. It is obvious that further data collection, which is presently ongoing on the site (Baraloto, 2001; Gourlet-Fleury, 1999), is necessary to complete the demographic timeline for this experiment and to furnish the data necessary for the calibration of the regeneration component of forest growth simulation models. Priority should be given to long-term studies of tagged individuals as well as to a better quantification and understanding of their physical and biotic environments throughout the various stages of plant establishment and growth. From the start, studies should be designed in such a way as to assure that the data collected is unambiguous (i.e. deaths and births are explicitly registered; observation intervals and growth rates are compatible or all individuals are tagged) and easily incorporated into population models.

Acknowledgements

This publication was made possible by financial support from INRA, the program SOFT, the Contrat de Plan État - Région, Guyane and a grant from the GIP ECOFOR, Paris (Research contract GIP ECOFOR, 6 November 1996 N° 98 codicil n 1). All field work and research was conducted by the staff of the INRA Station de Recherches Forestières at Kourou, French Guiana (France) under the responsibilities of program directors M. Bariteau (1986–1990), P. Montpied (1990–1994) and J. M. Rankin-de Mérona (1994–1997). Logistic support was also provided by the CIRAD-Forêt Natural Forest Program of CIRAD-Guyane. The authors wish to thank the members of the INRA staff at Kourou, whose dedication under all field conditions made the inventory campaigns successful, and S. Gourlet-Fleury of CIRAD-Forêt, whose discussions and encouragement greatly contributed to this work. We also thank the reviewers for their constructive comments on the manuscript.

References

Augsburg C.K., 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. J. Ecol. 72, 777–795.

Baraloto C., 2001. Tradeoffs between neotropical tree seedling traits and performance in contrasting environments, PhD dissertation, University of Michigan, 302 p.

Canham C.D., 1989. Different responses to gaps among shade tolerant tree species. Ecology 70, 548–550.

Coomes D.A., Grubb P.J., 1998. Responses of juvenile trees to above- and below-ground competition in nutrient-starved Amazonian rain forest. Ecology 79, 768–782.

DeStevens D., 1994. Tropical seedling dynamics: recruitment patterns and their population consequences for three canopy tree species in Panama. J. Trop. Ecol. 10, 369–383.

Favrichon V., 1994. Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise. Revue d'Ecologie (La Terre et la Vie) 49, 379–403.

Forget P.M., 1997. Effect of microhabit on seed fate and seedling performance in two rodent-dispersed tree species in rain forest in French Guiana. J. Ecol. 85, 693–703.

Gomez-Pompa A., Burley F.W., 1991. The management of natural tropical forests. In: Gomez-Pompa A., Whitmore T.C., Hadley, M., Rain Forest Regeneration and Management. MAB vol. 6. pp. 3–18.

Gourlet-Fleury S., 1999. Régénération de l'angélique (*Dicorynia guianensis* Amshoff, Caesalpiniaceae) en Guyane française. Project supported by the GIP ECOFOR.

Gourlet-Fleury S., et Montpied P., 1995. Dynamique des peuplements denses forestiers en zone tropicale humide : ébauche d'un modèle d'arbre à Paracou (Guyane française). Revue d'Ecologie (La Terre et La Vie) 50, 283–302.

Grubb P.J., 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107–145.

Harper J.L., 1977. Population Biology of Plants. Academic Press, New York, 892 p.

Higuchi N., Jardim F.C.S., dos Santos J. , Cruz de Alencar J., 1985. Inventario diagnostico da regeneraçao natural. Acta Am. 15.

Hubbell S.P., Foster R.B., O'Brien S.T., Harms K.E., Condit R., Wechsler B., et al., 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283, 554–557.

Janzen D.H., 1970. Herbivores and the number of tree species in tropical forests. Amer. Natur. 104, 501–528.

Koestel G., Rankin-de Mérona J.M., 1998. Physical damage on tropical tree saplings: quantification and consequences on competition for height growth in a neotropical rain forest in French Guiana. Ann. Sci. Forest. 6, 727–742.

Montpied P., 1995. La régénération naturelle en forêt tropicale humide, effet de traitements sylvicoles d'intensité variable. Bilan des inventaires INRA à Paracou, Guyane française 1986–1992, in: Recherches sur les Ecosystèmes Forestiers de Guyane: Actes du Séminaire Interne de Silvolab, GIS Silvolab-Guyane, Kourou, pp. 51–69.

Nicotra A.B., Chazdon R.L., Iriarte S.V.B., 1999. Spatial heterogeniety of light and woody seedling regeneration in tropical wet forests. Ecology 80, 1908–1926.

Oldeman R.A.A., van Dijk J., 1991. Diagnosis of the temperament of tropical rain forest trees. in: Gomez-Pompa A., Whitmore T.C., Hadley M. (Eds.), Rain Forest Regeneration and Management. MAB Paris, vol. 6. pp. 21–65.

Osunkoya O.O., Ash J.E., Hopkins M.S., Graham A.W., 1992. Factors affecting survival of tree seedlings in North Queensland rainforests. Oecologia 91, 569–578.

Osunkoya O.O., Ash J.E., Hopkins M.S., Graham A.W., 1993. Growth of tree seedlings in tropical rain forests of North Queensland, Australia. J. Trop. Ecol. 9,9–18.

Osunkoya O.O., Ash J.E., Hopkins M.S., Graham A.W., 1994. Influence of seed size and seedling ecological attributes on shade tolerance of rain forest tree species in northern Queenslands. J. Ecol. 82, 149–163.

Sarukhan J., 1978. Studies on the demography of tropical trees. In: Tomlinson P.B., Zimmerman M.H. (Eds.), *Tropical Trees as Living Systems*. Cambridge University Press, Cambridge, 1978, pp. 163–184.

SAS Institute, 1989. SAS/STAT Guide for Personal Computers. Version 6 ed. Cary, NC, USA, 1028 p.

Schmitt L., Bariteau M., 1990. Gestion de l'écosystème forestier guyanais. Étude de la croissance et de la régénération naturelle. Dispositif de Paracou. Bois et Forêts de Tropiques. 220, 3–24.

Schultz J.P., 1960. Ecological studies on rain forest in northern Suriname. Verh. K. Ned. Akad. Wet., Afd. Natuurk. Second series, Part 53, no.1. 267 pp., Amsterdam, The Netherlands.

Swaine M.D., Whitmore T.C., 1988. On the definition of ecological species groups in tropical rain forests. Vegetation 75, 81–86.

Swaine M.D. (Eds.), 1996. The Ecology of Tropical Forest Tree Seedlings. UNESCO/Parthenon, Paris.

Vieira G., Hosokawa 1989. Composoçao floristica da vegetaçao da regeneraçao natural um ano apos diferentes niveis de exploraçao de uma floresta tropical humida. Acta Am. 19.

Welden C.W., Hewett S.W., Hubbell S.P., Foster R.B., 1991. Sapling survival, growth and recruitment: relationship to canopy height in a neotropical forest. Ecology 72, 35–50.

Whitmore T.C., 1990. An Introduction to Tropical Rain Forests. Oxford University Press, 226 p.

Whitmore T.C., 1975. Tropical Rain Forests of the Far East. Clarendon Press, Oxford, 282 p.

Ecology and Management of a Neotropical Rainforest

Chapter 4

Growth behaviour of trees and relationship with some descriptors of the environment

Sylvie Gourlet-Fleury, Nicolas Picard

Abstract – In tropical rainforests, trees over 10 cm diameter at breast height (DBH) show a great variability in diameter increments. We first characterise the phenomenon on the Paracou plots and examine its evolution over time and according to silvicultural treatments. Among the many factors which can explain the variability of growth, some can be more or less easily examined with the data available on the site: annual rainfall, botanical identity, size of the trees, topography and soils characteristics, competition for light, water and nutrients. The last effect can be estimated through the use of competition indices, either one- sided or two-sided (showing the competition for light or for all types of resources, respectively). We have tried to gradually incorporate the most influential factors in a model describing individual growth, and have shown that the residuals include tendencies suggesting that explanatory factors still have to be taken into account. In addition to other results, this work led us to build groups of species which can be qualified as homogeneous as far as diameter increment is concerned. The methods to further improve the explanations of growth variability are discussed.

Keywords: Diameter increment, Topography, Pedology, Species groups, Competition indices, Growth model, Plot effect

1. Introduction

Tree growth, in height as well as in diameter, is of particular importance to foresters for two main reasons: (i) it determines for a good part – mortality being the other part in natural forests – the quantity and quality of the products they will harvest from the forest at a given time; (ii) it is possible to manipulate growth to a certain extent through silvicultural operations. Extensive experience has been gained in this field in temperate forests, especially in regular stands, for more than two centuries. Studies in tropical forests are more recent, and face considerable difficulties due to (i) the highly heterogeneous stands encountered: hundreds of species, most of them represented by few individuals, present at all stages of their development; (ii) the impossibility, for most of the species, to determine the age of an individual; (iii) the lack of representative permanent sample plots of significant size (large enough to take into account the local heterogeneity), accurately monitored over a long period (Dawkins and Phillips, 1998).

With its 15 years of existence, its 75 ha regularly fully inventoried, and the type of silviculture implemented resulting in very contrasted local environments around the trees, the Paracou experimental site offers well-adapted conditions to study in more depth this essential component of dynamics. The present chapter thus aims, after a brief review of the main factors known to influence growth, at presenting our efforts, successes and failures to explain the variability observed at Paracou by means of modelling, at pointing out the main limitations of the actual experiment and at discussing how we chose to proceed in the future.

2. Main factors influencing the growth of trees: what happens at Paracou?

Growth is a consequence of the assimilatory process of photosynthesis and the subsequent carbon allocations inside the tree (see Assmann, 1970; Deleuze, 1996 for detailed reviews). Factors influencing these processes are multiple and interconnected. Assmann (1970) distinguished between 5 main types of abiotic and biotic factors playing a role in tree growth, as illustrated on Fig. 1: climate, soil, position of the tree in the stand ("good or poor effect position", in fact social status), phenotype (outward shape of the tree) and finally genotype.

With the data available at Paracou, the extensive investigation of growth and its deterministic components is possible only to a certain extent. We quickly review each potential influencing factor independently of each other, before developing a more integrated approach through modelling.

2.1. Evaluation of growth itself

The development of a tree is driven by its height increment (primary growth) on which diameter increment (secondary growth) depends to a more or less important extent. The two processes are not fully coupled in time, their relative importance depends on the stage of the life cycle and the environmental conditions encountered, especially with respect to light. Roughly speaking, in the early stages, priority is given to the search for light and thus height growth, while in the late stages (and generally when the canopy has been reached), it is given to strengthening of the structure, resulting in diameter growth (see Cusset, 1980; Oldeman, 1974 and the paragraph "Phenotype" later in this text). The consequence is that height is an important explicative variable of individual growth, which unfortunately is not available at Paracou on a systematic basis. Growth can only be studied through diameter increment, which partially hinders the

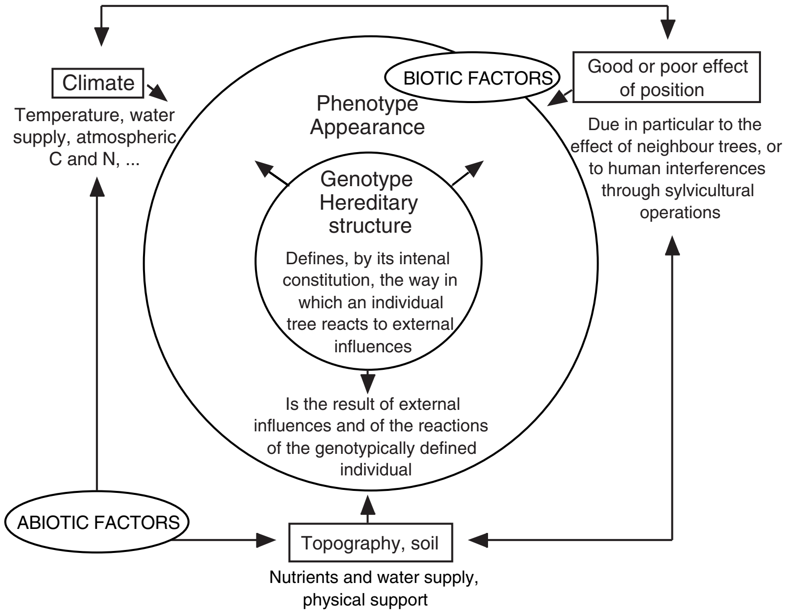


Fig. 1. Structure of growth influences upon an individual tree in a stand. Diagram taken from Assmann (1970) and slightly modified.

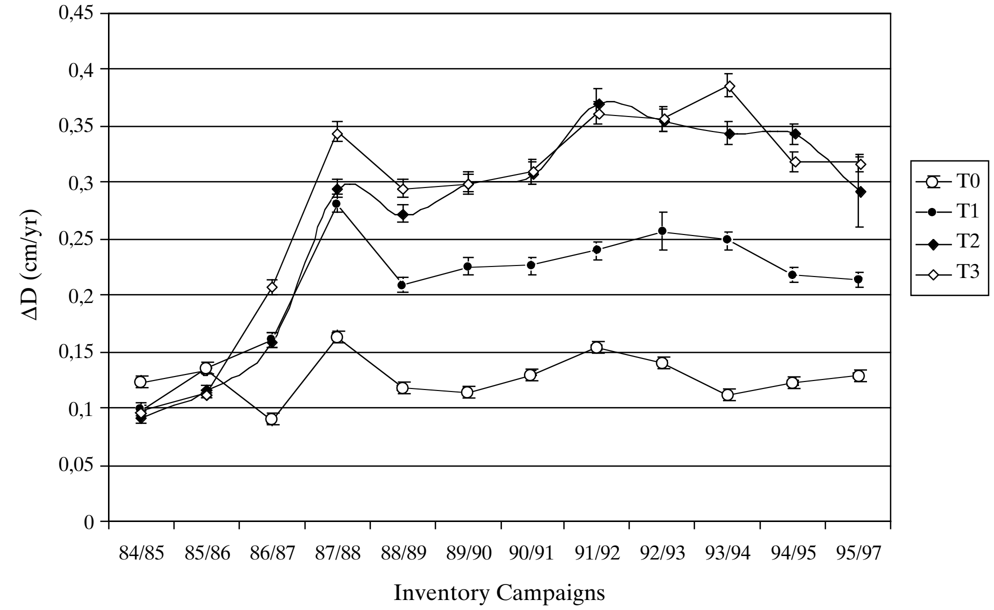


Fig. 2. Mean annual diameter increments at Paracou between 1984 and 1997, according to the 4 groups of plots T0, T1, T2 and T3. Treatments were applied between the end of 1986 and the beginning of 1988. Means are plotted with their 95% confidence interval (a minimum number of 5800 trees was used in each group).

efficiency of the explicative models we tried to build.[1] The yearly evolution of mean diameter increments at Paracou is illustrated in Fig. 2 for the 4 groups of plots: T0 (control plots), T1 (logging for timber), T2 (logging for timber + poison-girdling), T3 (logging for timber and fuelwood + poison-girdling). Let us recall that the treatments were applied between the end of 1986 and the beginning of 1988. During this period, on a mean basis, the plots of T1 lost 19.9% of their trees and 18.9% of their basal area (20.8% and 36.4% for T2, 32.1% and 45.2% for T3, respectively): see Part I for a detailed presentation of plots, treatments and measurements, and Part IV, Chapter 5, Table 1, for the evolution of density and basal area in the different groups of plots.

Each year, the girth of trees is measured at breast height (1.30 m) and rounded up or down to the nearest centimetre. Growth being evaluated through diameter increments, in order to limit the effects of year-to-year measurement inaccuracy and errors, it is worth working with time steps of more than 1 year. In the following text, we use 3-year time steps as often as possible (see Gourlet-Fleury, 1997 for a justification), except before the silvicultural treatments, where only two annual periods were available.

Four periods are thus accounted for:

- 1984-1986, which allows the estimate of mean annual diameter increments (ΔD, in cm/year) in undisturbed stands on all the plots. ΔD is calculated as a simple mean using the measurement values of 1984 and 1986;
- 1988-1991, 1991-1994 and 1994-1997, periods following the silvicultural treatments. For those periods, ΔD is smoothed by linear regression: for each tree, we fit the model $D(t) = \Delta D^{*} t + c$ (with *c* constant), using data from the 4 successive years of each period.

In all cases, diameter increments are calculated only for those trees showing no anomaly on their trunks during the period concerned. Note that increment values can be negative due to (i) water stress linked to season, competition, injury or disease (Durrieu de Madron, 1993; Prévost and Puig, 1981) and (ii) measurement errors, even if the smoothing of ΔD through regression limits the risk. In the following

---

[1] A model of height growth was, however, developped at Paracou, on the basis of theoretical considerations of growth processes; see Chapter 6, Part IV, or Picard et al. 2001.

text, we consider only those trees with increments exceeding –0.2 cm/year.

2.2. Climate

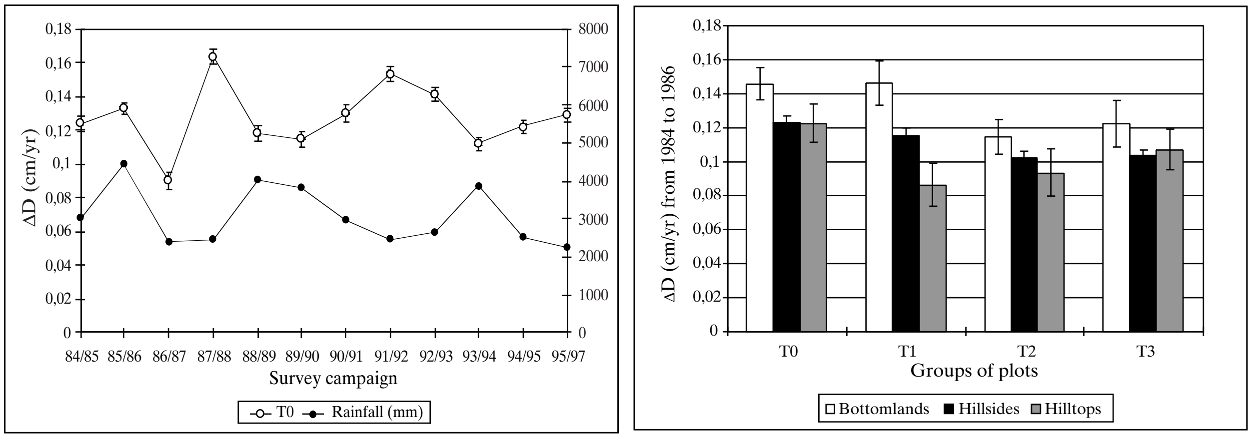
The main parameter available at Paracou is the amount of rainfall, monitored near the camp on a weekly and, more recently, on a daily basis. Fig. 3a shows the evolution of rainfall cumulated between September of one year and August of the next year, that is to say between two successive inventories of the trees. This is compared to the evolution of yearly diameter increments on the control plots. If the two periods 1985/1986 and 1986/1987 are omitted, a negative correlation appears between the two series of data (Pearson correlation coefficient: $r = -0.69$, $P = 0.028$), as well as an apparent periodicity in the two phenomena. Peaks in rainfall tend to be followed by peaks in increments 2 years later: the successive values of the Pearson correlation coefficient between mean diameter increments and rainfall at year t-1, t-2 and t-3 are respectively –0.59 ($P = 0.071$), 0.80 ($P = 0.010$) and 0.41 ($P = 0.307$). It must be noted that the evolution of density and basal area on the control plots, being almost monotonous, cannot explain by itself the periodicity observed in the increments.

Relationships and periodicity are less pronounced in the treated plots, due to other important influencing factors linked to the silvicultural disturbances. However, despite the stimulating effects of logging and thinning, a relative decrease in diameter increments is clear over the period 1988-1991 (Fig. 2), the same as for the control plots. Maximum increments are reached during the period 1991-1994 for T2, as in T0, but are delayed one year for T1 and 2 years for T3 for non-evident reasons. This could be a combined effect of treatments and rainfall.

2.3. Topography and soils

At Paracou, the soils have been described only on five of the plots, with differing levels of detail (see Part I for more information). To date, the only systematic information we can use on the whole experimental area is topography, known from 5 m contour lines. From Barthès' (1998) studies on the five above-mentioned plots, we know that:

- bottomlands (slope ≤ 10° and altitude ≤ 5 m) are preferentially associated with deep sandy soils, permanent water layers, hydromorphy at the top of the soils and low carbon levels;
- hillsides (slope > 10° whatever the altitude) are preferentially associated with superficial soils and thus low water stocks;



(a) **(b)**

Fig. 3. Apparent links between mean diameter increments and two abiotic factors. (a) Yearly increments on the control plots (T0) versus annual rainfall. More than 10,000 trees are used to calculate means and 95% confidence intervals each year. (b) Mean diameter increments between 1984 and 1986 (before the implementation of treatments) and topography, on the basis of groups of plots. For each group, more than 900 trees, 7000 trees and 500 trees respectively in the three categories of landfacets are used to calculate means and 95% confidence intervals.

- hilltops (slope = 0, altitude > 5 m) are often characterized by deeper soils and high carbon contents, and sometimes by tracks of hydromorphy at the top of the soils.

Prévost and Puig (1981) underlined the importance of water availability for tree growth in the forests of French Guiana, especially during the critical period of the dry season (see also the review by Barthès, 1990). According to their results and to Barthès' observations, we could expect mean diameter increments to be higher in bottomlands and lower on hillsides. This is confirmed by the results at Paracou for undisturbed stands (Fig. 3b).

In all the groups of plots, the topographic effect on mean diameter increments is significant (T0: $F_{(2,\infty)} = 12.16$, $P = 0.0001$; T1: $F_{(2,\infty)} = 22.83$, $P = 0.0001$; T2: $F_{(2,\infty)} = 3.50$, $P = 0.030$; T3: $F_{(2,\infty)} = 4.60$, $P = 0.010$), even if less pronounced in T2 and T3. Bonferroni tests (multiple comparison of means) indicate bottomlands as being the place where increments are higher. Except in T1, hillsides and hilltops do not prove significantly different (note however that mean increments are far better estimated on hillsides, covering most of the area of the plots, which can induce a bias in the analysis). In T1, increments are significantly lower on hilltops.

After the implementation period of the silvicultural treatments, the topographic effect remains significant except in T2, and bottomlands are still the most favourable places in all cases.

2.4. Position in the stand

The "good or poor effect position", or social status in the stand (cf. Fig. 1) mainly refers to the social relationships between a tree and its neighbours, on which the access to light, water and nutrients depends. It is expected to (i) be sensitive, to a certain extent, to the global characteristics of the stand: density and basal area (high densities and/or basal areas are supposed to induce higher competition for the resources); (ii) vary greatly with silvicultural operations, which tend to alleviate all kinds of competition pressure (competition for light, space, soil resources) through the elimination of the biggest trees and a general decrease of density. We thus examine, in a first rough approach, the plot and treatment effects on diameter increments (see Figs. 4 and 5).

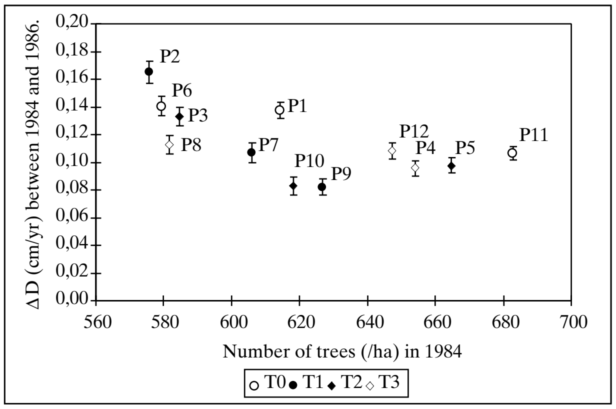


Fig. 4. Position of the plots according to their density in 1984 and their mean diameter increments before implementation of the treatments. Means are plotted with their 95% confidence interval.

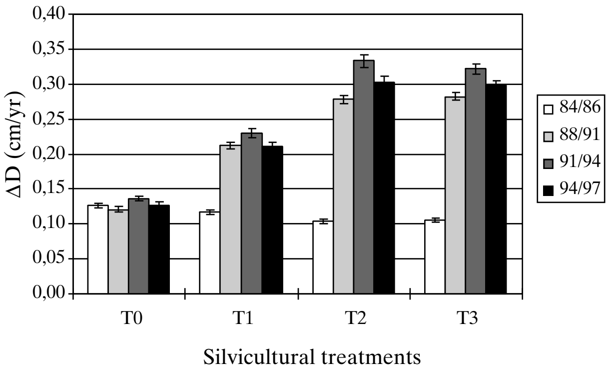


Fig. 5. Mean annual diameter increment (cm/year) according to the treatment and period of time studied. Treatments were applied between the end of 1986 and the beginning of 1988.

2.4.1. The period 1984-1986

Before the application of the treatments, mean annual diameter increments at Paracou varied between 0.082 and 0.165 cm/year (in P9 and P2, respectively) (see Fig. 4). The plot effect is highly significant (one-way analysis of variance: $F_{(11,\infty)} = 59.43$, $P = 0.0001$). Roughly speaking, if compared to the situation of the plots as described in Fig. 12, Part I, the lowest mean increments are observed on plots with high total density of trees (P4, P5, P11) or high densities of trees in the mean diameter classes (P7, P9), while the highest mean increments are observed on the less dense plots (P2, P6), P10 and P1 being noticeable exceptions in each category. A significant negative relationship exists between mean increments and densities on the 12 plots (Pearson correlation coefficient: $r = -0.61$, $P = 0.036$), while the link with cumulated basal area is not significant ($r = -0.46$, $P = 0.135$).

Note. We saw in Part I that the treated plots were chosen at random inside three more or less homogeneous blocks, defined in 1985 according to the size structure characteristics of the main valuable species. They were block 1 (P1, P2, P3, P8), block 2 (P6, P7, P10, P12) and block 3 (P4, P5, P9, P11). A hierarchical analysis of variance "plot(block)" shows a significant effect of both block and plot on increments ($F_{(2,\infty)} = 167.72$, $P = 0.0001$, mean square of errors $MSE_{block}/MSE_{plot(block)} = 4.74$ to be compared to $F_{0.05(2,9)} = 4.26$), but the effect mainly comes from plots, showing that complete homogeneity inside blocks was not achieved. The principle of choosing plots at random inside blocks should have guaranteed the lack of any "treatment effect" on increments before the implementation of treatments. In fact, there is a significant effect of treatment (i.e. the grouping of plots according to the treatment they were to receive), and a Bonferroni test of multiple comparison of means separates three groups: T0 (greatest increments), T1 (intermediate increments) and T2/T3 (lowest increments) (see Fig. 5). This effect, however, is only a plot effect as shown by the results of a hierarchical analysis of variance "plot(treatment)" ($F_{(3,\infty)} = 34.05$, $P = 0.0001$, $MSE_{treatment}/MSE_{plot(treatment)} = 0.51$, to be compared to $F_{0.05(3.8)} = 4.07$).

2.4.2. Post-treatment periods

Mean diameter increments systematically increased after disturbance, whatever the intensity of the treatment (see Figs. 2 and 5). Between 1988 and 1991, increments were multiplied by 1.8 in T1 and by 2.7 both in T2 and T3. They still increased during the following period (1991-1994): twofold in T1 and more than threefold in T2 and T3 compared to the 1984-1986 period. A slow down is noticeable in the period 1994-1997, increments, however, remaining at least at the level of 1988-1991.

The treatment effect is highly significant in all cases (1988-1991: $F_{(3,\infty)} = 888.13$, $P = 0.0001$; 1991-1994: $F_{(3,\infty)} = 783.66$, $P = 0.0001$; 1994-1997: $F_{(3,\infty)} = 793.95$, $P = 0.0001$). Bonferroni tests systematically separate T0 as the group of plots where increments are the lowest, T1 as an intermediate group and T2/T3 as a group showing the highest increments. The t-tests performed on paired data (increments before and after treatment, for trees remaining alive between 1984 and 1997) confirm that increments in treated plots are significantly higher, not only compared to the control plots, but also compared to the situation in the plots themselves before disturbance.

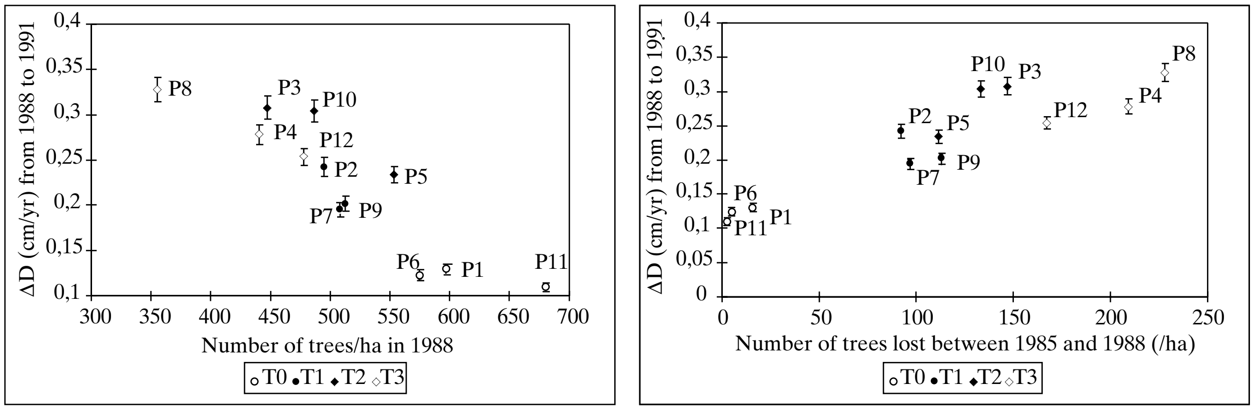
For the three periods, a hierarchical analysis of variance "plot(treatment)" shows that the differences observed come both from a real treatment effect and from a plot effect ($MSE_{treatment}/MSE_{plot(treatment)} = 18.51$, 9.38 and 13.0 respectively for 1988-1991, 1991-1994 and 1994-1997, values to be compared to $F_{0.05(3.8)} = 4.07$). This is illustrated for the 1988-1991 period in Fig. 6a, b, where each plot is represented according to its density in 1988 (respectively, the number of trees lost during the treatments) and the mean value of diameter increments from 1988 to 1991. On a mean basis, the more intensive the treatment, the lower the final density, but great variability occurred among the plots inside the treatments, with some visible inconsistencies as for P4 or P12 vs. P3 and P10, or P2 vs. P5.

It is very important to notice that, whatever the period, mean diameter increments are not significantly different in treatments 2 and 3. It seems that decreasing the density through silvicultural operations in order to relieve competition cannot produce results beyond a certain limit, probably due to local microclimate modifications hindering photosynthetic processes (see further).

2.5. Phenotype

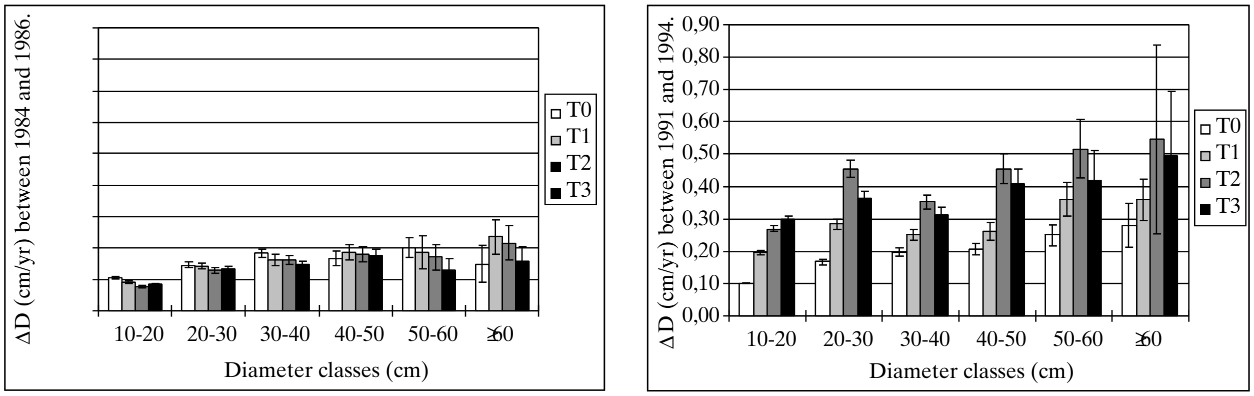
This factor is assessed by the only dendrometric variable systematically available at Paracou, that is to say DBH.

In undisturbed stands, a significant effect of the diameter class on diameter increments can be shown globally ($F_{(5,\infty)} = 245.92$, $P = 0.0001$) as well as inside each plot group (see Fig. 7). Bonferroni tests systematically separate the first diameter class, 10-20 cm, as the one where increments are the lowest and, depending on the treatment, the three classes 40-50, 50-60 and ≥ 60 cm (sometimes together with the 30-40 cm class) characterised by the highest increments. This is consistent with what we know about the height development of the trees (Collinet, 1997; King, 1996): the "liberation point", that is the height at which the trees are freed from the limiting



(a) **(b)**

Fig. 6. Position of the plots according to (a) their density in 1988 or (b) the number of trees they lost during the treatments, and the mean diameter increments after the treatments were implemented. Means are plotted with their 95% confidence interval.



(a) **(b)**

Fig. 7. Mean diameter increments according to diameter classes and treatments before (a) and after (b) the implementation of treatments. Means are represented with their 95% confidence interval. Note that means are far better estimated in the small classes where trees are numerous. In the ≥ 60 cm class, more than 150 trees were used in each group of plots, but after treatment, only 11 and 15 trees could be used in T2 and T3 respectively for the calculations.

light factor, corresponds for most sub-canopy and canopy species to the class 25/30-40 cm DBH. In the lower classes, the "$H = 100*D$" relationship established by Oldeman (1974) is more or less respected; height growth prevails upon diameter growth and trees are highly sensitive to competition for light. In the upper classes, diameter growth prevails upon height growth and trees are more sensitive to competition for water and nutrients (Gourlet-Fleury, 1998, and see Section 3 hereafter).

After the implementation of the treatments, the diameter effect remains significant in all the groups of plots, whatever the period considered: the first diameter class still shows the lowest increments, while the classes 40-50 cm and 50-60 cm exhibit the highest increments (the class ≥ 60 cm being excluded from the analysis due to the low numbers of individuals). The first diameter class (10-20 cm) is the most sensitive to the treatments, with the highest multiplicative factors between 1991 and 1994, reaching 3.5 in T2 and 3.6 in T3. However, it is striking to see that in all the classes the reaction is clearly positive: trees already present in the canopy are able to benefit from the opening of the stands.

The t-tests performed on paired data allowed to conclude that the treatment effect on increments is long lasting in all the diameter classes, even if a slow down is detectable between 1994 and 1997 in the first class. This slow down can be explained by the massive arrival of pioneer trees (see Chapter 5, this Part), which compete mainly, in the first stage, with the small trees.

2.6. Genotype

Information is collected at Paracou to study the state and evolution of the genetic diversity of a limited number of species (see Part III). The data, which are adapted to the study of gene flows, will probably never be useful for growth studies. The only information that can be used on a systematic basis is the allocation to a "species", with some limitations due to the relative lack of accuracy of botanical descriptions on the site (200 species or groups of species (SGS) determined, whereas the real number of species present is believed to reach 600: see Part I).

The contrasted growth behaviour of species is well known and has long been documented (see Favrichon, 1994, 1995 for an extensive review), an opposition being frequently made between fast-growing pioneers, highly heliophilous, also called "hard gamblers" by Oldeman and Van Dijk (1989) and slow-growing shade-tolerant species or "hard strugglers". In fact, species are distributed along a continuum between these two extremes, as illustrated in Fig. 8.

Not surprisingly, the SGS effect on increments at Paracou is highly significant in all the groups of plots, whatever the period considered. For 1984-1986, the results of one-way analysis of variance performed with 87 SGS well represented over the whole area are the following: $F_{(86,\infty)} = 19.51$, $P = 0.0001$ (T0), $F_{(86,\infty)} = 20.50$, $P = 0.0001$ (T1), $F_{(86,\infty)} = 21.44$, $P = 0.0001$ (T2), $F_{(86,\infty)} = 19.51$, $P = 0.0001$ (T3). The values of F are multiplied at least by three after the treatments, some species being far more sensitive than others to the opening of the stands.

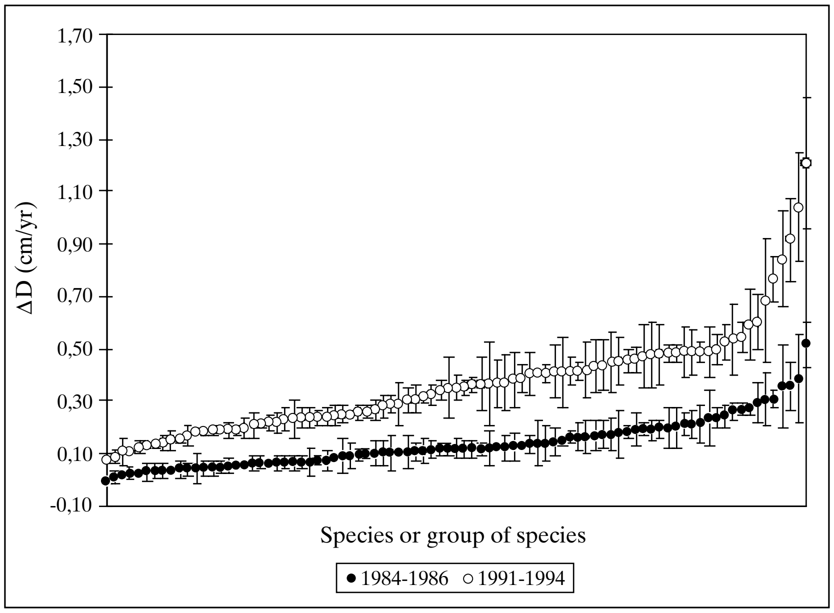


Fig. 8. Mean diameter increment of 87 SGS before and after implementation of the treatments, in the six plots of T2 and T3. SGS are ranked by mean diameter increment. Note that the rank of each SGS does not necessarily match between the two periods. Means are associated with their 95% confidence interval. There is a minimum number of 20 trees per SGS.

2.7. The problem of interactions

As underlined on Assmann's diagram (Fig. 1), each of the previously examined factors interacts with the others. We saw an example with annual rainfall, which probably interacted with the effects of the treatments. The global structure of a stand is influenced by the characteristics of the substrate (Paget, 1999, discussed in Part I), which also have more local effects: bottomlands, for instance, are preferentially occupied by particular species, either because they are better adapted to these special conditions or because they are less competitive elsewhere. Density and basal area are less important in these places and trees are usually smaller. Good or poor effects of position of a tree in a stand depends on its diameter and the species it belongs to, but also to a certain extent on the global structure of the stand, thus indirectly on the substrate. Belonging to a species possibly gives information on the diameter (usually small in species of the understorey, for example!) and in some cases on the place where it does, or more frequently does not, grow.

The rigorous assessment of the effect of each factor on diameter increments would require controlling all the others, which is simply impossible in such heterogeneous stands. Bottomlands provide a good example of this difficulty. The higher increments that are observed in this landfacet can be explained either by the maintenance of a water stock during the dry season, by the belonging of the trees to certain species or by lower densities, that is to say lower competition levels. Comparisons with other landfacets should thus be made for the same species, diameter class and density conditions, but most often the number of individuals that match all these conditions is too small.

To overcome this problem, a possible way is to progressively "eliminate" the influence of each factor before examining the next one. That is to say, to build models incorporating step by step these factors as explicative variables, and then to study the effect of the next factor on the residuals of the models. This is one of the objectives of a modelling programme that began in 1992 at Paracou and is still going on. We focus, in the next paragraph, on the results established by the individual-based, spatially explicit approach of this programme.

3. Modelling diameter increments: an integrative approach

We summarise here the modelling work extensively presented in Gourlet-Fleury (1997, 1998), Gourlet-Fleury et al. (1999), Gourlet-Fleury and Houllier (2000) before discussing its main limitations, particularly in the light of a test performed on a new data set (namely data from the period 1994 to 1997).

Other attempts to explain the individual diameter increments with a modelling approach were also made by Mercier (1997) and Picard (1999). Contrary to Gourlet-Fleury (1997) and Gourlet-Fleury et al. (1999), the authors did not try to explore in a systematic way the effects that may influence the diameter growth. They rather relied on a priori assumptions of what the growth process was, and focused on specific explanatory variables: the available area around trees for Mercier, and a one-sided local index of competition for light for Picard (see Chapter 6, this Part, Section 2.1.2, the description of the "L" variable). Both attempts were thus less successful in explaining the variability of diameter increments.

3.1. Building an individual-based, spatially explicit model

A first step consisted in evaluating and quantifying the "good or poor position" of a tree more accurately than by the mere use of the variables "global density" and "basal area" at the stand scale, which could only be justified in homogeneous stands (Franc et al., 2000). This led us to identify some efficient competition indices based on the local number and diameter of the neighbours of each tree, and to acknowledge the importance of:

- the past local dynamics around a tree: local densities being equal at a given moment, a tree grows better if some of its neighbours disappeared during the previous years.
- The diameter of the tree, i.e. its developmental stage: (i) the competition indices that we studied are only weakly linked to the diameter increments in intermediate classes (25/30-40 cm). This can be explained by the diversity of the status encountered in those classes. Trees belonging to the understorey species reach their maximum size, while trees belonging to the overstorey species are in the process of reaching the canopy. Diameter increments are likely to

depend on this status before being sensitive to competition indices that do not take height into account. (ii) One-sided competition indices (mostly integrating competition for light) are as efficient as two-sided competition indices (integrating competition pressure on all types of resources: light, water and nutrients) in small diameter classes, while big trees are mainly sensitive to two-sided competition.

- The species considered, being more or less sensitive to different types of competition according to its temperament.

In a second step, we searched for an adequate formulation of a model integrating diameter and competition indices as our first explicative variables, and decided to follow the functional "potential × modifier" approach. In this category of models, growth is described as:

- a function of intrinsic tree and site potentialities, "potential growth", frequently adjusted by a sigmoid curve, which can be biologically interpreted. We retained the Korf equation, also known as the Lundqvist-Matern equation (Zeide, 1993), as well as the more parsimonious Gompertz equation (with two parameters instead of three) as the most suitable for our data;
- modified by the effect of tree local environment (e.g. stand density and/or tree-to-tree competition for resources). The "modifier" component is usually a more or less complex function of empirical competition indices, which are supposed to account for resource partitioning among trees.

The third step was the calibration work. We focused on 8 of the 12 plots, two plots per treatement, in order to keep an independent data set for validation work. We also focused on two particular periods: (i) the 1985-1988 period covering the completion of silvicultural operations was used to calculate dynamic competition indices (NBD, NBT, see later in text) rendering the evolution of local density, which was expected to be the most contrasted during this period; (ii) the 1988-1991 period was used to calculate the tree increments. As this second period followed the silvicultural disturbances, tree reactions to the modification of their environment were also expected to be the most contrasted. As a consequence, the growth model has a 3-year time step.

Adjustments were made by ordinary least square regression after log-transformation of the dependent variable, diameter increment. Instead of using two separate data sets to estimate the parameters of "potential growth" and "modifier component" respectively, as usually done by modellers, we directly fitted complete models to our whole set. This changes the initial meaning of "potential" and "modifier" a little: according to the values of the competition indices, the modifier component can be greater than 1 (indicating a favourable environment which stimulates growth) or less than 1 (indicating a competitive environment which decreases growth). The potential component then represents the growth of a tree in a "neutral" environment, with a modifier value of 1.

3.1.1. Relating diameter increment, diameter and local environment

The best model relating this set of factors was found to have the following expression (see Fig. 9 for an illustration):

$$\begin{aligned}\mathrm{Log}(\Delta D + 0.287) = a' + \Big[&\mathrm{Log}(m) + \mathrm{Log}(D) \\ &+ \Big(1 + \frac{1}{m}\Big)\mathrm{Log}[\mathrm{Log}(K) - \mathrm{Log}(D)]\Big] \\ &+ [b\mathrm{Log}(\mathrm{NBD} + 1) + c\Delta\mathrm{NBD} \\ &+ d(\Delta\mathrm{NBD})^2] + \varepsilon \qquad [1]\end{aligned}$$

with

$$\begin{aligned}\mathrm{Log}(\text{potential}) = \mathrm{Log}(a) + \mathrm{Log}(m) + \mathrm{Log}(D) \\ + \Big(1 + \frac{1}{m}\Big)\mathrm{Log}[\mathrm{Log}(K) - \mathrm{Log}(D)]\ \text{(Korf model)},\end{aligned}$$

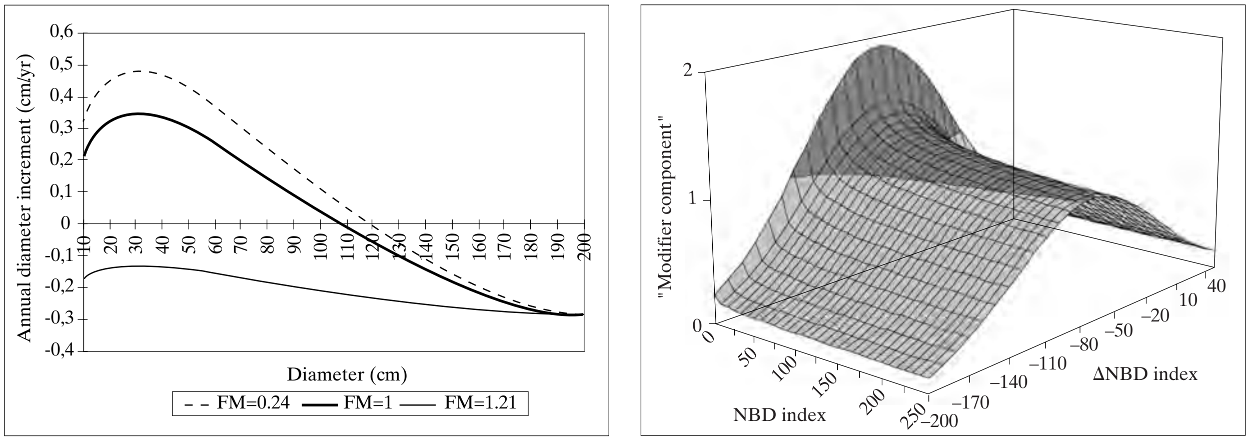
$$\begin{aligned}\mathrm{Log}(\text{modifier}) = [b\mathrm{Log}(\mathrm{NBD} + 1) + c\Delta\mathrm{NBD} \\ + d(\Delta\mathrm{NBD})^2 + e]\end{aligned}$$

and $a' = \mathrm{Log}(a) + e$.

D is the DBH in 1988, immediately after the completion of silvicultural treatments, ΔD the annual diameter increment of the tree, smoothed over the period 1988-1991 (cm/year). The constant 0.287 was added to ΔD in order to take the negative values of diameter increment into account (for a thorough discussion about the effect of this translation, see Gourlet-Fleury, 1997). NBD and ΔNBD are one-sided competition indices:[2] NBD is the total number

---

[2] NBD refers to « NomBre de voisins Dominants » in French. This notation is kept in order to be consistent with the thesis work of Gourlet-Fleury (1997) and to facilitate the task of readers.



(a) **(b)**

Fig. 9. Characteristics of the diameter growth model. (a) Domain of variation: FM is the value taken by the modifier component (0.24: minimum, 1.21: maximum, according to the values taken by NBD and ΔNBD in our calibration data set). FM = 1 indicates the neutral situation. (b) Behaviour of the modifier component according to the values simultaneously taken by the indices NBD and ΔNBD (taken from Gourlet-Fleury and Houllier, 2000).

of neighbours with a DBH greater than or equal to the subject in 1988 and located less than 30 m from it; ΔNBD is the past variation of the NBD index, that is to say 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 – occurred; positive values, on the contrary, result from a better growth of the neighbours and render an increase in competition. ΔNBD is particularly efficient in rendering the effect of silvicultural treatments. The behavior of the "modifier", that is the function of NBD and ΔNBD that modulates tree growth is illustrated in Fig. 9b.

a, m and *K* are the parameters of the Korf model: *a* is the inverse of a time constant, *m* regulates the location of the inflexion point and *K* is the maximum value *D* can reach. *b, c,* d and *e* are the other regression parameters (*a* and *e* cannot be estimated separately, and have therefore been grouped into one single parameter *a′*). Their values, all significantly differing from zero, are reported in the Annex (Table 1). The behaviour of the "potential component" is illustrated in Fig. 9a, for three different values of the "modifier" (noted "FM" on the Figure).

This model explains 23% of the variability observed on the logarithms of the increments (pseudo – $R^2 = 1 - [\mathrm{SSR}/\mathrm{CSS}] = 0.230$, with sum of squared residuals (SSR) = 1320 and centred sum of squares (CSS) = 1715) and exhibits some interesting properties: (i) the modifier always decreases when NBD increases, that is, individual growth decreases when stand density increases; (ii) the relation between the modifier and ΔNBD is a second-order polynomial. For high positive values of ΔNBD, growth logically decreases. When NBD decreases or ΔNBD takes negative values (for example, as a consequence of silvicultural treatments), the modifier first increases and so does the growth, but only to a certain point: if too many neighbours disappear, then growth is slowed. This is consistent with what is observed at Paracou in T3, where increments are not significantly different from those registered in T2 (see Fig. 5), or along the recently opened roads where rapid death of trees on the border lines currently occurs.

Diameter classes still have as light significant effect on the residuals of this model ($F_{(4,\infty)} = 2.84$, $P = 0.023$, to be compared to the results of a one-way analysis of variance on the logarithms of the increments on the same data set: $F_{(4,\infty)} = 72.19$, $P = 0.0001$) but: (i) there is no logical ordering of the diameter classes according to the mean of the residuals, and (ii) tests of multiple comparisons of means do not separate the classes. The competition indices correctly account for the treatment effect, as shown by a hierarchical analysis of variance "plot(treatment)" ($\mathrm{MSE}_{\mathrm{treatment}}/\mathrm{MSE}_{\mathrm{plot(treatment)}} = 2.80$, value to be compared to $F_{0.05(3.4)} = 6.59$), but a significant plot effect remains. This plot effect is, as expected, accompanied by a strong and distinct species effect (results of a two-ways analysis of variance with interaction, see Gourlet-Fleury and Houllier, 2000).

3.1.2. Taking species information into account

As it was not possible to fit a growth model to each species encountered, we concentrated on building species groups with diameter increment as homogeneous as possible. We first tried to use Favrichon's work (1994, 1995), which defined five ecological groups based on the size structure of species populations and on their diameter growth in both control and treated plots: (1) understorey shade-tolerant, (2) canopy shade-tolerant, (3) emergent mid-tolerant, (4) canopy shade-intolerant and (5) pioneer taxa. We fitted specific growth sub-models for each of those groups, but efforts to eliminate the species effects on the residuals remained unsuccessful. We thus iteratively modified this first classification until we reached a point where no residual species effect remained.[3] This gave us 15 "growth groups", aggregated into five super-groups defined by species maximum size and species sensitivity to social position (summarized in Table 1).

Diameter increments in these 15 groups are described by "potential × modifier" sub-models adapted to each case: according to the species group considered and its sensitivity to the social status, modifiers were built with one-sided or two-sided competition indices. Those modifications caused model [1] to be less efficient than a more simple Gompertz model in several cases, and this led us to modify the expression of the potential component. For all the groups we thus remained with:

$$\mathrm{Log}(\Delta D + 0.287) = \mathrm{Log}(\mathrm{potential}) + \mathrm{Log}(\mathrm{modifier}) + \varepsilon$$

$$\text{with} \quad \mathrm{Log}(\mathrm{potential}) = \mathrm{Log}(a) + \mathrm{Log}(D) + \mathrm{Log}[\mathrm{Log}(K) - \mathrm{Log}(D)] \quad \text{(Gompertz equation)} \quad [2]$$

and 7 possible formulations of the modifier component, using various competition indices (see Table 2 in the Annex for a definition of the groups and a link with the modifiers):

$$\mathrm{Log}(\mathrm{modifier}) = b(\mathrm{NBD})^{1/2} + c\Delta\mathrm{NBD} + d(\Delta\mathrm{NBD})^2 + e \quad [\mathrm{M1}]$$

$$\mathrm{Log}(\mathrm{modifier}) = b(\mathrm{NBD})^{1/2} + c\Delta\mathrm{NBD} + d(\Delta\mathrm{NBT})^2 + e \quad [\mathrm{M2}]$$

$$\mathrm{Log}(\mathrm{modifier}) = b\mathrm{Log}(\mathrm{NBD} + 1) + c\Delta\mathrm{NBD} + d(\Delta\mathrm{NBT})^2 + e \quad [\mathrm{M3}]$$

$$\mathrm{Log}(\mathrm{modifier}) = b\mathrm{NBD} + c\Delta\mathrm{NBD} + d(\Delta\mathrm{NBD})^2 + e \quad [\mathrm{M4}]$$

$$\mathrm{Log}(\mathrm{modifier}) = c\Delta\mathrm{NBD} + d(\Delta\mathrm{NBD})^2 + e \quad [\mathrm{M5}]$$

$$\mathrm{Log}(\mathrm{modifier}) = c\Delta\mathrm{NBD} + d(\Delta\mathrm{NBT})^2 + e \quad [\mathrm{M6}]$$

$$\mathrm{Log}(\mathrm{modifier}) = c\Delta\mathrm{NBD} + e \quad [\mathrm{M7}]$$

D, ΔD, NBD and ΔNBD are defined as for model [1]. NBT is the total number of neighbours ≥ 10 cm DBH located less than 30 m from the subject tree,[4] in 1988 (two-sided competition index). ΔNBT is the past variation of the NBT index, that is to say between 1985 and 1988. a and K are the parameters of the Gompertz model and are defined as for the Korf model. b, c, d and e are the other regression parameters (a and e cannot be estimated separately, and have therefore been grouped into one single parameter a'). Their values, all significantly differing from zero, are reported in the Annex (Table 2) for each group. We will further refer to this set of equations as model [2].

All these models exhibit the same type of behaviour as model [1]. Particularly important, the K parameter could be estimated more realistically and, in all but two cases, more accurately. Fig. 10 illustrates the growth curve of five of the groups in a simplified case where the modifier component is set to 1 (neutral environment). According to the respective values of the parameters a' and K, a distinction can be made between: (i) species which quickly reach their asymptotic size (e.g. groups g4.1 or g5.1) and the others, and (ii) species which reach the canopy and emerge (e.g. group g3.2) or which stay in lower strata.

---

[3] Details about the species grouping and the method used to build the sub-models will be found in Gourlet-Fleury (1997), pp. 119-133.

[4] NBT refers to "NomBre Total de voisins" in French. See note 2 for justification.

Table 1

Brief description of the 15 groups defined with the growth modelling approach. See the complete description in Annex, Table 2. Inside each supergroup, subgroups differ by the mean value of the model [1] residuals

Main groups	*Group 1*	*Group 2*	*Group 3*	*Group 4*	*Group 5*
Description	Species of small potential size, showing low sensitivity to social status	Species of medium to large potential size, showing low sensitivity to social status	Species of large potential size, showing medium to high sensitivity to social status	Species of medium to large potential size, showing medium to high sensitivity to social status	Species of small potential size, showing medium to very high sensitivity to social status
Subgroups	*4*	*4*	*2*	*2*	*3*
Representative species	g1.1 *Catostemma fragrans* Bentham (Bombacaceae)	g2.1 *Bocoa prouacensis* Aublet (Caesalpiniaceae)	g3.1 *Qualea rosea* Aublet (Vochysiaceae)	g4.1 *Recordoxylon speciosum* (R. Ben) Norm. and Marq (Caesalpiniaceae)	g5.1 *Drypetes variabilis* Uittien (Euphorbiaceae)
	g1.2 *Iryanthera sagotiana* (Bentham) Warburg (Myristicaceae)	g2.2 *Lecythis poiteauii* Berg (Lecythidaceae)	g3.2 *Sclerolobium melinonii* Harms (Caesalpiniaceae)	g4.2 *Symphonia globulifera* Linnaeus f. (Clusiaceae)	g5.2 *Couepia* cf. *caryophylloïdes* R. Ben (Chrysobalanaceae)
	g1.3*	g2.3 *Licania* cf. *micrantha* Miq (Chrysobalanaceae)			g5.3 *Inga cayennensis* Sagot ex Bentham (Mimosaceae)
	g1.4 *Sloanea* cf. *guianensis* (Aublet) Bentham (Elaeagnaceae)	g2.4 *Eperua falcata* Aublet (Caesalpiniaceae)			

*This group gathers a lot of uncorrectly identified species belonging to the genus *Licania*.

There is a rough agreement between Favrichon's classification and this one, especially for extreme behaviours like shade-tolerance in the understorey (groups g1.1-g1.4) and shade-intolerance of pioneers (group g5.3). However, considering the sensitivity of the trees to social position through competition indices led us to different conclusions regarding the "shade-(in)tolerance" character of the species examined (see Gourlet-Fleury, 1997; Gourlet-Fleury and Houllier, 2000 for more details). Compared to model [1], which could explain 23% of the variability observed on the logarithms of the increments, the model based on Favrichon's species classification and the model based on our species classification led respectively to a pseudo – R^2 of 0.370 and 0.416 on the same data set, which represents a definite improvement.

3.1.3. Trying to incorporate the plot effect

We still observe on the residuals of model [2] a significant plot effect (for the eight calibration plots:

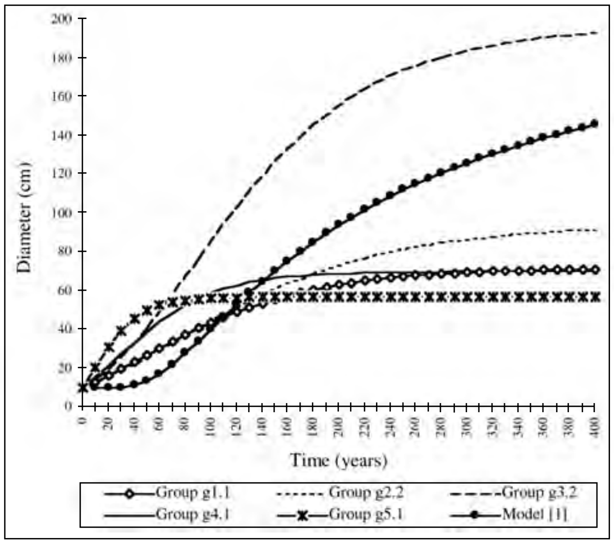


Fig. 10. Potential component of the growth sub-models fitted to 5 of the 15 species groups, and comparison with the potential component of the average model [1]. Trees are assumed to grow in a "neutral environment", that is, the modifier component value is set to 1. Note that the data set has been translated before fitting (the dependent variable is Log(ΔD + 0.287)), to take negative growth values into account (taken from Gourlet-Fleury and Houllier, 2000).

$F_{(7,\infty)} = 26.19$, $P = 0.0001$, to be compared to the results of a one-way analysis of variance on the logarithms of the increments on the same eight plots during the period 1984-1986: $F_{(7,\infty)} = 63.40$, $P = 0.0001$). A Bonferroni test significantly separates P10 as the plot where the increments are the most underestimated, followed by the group P1/P6. The other plots do not significantly differ from each other. Fig. 11 illustrates the relative position of each plot according to the mean value of the model residuals and the mean density at the beginning of the experiment in 1984, or the logging intensity. The model was used to predict the increments of the trees during the period 1988-1991 on the four validation plots: they are plotted for comparison on the same figure.

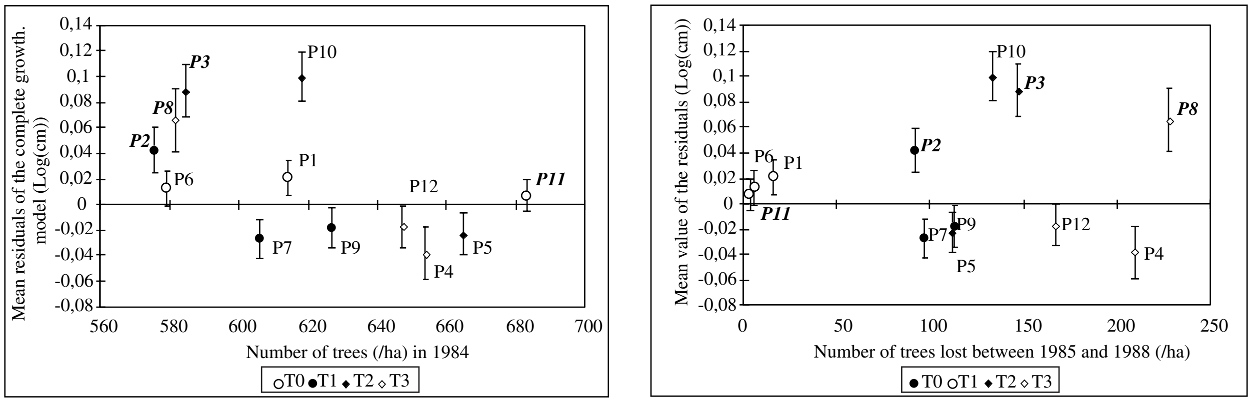
The comparison of Fig. 11a with Fig. 4 reveals striking similarities. With the exception of plot P10, the relative position of each plot is almost the same, and this is also true for the four validation plots.[5] It is as if our complete growth model had strictly taken into account the disturbance effects linked to the silvicultural treatments (as well as the interactions between treatments and species), as is revealed on Fig. 11b, and had left the initial plot effect untouched.

We interpret this plot effect as a substrate effect, but we are unfortunately limited in the investigation of this hypothesis by the restricted body of knowledge available at Paracou. The level of soil descriptions carried out on the site (see Part I) is altogether incomplete and insufficiently detailed to allow significant progress in the explanation of growth. The only information that can be used on a systematic basis deals with the landfacets, as we saw in Section 2.3. The factor "landfacets" still has a significant effect on the residuals of the complete model (for the eight calibration plots: $F_{(2,\infty)} = 9.64$, $P = 0.0001$, to be compared on the same data set to the results of a one-way analysis of variance on the logarithms of the increments: $F_{(2,\infty)} = 5.43$, $P = 0.0044$). Increments prove to be significantly underestimated in bottomlands and, in the case of the eight calibration plots, significantly overestimated on hilltops. There is no bias in the prediction of increments on hillsides, which may not be surprising as this landfacet covers most of the site.

We tried to integrate the landfacet information in our model in the following way (Gourlet-Fleury and Houllier, 2000): (i) we defined three dummy variables: f_1 for the bottomlands, f_2 for the hillsides and f_3 for

---

[5] The particular situation of plot P10 was discussed in detail in Gourlet-Fleury (1997). We still do not have any satisfactory explanation of the behaviour of this plot. It cannot be excluded that this is an artefact resulting from a poor specification of the model.



(a) **(b)**

Fig. 11. (a) Position of the plots according to their density in 1984 and the mean value of the residuals of the complete growth model. (b) Position of the plots according to the intensity of the silvicultural treatments and the same mean value of the residuals. Means are plotted with their 95% confidence interval. Plots in bold italic type are the validation plots, not taken into account for the parameters estimation phase.

the hilltops. (ii) We assumed that favourable site conditions had an effect on the potential component of the increment model, more exactly on parameter a which, in the Korf as well as in the Gompertz model, regulates the time needed to reach the asymptote (i.e. the maximum diameter, for a tree). (iii) For each of our 15 species groups, we tried to fit the following model:

$$\mathrm{Log}(\Delta D_k + 0.287) = \mathrm{Log}(D_k) + \mathrm{Log}[\mathrm{Log}(K_k) - \mathrm{Log}(D_k)] + \mathrm{Log}(\mathrm{FM}_k) + \sum_{s=1}^{3} f_s a'_{s,k}$$

where subscript k refers to species groups, subscript s to topographical situations, and FM_k is the modifier component adapted to each group.

We could estimate all the parameters for only 7 out of the 15 species groups, in fact for those groups for which mean residuals of model [2] were classified in the following logical order with respect to landfacets: bottomlands > hillsides > hilltops. However, the site information did not improve the model significantly: (i) a Bonferroni test of the equality of parameters a'_1, a'_2 and a'_3 in each species group, led only once to reject the null hypothesis with a global risk of error of 0.05 (group g2.2); (ii) the decrease in global residual variance of the refined growth model was negligible, relative to the number of added parameters; (iii) a significant plot effect remained on the new residuals.

3.2. Validation of the model and residual effects

At this stage, we have a model with 65 parameters, on the residuals of which:

- a slight diameter class effect remains ($F_{(4,\infty)} = 3.40$, $P = 0.0088$). The F-value is higher than what occurred when species groups were not taken into account ($F = 2.84$, $P = 0.023$); interactions between the two variables "diameter" and "species" are not optimally described. However, no logical ordering of the classes and no separation between them through tests of multiple comparisons of means were observed. The class for which diameter increments are the less well predicted is, not surprisingly, the height transition 30-40 cm class for which no competition index proved efficient.
- No treatment effect is left as shown by the results of a hierarchical analysis of variance "plot(treatment)" using the eight calibration plots ($\mathrm{MSE}_{\mathrm{treatment}}/\mathrm{MSE}_{\mathrm{plot(treatment)}} = 1.00$, value to be compared to $F_{0.05(3.4)} = 6.59$).
- No species effect is left.

We used supplementary data to explore whether or not residual effects had been forgotten. The four validation plots that were deliberately set aside, as well as the whole set of plots at a later stage (i.e. after 1991), were available for the validation data set. As the same trees were repeatedly measured, the longitudinal data analysis provided a more suitable framework. The growth model is thus:

$$\text{Log}(\Delta D_{it} + 0.287) = \text{Log}(\text{potential}_{it}) + \text{Log}(\text{modifier}_{it}) + \varepsilon_{it}$$

where subscript i indicates the tree and subscript t indicates the period. If all effects have been taken into account, we should have the following properties: $E(\varepsilon_{it}) = 0$ and $\text{Cov}(\varepsilon_{it}, \varepsilon_{ju}) = \sigma^2\delta_{ij}\delta_{tu}$, where δ_{xy} is the Kronecker symbol (i.e. $\delta_{xy} = 0$ if $x \neq y$, $\delta_{xy} = 1$ if $x = y$). With the validation data set, the following verifications can be made:

- with the four validation plots, we can test whether $E(\varepsilon_{i,\ 1988-1991}) = 0$;
- with the data after 1991, we can test any of the following hypothesis: $E(\varepsilon_{i,\ 1991-1994}) = 0$,

or $E(\varepsilon_{i,\ 1994-1997}) = 0$,
or $\text{Cov}(\varepsilon_{i,\ 1988-1991}, \varepsilon_{i,\ 1991-1994}) = 0$,
or $\text{Cov}(\varepsilon_{i,\ 1988-1991}, \varepsilon_{i,\ 1994-1997}) = 0$.

3.2.1. Spatial effect

We first tested whether $E(\varepsilon_{i,\ 1988-1991}) = 0$.

Model [2] was used to predict diameter increments over the 1988-1991 period on the four plots set aside for validation: P2, P3, P8 and P11. The following statistics were calculated, with O referring to “observed values” and P referring to “predicted values”:

- $B = \dfrac{\sum_{i=1}^{n}(O_i - P_i)}{n}$: mean bias.
- $\text{MSE} = \dfrac{\sum_{i=1}^{n}(O_i - P_i)^2}{n-1}$: mean square of errors. This statistic is an estimate of the residual variance $\bar{\sigma}^2$ when $B = 0$. When $B \neq 0$, the unbiased estimate of the residual variance is $\bar{\sigma}^2 = \dfrac{\sum_{i=1}^{n}(O_i - P_i - B)^2}{n-1}$.
- $\text{pseudo} - R^2 = 1 - \dfrac{\sum_{i=1}^{n}(O_i - P_i)^2}{\sum_{i=1}^{n}(O_i - \bar{O})^2}$: “modelling efficiency”.

The results are presented in Table 2.

Diameter increments on the validation plots are globally underestimated by model [2]. More precisely, as can be seen in Fig. 11, underestimates occur on plots P2, P3 and P8, while predictions are close to observations on plot P11. P2, P3 and P8 are among the plots where in general initial density of the stands was low and mean diameter increments were high (see Fig. 4). We suspect a global substrate effect that we are unable to demonstrate at present; thus, for the moment, spatial extrapolation of the predictions appears hazardous. This so-called substrate effect, however, does not hinder the efficiency of the model which even proves slightly more accurate on the validation data set than on the calibration data set $(\text{pseudo} - R^2 = 0.445)$.

Table 2
Evaluation of the performance of growth model [2] taking species groups into account, when considering the four plots set aside from the calibration set: 10,745 trees are considered in the calibration set (eight plots), 5074 trees are considered in the independent set (four plots).

Statistics	*Calibration data set*	*Independant data set*
B (Log(cm))	0.002	0.041
T[a]	0.53 ns	9.29***
MSE (Log(cm)^2)	0.093	0.100
$\bar{\sigma}^2$ (Log(cm)^2)	0.093	0.098
$\text{pseudo} - R^2$	0.420	0.445

[a] T is the Student statistics allowing the test of the null hypothesis ($B = 0$). ns: non-significant; ***: $P < 0.001$.

3.2.2. Time (climate?) effect

On the calibration plots, we made use of the model to predict increments on the two available periods following that used to calibrate the model: namely 1991-1994 and 1994-1997. Table 3 shows the main results of this evaluation.

We first studied the bias, by testing the hypothesis: $E(\varepsilon_{i,\,1991-1994}) = 0$ and $E(\varepsilon_{i,\,1994-1997}) = 0$.

It can be seen from Table 3 that the performance of the model decreases as early as the first period following calibration, indicating that some important factor was neglected during the building phase. Although the residuals of the model do not sum to zero on each plot (plot effect described in the Section 3.1.3), this bias at the plot level increases with time and can be related to the level of disturbance experienced by the plot (see Fig. 12; the same feature was obtained with the 1991-1994 period). This of course can be explained by the long lasting positive effect of the silvicultural treatments, illustrated in Fig. 5. The growth model with a 3-year time step does not keep track of these major events: competition indices calculated for the periods following 1985-1988, especially ΔNBD, cease to account for the opening of the stands.

However, delayed silvicultural effects are not the only source of bias. We observed on Fig. 3a that diameter increments seem to be sensitive to rainfall, peaks in annual cumulated amounts being followed by peaks in increments 2 years later. Under this hypothesis, we expect the growth model to underestimate growth more severely after rainy years than after drier ones, that is, we expect the bias to follow the same pattern as diameter increments. On the control plots, where artificial disturbances do not interfere, the results are coherent (see Fig. 13).

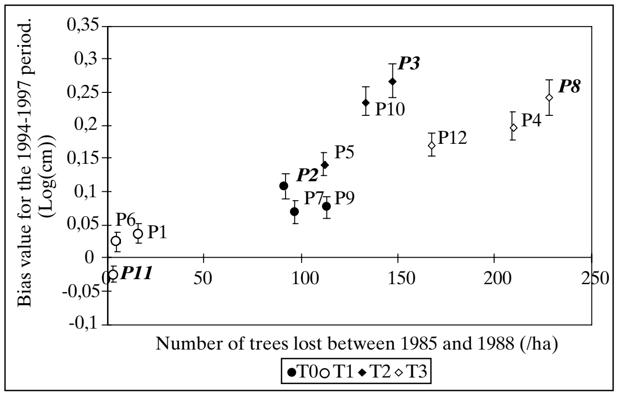


Fig. 12. Relationships between the value of the bias observed when using the model to predict increments over the period 1994-1997, and the intensity of the disturbance experienced in the plots. Means are plotted with their 95% confidence interval.

Between the two periods 1991-1994 and 1994-1997, there was a decrease in mean diameter increments in all the plots except plot P1, amounting to 13% (between 7% and 19%). In the same way, there was a decrease in bias in all but two plots (P4 and P5), as shown by the mean bias value in Table 3. The decrease, in all cases, was independent of the treatment. We thus suggest that, during the two periods, two factors not taken into account in the growth model added their effects:

- 1991-1994: maximum delayed response to the silvicultural treatments + peak in increments following the rainy years 1988-1989 and 1989-1990;

Table 3
Evaluation of the performance of growth model [2] taking species groups into account, when considering two periods succeeding the period used for the calibration. Data come from the eight calibration plots: 10,745 trees in the calibration set, 9831 trees in the “temporal validation” sets.

Statistics	*Calibration data set*	*Period 1991–1994*	*Period 1994–1997*
B (Log(cm))	0.002	0.146	0.110
T^a	0.53 ns	46.38***	34.67***
MSE (Log(cm)^2)	0.093	0.119	0.110
$\bar{\sigma}^2$ (Log(cm)^2)	0.093	0.098	0.098
pseudo – R^2	0.420	0.191	0.269

[a]For footnote, cf. Table 2.

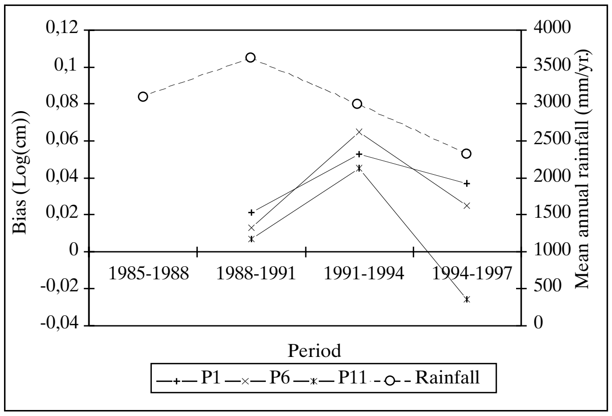


Fig. 13. Evolution of the bias observed on the three control plots, compared to the evolution of rainfall cumulated over 3-year periods.

- 1994-1997: delayed but weakening response to the treatment + decrease in increments following the relatively dry years 1990-1991, 1991-1992 and 1992-1993.

Although prediction of the occurrence of rainy years cannot easily be achieved, the delayed treatment effect can be artificially taken into account in the growth model through a variable memorizing the elapsed time since disturbance (see Vanclay, 1991, for an example). This variable would temporarily increase the modifier value. However, the challenge remains to understand the underlying mechanisms explaining this delayed effect, such as increase in the soil richness due to the decomposition of a great quantity of logging remnants, better water supply and so on.

In a second stage, we studied the temporal correlation by testing the hypothesis:

$$\mathrm{Cov}(\varepsilon_{i,\,1988-1991}, \varepsilon_{i,\,1991-1994}) = 0 \text{ , and}$$

$$\mathrm{Cov}(\varepsilon_{i,\,1988-1991}, \varepsilon_{i,\,1994-1997}) = 0 \text{ .}$$

In addition to the positive bias that appears between 1991 and 1997, a linear relationship exists between the residuals of the growth model (period 1988-1991) and the prediction errors on the period 1991-1994, as well as between the prediction errors of the two following periods, 1991-1994 and 1994-1997. Pearson correlation coefficients significantly differ from zero ($P \leq 0.0001$) and amount respectively 0.39 and 0.51, with little variation from one plot to the other.

These observations mean that trees for which the diameter increment has been underestimated (or overestimated) for the calibration period 1988-1991 tend to retain underestimated (or overestimated) predictions during the following periods. Two interpretations are possible.

- First, the residuals $\varepsilon_{i,\,t}$ are not independent but can be written as: $\varepsilon_{i,\,t} = X_i + \eta_{i,\,t}$, where X_i are random variates and the $\eta_{i,\,t}$ are independent from X_i and of each other. This produces a temporal correlation between the residuals, due to the existence of a fixed (i.e. time-independent) factor not taken into account in model [2]. This factor could be linked to the substrate, as we noted that a global plot effect remained on the residuals.
- Second, there exists a stochastic process ρ_i such that: $\varepsilon_{i,\,t} = \rho_i(t)$, that is , intrinsic phenomena which cause a tree that grew rapidly (or slowly) during one period to go on growing rapidly (or slowly) afterwards, independently of any other factor. This produces a temporal autocorrelation. One may think about successful/unfavourable genotypes, or about decaying trees that decrease their growth before dying, whatever the environmental characteristics of their location.

These two sources of temporal correlation probably occur together at Paracou.

4. Synthesis and conclusion

Working with the Paracou data set and making use of as many types of information available on the site as possible, we could verify, or at least suggest, the influence of several factors on the diameter increments of the trees ≥10 cm DBH monitored on the site. This influence was first suspected when analysing each factor separately from the others, and in a second step, confirmed and possibly quantified after having taken into account through modelling some of the multiple interactions existing between them.

4.1. Biotic factors

Diameter increments are sensitive to the number and size of neighbouring trees, competition for light and nutrients being on average more perceptible within a radius of 30 m as previously shown by Gourlet-Fleury (1998). This result is coherent with the fact that trees ≥10 cm DBH are aggregated at this scale on the plots (Picard et al., 2001 or see Chapter 6, this Part). The rapid change of these characteristics, as measured on 3-year time-step, also influences increments on both a short and a longer term basis: a tree grows better, whatever the number and size of its neighbours at time t, if these number and size have suddenly decreased in the past. Significant disturbances, like those induced by silvicultural operations, have a lasting effect of at least 10 years, as has been shown here. The increase in growth is greater in direct relationship to the local decrease in competition; however there is a limit. When trees lose too many of their neighbours, their growth slows down. This could be interpreted as a negative reaction of the leaves to drying of the atmosphere following significant modification of the local microclimate, and could explain why, on a mean basis, increments are not significantly higher in the plots of T3 than in the plots of T2. The limit occurs more rapidly for trees located in very dense neighbourhoods. The shape of the link between increments and competition indices also indicates that it is better interesting for a tree to lose dominant neighbours throughout its life than to always be a dominant. These observations have practical consequences from a silvicultural viewpoint.

Diameter increments clearly depend on the initial diameter of the trees, and on the species they belong to. They tend to be very low in small diameter classes, all the more so when they belong to shade-tolerant, understorey species, whereas they are high in intermediate and big classes, especially if they belong to light-demanding canopy species.

Those three factors (neighbourhood, diameter, species) control tree reactions to the opening of the canopy. They are interdependent, which probably explains why adding one factor does not much improve the predictive ability of the model. The pseudo – R^2 of the complete model that incorporates all of them, 0.42, is comparable to figures obtained in other tropical forests – Vanclay (1991) in Queensland: 0.45, Chai and LeMay (1993) in Sarawak: 0.38; Wan Razali (1986) for the Dipterocarpaceae group of species in Peninsular Malaysia: 0.49; Moravie et al. (1999) for a top canopy dipterocarp species of the Western Ghats of India: 0.60.

4.2. Abiotic factors

Diameter increments seem to be sensitive to the amount of cumulated annual rainfall. If we hypothesize that Guianan forests grow better when they have more water, which seems to be the case given the characteristics of the stands along the rainfall gradient on the coast, the observed pattern indicates a delayed reaction of the trees over 2 years: high diameter increments follow rainy years, and growth tends to decrease after drier periods.

Diameter increments appear to be sensitive to the substrate; indications are given by three different types of results. (i) Growth tends to be higher, or highly underestimated by our growth model, in bottomlands, which seems coherent with the former point. The importance of the availability of water during the dry season could compensate for the constraints linked to hydromorphy during the rest of the year. However, this point remains to be clarified, as some studies dealing with well-identified species, such as *Carapa procera*, do not lead to the same conclusions (Angelier et al., 2000). According to these researchers, high growth in bottomlands could result merely from higher light availability and lower competition levels, due to a higher frequency of small tree fall gaps. The discrepancy between their results and ours could come from the fact that our growth model, which is supposed to have taken into account the main confusing factors such as local competition and species effect remains rather imprecise: only 15 species groups describe the behaviour of more than 300 species, and competition is evaluated over 30 m radius circles, which can be totally inadapted to the study of bottomland effects (narrow areas). (ii) Increments are lower in dense stands; the introduction of local competition indices into the growth model correctly accounted for the treatment effects, but did not prove efficient enough to explain the differences observed between overstocked and understocked plots. This could be explained by the global characteristics of the plots substrate, but the data bank available at present on the Paracou soils is not complete enough to allow the test of this hypothesis. (iii) Finally, a significant temporal correlation, partly disturbed by the implementation of the silvicultural treatments, can be observed on the residuals of the growth model. We explain it by the existence of a local set of environmental conditions which do not vary over time and which are therefore probably linked to the substrate.

4.3. Prospects

The prospects of furthering our understanding of diameter growths observed at Paracou can be classified in two categories: the first, more immediate than the second, is mainly empirical and relies on statistical studies of correlations. It will deal with the search for variables, mainly environmental, that will maximise the explanation of diameter increments through the use of a suitable equation. Most of the work will consist in:

- improving the competition indices, by taking two main factors into account: (i) a variation of the size of the competitive neighbourhood, according to the group of species and the diameter of the subject tree considered; (ii) the differential competitiveness of the species, defined on the basis of information resulting from recent ecophysiological studies on water use efficiency and the use of different sources of N_2 (Bonal, 2000; Guehl et al., 1998; Roggy, 1998).
- Improving our knowledge on the Paracou soils, in order to increase the precision of the original maps of Barthès (see Part I) and to test our hypothesis of a stand density being linked to a global substrate "quality". This work has been undertaken by Angelier et al. (2000) and by V. Freycon (personal communication).
- Using other or more precisely defined tree characteristics such as: (i) total height. Data have been collected in several sub-plots in order to estimate the explicative potential of this information, which can be used as a direct explicative variable of diameter increment or as a characteristic of neighbours inside competition indices. (ii) Species identity. Improvement of botanical identification of the trees on the site will help to refine our species groups; this is expected to decrease the observed variability of increments inside each group and to reinforce the link between increments and some competition indices supposed to render the social status sensitivity.

The second category is the need for a more process-based approach and still requires further reflexion. Studies have recently been undertaken dealing with:

- a more precise approach to what a tree is and how a tree grows: this involves detailed architectural studies aimed at describing and understanding the chronological sequences of the development of a tree through building of growth units and metamorphosis and reiteration phenomena (Bongers and Sterck, 1998; Drénou, 1994; Sterck, 1997). At present, *Dicorynia guianensis* is being extensively studied on the site (Nicolini et al., 2003).
- A more precise approach to how a tree takes resources from its environment: this includes intensive work initiated about 10 years ago on the part played by mycorrhizas in the survival and growth of trees (Béreau and Garbaye, 1994; Béreau et al., 1997, see also Chapter 4, Part II). It also refers to the work of Guehl et al. (1998), Roggy (1998) and Bonal (2000) (see also Chapters 2 and 5, Part II) on water use efficiency and N_2 uptake according to species.
- A more precise quantification of the resources in natural stands. The most studied are light (Baraloto, unpublished data; Ferment et al., 2001), CO_2 concentration in the air (see Chapter 3, Part II), N_2 and P (Baraloto, unpublished data). Questions still remain concerning measurement methods as well as the part played by resources in photosynthesis and biomass increment.

There still exists a gap between the empirical and the process-based approaches, which is not new in ecology and probably more acute in such complex and poorly studied ecosystems as tropical rainforests. Important questions are: what information do we lack between the two extremes "DBH" and "collection of growth units" or $\delta^{13}C$ value in the leaves? Between the landfacet "bottomlands" and the "extractable phosphorus" of the soil? Must the impact of logging on diameter increment, through the creation of a gap, be described by studying the detailed evolution of the photosynthetically active radiation (PAR), the detailed response of the leaves to this evolution given the increased dryness of the air, the advantage of belonging to a species that can make use of N_2 flushes in the soil after logging, the detailed consecutive evolution of crown architecture and, consequently, the modified allocation of photosynthetates to the increase of girth? What is the good scale of integration of these processes? The Paracou site is a place where the multi-disciplinary community can profitably seek more precise answers than "it depends …".

References

Angelier A., Bricka L., Cassagnaud M., Laurent M.P. (encadrées par B. Ferry et H. Laborde), 2000. Cartographie des bas-fonds du dispositif expérimental de Paracou. Mémoire du module "FTH" de l'ENGREF-Kourou, 35 p.

Assmann E., 1970. The principles of forest yield study. Pergamon Press, 506 p.

Barthès B., 1988. Où pousse cet arbre? Premiers résultats de l'étude des relations sol-végétation en forêt de Paracou (Guyane). Cas du Wapa et du Gonfolo. Rapport interne 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).

Béreau M., Garbaye J., 1994. First observations on the root morphology and symbioses of 21 major tree species in the primary tropical rain forest of French Guyana. Ann. Sci. Forest. 51, 407–416.

Béreau M., Louisanna E., Garbaye J., 1997. Effect of endomycorrhizas and nematodes on the growth of seedlings of *Dicorynia guianensis* Amshoff, a tree species of the tropical rain forest in French "Guiana. Ann. Sci. Forest 54, 271–277.

Bonal D., 2000. Variabilité interspécifique de l'efficience d'utilisation de l'eau en forêt tropicale humide guyanaise: groupes fonctionnels, interprétation écophysiologique, intégration à l'échelle du couvert. Thèse de l'Université Henri Poincaré, Nancy I, spécialité "Biologie Forestière". 51 p. + articles + annexes.

Bongers F., Sterck F.J., 1998. The architecture, allometry and development of tropical rain forest trees. Philos. Trans. Br. Ecol. Soc., London.

Chai F.Y.C., LeMay V.M., 1993. Development and testing of diameter increment models for mixed swamp forests of Sarawak. Forest Ecol. Manag. 58, 51–64.

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. + annexes.

Cusset G., 1980. Sur des paramètres intervenant dans la croissance des arbres. La relation hauteur/diamètre de l'axe primaire aérien. Candol. 35 (1), 231–255.

Dawkins H.C., Philip M.S., 1998. Tropical moist forest silviculture and management. A History of Success and Failure. CAB International, Wallingford, UK, 359 p.

Deleuze C., 1996. Pour une dendrométrie fonctionnelle: essai sur l'intégration de connaissances écophysiologiques dans les modèles de production ligneuse. Thèse de doctorat de l'Université Claude Bernard Lyon I. 305 p.

Drénou C., 1994. Approche architecturale de la sénescence des arbres. Le cas de quelques angiospermes tempérées et tropicales. Thèse de doctorat de l'Université de Montpellier II, 263 p.

Durrieu De Madron L., 1993. Mortalité, chablis et rôle des trouées avant et après exploitation sur le dispositif d'étude sylvicole de Paracou – Guyane Française. Thèse de 3^{e} cycle – ENGREF/CIRAD, 203 p. + annexes.

Favrichon V., 1994. Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise. Revue d'Ecologie (La Terre et la Vie) 49, 379–403.

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. + annexes.

Ferment A., Picard N., Gourlet-Fleury S., Baraloto C., 2001. A comparison of five indirect methods for characterizing the light environment in a tropical forest. Ann. Forest Sci. 58 (8), 877–891.

Franc A., Gourlet-Fleury S., Picard N., 2000. Une introduction à la modélisation des forêts hétérogènes. Collection « Forêt » des éditions de l'ENGREF – Nancy, 312 p.

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. + annexes.

Gourlet-Fleury S., 1998. Indices de compétition en forêt dense tropicale humide: étude de cas sur le dispositif sylvicole expérimental de Paracou (Guyane française). Ann. Sci. Forest 55 (6), 623–654.

Gourlet-Fleury S., Bar-Hen A., Fauvet N., 1999. The silvicultural experimental plots of Paracou in French Guiana: example of use and limits of the available data for developing individual growth models. In: Kleinn, C., Köhl, M. (Eds.), Proceedings of the IUFRO S4.11 International Symposium: Long-Term Observations and Research in Forestry, CATIE, Turrialba, Costa Rica, February 23–27, 1999.

Gourlet-Fleury S., Houllier F., 2000. Modelling diameter increment in a lowland evergreen rain forest in French Guiana. Forest Ecol. Manag. 131 (1–3), 269–289.

Guehl J.M., Domenach A.M., Bereau M., Barigah T.S., Casabianca H., Ferhi A., et al., 1998. Functional diversity in an Amazonian rainforest of French Guyana: a dual isotope approach (_15N and 13C). Oecologia 116, 316–330.

King D.A., 1996. Allometry and life history of tropical trees. J. Trop. Ecol. 12, 25–44.

Mercier F., 1997. Analyse et modélisation de la dynamique forestière guyanaise à l'aide de diagrammes de Voronoï. Thèse de doctorat de l'Université Claude Bernard Lyon I/CIRAD. 181 p.

Moravie M.A., Durand M., Houllier F., 1999. Prediction of diameter increment of *Vateria indica* L. in a moist evergreen forest in the Western Ghâts of India: efficiency and meaning of competition indexes. Forest Ecol. Manag. 117, 221–240.

Nicolini E., Caraglio Y., Pélissier R., Leroy C. and Roggy J.-C., 2003. Epicormic Branches: a Growth Indicator for the Tropical Forest Tree, *Dicorynia guianensis* Amshoff (Caesalpiniaceae). Ann. Botany 92: 97–105.

Oldeman R.A.A., 1974. L'architecture de la forêt guyanaise. Mémoires ORSTOM vol. 73. 198 p + annexes.

Oldeman R.A.A., Van Dijk J., 1989. Diagnosis of the temperament of tropical rain forest trees. In: Gomez-Pompa A., Whitmore T.C., Hadley M. (Eds.), Rain Forest Regeneration and Management. UNESCO – Man and the Biosphere Series, vol. 6. pp. 21–63.

Paget D., 1999. Etude de la diversité spatiale des écosystèmes forestiers guyanais. Réflexion méthodologique et application. Thèse de doctorat de l'Ecole Nationale du Génie Rural, des Eaux et des Forêts de Paris/CIRAD. 151 p. + annexes.

Picard N., 1999. Passage d'un modèle individuel à un modèle de distribution de la dynamique forestière. Application à une forêt dense tropicale humide de Guyane française. Thèse de doctorat de l'Ecole Nationale du Génie Rural, des Eaux et des Forêts de Paris/CIRAD. 236 p. + annexes.

Picard N., Bar-Hen A., Franc A., 2001. Spatial pattern induced by asymmetric competition: a modelling approach. Nat. Resou. Model. 14 (1).

Prévost M.F., Puig H., 1981. Accroissement diamétral des arbres en Guyane: observations sur quelques arbres de forêt primaire et de forêt secondaire. Bulletin du Muséum National d'Histoire Naturelle 3, 147–171.

Roggy J.C., 1998. Contribution des symbioses fixatrices d'azote à la stabilité de l'écosystème forestier tropical guyanais. Thèse de l'Université Lyon I. 124 p.

Sterck F.J., 1997. Trees and light: tree development and morphology in relation to light availability in a tropical rain forest in French Guiana. Thesis Landbouwuniversiteit Wageningen, 121 p.

Vanclay J.K., 1991. Aggregating tree species to develop diameter increment equations for tropical rainforests. Forest Ecol. Manag. 42, 143–168.

Wan Razali B.W.M., 1986. Development of a generalized forest growth and yield modelling system for mixed tropical forests of peninsular Malaysia. PhD thesis, University of Washington, 177 p.

Zeide B., 1993. Analysis of growth equations. Forest Sci. 39 (3), 594–616.

ANNEX

Table 1
Parameters of the diameter growth model (Equation [1]), estimated from the calibration data set: 10,745 trees from eight plots (all species together)

Parameter	*Estimate*	*Asymptotic standard error*
a' (Log(a) + e)	–5.21	0.11
M	1.088	0.15
K (cm)	208	25
b ($\times 10^{-3}$)*	–114.08	14.08
c ($\times 10^{-3}$)*	–18.32	0.59
d ($\times 10^{-3}$)*	–0.13	0.01

*Values in the table were obtained by multiplying the actual value by 10^{-3}.

Table 2
Values of the parameters of the 15 sub-models of growth increment, taking the "species" factor into account (the line titled "modifier used" refers to the equations given in the main text). The 15 species groups are allocated to five 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 contains non-identified species belonging mainly to Chrysobalanaceae ("gaulettes"). See Gourlet-Fleury (1997), 119–133 for more details.
Table 2a
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/year)	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
Modifier used	[M6]	[M6]	[M6]	[M6]
Parameters	Estimate (s)	Estimate (s)	Estimate (s)	Estimate (s)
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 ($\times 10^{-3}$)**	0.00	0.00	0.00	0.00
c ($\times 10^{-3}$)**	–9.97 (0.84)	–12.66 (1.02)	–15.70 (1.37)	–11.40 (0.89)
d ($\times 10^{-3}$)**	–0.050 (0.009)	–0.070 (0.011)	–0.053 (0.014)	–0.053 (0.010)

*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 $a' = \text{Log}(a) + e$.
**Values in the table were obtained by multiplying the actual value by 10^{-3}.
***This group contains many incorrectly identified species belonging to the genus *Licania*.

Table 2b

Super-group 2: average to large 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/year)	0.06	0.09	0.12	0.17
Typical species	*Bocoa prouacensis* Aublet Caesalpiniaceae	*Lecythis poiteauii* Berg Lecythidaceae	*Licania cf micrantha* Miq Chrysobalanaceae	*Eperua falcata* Aublet Caesalpiniaceae
Modifier used	[M6]	[M5]	[M5]	[M5]
Parameters	Estimate (s)	Estimate (s)	Estimate (s)	Estimate (s)
$\underline{a}'$[*]	–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 ($\times 10^{-3}$)[**]	0.00	0.00	0.00	0.00
c ($\times 10^{-3}$)[**]	–13.72 (1.84)	–22.47 (1.55)	–20.91 (1.62)	–30.64 (2.76)
d ($\times 10^{-3}$)[**]	–0.044 (0.014)	–0.174 (0.027)	–0.153 (0.029)	–0.278 (0.045)

[*] For expansion see Table 2a (*) footnote.

[**] Values in the table were obtained by multiplying the actual value by 10^{-3}.

Table 2c

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/year)	0.27	0.50	0.16	0.31
Typical species	*Qualea rosea* Aublet Vochysiaceae	*Sclerolobium melinonii* Harms Caesalpiniaceae	*Recordoxylon speciosum* (R, Ben) Norm. et Marq Caesalpiniaceae	*Symphonia globulifera* Linnaeus f. Clusiaceae
Modifier used	[M4]	[M7]	[M1]	[M1]
Parameters	Estimate (s)	Estimate (s)	Estimate (s)	Estimate (s)
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 ($\times 10^{-3}$)[**]	–1.19 (0.47)	0.00	–47.25 (10.45)	–27.28 (10.49)
c ($\times 10^{-3}$)[**]	–28.82 (3.22)	–19.03 (4.32)	–24.15 (2.72)	–29.89 (2.60)
d ($\times 10^{-3}$)[**]	–0.257 (0.056)	0.00	–0.125 (0.044)	–0.192 (0.042)

[*] For expansion see Table 2a (*) footnote.

[**] Values in the table were obtained by multiplying the actual value by 10^{-3}.

Table 2d

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/year)	0.09	0.18	0.25
Typical species	*Drypetes variabilis* Uittien Euphorbiaceae	*Couepia* cf. *caryophylloïdes* R. Ben Chrysobalanaceae	*Inga cayennensis* Sagot ex Bentham Mimosaceae
Modifier used	[M3]	[M3]	[M2]
Parameters	Estimation (s)	Estimation (s)	Estimation (s)
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 ($\times 10^{-3}$)**	–234.94 (48.31)	–223.95 (30.02)	–47.73 (18.58)
c ($\times 10^{-3}$)**	–17.33 (1.18)	–17.72 (1.16)	–21.93 (1.88)
d ($\times 10^{-3}$)**	–0.069 (0.014)	–0.055 (0.011)	–0.107 (0.021)

*For expansion see Table 2a (*) footnote.

**Values in the table were obtained by multiplying the actual value by 10^{-3}.

Ecology and Management of a Neotropical Rainforest

Chapter 5

Consequences of silvicultural treatments on stand dynamics at Paracou

Sylvie Gourlet-Fleury, Vincent Favrichon, Laurent Schmitt, Pascal Petronelli

Abstract – The different components of stand dynamics – growth, mortality and recruitment –were affected by silvicultural treatments of growing intensity applied in the Paracou plots, resulting in contrasted behaviours in the stands. We first present and discuss the evolution over time of the plots in terms of their total number of trees and basal area. We then examine the evolution of the diameter structures, the dynamic components and the basal area balance for the global set of species and for the marketable species, emphasising the differences between treatments. Estimates of the time required to return to a hypothetical initial state are made according to different methods. One of the conclusions is that a felling cycle of 50 years in stands identical to those logged-over at Paracou, could allow recovery of 80–90% of the initial number of valuable trees above the diameter cutting limit, but with a shift in the floristic composition. We discuss some practical consequences for forest managers of the results found at Paracou and comparisons are made with other known experimental designs such as CELOS in Suriname and Tapajos in Brazil.

Keywords: Rainforest dynamics, Logging, Silviculture, Recovery, Felling cycles

1. Introduction

The experimental site of Paracou was originally designed to answer two main questions asked by forest managers (see Part I).

- What are the possibilities of recovering[1] the commercial standing volume in logged-over forests of the coastal part of French Guiana?
- Is it possible to stimulate this recovery with appropriate silvicultural techniques and rules that are easy to apply on a large scale, in order to achieve sustainable production in these forests?

At that time, the centre of interest was clearly the timber resources; however, since then, an awareness of the potential value of biodiversity has both widened and constrained the objectives of management plans (Dutrève et al., 2001; Leslie, 1997; Mankin, 1998; Mengin-Lecreulx, 2000) and enlarged the set of questions addressed to researchers.

To manage any kind of resource, it is necessary, as recalled by Houllier (1992), (i) to describe and quantify it, (ii) to study its past evolution, and (iii) to predict its dynamics in the future. This can be done on several scales. In French Guiana, the first point has

---

[1] In this chapter, we will use the term "recovery" to designate the return to initial state, whatever the variable considered.

been dealt with over the entire coastal part of the department, by means of more or less systematic inventories (Fleury, 1995), and studies are now underway to determine the main factors which influence localisation of the resource (Paget, 2000; Sabatier et al., 2001). The other two points have been classically approached on the local scale: the second point by means of the design of permanent sample plots, first near Saint-Laurent in disturbed stands of unknown history (Gazel, 1983) and then at Paracou; the third point has been addressed by means of modelling (see Chapter 6, this Part).

The need for answers about the future of logged over stands and the type of silviculture to apply led the researchers at Paracou to deliberately disturb parts of "primary forest" according to well-established, simple and contrasted rules, as has been done in several other sites in moist tropical forests (Favrichon, 1997; Favrichon et al., 1998; Sist, 1998, in previously logged over forests). The purpose of the annual survey of the permanent sample plots was to provide a quantified view of the preceding and subsequent evolution of the stands on the basis of a precise study of the three components of their dynamics – growth, mortality and recruitment – before inferring information of practical use for managers.

The present chapter examines how close (or how far) we are from a clear answer to the two questions above. To do so:

- we will analyse the impact on the dynamics of the stands of the disturbances induced by the silvicultural treatments applied on the 12 oldest plots at Paracou. We will examine the evolution of the global characteristics of the stands, "number of trees/ha", or mean density, "basal area/ha", and diameter class structure, providing details for each of the components of the dynamics – growth, mortality and recruitment (i.e. ingrowth ≥ 10 cm DBH) – so as to highlight which components are mainly responsible for the evolution.
- We will use the trends observed over 9 years following disturbance to examine the possible future of the stands and discuss the consequences in terms of silviculture and management, especially as far as felling cycles are concerned.
- We will discuss our conclusions and recommendations in the light of the conclusions of other known experiments in the Amazonian region.

This chapter will consider either floristic groups or particular species, depending on the question dealt with. The groups will be (i) the global group of all species pooled together; (ii) the group of initial "timber species", that is to say the 58 species or groups of species (SGS) that were logged at Paracou (cf. Part I, Section 2.1) and (iii) the group of 20 valuable species currently logged in French Guiana. These groups are not ecologically based and, of course, are heterogeneous in terms of species behaviour, but our concern in this particular chapter is the evolution of the commercial timber.

Finally, this chapter is based on the assumption that the silvicultural treatments are the global cause for changes in the components of the stand dynamics. It will not address questions about the detailed underlying processes involved. Readers who are particularly interested in these matters will find details in this Part, Chapters 2 and 3 (regeneration processes) and Chapter 4 (growth).

2. Impact of the treatments and subsequent evolution of the stands

2.1. In terms of density and basal area

2.2.1. Intensity of experimental disturbances and immediate impact

Let us recall that three types of silvicultural treatments were applied at Paracou between 1986 and 1987 (logging) and 1987 and 1988 (poison-girdling), each one on three plots; nine plots were thus disturbed, while three complementary plots remained undisturbed as control plots (see Part I, Section 2.1 and Tables 1 and 2 for details). The control plots are referred to as T0, and the treated plots as follows: T1 (logging for timber), T2 (logging for timber + poison-girdling) and T3 (logging for timber and fuelwood + poison-girdling). Fifty-eight species or groups of species (SGS) with interesting timber characteristics were targeted for logging, 10 of them with a diameter cutting limit (DCL) of 60 cm DBH, the 48 others with a cutting limit of 50 cm DBH. In 1984, altogether they accounted for about 30% of the total number of trees in the stands and almost 50% of the total basal area. The 20 species currently logged in French Guiana represent about 42% of this valuable group in terms of numbers and 50% in basal area. Logging for fuelwood and poison-girdling concerned non-valuable timber species and trees of commercial species with major defects. The intensity of tree removal by logging, linked damages and poison-

Table 1

Characteristics of the plots before and after treatment, and intensity of disturbance experimented according to the treatment. All data are given on a per hectare basis. Data are presented in total number of trees of DBH ≥ 10 cm and corresponding basal area, as means on each group of three plots. NB1: the sum of dead trees does not match with the differences respectively between 1986 and 1987 (logging), and 1987 and 1988 (poison-girdling) because of natural mortality. NB2: from 1995 on, the systematic survey of living trees has been done every 2 years.

Year	*T_0 (plots 1, 6, 11)*		*T_1 (plots 2, 7, 9)*		*T_2 (plots 3, 5, 10)*		*T_3 (plots 4, 8, 12)*	
	N	*G (m^2)*	*N*	*G (m^2)*	*N*	*G (m^2)*	*N*	*G (m^2)*
1984	625.5	30.9	602.9	30.6	622.8	31.9	627.6	32.1
1985	626.0	30.9	606.2	30.6	626.8	32.0	626.2	32.0
1986	625.9	31.0	606.2	30.7	626.7	32.1	625.0	32.1
Trees felled*	0	0	10.2	3.3	10.9	3.8	28.9	6.3
% of 1986	–	–	*1.7*	*10.7*	*1.7*	*11.8*	*4.6*	*19.6*
Trees destroyed by logging operations	0	0	78.2	2.3	84.7	2.6	148.5	4.2
% of 1986	–	–	*12.9*	*7.5*	*13.5*	*8.1*	*23.8*	*13.1*
1987	621.6	30.8	511.4	25.0	523.4	25.5	441.6	21.3
Trees killed by poison-girdling (dead in 1988)	0	0	0	0	21.4	5.2	10.6	3.6
% of 1986	–	–	–	–	*3.4*	*16.2*	*1.7*	*11.2*
1988	617.8	30.7	505.6	24.9	496.1	20.4	424.6	17.6
1989	614.8	30.7	507.5	25.0	488.5	19.3	423.5	17.1
1990	613.9	30.8	508.4	25.1	489.6	19.2	430.6	17.2
1991	615.7	30.8	521.1	25.3	504.5	19.4	449.1	17.3
1992	614.1	30.9	529.1	25.5	513.3	19.7	469.6	17.7
1993	611.1	30.9	532.8	25.7	525.1	20.1	486.7	18.1
1994	607.5	30.9	529.9	25.8	527.0	20.3	490.3	18.5
1995	608.4	31.1	537.9	26.0	546.4	20.8	524.2	19.2
1996	–	–	–	–	–	–	–	–
1997	604.4	31.1	554.0	26.5	583.2	21.9	594.2	20.6

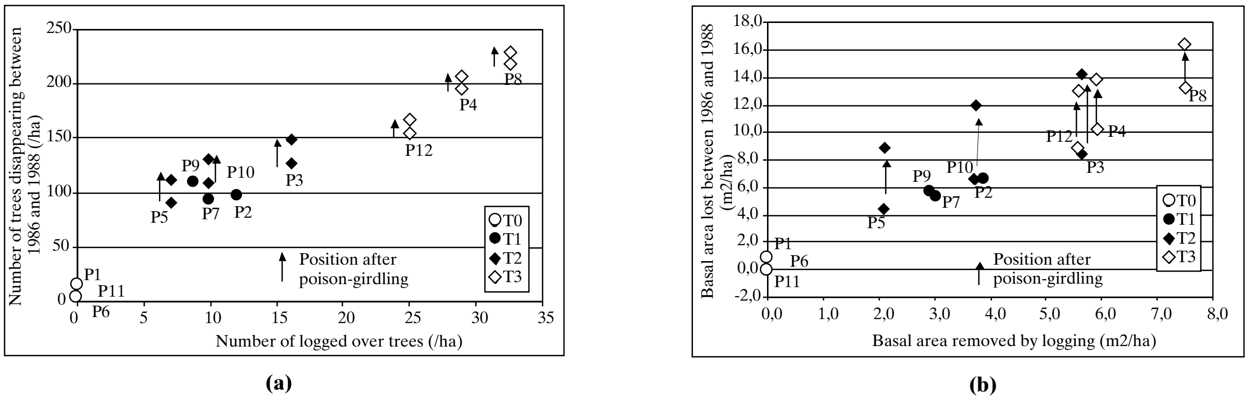
*Among those trees, respectively 1.2 for T_1, 1.4 for T_2 and 2.3 for T_3 were logged for timber under the DCL, namely between 40 and 50 cm DBH. This was done in the three first logged plots P_2, P_3 and P_8, following an initial protocol abandoned afterwards. For T_3, the number of 28.9 trees/ha is split between 9.9 trees ≥ 50 or 60 cm DBH (according to the DCL of the species considered) logged for timber and 19.0 trees logged for fuelwood.

girdling, respectively, is detailed in Table 1, as well as the annual evolution of the parameters of the stands at the treatment level. Extraction of timber trees by logging represented, on a mean basis, 10 trees/ha, 3.5 m^2 and 50 m^3/ha on the nine treated plots.

The loss of trees induced by the treatments resulted mainly from damage directly linked to felling operations, as illustrated in Fig. 1a,b. In comparison, the additional loss due to poison-girdling (see arrows in Fig. 1) was marginal in terms of numbers but not in terms of basal area. This illustrates the main interest of such a thinning technique: it increases the light supply to the stand without increasing damage to the remaining trees.

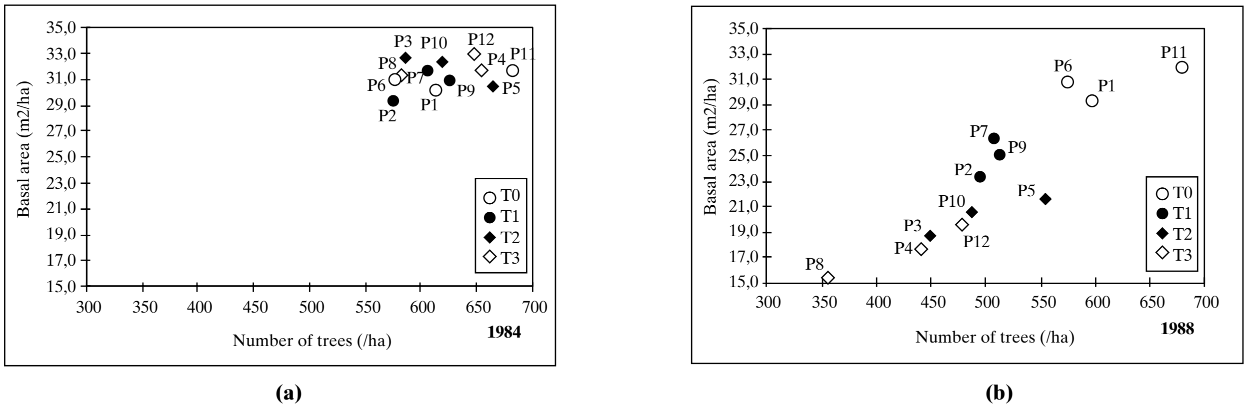
The logging and thinning rules were applied to plots in which the initial characteristics differed from each other, reflecting the heterogeneity of the natural forest stands on a local scale (see Part I for a detailed description and discussion). As an example, the mean densities (trees ≥ 10 cm DBH) in 1984 ranged between 576 trees/ha in P2 and 683 trees/ha in P11, 19% more than in P2! (Fig. 2a). Basal area ranged between 29.3 m^2/ha in P2 and 33 m^2/ha in P12, a significant difference that is equivalent to the mean basal area removed during logging operations between 1986 and 1987. The protocol of the experiment took this heterogeneity into account, and it can be seen in Fig. 2b that the range of natural variation was covered inside each treatment.

Depending on the stand structure and richness in exploitable trees, the treatments had a more or less severe impact on the plots, either preserving (T1) or



(a) **(b)**

Fig. 1. Position of the plots according to the degree of disturbance experimented when applying the silvicultural operations. The x-axis represents the logging intensity and the y-axis the stand loss between 1986 and 1988 when poisoned trees are not taken into account. (a) Information in terms of number of trees/ha. (b) Information in terms of basal area. For the plots of T_2 and T_3, the arrows indicate the shift in stand loss specifically due to poison-girdling.



(a) **(b)**

Fig. 2. Total number of trees (≥10 cm DBH) and cumulated basal area characteristics of each Paracou plot: (a) in 1984, before the implementation of the treatments (natural stands) and (b) in 1988, immediately after.

increasing (T2, T3) the initial heterogeneity (see Fig. 2b). P3 (T2), which was very rich in trees ≥ 60 cm DBH (see Part I, Fig. 12b,d), finally underwent a disturbance level similar to that of the T3 plots, while P12 (T3) experienced the opposite situation.

2.1.2. Subsequent evolution

From 1988 to 1997, the evolution of density and the corresponding basal area in the plots showed a double trend as illustrated in Fig. 3: (i) within the group of T2/T3 plots, the increase in the number of trees and basal area was greater when the disturbance linked to the treatments was higher and the level of density and basal area in 1988 was low (compare Fig. 3 with Fig. 2b), and (ii) for the same increase in basal area, the increase in the number of trees was far higher in the T2/T3 plots than in the T1 plots, illustrating the effect on recruitment of a greater opening of the stands (see Section 2.4). On a mean basis, the gain in basal area over the period 1988–1997 was the same for T1 and T2, due to high mortality phenomena in the plots of T2, especially P5, between 1988 and 1989 (see Section 2.3).

Fig. 4 shows the annual evolution of the same parameters at the treatment level. On the control plots, the number of trees slowly and continuously decreased since 1984, while the basal area increased, whatever the set of species considered. The trends observed on the control plots were slight compared to those of the treated plots. These trends can correspond to normal fluctuations around an equilibrium value, or result either from a large ancient disturbance or from a recent anthropogenic global change (increased atmospheric CO_2 and/or N and P deposition from Saharan dust) as hypothesised by Phillips et al. (1998). More time is needed to reach a conclusion.

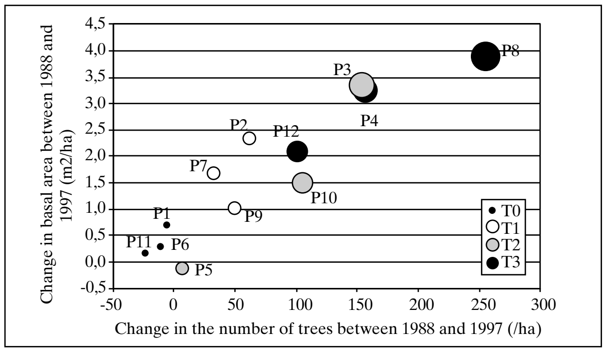


Fig. 3. Position of the plots according to the changes in their number of trees and cumulated basal area over the period 1988–1997. Each plot is figured out by a circle, whose radius is proportional to the basal area lost between 1986 and 1988, in increasing order and in m^2/ha: P11 (–0.09), P6 (0.07), P1 (0.89), P7 (5.35), P9 (5.59), P2 (6.48), P5 (8.92), P10 (11.98), P12 (13.03), P4 (13.97), P3 (14.29) and P8 (16.36).

On the treated plots, the mean density has increased rapidly since 1990, especially in T2 and T3. In 1997, the most heavily affected plots (T3) almost reached the level of the controls, and two plots (P3 in T2 and P8 in T3) were denser than they were before treatment. Plots of T2 and T3 show greater mean densities than in T1. Logically, basal area evolves more slowly and in 1997 remained lower in T2 and T3 than in T1.

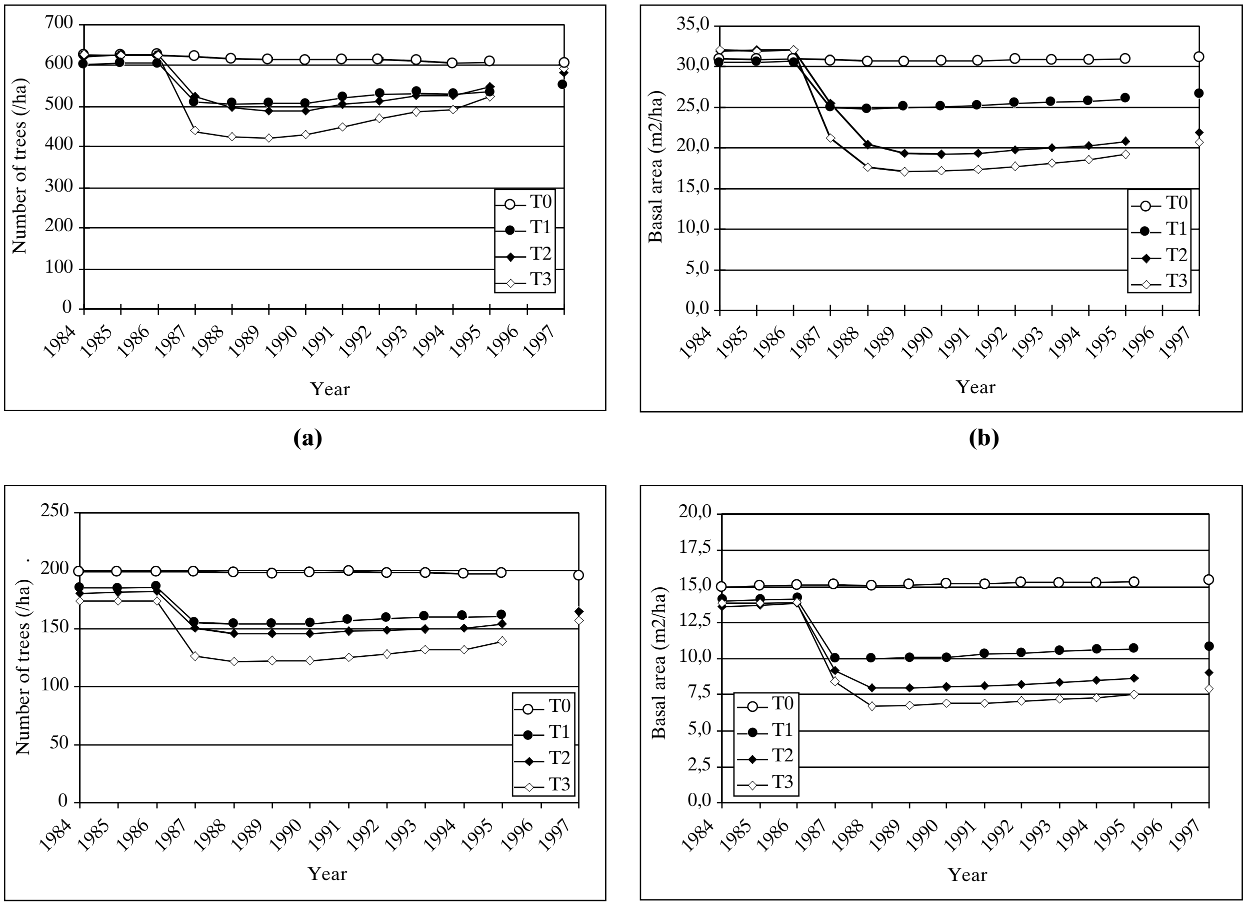
In the set of valuable species, the trends are similar but less pronounced. The plots of T2 and T3 did not recover their number of trees as quickly as the whole stands because valuable species do not encompass the group of pioneer trees (see Part I, Table 2 of Annex 1). Their proportion in the stands thus decreased slightly since 1989, not only in number but also in basal area for T3. This trend is even more pronounced in the set of the 20 currently most researched species, which contains only one real heliophilous species (*Simarouba amara* Aublet, Simaroubaceae).

2.2. In terms of the diameter structure

When all species in the undisturbed stands are considered, the size-class distribution of the trees can be fit by a negative exponential function (which, however, tends to underestimate the numbers in the first size class), as classically observed at this scale in these forests (Rollet, 1974). The percentage of the 58 valuable SGS in the classes increases from less than 25% of all trees between 10 and 20 cm DBH to 60–80% of trees greater than 60 cm DBH; this illustrates the status of most of these species, which are able to reach the canopy or, at least for some of them, the sub-canopy (see Fig. 5b,d,f, curves for 1984). It also explains their importance, about 50%, in the cumulated basal area of the stands.

2.2.1. Immediate impact on the stands

In the treated plots, all the diameter classes were disturbed between 1986 and 1988: the large diameter classes by logging and poison-girdling, the smaller ones by damage (Fig. 5a,c,e). The set of valuable species ≥50 cm DBH in the stands logically decreased everywhere, before increasing again between 1988 and



(a)

(b)

(c)

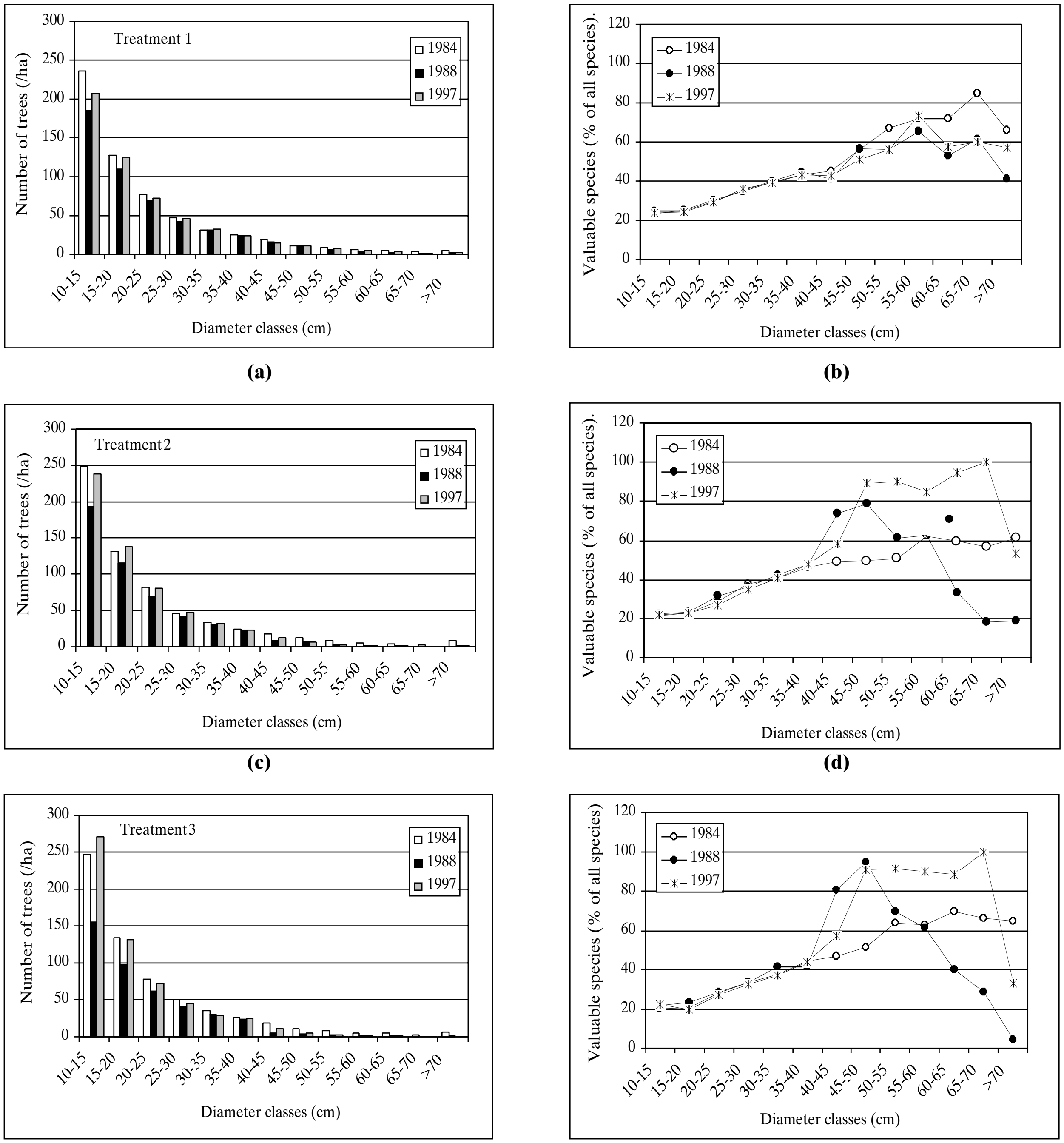
(d)

Fig. 4. Evolution of the living trees according to silvicultural treatments: (a) total number per hectare, DBH ≥ 10 cm, all species; (b) basal area per hectare, same trees; (c) total number per hectare, DBH ≥10 cm, 58 valuable SGS and (d) basal area per hectare, same trees.

1997 as the larger classes were supplied with the ingrowth from intermediate classes (Figs. 5b,d,f and 6). In T2 and T3, systematic elimination of the non-valuable species above 40 cm DBH, either by poison-girdling or by logging for fuelwood, greatly increased the percentage of valuable trees in these diameter classes and partly compensated for losses due to logging for timber (Fig. 5d,f, curves for 1988 and 1997). In diameter classes below 40 cm DBH, damage affected all species equally and there was no modification in the balance between valuable and non-valuable species.

Considering only the set of valuable species, logging for timber between 1986 and 1987 almost equally depleted the exploitable stock at the treatment level, leaving in the stands between 26% (in T2) and 36% (in T1) of trees ≥ DCL, which either had defects or were forgotten by loggers (Schmitt, 1989) (Fig. 6). Between 1987 and 1988, the remaining stock was further similarly depleted by thinning in T2 and T3, T3 being the most affected due to the presence of many large individuals in plot P8. The size of this new loss indicates that most of the remaining trees above DCL in T1 probably showed defects.

For the same set of valuable species, the classes below DCL (the future crop trees) were depleted by damage due to logging, logging for timber of some trees under DCL (see footnote, Table 1) and elimination through poison-girdling or logging for fuelwood of trees ≥ 40 cm DBH which had defects. As previously discussed, this indicates that some future crop trees remaining in T1 show defects; a direct estimation of their numbers can be made by comparing T1 and T2 in Fig. 6.



(a) (b)

(c) (d)

(e) (f)

Fig. 5. Evolution of the size–class structure in the treated stands, between 1984 and 1997. The situation after the treatments (1988) is also stated: (a) T1, all species; (b) T1, importance of the set of valuable species; (c) T2, all species; (d) T2, importance of the set of valuable species; (e) T3, all species and (f) T3, importance of the set of valuable species.

2.2.2. Subsequent evolution

Between 1988 and 1997, the increase in number of the first diameter class (10 to 15 cm) was proportional to the severity of the disturbance, with numbers exceeding initial values in 1997 in T3 (Fig. 5e). The intermediate classes, from 15 to 35 cm DBH, recovered their initial numbers in 1997, except in T3, which suffered the higher logging intensity and damage.

In the large diameter classes, the degree of recovery observed depended on the set of species, the treatment and the diameter limit considered (Table 2).

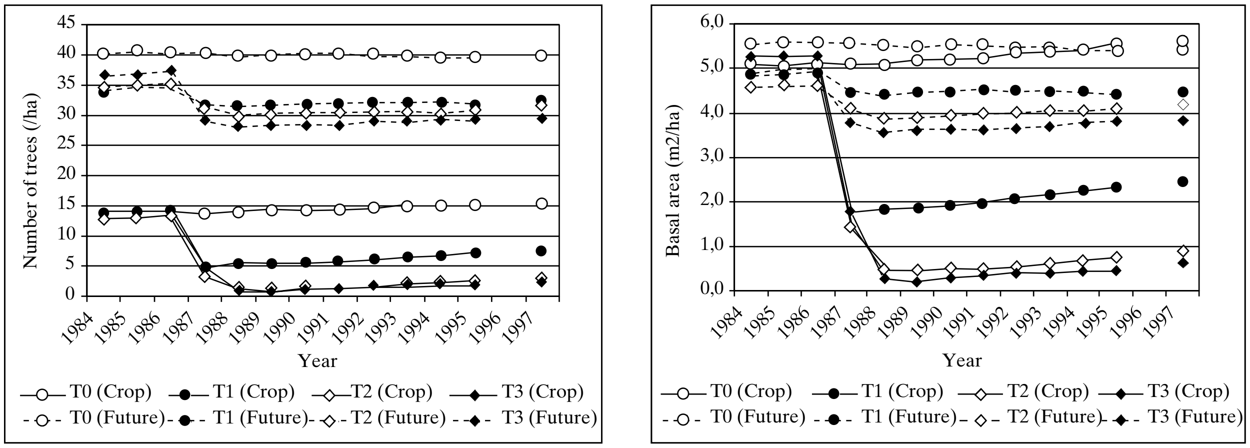
In T1, about 20% of the large trees were recovered in 1997, whatever the DCL and the set of trees considered. Using the hypothesis of a constant rate of recovery (2% per year), the total stock would be regained within a minimum of 50 years (2.5% and 40 years, respectively, for the valuable stock of large trees). However, the mean diameter of trees above DCL would probably be smaller than in untouched forest, as indicated by the low rates registered in the classes ≥ 65 cm. Results are the same for the set of 20 species currently exploited in French Guiana.

In T2 and T3, the upper diameter classes globally lost trees between 1988 and 1997. Ingrowth above 50 cm DBH did not compensate for the high mortality rates which occurred after treatment. This mortality phenomenon involved mainly the non-valuable species; for the set of valuable trees, as illustrated in Fig. 6, an

Table 2
Annual rate of recovery in the upper diameter classes, according to the set of species considered. AS: all species; VS: valuable species. The rate is the ratio between the number of trees appeared between 1987 (respectively 1988 for T_2 and T_3) and 1997, and the number of trees lost between 1984 and 1987 (respectively 1988 for T_2 and T_3), divided by the number of years and multiplied by 100.

Treatments	*T_1 (period 1987–1997)*		*T_2 (period 1988–1997)*		*T_3 (period 1988–1997)*	
Diameter classes (≥ cm)	*AS (%)*	*VS (%)**	*AS (%)*	*VS (%)**	*AS (%)*	*VS (%)**
50	2.1	2.5	–0.6	1.7	–0.5	1.0
55	1.6	1.5	–1.0	0.4	–0.9	–0.4
60	1.9	2.4	–1.6	1.3	–0.9	1.3
65	1.3	1.5	–2.1	0.2	–1.4	0.5
70	0.9	0.9	–1.9	0.0	–1.8	0.0

*For the diameter classes ≥ 50 and 55 cm, the set of valuable species considered is the set of species which diameter cutting limit was 50 cm DBH (48 SGS). For the upper classes, the valuable species considered are those with a DCL of 60 cm DBH (10 SGS).



(a) (b)

Fig. 6. Evolution, according to silvicultural treatments, of the larger diameter classes for the set of 58 valuable SGS. DCL = 50 or 60 cm according to the SGS: (a) number per hectare, crop trees (“Crop”: DBH ≥ DCL) and future crop trees (“Future”: DCL-20 ≥ DBH ≥ DCL) and (b) basal area per hectare, same trees.

increase in the number of trees and basal area is evident for all treatments, even for T2 and T3.

Having suffered heavy depletion of their stocks, T2 and T3 do not perform as well as T0 and T1, where increments are spread over more numerous trees, but their potential for recovery can be seen in the behaviour of the class below DCL, where a net increase in both numbers and basal area has occurred, whereas it tends to stagnate in T0 and T1. Diameter structures are evolving significantly in these treatments, thus using the observed rates to forecast how fast the stands will be restocked is uncertain.

2.3. Effects on mortality

Three types of mortality are currently monitored at Paracou: standing death (SD), primary windthrow (W1), and secondary windthrow (trees broken or unbalanced by a primary windthrow, W2). On the control plots, between 0.7% (4.5 trees/ha) and 1.4% (9.1 trees/ha) of living trees died each year between 1984 and 1997. Over this period, 48% of them died standing, 30% were primary windthrows and 22% were secondary windthrows (Fig. 7). Mortality is highly variable from one year to the next and generally has important consequences on the annual balance of basal area (see Section 2.6).

Schmitt (1989) has precisely described the implementation of the silvicultural treatments and their direct impacts on the stands in terms of damage and immediate mortality (see Table 1). A detailed study of the mortality phenomena, both natural and treatment-induced, and of its determinism at Paracou can be found in Durrieu de Madron (1993, 1994).

Fig. 7 shows that the treatments temporarily increased mortality among the trees remaining on the stands, mainly during the 3 to 4 years following logging, and for a longer period in T2 than for the others. Four periods can be highlighted:

- first, during logging operations (1986–1987), the number of W1 was almost doubled compared to the control in all the treatments with a simultaneous increase in W2 in T2 (Fig. 7d,e).
- One year later, between 1987 and 1988, the natural mortality rate reached 2.5% in T1 and T2, and 3.4% in T3. This was the maximum observed in T1 and T3, in absolute numbers and in rate (Fig. 7a,b). Mortality concerned mainly injured trees which did not die immediately during logging operations. In 1987, injured trees represented 9% of the living trees in T1 and in T2 (about 54 trees/ha) and 13.4% in T3 (84 trees/ha). In 1997, about 30% had died, most of them between 1987 and 1988. During this year, injured trees accounted for about 40% (T1 and T2) and 59% (T3) of the total mortality: the differences observed between T0 and the three treatments on SD and W1 are almost entirely due to these trees (Fig. 7c,d).
- Between 1988 and 1989, mortality began to decrease in numbers and rate in T1 and T3, while a peak occurred in T2 where the mortality rate reached 3.1%. During this period, the plots of T2 and, to a lesser extent T3, experienced the consequences of poison-girdling applied during the previous year; respectively, 28.7 trees/ha ≥ 40 cm DBH and 14.8 trees/ha ≥ 50 cm DBH were poisoned and 70–75% of them died within the first year (cf. reported numbers in Table 1); most of the others disappeared between 1988 and 1989. The peak of mortality in T2 came from an increase in W2, entirely explained by the damage caused by the fall of poisoned trees (about 3.7 trees broken/ha). The increase in W1 could be due to an additional instability linked to these damages.
- From 1989 onwards, a return to the control level is observed in T1, but this was delayed until 1992 for T3 and 1995 for T2, due to a relatively high number of secondary windthrows. The T2 treatment lost, due to “natural” mortality, the greatest number of trees between 1986 and 1997, mainly through windthrows. Except for the peak of 1988–1990, this high rate is not easy to interpret, as the mean diameters of W1 in T2 were not significantly different from those of T1 and T3. The underlying mechanisms and the possible role played by poison-girdling in generating instability in these stands remains to be studied in more depth.

In conclusion, the silvicultural treatments applied at Paracou indirectly affected the natural mortality phenomena in three ways: (i) injuries, leading to death by SD or W1 one year after logging, (ii) the opening of the stands which induced local instability and a consequent increase in windthrows, and (iii) poison-girdling which led to an additional increase in windthrows due to the fall of poisoned trees. The effect was greater in T2 than in T3, where a lower number of trees remained in the stands after logging. It must be noted that the effect of the treatments on natural mortality, as compared to the controls, is almost never significant. Comparisons of mortality rates, assuming that the number of dead trees follows a binomial distribution, were performed year after year between each of T1, T2, T3 and T0 values. The

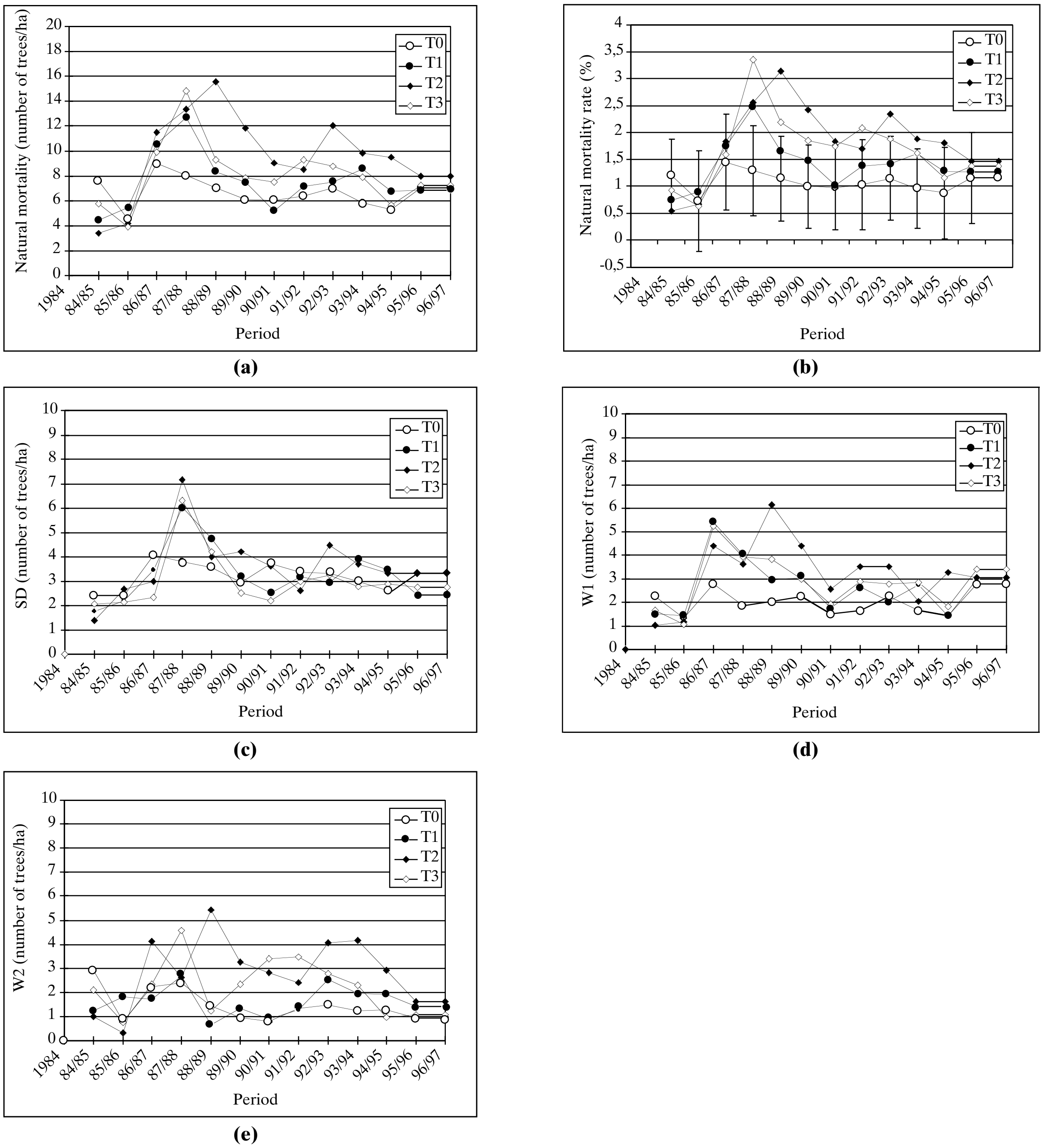


Fig. 7. Evolution of natural mortality in the stands (untouched + injured trees). (a) All types, in number of trees/ha/yr. (b) All types, mortality rate (%). For T0, annual rates are plotted with their 95% confidence interval, considering that the number of dead trees follows a binomial distribution. (c) Standing death, in number of trees/ha/yr. (d) Primary windthrows in number of trees/ha/yr. (e) Secondary windthrows, in number of trees/ha/yr.

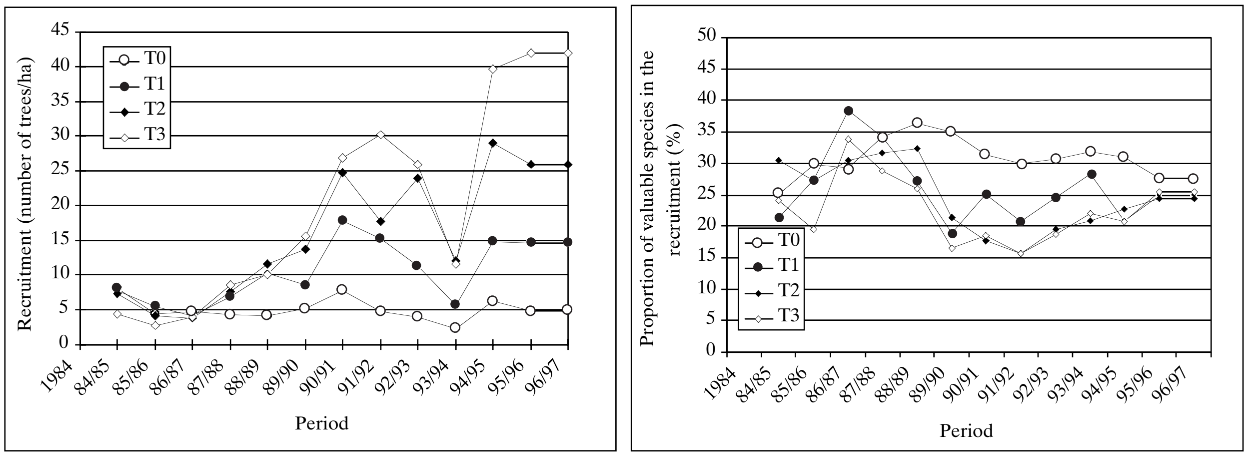
only significant differences were found between T3 and T0 in 1987–1988 ($P = 0.023$) and T2 and T0 in 1988–1989 ($P = 0.019$).

The pattern of natural mortality in the set of valuable species is similar to that of the whole set of species; the percentage of total mortality due to the death of valuable trees oscillated between 15% and 30% around a constant mean across the years in all treatments, with a tendency to decrease in T2 and T3, and to increase in T0 and T1 between 1991 and 1997. In the control plots, the mortality rate of the valuable trees varied between 0.5% and 1.1% according to year (1–2 trees/ha). This rate reached 2.2 to 2.5% in the treated plots, about 2.5 times the level of the controls between 1987 and 1988. The mortality rate increased to 2.6% in T2 between 1988 and 1989. A return to normality was observed from 1989 onwards in T1 and T3, and from 1994 onwards in T2.

2.4. Effects on recruitment

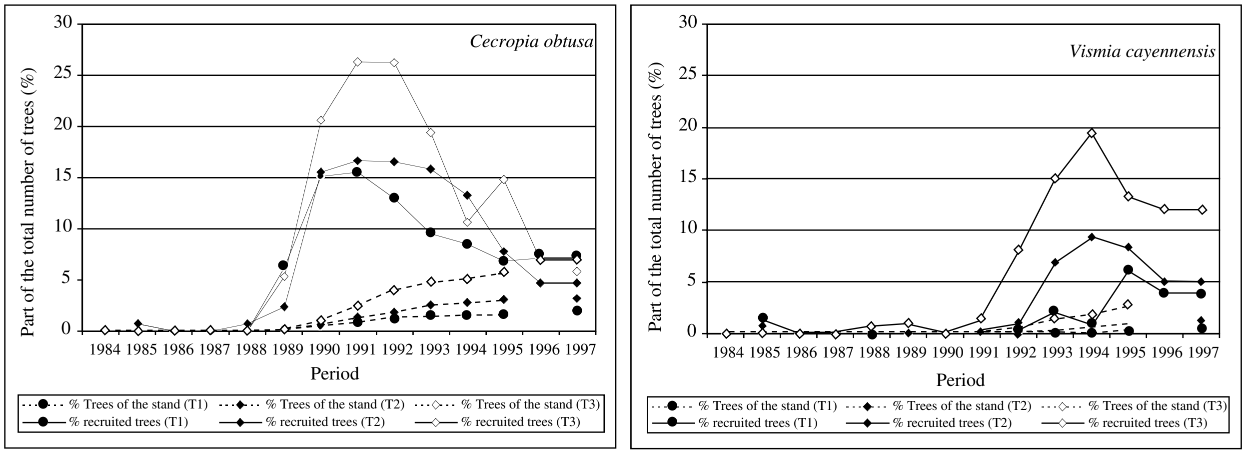
On the control plots, between 0.7% (4 trees/ha/yr) and 1.3% (8 trees/ha/yr) of the living trees were recruited between 1984 and 1997. Fig. 8a illustrates the effect of treatments on this component. In T1, the recruitment rate reached 2.8% (14 trees/ha/yr) between 1994 and 1997, almost three times the rate observed in the controls during the same period. In T2, this rate reached 5.5% (24 trees/ha/yr) and in T3, 8.1% (41 trees/ha/yr, 10% of the living trees, 8 times the normal level of recruitment!). Subsequent inventories (unpublished data) show that the maximum was still not reached in 1997 in any of the treatments.

It can be seen that (i) from 1988 to 1994, the level of recruitment was almost the same in T2 and T3, higher than in T1; (ii) from 1994 onwards, T3 broke away from T2. This two-step evolution can be explained by the pattern of recruitment of several pioneer species which played an important part in the behaviour of the disturbed stands: *Cecropia obtusa* Trec and *Cecropia sciadophylla* Martius (Moraceae), *Vismia cayennensis* (N,J, Jacquin) Persoon (Clusiaceae) and *Tapirira guianensis* Aublet (Anacardiaceae). The two *Cecropia* species, with some individuals growing at a speed of 8 cm diameter/yr, appeared above the 10 cm DBH inventory threshold as soon as 1988, 2 years after logging (see Fig. 9a for *C. obtusa*). *T. guianensis* and *V. cayennensis* germinated in the openings at the same time as the *Cecropia* species, but as they grew more slowly, they were recruited 2 to 3 years later (see Fig. 9b for *V. cayennensis*). The recruitment of these four species was greater when the disturbance had been high, particularly for *T. guianensis*. Pooled together, between 1994 and 1995 these species represented 29.6% of the recruitment in T2 (19.4 trees/ha) and 47.4% in T3 (39.7 trees/ha)! In 1997, their total number in the stands equalled 53.3 trees/ha in T2 (out of 82.1 trees for all the pioneer species present in the stands) and 91.3 trees/ha in T3 (137.6 pioneer trees in total), that is respectively 9% and 15% of the total set of living trees. This considerable set of fast-growing trees, almost absent in the undisturbed stands, probably increased the level of inter-tree competition



(a) **(b)**

Fig. 8. Evolution of the annual recruitment at Paracou: (a) number of trees recruited each year, all species pooled together and (b) proportion of the total number of recruited trees belonging to the set of 58 valuable SGS. Note: values for 1995/1996 and 1996/1997 are the annual mean calculated over the period 1995/1997; the low value registered on the 1993–1994 period in all the groups of plots is a bias due to problems in the organisation of the inventory of 1994.



(a) **(b)**

Fig. 9. Compared evolution of the importance of two pioneer species in the total stand and in the annual recruitment, according to the intensity of disturbance (treatments): (a) *Cecropia obtusa* and (b) *Vismia cayennensis*.

in the stands, at least in T2 and T3, and may explain why mean diameter increments are now slowing down in those treatments (see Section 2.5). Finally, the 1995–1997 period shows a decrease in the proportion of these main pioneer species in the recruited pool (Fig. 9), announcing a new shift in the environmental conditions of the treated plots.

The recruitment rate in the set of valuable trees, varied between 0.6% and 1.2% per year (1.2–2.5 trees/ha) on the control plots. After treatment, trends were similar to those observed for the whole set of species, with absolute numbers of recruited trees being multiplied, respectively, by 2.7 (T1), 4.7 (T2) and 7.8 (T3) compared to the controls over the period 1994–1997, and 2.3 (T1), 3.8 (T2) and 13.3 (T3) compared to their own level of recruitment before treatment. Fig. 8(b) shows how their numbers evolved in the global pool of recruited trees. From 1984 to 1988, the proportion oscillated around the mean value representing the size of the stock in the stands (from 28% in T3 to 32% in T0). From 1988 onwards, the effect of disturbances began to be seen and the proportion of valuable trees decreased until 1995, before rising again due to the evolution pattern of pioneer trees during this period.

2.5. Effects on growth

An in-depth study of the growth behaviour of trees at Paracou is presented in Chapter 4, this Part. In particular, the evolution of mean annual diameter increments over the periods 1984–1986, 1988–1991, 1991–1994 and 1994–1997 is shown in Table 1 and illustrated in Fig. 5, Section 2.4 of this chapter. The most important features are as follows:

- before the application of the treatments, mean annual diameter increments at Paracou varied between 0.082 and 0.165 cm/year (in P9 and P2, respectively), with a highly significant plot effect; increments tended to be lower where tree density was higher. Moreover, increments were significantly lower in the 10–20 cm diameter class, while they were higher in the classes exceeding 40 cm DBH.
- After treatment, mean diameter increments systematically increased. They were multiplied by 1.8 in T1 and by 2.7 in both T2 and T3 between 1988 and 1991. They continued to increase during the following period (1991–1994): 2-fold in T1 and more than 3-fold in T2 and T3 compared to the 1984–1986 period, although a slowdown was noticeable in the period 1994–1997. The diameter class effect remained highly significant in the treated plots whatever the period considered, with the same pattern as before treatment. The small trees were most sensitive to the treatments, with the highest multiplicative factors occurring in the 10–20 cm diameter class; however, all the trees benefited from the opening of the stands, even the largest ones. The treatment effect appears to be long lasting in all the diameter classes, even if a slowdown, possibly explained by the massive arrival of pioneer trees, is detectable from 1994 onwards in the smallest class.

- Whatever the period and diameter class considered, mean diameter increments were not significantly different in treatments 2 and 3 and are slightly lower in T3 than in T2.

In the undisturbed stands, diameter increments monitored on the set of valuable species are about 45% higher than on the whole set of species, varying between 0.119 and 0.244 cm/yr in P9 and P2, respectively. This illustrates the ecological status of the species of commercial interest, as already mentioned in Section 2.2. Sixty-eight per cent of these (78% of the total number of valuable trees and 89% of the valuable basal area) belong to the three canopy groups defined by Favrichon (1994, 1995), with a majority of semi-tolerant or heliophilous species characterised by mean wood densities. On the contrary, the major part of the non-valuable species consists of slow-growing, high wood density species of the understorey and subcanopy.

The opening of the stands in 1987 and 1988 gave place, in varying degrees, to fast-growing noncommercial pioneer species. As a result, the increase in mean increments was slightly higher in the whole set of species than in the valuable species (increments in this latter set were multiplied by 1.7 in T1 and 2.4 in T2 and T3 between 1988 and 1991) and the absolute differential between valuable species and the total pool of species remained fairly stable.

The main trends found for the whole set of species remain globally true for the valuable set: (i) before treatments, a highly significant plot effect existed ($F_{(11,00)}$ = 22.58, P = 0.0001), with a globally good accordance between low stand densities and high diameter increments, and increments were significantly lower in the 10–20 cm diameter class than in the others ($F_{(5,00)}$ = 64.95, P = 0.0001) (Fig. 11a); (ii) the reaction to treatments reached its maximum during the period 1991–1994, with increments decreasing from 1994 onwards (Fig. 10, to be compared to Fig. 5, Section 2.4 in Chapter 4, this Part). The first diameter class was the most reactive, while the greatest diameter increments were registered in the upper classes (≥40 cm DBH) (Fig. 11, compare to Fig. 7, Section 2.5 in Chapter 4, this Part). No significant differences were noted between T2 and T3, increments being most often higher in T2.

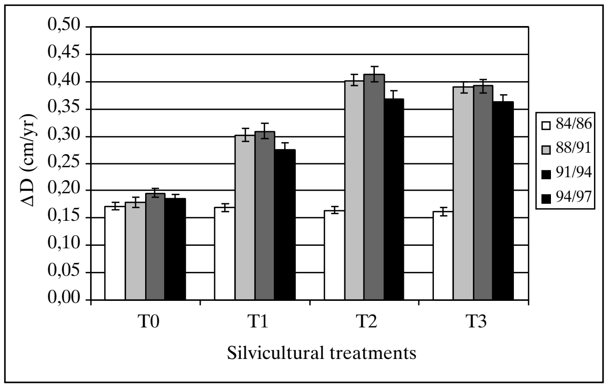


Fig. 10. Mean annual diameter increment (cm/year) according to the treatment and period of time studied in the pool of 58 valuable SGS. Treatments were applied between the end of 1986 and the beginning of 1988. Mean values are plotted with their 95% confidence interval.

2.6. Effects on the basal area balance

The basal area balance between 2 years of inventory, t_1 and t_2, is calculated as follows:

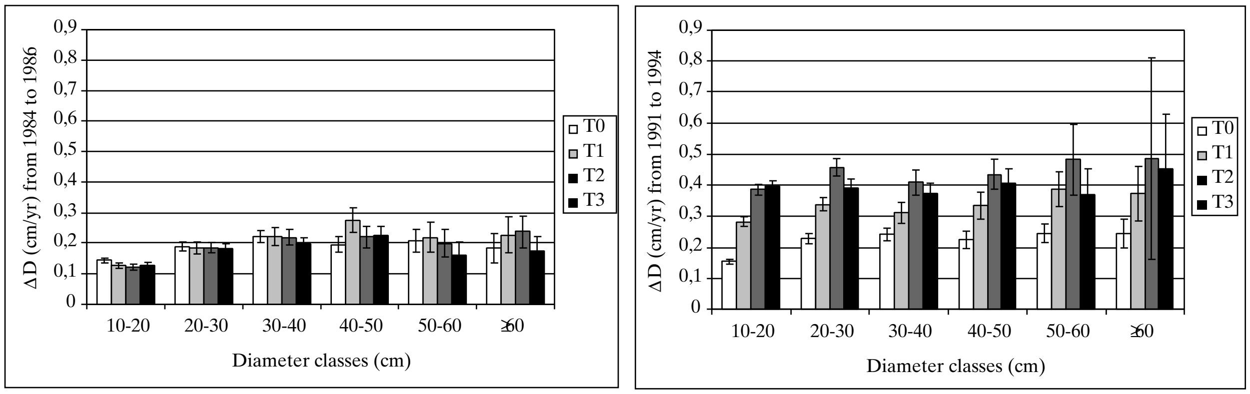
$$B_{t_1,t_2} = A_{t_1,t_2} - M_{t_1,t_2} + R_{t_1,t_2} \qquad [1]$$

where A is the increment in basal area due to the growth of living trees between t_1 and t_2, M is the basal area lost to mortality and R is the basal area gained through the recruitment of new trees.

The annual fluctuation of the balance closely follows that of mortality (Fig. 12a,b). Most often, growth and recruitment overcompensated for mortality and the balance is slightly positive, as already noted in Section 2.1. This phenomenon was more regular for the set of valuable species, which did not experience the high mortality in the period 1984–1989 undergone by the global set and was responsible for the positive balance of the whole stands (compare the curves of the cumulated balance in Figs. 12a and 12b). As a consequence, their relative importance in the stands slightly increased between 1984 and 1997.

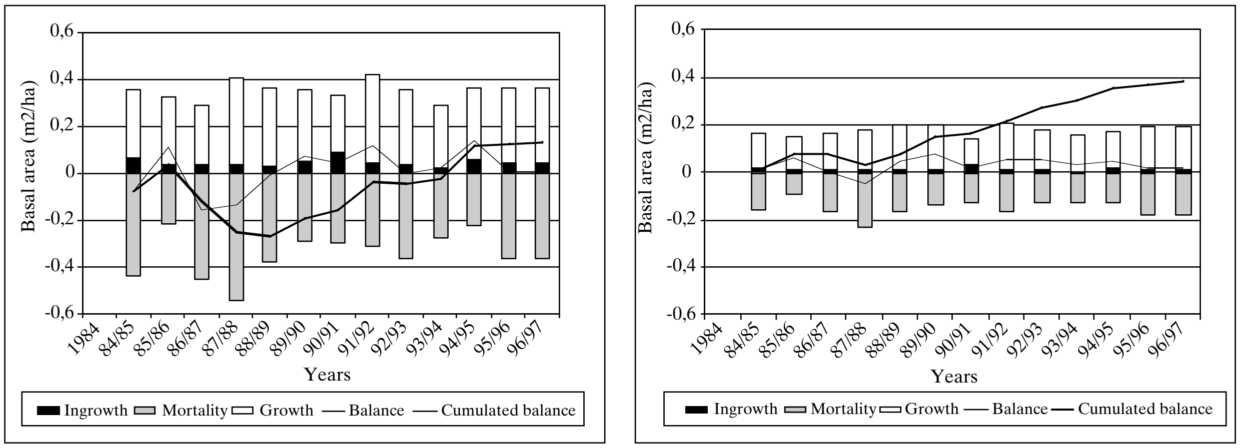
In the treated plots, the annual balance remained highly negative over the period 1986–1988 (T1), 1986–1989 (T3) and 1986–1990 (T2), due to the high mortality linked to logging and poison-girdling. From 1990 onwards, the balance was positive everywhere and its value was highest when the treatment had been severe.

Fig. 13 represents the evolution of the cumulated basal area and its components A, M and R, considering the 1988–1989 value as the origin (the first non-null



(a) **(b)**

Fig. 11. Mean diameter increments according to diameter classes and treatments (a) before and (b) after the implementation of the treatments. Mean values are represented with their 95% confidence interval. Note that mean values are far better estimated in the small classes where trees are numerous. In the ≥60 cm DBH class, more than 130 trees were used in each group of plots, but after treatment only 6 and 11 trees could be used in T2 and T3 respectively for the calculations.



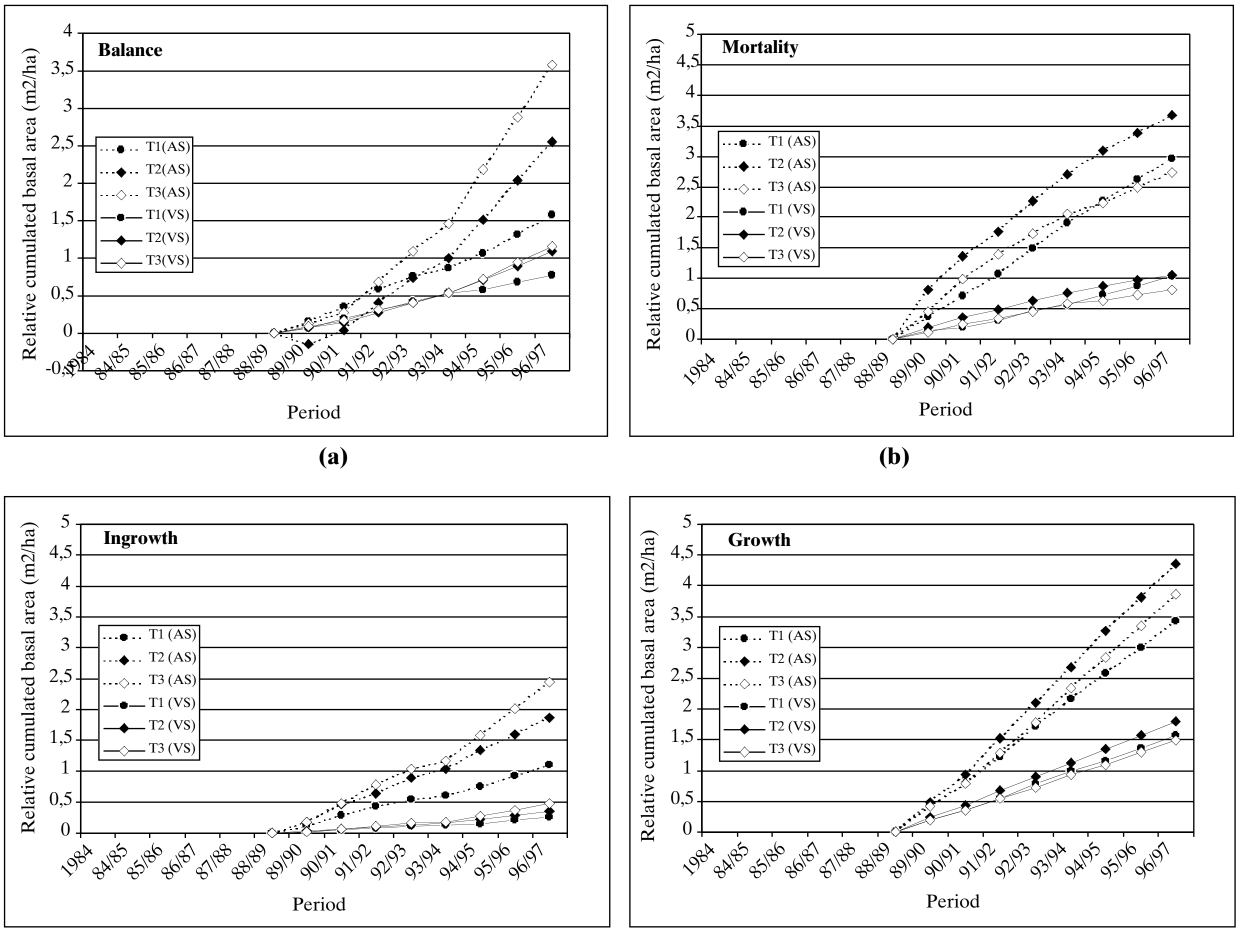
(a) **(b)**

Fig. 12. Evolution of the balance and its components on the control plots. (a) Whole set of species and (b) set of 58 valuable SGS. The cumulated balance is calculated as $\sum_{i=1985}^{t} B_{i-1,i}$ for t = 1985–1997.

value over the 1989–1990 period; as of this point, it was possible to be rid of the high mortality levels which occurred immediately after treatment). Fig. 13a shows that the rate of basal area recovery increased with the intensity of the treatments. Compared to T2, the high rate observed in T3 over the 1989–1997 period resulted mainly from the following:

- lower losses due to mortality (Fig. 13b): the treatment and associated damage left few living trees in the plots, of reduced mean size, thus limiting the subsequent impact of this component.
- High gains through recruitment (Fig. 13c), due to the invasion of pioneer species.

The evolution of balance in T2 was penalised by high mortality rates (Section 2.3) but benefited, in return, from high values of basal area increment due to growth (Fig. 13d); although mean diameter increments were not significantly different between



(a) **(b)**

(c) **(d)**

Fig. 13. Evolution of the cumulated basal area balance and its components, according to the treatments applied and relative to the value observed in 1988/1989. (a) Balance: the variable plotted is $\sum_{i=1990}^{t} B_{i-1,i}$, for i = 1990 to 1997; (b) B is replaced by M for the mortality component; (c) by R for the ingrowth component and (d) by A for the growth component. The two sets of species considered are all species (AS) and valuable species (VS). Note that over this period, T2 cumulated more basal area than T1, which is not the case over the 1988-1997 period (see Fig. 3) due to the high mortality phenomena occurring between 1988 and 1989.

T2 and T3, they were generally higher in T2 (Section 2.5) and concerned more trees left in the stands after treatment.

Between 1984 and 1997, the cumulated basal area due to mortality was almost as great in T2 (18.22 m^2/ha) as in T3 (19.68 m^2/ha); the main difference was in the spread of the process over time. This could partially explain the higher values of diameter increments observed in T2; the level was high but the mortality was distributed over time and this prevented many trees from suffering sudden and drastic modifications of their local environment, as is supposed to be the case in T3.

In the set of valuable species, the balance trend in T2 was similar to that of T3, due mainly to the growth component. For this set, basal area increment due to growth was particularly low in T3, even less than in T1, while (i) the logging rules applied to these species were the same in all the treatments and (ii) the mean diameter increments observed in T3 were 50% higher than those observed in T1 between 1988 and 1997. This difference between T1 and T3 results from the impact of additional logging for fuelwood carried out in T3, resulting in damage to the trees remaining in the stands.

If the cumulated basal area balance evolution is examined for the fraction of exploitable trees, i.e. valuable trees above the DCL (Fig. 14a, to be compared to Fig. 6b), it can be seen that T1 behaves more favourably than T2 and T3, where more valuable trees were lost either through logging or poison-girdling. T2 and T3 did not gain more basal area between 1989 and 1997 than even the control plots. However, the trend will reverse as the intermediate classes below DCL recover their potential (Fig. 14b).

Considering all the trees ≥ 10 cm DBH, the basal area balance cumulated between 1989 and 1997 in the valuable set of species represented 50% (T1), 43% (T2) and 32% (T3) of the total balance. These data can be compared to the proportion of the 58 SGS in the total basal area of the stands in 1984: 45.8% (T1), 42.7% (T2) and 43.1% (T3). Thus, the global size of this group remained stable in the plots of T1 and T2, while it decreased in the plots of T3.

3. The possible future of the stands

3.1. Recovery of the stands after disturbance, given the constant rate hypothesis

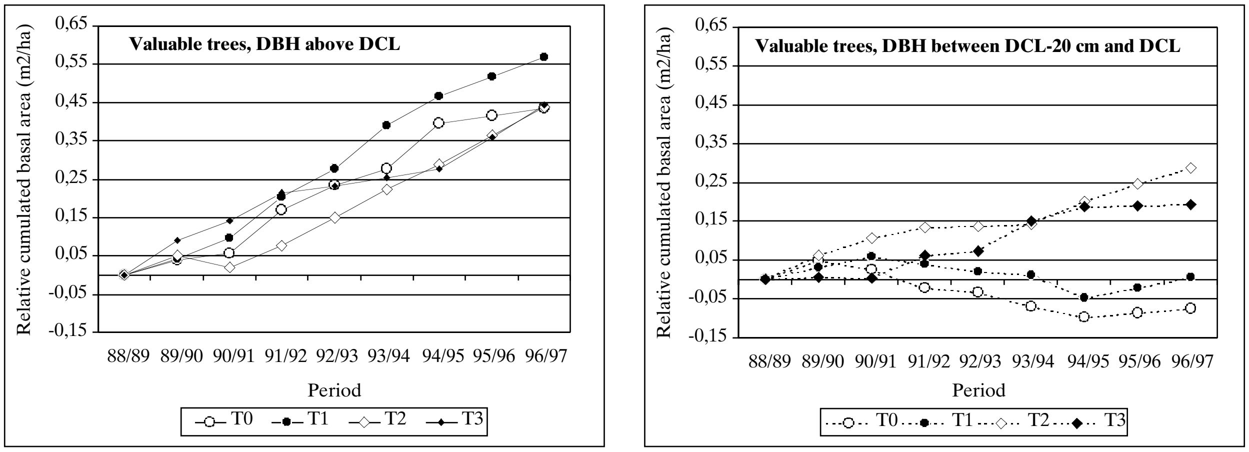
We are particularly interested by the time required for this recovery, or "return time", for two specific variables:

1. the total basal area of the stand, as an indicator of the speed at which the environment of the trees will become competitive again. Complemented by the basal area in large diameter classes, particularly for the set of valuable species, this also gives an idea of whether these species will retain their global production potential. However, it gives no indication about the composition of this recovered basal area (recruited trees, increments of small, medium and/or big trees, etc.). For the valuable species in large diameter classes, part of the recovered basal area will result from the growth of defective trees left by the logging operations.

2. The number of trees having a diameter greater than the DCL; when considering the valuable set of species, this represents the exploitable stock of the stand. The time required for recovery is an indicator for the cutting cycle in managed forests of the area. The information for this variable complements the information on the total basal area of the stand.

To gain insight concerning these two points, we considered as a constant the mean annual recovery rate observed between 1989 and 1997 for each variable, and we deduced from this the time needed to reach the initial value. However, this method can yield results which are too optimistic due to the following:

- as the structure of the disturbed stands evolves, the components of the dynamics also evolve. The stimulating effect of logging, which opens the stands, is probably not a long-lasting one. This is indicated by the trends observed for growth data (Section 2.5). As stand density or basal area (and thus the overall competitive



(a) **(b)**

Fig. 14. Evolution of the cumulated basal area balance, according to the treatments applied and relative to the value observed in 1988/1989: (a) valuable trees, DBH ≥ DCL and (b) valuable trees, DBH between DCL –20 cm and DCL.

pressure) increases, diameter increments slow down and ingrowth into the first diameter class is likely to decrease; variables should evolve according to a Chapman-Richards curve rather than in a straight line.

- For the upper classes, predictions do not take into account the diameter structure in the smaller classes. This structure, in addition to increment rates, greatly influences the feeding rate above DCL.

These drawbacks can be overcome by using more or less simple dynamics models, which are more or less easy to calibrate, realistic and effective: these questions are addressed in Chapter 6, this Part (see Fig. 3 in particular). As it is simple and quick, we used the constant rate method as a first step to obtain rough estimates; its limitations must be kept in mind when reading the rest of this section. In a second step, we refined the approach to study the recovery of the valuable stock of species (Section 3.2).

The results presented in Table 3 indicate that the basal area of the whole stands will be quickly recovered in all the treatments in less than 40 years. In T2 and T3, the reaction of the stands is not stabilised

Table 3

Time of recovery of the initial stand basal area, given the observed rate of increment between 1989 and 1997 and according to the diameter classes and set of species considered. AS: all species; VS: valuable species. For the upper diameter classes, the VS were split between species with a DCL of 50 cm and species with a DCL of 60 cm. See also Fig. 12(a) and Fig. 13(a).

Treatments	*Mean annual balance (m^2/ha/year)*		*Basal area lost between 1986 and 1989*		*"Return time"* (years)*	
All diameters	*AS*	*VS*	*AS*	*VS*	*AS*	*VS*
T_1	0.19	0.09	5.7	4.0	29.6	43.7
T_2	0.32	0.13	12.8	5.9	39.8	44.6
T_3	0.45	0.14	15.0	7.1	33.5	50.9
Diameters ≥ 50 cm dbh	*AS*	*48 SGS with DCL = 50 cm*	*AS*	*48 SGS with DCL = 50 cm*	*AS*	*48 SGS with DCL = 50 cm*
T_1	0.038	0.035	3.280	1.372	86.3	39.6
T_2	< 0	0.033	7.956	2.015	–	61.1
T_3	< 0	0.026	8.292	2.580	–	99.2
Diameters ≥ 60 cm dbh	*AS*	*10 SGS with DCL = 60 cm*	*AS*	*10 SGS with DCL = 60 cm*	*AS*	*10 SGS with DCL = 60 cm*
T_1	0.026	0.036	2.463	1.624	95.2	44.8
T_2	< 0	0.022	5.622	2.657	–	121.5
T_3	< 0	0.030	6.058	2.508	–	85.0

*This way of calculating the return time must be considered with caution, as it depends on the period considered to evaluate the mean annual balance. If the 1988–1997 period is taken as the reference, the return time, for all diameters, increases between 4 (T1) and 56 years (T2) because mortality is still high at the beginning of the period. If we consider 1989–1996, the return time increases between 2 (T1) and 5 years (T2) because the reaction potential of the stand is less correctly taken into account.

(Fig. 13a); the total basal area recovery will probably be faster than evaluated here. It will first concern mainly the small and medium size trees. In large diameter classes, recovery will be longer, i.e. around 86 years in T1. In T2 and T3, where both the number of large trees (Table 2) and the basal area decreased between 1989 and 1997, the return time is still impossible to evaluate.

The total basal area of valuable species could be recovered between 40 and 45 years, except in T3, where species experienced more damage. In T1, this result also holds for diameter classes above the DCL; considering the pool of 58 SGS, the basal area of the upper classes would be recovered within 43 years according to trends observed between 1989 and 1997. In T2 and T3, as already seen, the initial loss was greater and basal area increases more slowly than in T1. Consequently, the estimated return time is doubled (85 and 92 years, respectively, for T2 and T3 for the 58 SGS). However, extrapolating the present behaviour of the upper classes in these plots is quite uncertain, given the evolution of the diameter structure below DCL. The predictions made are probably too pessimistic.

The recovery time estimated for the valuable stock of species in T1 is the same (40 years), whether considering the rate of ingrowth above DCL (Table 2) or the evolution of basal area. Because a part of this evolution is due to the growth of the remaining big trees, however, the similarity of both estimates tends to indicate that the new trees recruited above DCL will be smaller at the end of the rotation than the trees logged for the first time. This also appears to be indicated by the low recovery observed in the classes ≥ 65 cm DBH, as stated in Section 2.2.

3.2. Recovery of the valuable stock in logged-over stands: a simple model approach

In order to overcome at least partially the limitations of the constant rate method, we simulated the evolution of the Paracou stands with a simple matrix model using non-regulated parameters (Caswell, 2001; Favrichon, 1995). We focused on the T1 treatment as being the more realistic for use in French Guiana given the present economical context.

The principle and formula used are described in Chapter 6, this Part, Section 2.2.1 (model [2]), but several adaptations were made:

- different sets of species were considered, with adapted distributions by diameter classes: the set of 58 valuable SGS, split between species with a DCL of 50 cm and species with a DCL of 60 cm, the reduced set of 20 currently logged species and the four most researched species in French Guiana, namely *Dicorynia guianensis* (Aublet) Amshoff (Caesalpiniaceae), *Qualea rosea* Aublet pooled with *Qualea albiflora* (Warm) Marcano-Berti (Vochysiaceae) and *Sextonia rubra* Mez (Lauraceae).
- The starting point was a mean stand (mean of the 12 Paracou plots) logged-over according to the T1 treatment, with logging damages similar to those observed in the T1 plots; the model input was the corresponding distribution by diameter classes in 1987 and the output was the number of trees with a DBH greater than the DCL.
- The b_{si} and m_{si} parameters of the transition matrix were taken as constants for each simulation. The b_{si} were calculated from diameter increments estimated for each diameter class considering (i) the 1988–1997 period following logging in the T1 plots, the values were used during the first 10 years of the simulations; (ii) the 1984–1986 period before implementation of the silvicultural treatments in all the Paracou plots. These values were used for the simulations of subsequent years to take into account the increase in competitive pressure in the stands. This can be considered pessimistic as, in reality, even if a decrease in the increment values was observed in the 1994–1997 period, the values are still higher than in the control plots. The m_{si} were estimated using as many observations of natural mortality as possible, grouping diameter classes to obtain meaningful information, and considering all the plots over the period 1984–1997 to obtain pessimistic estimates.
- For each set of species, the recruitment vector r_s was calculated so as to maintain a constant number of trees in the first diameter class.

For each set of species, 10,000 repetitions of the simulation over at least 100 years were carried out, using values of the matrix parameters sampled inside their variation domain: (i) for the diameter increments, sampling was achieved according to the observed frequency distribution of increments between the 5th and the 95th percentile of the real distribution in each diameter class, and (ii) for the mortality rates, systematic sampling was carried out between the minimum and the maximum values observed in the treatments T0 toT3. We then computed the mean of the 10,000 values obtained for the output variable (here the number of trees above the DCL, see Gourlet-Fleury et al., 2002, for a justification of the method); the result obtained is considered as the most likely given the variability observed on the increment and mortality rates.

The growth and mortality values used to assess the parameters of the matrix model for the main set of 58 valuable SGS are summarized in Table 4 (other sets were used for the other sets of species).

Three main observations can be made on the basis of the results of these simulations (see Table 5 and Fig. 15):

- considering a delayed effect, of no more than 10 years, of the opening of the stands on diameter increments, it is unlikely that the stock of valuable trees logged over in a previously undisturbed forest at a rate of 10 trees/ha will be recovered within a felling cycle of 50 years, and even less so within 40 years as scheduled at present in French Guiana (but for a lower mean level of extraction). Between 80% and 90% of the valuable stock (either the 58 SGS or the 20 currently logged species) could nevertheless be recovered after this time (between 75% and 85% after 40 years).

Table 4
Dynamics characteristics used for the calibration of the matrix model. The 58 SGS were split into two subsets according to their diameter cutting limit, and studied independently.

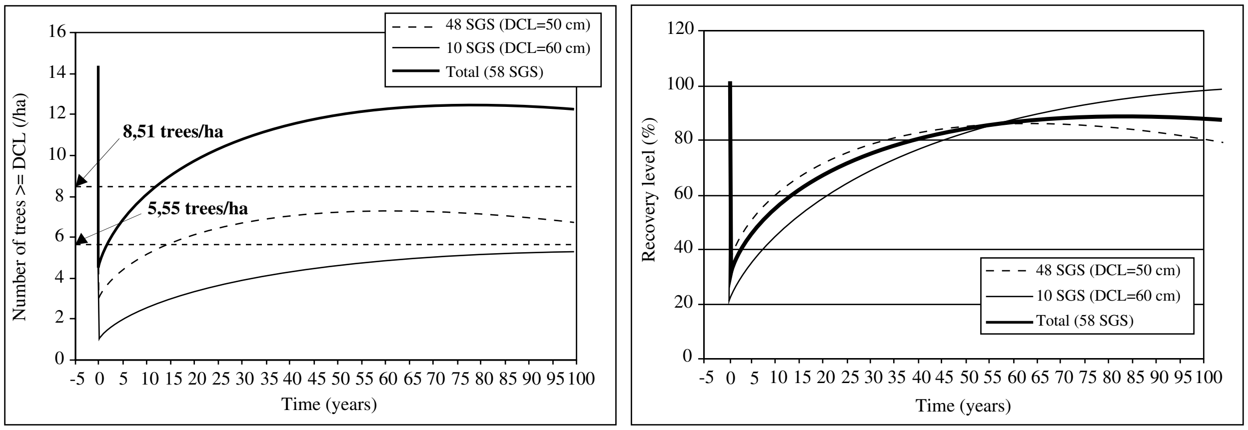
	Growth characteristics (cm/year)						*Mortality rates (%)*	
	First period (10 years)			*Second period (≥ 10 years)*			*Minimum*	*Maximum*
Diameter classes (cm)	*ΔD_{min} (5th perc.)*	*Median (mean)*	*ΔD_{max} (95th perc.)*	*ΔD_{min} (5th perc.)*	*Median (mean)*	*ΔD_{max} (95th perc.)*	*All simulation*	
48 SGS (DCL = 50 cm)								
10–20	0.00	0.18 (0.23)	0.64	0.00	0.08 (0.11)	0.48	0.83	1.24
20–30	0.02	0.22 (0.28)	0.74	0.00	0.08 (0.16)	0.56	0.96	1.81
30–40	0.02	0.20 (0.26)	0.72	0.00	0.16 (0.17)	0.56	1.01	1.72
40–50	0.00	0.22 (0.31)	0.92	0.00	0.16 (0.19)	0.64	“	“
≥ 50	0.04	0.24 (0.33)	0.87	0.00	0.16 (0.16)	0.64	1.03*	2.26*
10 SGS (DCL = 60 cm)								
10–20	0.02	0.34 (0.37)	0.82	0.00	0.16 (0.19)	0.64	0.86	1.25
20–30	0.08	0.45 (0.46)	0.94	0.00	0.24 (0.27)	0.64	0.73	1.25
30–40	0.04	0.32 (0.39)	0.86	0.00	0.32 (0.31)	0.80	0.39	1.63
40–50	0.04	0.34 (0.39)	0.89	0.00	0.24 (0.29)	0.72	0.88	1.31
50–60	0.06	0.42 (0.44)	0.86	0.00	0.24 (0.27)	0.80	“	“
≥ 60	0.12	0.41 (0.45)	1.11	0.00	0.16 (0.20)	0.64	0.37*	1.50*

*Usually, there are not enough trees in the last diameter class to correctly assess a mortality rate. The rate used in the model is, in fact, calculated over the pooled three greater classes: classes ≥ 30 cm when the DCL is 50 cm DBH and classes ≥ 40 cm when the DCL is 60 cm DBH.

Table 5
Initial state of the stock of trees greater than the DCL, and possibility of recovery after logging for different subsets of species: 58 SGS, 20 actually logged species and each of the most researched species

	Initial stock	*Logged trees*	*Recovery after 50 years*	*Return time*	*Maximum of recovery**
	Number/ha of trees ≥ DCL	*Number/ha of trees ≥ DCL*	*Number/ha (%) of trees ≥ DCL*		*Number/ha (%) of trees ≥ DCL, time*
58 valuable SGS					
48 SGS which DCL = 50 cm	8.51	5.16	7.12 (83.7%)	–	7.16 (84.1%) after 58 years
10 SGS which DCL = 60 cm	5.55	4.34	4.56 (82.2%)	135 years	–
Total 58 SGS	**14.06**	**9.50**	**11.69 (83.1%)**	**–**	**12.17 (86.6%) after 82 years**
20 actually logged species					
10 species which DCL = 50 cm	0.81	0.29	1.086 (133.4%)	21 years	–
10 species which DCL = 60 cm	5.04	1.09	4.200 (83.3%)	–	4.76 (94.4%) after 96 years
Total 20 species	**5.85**	**4.47**	**5.287 (90.3%)**	**85 years**	**–**
Most researched species					
Dicorynia guianensis (DCL = 60 cm)	0.72	0.08	0.65 (90.4%)	61 years	–
Qualea rosea + *Qualea albiflora* (DCL = 60 cm)	2.08	0.28	1.34 (64.5%)	–	1.43 (68.9%) after 86 years
Sextonia rubra (DCL = 60 cm)	0.84	0.09	0.26 (30.8%)	–	0.27 (31.9%) after 76 years
Total 4 species	**3.64**	**0.45**	**2.25 (61.8%)**	**–**	**2.57 (70.6%) after 112 years**

*The maximum of recovery indicates the point when tree death above the DCL is no longer compensated by ingrowth for the set of species considered.



(a) **(b)**

Fig. 15. Evolution of the number of trees greater than the DCL for the two subsets of valuable species: (a) in absolute numbers/ha and (b) in percentage of the initial number of trees greater than the DCL (i.e. before logging).

- The level of recovery will depend on the species or set of species considered. Within the 20 valuable species, the subset of the 10 species having a smaller DCL will increase at the expense of the larger ones. On the other hand, although recovery of the species *Dicorynia guianensis* appears possible at a satisfactory level, this is not the case for the two species of *Qualea*, and the situation of *Sextonia rubra* is quite worrying (Table 5, Fig. 16).
- If the same level of extraction is maintained, one could be tempted to recommend lengthening of felling cycles so as to increase recovery levels. We do not think that this would necessarily be a good solution: (i) because some large trees will still be lost due to natural mortality: in half of the cases, simulations even show that after reaching a maximum level (still lower than the initial value before logging), the number of trees ≥ DCL decreases over time due to an ingrowth in large diameter classes which is not high enough to compensate for mortality rates (see Table 5, "maximum recovery") and (ii) because the opening of the stands is the driving force of growth. Most often, due to high costs, logging is the only silvicultural operation carried out in the course of a felling cycle and it should not be postponed. Another option would be to reduce logging an intermediate level between what was done at Paracou and the present level in managed forests. In this case, however, the stands will be less opened and growth is likely to be less stimulated than in T1; better results in terms of recovery and length of felling cycles would not necessarily be obtained.

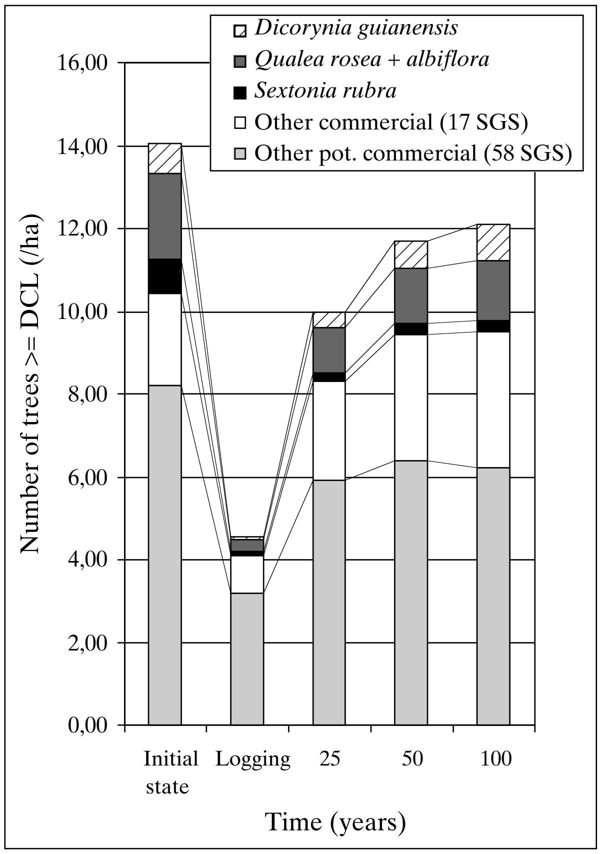


Fig. 16. Evolution of the valuable stock of 58 SGS in total number of trees greater than the DCL and from the viewpoint of its composition in several subsets, comprising the most desired species. Full recovery of the number of exploitable trees is unlikely, even within 100 years. Moreover, the floristic composition will change.

If the level of diameter increments observed in the T1 plots over the period 1988–1997 could be maintained, recovery could be complete within 40 years for the global set of 58 SGS; this is coherent with the estimates made in Section 3.1. The result would be the same for the subset of 20 currently logged species. Recovery could be possible between 50 and 60 years for *Dicorynia guianensis* and would still require more than 70 years for *Qualea* spp. Given the observed dynamics of *Sextonia rubra*, complete recovery appears impossible for this species.

Several options that could be used by forest managers are discussed below.

4. Discussion and recommendations

It is impossible for a primary forest to quickly recover all the aspects of its initial state after logging. As the initially logged standing volume "has accumulated over a long period, the commercial timber is likely to be of a quality and volume that will probably not be matched in future cuts (because it contains slow-growing specimens and species, large diameters, etc.), unless the logged forest is closed to further exploitation for a century or more. In this sense the first crop is, in practical terms, not repeatable." (Poore et al., 1989).

At Paracou, long-term observations on the dynamics of the stands subjected to disturbances of growing intensity confirm this statement. Changes can be measured through the differential evolution of some major parameters. The total number of trees increases quickly after disturbance and will reach, and even exceed, the initial values within 15 years, due to the recruitment of fast-growing species benefiting from canopy openings. The reaction of the stands is all the more pronounced (number of new trees, importance of the pioneer and heliophilous species) when the disturbance is heavy. Basal area follows the same pattern, but more slowly because growth is spread over less trees of large and intermediate size and an increasing number of small trees. However, because one consequence of canopy opening is to favour, at least at first, light-demanding species, a return to the initial value can be rapid. An optimistic estimate for Paracou is between 30 and 40 years, where current rates of recovery would be maintained. Recovery will be delayed for the set of valuable species, which (i) do not contain the fastest growing species and (ii) are confronted with competition from the sometimes "explosive" development of the fast-growing species.

The difficulty of recovering the initial state of stands after logging is particularly evident when examining the evolution of the diameter structures. It appears reasonable to find the initial number of trees, commercial and non-commercial, above DCL after 40 or 50 years, but their mean diameter will be smaller than before. To recover trees ≥ 70 cm DBH (10–20 cm above the DCL according to the species considered), more than 100 years would be required (Table 2, T1). Where disturbance was heavy as in T3, the upper classes above 40 cm were almost completely cleaned out and kept losing trees nine years after the treatment, while the intermediate classes were greatly depleted (Fig. 5). The stock of commercial species above DCL suffered from the depletion of the intermediate classes, and recovery will be slow until these classes are filled again. Simple recovery of the number and basal area of this valuable stock would take more than 80 years.

Another aspect is the floristic evolution of the stands. We have already described the immediate effect of canopy openings on the recruitment of pioneer and heliophilous species, most of which could be there for several decades. However, openings will also have different effects on the growth and probably mortality of most of the species present in the previously undisturbed stands, according to their temperament and diameter structure. This is illustrated, for the plots of T1, by the histogram in Fig. 16 showing the relative decline of *S. rubra* to the benefit of some species such as *Virola michelii* Heckel + *Virola surinamensis* (Rolander) Warburg (Myristicaceae), *Simarouba amara* Aublet (Simaroubaceae), *Manilkara bidentata* (A, de Candolle) Chevalier (Sapotaceae), *Tabebuia serratifolia* (Vahl) Nicholson (Bignoniaceae) (Gourlet-Fleury, 2000), present in the set of the 20 most researched species. When the increase in diameter increments is maintained (as in our simulations described in Section 3.2, or accentuated as was done by Gourlet-Fleury, 2000), the effect can be reinforced in favour of fast-growing species, depending on their abundance in the intermediate diameter classes.

Our estimates of return time are hindered by uncertainty about the duration of the disturbance effects on the plots' dynamics. Mortality rates are still a little higher than they were before treatment, diameter increments began to decrease in 1994 but are still higher than in the control plots, and recruitment rates remain very high in T2 and T3. Fig. 13 shows that not only does the basal area increment rate in T1 remain constant, but it also increases in T2 and T3 due to recruitment. A slight slowdown is, however, noticeable from 1994 onwards in the basal area increment of the valuable set of species in T1, but it is too soon to know if this is the beginning of a strong trend.

Other studies in the region or elsewhere provide elements for comparison, although they must be considered with great care. In fact, the dynamics of stands appear to be highly variable, depending on their floristic composition, the diameter structure of the populations and the fertility of the site. This variability can be observed on very local scales, as shown by the Paracou plots themselves (see Figs. 2 and 3). Additional difficulties in comparison may be caused by the diameter limit used to inventory the trees, the use of volumes rather than basal areas, the composition of the marketable set of species and the DCL.

Nevertheless, an example for comparison can be the silvicultural experiments carried out since 1965 in the Mapane region in Suriname ("CELOS experiments", De Graaf, 1986). Given the data available, the stands of the sites studied show many similarities with the Paracou stands, although the trees seem to be somewhat smaller. Basal areas before disturbance of all trees ≥ 5 cm DBH vary between 25 and 30 m^2/ha. DCL is 45 cm DBH. There are 51 commercial SGS, among which at least 29 are common to our set of 58 valuable SGS.

In Experiment 97/2, simple logging for timber was performed. In one of the plots (Goliath), this yielded 31 m^3/ha from 8.2 trees (to be compared with 50 m^3 in Paracou, from 10.2 trees) corresponding to 2.6 m^2/ha (3.3 m^2/ha in Paracou) and 2.4 m^2/ha of loss through damages (2.3 m^2/ha in Paracou). After 9 years of observations, the increment in total basal area was only 0.3 m^2/ha (0.03 m^2/ha/yr, to be compared to 0.2 m^2/ha/yr at Paracou). This lower figure can be explained by high mortality rates in the upper classes. However, at the same time, the set of valuable species ≥ 45 cm DBH increased from 2.0 to 2.6 m^2/ha, while that of Paracou increased from 1.8 to 2.4 m^2/ha, the equivalence indicating a lesser performance at Paracou, where the mean trees are larger.

These results were judged disappointing enough to lead De Graaf to recommend the use of refinement immediately after logging, and then every 8 years during a 20 year felling cycle, with an intensity intended to decrease the total basal area to 10 m^2/ha. Such a schedule was implemented in 1975 in Experiment 67/9B, with immediate consequences on the stands that can be compared to those produced by T3; logging for timber was performed, yielding 20 m^3 or 1.7 m^2/ha and damaging a further 2 m^2/ha; the total basal area decreased from 30 to 26 m^2/ha. All non-valuable trees ≥ 20 cm DBH were then poison-girdled and basal area decreased to 10 m^2/ha (17.6 m^2/ha in the T3 of Paracou, after a total loss of 14 m^2/ha in the stands). Inventories were made every year between 1976 and 1981, and once again in 1995; this allowed De Graaf and colleagues to examine a 20 year period of stand dynamics after heavy disturbance, even though the initial schedule was disrupted due to political problems (De Graaf and colleagues, 1999). During the first six years, the increase in basal area was 1.4 m^2/ha/yr (0.24 m^2/ha/yr for the marketable set of species), whereas, during the first 8 years, it was only 0.44 m^2/ha in the T3 of Paracou (0.14 m^2/ha for the valuable set of species)! During the following 14 years, the rates considerably slowed to 0.6 m^2/ha for all species and 0.11 m^2/ha for the marketable set. At the end of the 20 year period, the initial basal area of the marketable species was completely recovered, and the fraction ≥ 45 cm DBH increased from 1.7 to 3.3 m^2/ha, i.e. the exploitable stock was recovered by 97%. Therefore, according to these results: (i) a slowdown in the dynamics of recovery must be expected between 6 and 20 years and (ii) it is possible to recover a marketable stock quickly when heavy refinement is implemented after logging; we will return to this second point.

Farther from Paracou are the sites of Tapajos (Para) and ZF2 at Manaus (Amazonas) in Brazil. Comparisons made between ZF2 and Paracou showed important similarities in the structure of the stands (Favrichon, 1997; Favrichon et al., 1998), although floristic compositions differ far more than between CELOS and Paracou. Three intensities of logging were applied in 1986, with consequences on the stands spreading between those of the T1 and T2 at Paracou. The dynamics of recovery was found to be slightly more rapid than in French Guiana, however, the period for which data are available does not allow to conclude about a potential slowing down with time. At the experimental site located in Tapajos National Forest, logging was heavier; the extraction of 16 trees/ha with a DCL of 45 cm DBH, yielding 75 m^3, resulted in an estimated loss of 43% of the initial basal area (deduced from data given by Silva et al., 1995, site RP012) of individuals ≥ 5 cm DBH. Given the dynamics observed on trees between 1981 and 1992, the initial basal area value could be reached in 25 years using the hypothesis of a constant rate of recovery. However, Silva and co-authors, when splitting their data set to examine the first 8 years of evolution separately from the subsequent 5 years, showed an important decrease in periodic diameter increments (divided by two between the two periods) and ingrowth ≥ 5 cm DBH (divided by 3 to 4, all species or commercial species), while mortality rates increased slightly. This resulted in a decrease of 31% in the mean annual increment of the volume of all trees ≥ 20 cm DBH (22% for the commercial species). Data over a longer period are provided for the same experiment in Alder and Silva (2000, Fig. 7). For the fraction of trees ≥ 45 cm DBH, all species and commercial species, a slight slowdown 8 years after logging is followed by a period of 10 years where the rate of volume increment remains constant. Another example from the same study deals with Experiment RP11. In this case, where about 62 m^3/ha were logged over, no slowing down in the recovery rate of the commercial volume ≥ 45 cm DBH was noticeable over a period of 12 years (three re-measurements were made). Given this recovery rate, more than 150 years would be necessary to return to the initial state.

The examples given above indicate that something should happen in the evolution of the stands between 6/8 and 20 years. Such a slowdown is reproduced by all simulation models. On the Paracou site, simulations tend to locate the inflexion point of evolution between 15 and 20 years after disturbance, depending on the dynamics model and the intensity of treatment considered (see Figs. 3 and 4; Chapter 6, this Part). According to these models, the initial basal area, all species considered, requires much more time to recover (when it does recover), than is estimated on the basis of constant rates; about 90–100 years would be necessary in the T1 plots according to Favrichon (1995, 1997) and more than120 years in the T2 plots. However, it is already evident in Figs. 3 and 4, Chapter 6, this Part, that these models tend to considerably underestimate the evolution of the number of trees and this should encourage us to be cautious with predictions. At Tapajos, simulations made with the cohort model CAFOGROM (Alder and Silva, 2000) reproduced quite correctly the evolution of logged over stands, allowing the authors to indicate a return to initial basal area within 30–40 years after felling. However, they noted that although the model proved successful over the period of 12–16 years for which data are available, the accuracy of longer-term projections remains to be seen.

Thirteen years after the first inventories and 9 years after the end of the silvicultural treatments, the plots of Paracou are thus entering a critical phase, where the effect of disturbances should decrease; periodic surveys appear more important than ever, as our medium-term predictions will depend on the intensity of changes.

4.1. What are the options for forest managers in French Guiana?

The intensity of logging implemented in the T1 plots of Paracou far exceeded what currently prevails in the forests managed by the National Forest Office, where a mean of 2–3 trees/ha are extracted. The experiment showed that an increase in the number of trees logged is perfectly conceivable, provided a market can be found for the timber of the additional species. From the several estimates that can be made through observations and modelling, it appears reasonable to expect a minimum recovery of 75–85% of the number of valuable trees above DCL within 40 years, and 80–90% within 50 years. However, these trees will probably be smaller than in previously undisturbed forest, and the floristic composition will differ.

All elements indicate that the potential of the valuable species as a set will be preserved; their relative importance in the stands remains stable over 9 years after disturbance and their initial basal area could be recovered within 45–50 years. However, the situation will not be the same according to the species considered; some will be favoured, while others could decline and even become endangered within the managed area. *Sextonia rubra* is one good example and, among the 20 most researched species, *Caryocar glabrum* (Aublet) Persoon (Caryocaraceae) would be another (Gourlet-Fleury, 2000). For such species, preserving some big trees as seed bearers or increasing the DCL could be wise until more is known about their real regeneration potential.

Lengthening felling cycles beyond 50 years does not guarantee, as already emphasized, the recovery of 100% of the initial stock, in particular because natural mortality can occur (cf. the plots of Experiment 97/2, De Graaf, 1986) and hinder its evolution. On the contrary, opening the forest stimulates its dynamics; it is possible, as observed in T2, to more than double the mean diameter increments of the valuable species for at least 9 years after the treatment. However, the results obtained at Paracou indicate that attention must be paid to some points.

Opening the stands has at least three consequences:
(1) it stimulates the growth of remaining trees. The more valuable trees left standing after felling operations, the better for the manager. It is particularly important to limit, as far as possible, damage to trees of the intermediate classes; in this respect, reduced-impact logging comprising directional felling should be actively promoted in French Guiana.
(2) It stimulates the recruitment of new trees, non-valuable as well as valuable.
(3) It can increase mortality rates by causing instability of trees around canopy gaps, thus reinforcing the opening effect on the other parameters.

Treatment T3 and its effects show that there is a limit not to be overstepped in these forests; the combination of heavy logging and poison-girdling left very few trees in the intermediate classes of the stands; the diameter increment of these trees was not stimulated more than in the T2 treatment, and the stands are now facing a considerable recruitment of pioneer and heliophilous species, which will sooner or later compete with the remaining valuable trees. Our observations do not match, for these treated plots, with the observations made by De Graaf et al. (1999), and we think that the silvicultural system proposed by De Graaf (1986) should be avoided in French Guiana, at least with the intensity advocated. There is little doubt that repeated openings, e.g. every 10 or 15 years in the course of a 40 or 45 year felling cycle, would favor growth of the valuable set of species, provided opening remains light enough to control invasion by undesirable species; light enough means that the basal area should not be decreased under 25 m^2/ha (cf. T1 treatment), and not 10 m^2/ha as in the CELOS silvicultural system. In general, we estimate that the intensity of disturbance reached in the T2 treatment, that is elimination of 1/3 of the initial basal area (from 30 to 20 m^2/ha), should not be exceeded.

Repeated interventions in the course of a felling cycle will probably never be economically feasible in the context of French Guiana. In addition to logging, which must itself be viewed as a silvicultural operation and be carried out as carefully as possible, a complementary opening (within the limits previously mentioned) can be considered, if thought justified by the manager. The advantage of T2 above T1 in terms of basal area recovery rate is yet not visible on the basis of the results; more basal area was eliminated and the stands are still affected by higher mortality rates (possibly not entirely linked to the treatment), but given the rapid evolution of intermediate classes, the situation should reverse in coming years. However, attention should be paid to two points:

- poison-girdling is not completely innocuous; as occurred in T2, it can still cause some damage in the stands when the largest trees fall. The elimination of large trees should be avoided when the operation does not benefit a minimum of valuable individuals. More generally, refinement, as performed at Paracou, is probably not the best way to open stands, all the more so if large areas are to be treated; the systematic elimination of undesirable species ≥ 40 cm DBH could have long-term consequences on biodiversity and limit the possibilities of adaptation to changes in market demand. Liberation of trees appears preferable, possibly completed or replaced by refinement over well-delimited areas, where the density of valuable trees is high, for example (Gourlet-Fleury, 1990, 1992; Fuhr and Plancheron, 2001).
- Although felling cycles could be shortened by stimulating growth in this way, it must be kept in mind that another consequence will be an accelerated shift in the floristic composition of both the commercial stock and the entire stand towards more light-demanding species. Independent of the possible unwanted effects of stimulating growth on the wood quality of some species, this would not be compatible with a wish to favour slow-growing, high wood density species so as to remain competitive on the export market.

A final and difficult point is the medium- to long-term effect of repeated felling cycles. Models can help to determine what should be the ideal length to systematically recover the same marketable volume (usually smaller than at first harvesting); Huth and Ditzer (2001) or Sist et al. (2003) performed such studies for Dipterocarp forests of Malaysia and Indonesia. However, the models rely on very simple descriptions of the floristic composition of the forests (usually three to five groups of species) and regeneration processes, which are of growing importance from the second felling cycle on. Results given by such models can be no more than indicative.

In the case of Paracou, the recruitment of new trees is difficult to model because, on a species basis, it is usually a rare event. Considering the set of the 20 most researched species in French Guiana, some such as *Carapa procera* A, de Candolle (Meliaceae), *Bocoa prouacensis* Aublet (Caesalpiniaceae), *Virola michelii*, *Virola surinamensis* and *Andira coriacea* Pulle (Fabaceae) or *Simarouba amara* appear to react positively to a growing intensity of disturbance, but the situation is more complex for the others, partly because it is difficult to determine what part is played by the intrinsic dynamics of the species (stock of juveniles present in the stands) and the opening of the canopy (Gourlet-Fleury, 2000). In this context, the accumulation of observations and studies on species ecology is of particular importance, especially as concerns the reproduction, growth and survival of juveniles (Chapter 3, this Part) and existing models must be improved to incorporate this new knowledge.

5. Conclusion

The experimental design of the stands of Paracou in 1982 has proven particularly useful to provide preliminary guidelines for forest managers. To date, we are able to partially answer the two major questions posed in the introduction to this chapter. We now have an idea of the time required to recover the commercial stock of logged over stands and we know to what extent silvicultural treatments can favour growth without completely disturbing the forest. We can also anticipate the problems that could arise with silvicultural systems such as CELOS, proposed for the forests of Suriname.

Using the results obtained at Paracou to make forest management decisions should nevertheless be done cautiously. We do not know to what extent these results are representative of what could be obtained in the forests of the coastal part of French Guiana, where large variations in soil richness and microclimatic conditions can be encountered. To progress on this subject, a research project associating the National Forest Office and CIRAD-Forêt and co-funded by the Department, the Region and the European Community began in late 2000 to establish and follow several permanent sample plots from the Regina-Saint-Georges region to Saint-Laurent du Maroni. This network will hopefully allow a better understanding of the determinants of forest dynamics, thus enhancing our ability to make predictions.

References

Alder D., Silva, J.N.M., 2000. An empirical cohort model for management of Terra Firme forests in the Brazilian Amazon. Forest Ecol. Manag. 130, 141–157.

Caswell H., 2001. Matrix population models. Construction, Analysis, and Interpretation, second ed. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, 722 pp.

Durrieu de Madron L., 1993. Mortalité, chablis et rôle des trouées avant et après exploitation sur le dispositif d'étude sylvicole de Paracou—Guyane Française. Thèse de 3ème cycle-ENGREF/CIRAD, 203 pp. + ann.

Durrieu de Madron L., 1994. Mortalité des arbres en forêt primaire de Guyane francaise. Bois et Forêts des Tropiques 239, 43–57.

Dutrève B., Julliot C., Brunaux O., 2001. Biodiversité et aménagement forestier en Guyane: approche méthodologique. Bois et Forêts des Tropiques 269 (3), 65–74.

Favrichon V., 1997. Réaction de peuplements forestiers tropicaux à des interventions sylvicoles. Bois et Forêts des Tropiques 254 (4), 5–24.

Favrichon V., Gourlet-Fleury S., Dessard H., Bar-Hen A., 1998. Parcelles permanentes de recherche en forêt dense tropicale humide. Eléments pour une méthodologie d'analyse de données. Série FORAFRI 1998, document no. 14. CIRAD-forêt/Coopération française/CIFOR, 67 pp.

Favrichon V., Maître H.-F., Higuchi N., 1998. Effects of silvicultural treatments in the tropical rain forest: a comparison between ZF-2 (Manaus, Brazil) and Paracou (French Guiana). In: Guariguata M.R., Finegan B. (Eds.), Proceedings of the CATIE/CIFOR/IUFRO Conference: Ecology and Management of Tropical Secondary Forest: Science, People and Policy. Turrialba, Costa Rica, November 10–12, 1997. Serie Técnica, Reuniones Tecnicas no. 4, 191–199.

Fleury B., 1995. Evolution récente de la gestion forestière et attentes du gestionnaire en Guyane française. Actes du séminaire interne de Silvolab-Guyane, tenu en Avril 1994: "Recherches sur les écosystèmes forestiers de Guyane", 83–93.

Fuhr M., Plancheron F., 2001. Forêts pilotes de Risquetout et Organabo, éclaircie mixte modalité 1—Aperçu sur la dynamique des peuplements 4 ans après intervention. Rapport interne de la STIR Tropicale, ONF Cayenne, 25 pp. + ann.

Gazel M., 1983. Croissance des arbres et productivité des peuplements en forêt dense équatoriale de Guyane. Rapport interne, ONF, 129 pp.

De Graaf N.R., 1986. A silvicultural system for natural regeneration of tropical rainforest in Suriname. Agricultural University, Wageningen, The Netherlands, 250 pp.

De Graaf N.R., Poels R.L.H., Van Rompaey R.S.A.R., 1999. Effect of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. Forest Ecol. Manag. 124, 123–135.

Gourlet-Fleury S., 1990. Simulation par l'ONF et le CTFT d'une éclaircie sélective sur une parcelle exploitée (parcelle 7) du dispositif de Paracou. Rapport interne CTFT, 11 pp.

Gourlet-Fleury S., 1992. Simulation d'éclaircies sur le dispositif sylvicole de PARACOU (Guyane française): recherche de méthodes d'intervention en forêt, après exploitation. Mémoire technique—DEA d'Analyse et de Modélisation des Systèmes Biologiques—I.A.S.B.S.E., Université Claude Bernard, LYON I, 34 pp. + ann.

Gourlet-Fleury S., 2000. Dispositif sylvicole expérimental de Paracou (Guyane française). Aperçus sur l'état et la dynamique des peuplements 13 ans après installation. Rapport interne CIRAD/Silvolab-Guyane, 253 pp. + ann.

Gourlet-Fleury S., Cornu G., Dessard H., Picard N., Sist P., 2002. Forest dynamics models in French Guiana to answer practical forest management issues. In: Sabogal C., Silva J.N.M., (Eds.), Manejo Integrado De Florestas Umidas Neotropicais por Industrias e Comunidades. Proceedings of the "Simposio Internacional da IUFRO" hold in Belem, 4–7 December 2000, 101-113.

Higuchi N., Veloso de Freitas J., Coïc A., 1992. Experimental Forest Management on a Sustainable Yield Basis at ZF2 (Manaus, Amazonas, Brazil). INPA-C.P.S.T., Manaus, Brésil, 19 pp.

Houllier F., 1992. Analyse et modélisation de la dynamique des peuplements forestiers. Applications à la gestion des ressources forestières. Mémoire présenté devant l'Université Claude Bernard-LYON I pour l'obtention de l'habilitation à diriger des recherches, 67 pp.

Huth A., Ditzer T., 2001. Long-term impacts of logging in a tropical rain forest—a simulation study. Forest Ecol. Manag. 142, 33–51.

Leslie A.J., 1997. Aménagement durable des forêts ombrophiles tropicales pour la production de bois. In: Ouvrages sur l'aménagement durable des forêts. Etude FAO Forêts no. 122, 19–36.

Mankin W.E., 1998. Defining sustainable forest management. Trop. Forest Update (ITTO Newsletter) 8 (3), 7.

Mengin-Lecreulx P., 2000. Prise en compte de la biodiversité dans l'aménagement et la gestion forestière. Note Régionale de l'Office National des Forêts, Cayenne, 13 pp + ann.

Paget D., 1999. Etude de la diversité spatiale des écosystèmes forestiers guyanais. Réflexion méthodologique et application. Thèse de doctorat de l'ENGREF, 155 pp. + ann.

Phillips O.L., Malhi Y., Higuchi N., Laurance W.F., Nunez P.V., Vasquez R.M., et al., 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. Science 282, 439–442.

Poore D., Burgess P., Palmer J., Rietbergen S., Synnott T., 1989. No timber without trees. Earthscan Publications Ltd, London, 252 pp.

Rollet B., 1974. L'architecture des forêts denses humides sempervirentes de plaine. Etude technique, C.T.F.T., 298 pp.

Sabatier D., Freycon V., collaborateurs, 2001. Analyse multi-échelles du couvert forestier guyanais. Rapport final du projet AME. Silvolab-Guyane, Kourou, 48 pp.

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 pp.

Silva J.N.M., de Carvalho J.O.P., Lopes J. do C.A., de Almeida B.F., Costa D.H.M., et al., 1995. Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging. Forest Ecol. Manag. 71, 267–274.

Sist P., 1998. Liberation thinnings in logged-over forests. In: Bertault, J.G., Kadir, K. (Eds.), Silvicultural Research in a Lowland Mixed Dipterocarp Forest of East Kalimantan. CIRAD, FORDA, PT Inhutani 1, Montpellier, CIRAD, 1998.

Sist P., Picard N., Gourlet-Fleury S., 2003. Sustainable rotation length and yields in a lowland mixed dipterocarp forest of Borneo. Ann. Forest Sci. 60, 803-814.

Ecology and Management of a Neotropical Rainforest

Chapter 6

Modelling the forest dynamics at Paracou: the contributions of four models

Nicolas Picard, Sylvie Gourlet-Fleury, Vincent Favrichon

Abstract – Four models of forest dynamics were built using the Paracou data base: (i) an individual-based space-dependent model, SELVA, which describes in detail the behaviour of the trees on the basis of diameter increment, standing death, treefall and recruitment; (ii) a simplified individual-based space-dependent model derived from gap models to explore theoretical questions on aggregation; (iii) a distribution-based model based on a Usher matrix; (iv) a hybrid model mixing a matrix model for trees < 40 cm DBH and an individual-based space-independent model for trees ≥ 40 cm DBH. The four models were compared in terms of their ability to predict the steady-state characteristics of the Paracou stands, as well as their dynamics following two levels of disturbance, and formal links between models showing various degrees of detail (according to whether they take into account individual trees and spatial interactions) were established using the simplified gap-like model. Among other results, we show that SELVA performs best at predicting the total number of trees and basal area at steady state and following a moderate level of disturbance such as conventional logging. The distribution-based and hybrid models show very similar behaviours. They perform better at describing the diameter distribution at steady state and the reaction of the stands after a high level of disturbance. The return to steady state after clear-cutting is predicted to be 250 years by these models, and 300 years by SELVA. The study of formal links between models led to the conclusion that individual-based and distribution-based models are equivalent provided they both take, or do not take , space-dependence into account. However, models working at the same level of stand description, either individual-based or distribution-based, do not yield the same predictions if they are, or are not, space-dependent. The respective interest and limitations, for managers, of the various models developed are discussed in the light of these results.

Keywords: Matrix model, Individual-based model, Space interaction, Comparison, Management application, Tropical rainforest

1. Introduction

The processes that drive forest dynamics may be inferred from its precise observation, including botanical, ecological, statistical and other, studies (Oldeman, 1974). But as soon as quantitative predictions must be made to test a theory, modelling appears as a relevant research tool (Vanclay, 1995). In the tropical zone, many models of forest dynamics have thus been developed for research purposes, in order to extricate the driving variables that influence the recruitment, growth and death of trees. We can mention, among other models, those of Wan Razali and Rustagi (1988) in Peninsular Malaysia ; Bossel and Krieger (1991) (FORMIX model), Ong and Kleine (1996) (DIPSIM model) or Köhler and Huth (1998) (FORMIND model) for the dipterocarp rainforest of Sabah, Malaysia ; Shugart et al. (1980) (KIAMBRAM model) or Vanclay (1989) for Queensland rainforests in Australia ; Moravie (1999) for the Western Ghats of India ; Alder (1995) for Ghana (GHAFOSIM model) and for Pará, Brazil (CAFOGROM model).

From a practical point of view, understanding the forest dynamics has implications for forest management. To assess whether a given management option is sustainable, it must be possible to predict the state of the forest in the future, after exploitation or any other man-made disturbance. Models could provide the link between scientific knowledge on the forest ecosystem and the practical rules required for decision making. They could predict the consequences of any silvicultural scenario, help to optimise management and to plan actions. Still, there is a large gap between research-oriented models and the prediction tools used by forest managers. Software such as TREMA (Hawthorne et al., 1999) or TIAMA (Tiama, 1999) are mainly data management software and use very simple rules to model the forest dynamics (constant diameter growth rate, constant mortality rate).

Nevertheless, some models of forest dynamics incorporate the impact of logging (including felling damage, skid trails, etc.) and more generally the impact of any management practice. As examples, we can mention the SYMFOR model in East Kalimantan, Indonesia (McLeish, 1999; Phillips et al., 2000a,b) and SIRENA II in Costa Rica (Alder, 1997). Some models even include an economic module for direct calculation of the costs and benefits (Boscolo and Vincent, 1998; McLeish, 1999).

Five models of forest dynamics were developed at Paracou for research purposes. The objective of this chapter is to compare four of these models and present their respective interests and limitations. To describe the models, we shall rely on the classification of Munro (1974) that is based on the level of stand description. We shall thus distinguish individual-based models, where the trajectory of every single tree is predicted, from distribution-based models, where the distribution of tree characteristics is predicted without identifying individual trees. We shall further classify the models according to the way tree interactions are considered (which was not specified in Munro's classification). We shall thus discriminate between space-dependent models, where a tree interacts with other trees in a local and spatially explicit neighbourhood, and space-independent models, where a tree interacts with all the trees on the plot.

Historically, the first model built at Paracou was a matrix model (Favrichon, 1995), that is a space-independent distribution-based model. The second was an individual-based space-dependent model, SELVA (Gourlet-Fleury, 1997). The third was an individual-based space-dependent model based on Voronoï diagrams (Mercier, 1997). However this model still requires major development, as it takes into account only recruitment and mortality and ignores growth. We shall thus disregard it in the main analysis, so as to maintain a common basis for comparison between models. Fourth, an individual-based space-dependent model whose equations are derived from gap models was built (Picard, 1999). Finally, a hybrid model, with a distribution-based component for small trees and an individual-based component for big trees, was derived from the matrix model (Picard, 1999).

We shall first present the four models: SELVA, the model derived from gap models, the matrix model and the hybrid model. Then, they will be compared in terms of ability to predict the stand dynamics in control and treated plots of Paracou. Some formal links that enable to shift from one type of model to another will also be described. Finally the successes and problems raised by this modelling work with respect to research purposes will be discussed, and the further developments that are required to face management issues will be presented.

2. Material and methods

2.1. Individual-based models

2.1.1. SELVA

A tree in SELVA is characterized by its diameter (denoted D) and its spatial coordinates (denoted $x \in R^2$). Time is discrete with a time step $\Delta t = 3$ years. As in most individual-based forest models, the forest dynamics in SELVA is split into three components: growth, mortality and recruitment.

Growth. The growth equation for a tree is stochastic and expressed as:

$$\Delta_t D = -C + \exp(\varepsilon) \times \underbrace{amD\left[\ln\left(\frac{K}{D}\right)\right]^{1/(1+m)}}_{\text{average growth}}$$
$$\times \exp\underbrace{\left\lfloor b\sqrt{NBD} + c\Delta_{t-\Delta t}NBD + d(\Delta_{t-\Delta t}NBD)^2\right\rfloor}_{\text{modification factor}} \qquad [1]$$

where C is a constant; a, m and K are the three parameters of a Korf growth curve (Zeide, 1993); b, c and d are empirical parameters (i.e. without any biological sense); NBD is a space-dependent tree interaction variable that is defined below; ε is a stochastic term; finally, Δ_t indicates an increment between two consecutive time steps, that is, for any variable X: $\Delta_t X = X(t + \Delta t) - X(t)$.

The first term with a bracket in [1] expresses average growth, for an isolated tree $(NBD(t) = 0, \forall t)$. It corresponds to a Korf curve. The second term with a bracket expresses the changes in this average growth due to tree interactions. It can be positive or negative, depending on whether the neighbourhood of the tree facilitates or reduces growth (competition). The stochastic terms ε are drawn at random, in a way such that two consecutive ε for a given tree are positively correlated (Pearson correlation between $\varepsilon(t)$ and $\varepsilon(t + \Delta t)$ equals 0.51). Eventually the competition index NBD is defined as the number of trees larger than the subject tree within 30 m from it:

$$NBD_i = \sum_{k=1}^{N} \mathrm{I}(D_k > D_i)\mathrm{I}(\|x_k - x_i\| \leqslant 30)$$

where N is the number of trees, $i \in \{1 \ldots N\}$ is the index of a tree, and $\mathrm{I}_{(p)}$ is the indicator function of proposition $p (\mathrm{I}(p) = 1$ if p is true, 0 otherwise$)$.

The choice of NBD as a competition index and the form of the growth equation are more precisely explained in Chapter 4, this part. More details may be found in Gourlet-Fleury (1997, 1998, 1999) and Gourlet-Fleury and Houllier (2000). Hence the growth equation has an "average × modification factor" shape, with multiplicative errors.

Mortality. Four types of death have been distinguished in SELVA: standing death, primary treefall, secondary treefall and complex treefall (Durrieu de Madron, 1993; Riéra, 1983). The first two phenomena are accounted for by independent death probabilities that are logistic functions of the tree characteristics and competition indices:

probability to survive =
$$\frac{\exp(\alpha_0 + \alpha_1 D + \alpha_2 \Delta D + \alpha_3 STT)}{1 + \exp(\alpha_0 + \alpha_1 D + \alpha_2 \Delta D + \alpha_3 STT)}$$

where α_0 to α_3 are empirical parameters and STT is the cumulative basal area in the circle of radius 30 m centred on the subject tree. At each time step, the occurrence of dying by primary treefall is drawn for each tree. If the tree survives, the occurrence of dying standing is then drawn.

Secondary treefall depends on the occurrence of a primary treefall. If a tree dies by primary treefall, each tree in the area affected by its fall undergoes a death probability that depends on the size of the tree that fell first. Complex treefall occurs according to a similar process, provided that the tree that died by primary treefall is greater than 40 cm DBH. Hence, if a tree greater than 40 cm DBH dies by primary treefall, each tree in its close neighbourhood undergoes a death probability that is a logistic function of the competition index STT. The process is recursive, which means that a tree that died by complex treefall can be the origin of another complex treefall, and so on.

Recruitment. Recruited trees have a diameter $D = 10$ cm. Recruitment in SELVA relies on a regular grid of 10 × 10 m square cells that is superimposed on the plot domain. Let R be the number of recruited trees in a given cell. It is stochastically drawn at each time step according to the following distribution:

$$Pr[R \leqslant n] = \frac{\exp(\beta_{0n} + \beta_{1n} ST)}{1 + \exp(\beta_{0n} + \beta_{1n} ST)} \quad \text{for } n = 0 \ldots 4$$
$$Pr[R \leqslant 5] = 1$$

where β_{0n} and β_{1n} are empirical parameters, and ST is the cumulative basal area on the subject cell plus its nine closest neighbours (which gives a 30 × 30 m square centred on the subject cell).

2.1.2. Model derived from gap models

A tree is characterised by its diameter D, its height (denoted H) and its spatial coordinates x. Time is discrete with a time step $\Delta t = 1$ year. The forest dynamics is also split into the three components: growth, mortality and recruitment.

Growth. The diameter growth rate is empirically related to diameter D and to an interaction variable L, after adjusting a Weibull distribution to ΔD (Picard et al., 2001):

$$\Delta_t D = \frac{\Gamma[1 + 1/(\beta_0 + \beta_1 D)]}{(\alpha_0 + \alpha_1 L)^{1/(\beta_0 + \beta_1 D)}}$$

where α_0, α_1, β_0 and β_1 are parameters, and Γ is the gamma function. The interaction variable L represents the cumulative proportion of the crown of the subject tree that is covered by the crown of neighbouring trees:

$$L_i = \frac{1}{\pi(\rho D_i)^2} \sum_{k=1}^{N} \omega(\|x_k - x_i\|, \rho D_i, \rho D_k) \mathrm{I}(H_k > H_i)$$

where ρ is a coefficient of proportionality between the tree diameter and its crown radius and $\omega(d,a,b)$ is the area of intersection of two discs of radius a and b, a distance d apart.

The height growth rate is derived from a volume growth equation that is taken from the literature on gap models:

$$\Delta_t(D^2 H) = D^2[\gamma P(L) - \theta H]$$

where γ is the potential gain in volume per unit of basal area when light is not limiting, θ is the respiration and wood maintenance rate, and $P(L) = [\alpha_0/(\alpha_0 + \alpha_1 L)]^{1/\beta_0}$ is a reduction factor that expresses competition for light. Given the diameter increment $\Delta_t D$ and the volume increment $\Delta_t(D^2 H)$, one can compute the height increment $\Delta_t H$. To calibrate the height growth equation, measurements of tree heights were conducted at Paracou on a sample of about 600 trees.

Mortality and recruitment. Mortality and recruitment are reduced to simple expressions. The death probability is supposed to be a function of diameter only, and is computed from the diameter distribution at steady state. For recruitment, we suppose that the total number of trees remains constant, so that each time a tree dies, it is immediately replaced by a young tree with a diameter of 10 cm. This simplification supposes that the stand is at steady state, which means that the model cannot be used to predict the forest dynamics after a disturbance.

2.2. Distribution-based models

2.2.1. Matrix model

The trees of each square of 1.5625 ha of a plot are broken down by diameter class and species group. Based on ecological features and on a cluster analysis of the dynamics characteristics of the species (Favrichon, 1994), five species groups were defined: (1) understorey shade-tolerant species (e.g. *Sandwithia guianensis* Lanj. Euphorbiaceae), (2) canopy shade-tolerant (e.g. *Vouacapoua americana* Aublet Caesalpiniaceae), (3) emergent mid-tolerant (e.g. *Dicorynia guianensis* Amshoff Caesalpiniaceae), (4) canopy shade-intolerant (e.g. *Jacaranda copaia* D.Don Bignoniaceae), (5) pioneers (e.g. *Cecropia sciadophylla* Martius Moraceae). Eleven diameter classes are used, ranging from 10 to 60 cm DBH with a constant width of 5 cm, the last class grouping all the trees greater than 60 cm DBH.

A species group $s = 1 \dots 5$ is then characterised by a vector $y_s \in R^{11}$ that gives the number of trees in each diameter class. The temporal evolution of y_s is defined by a transition matrix A_s, called a Usher matrix (Buongiorno and Michie, 1980; Buongiorno et al., 1994, 1995; Usher, 1966, 1969):

$$y_s(t + \Delta t) = A_s(t) y_s(t) + r_s(t) \qquad [2]$$

with a time step $\Delta t = 2$ years. The vector r_s represents recruitment. As recruited trees have a diameter of 10 cm, only the first component r_{s1} of r_s is non-null. The transition matrix A_s possesses non-zero elements only on its diagonal and on its subdiagonal:

$$A_s = \begin{bmatrix} \ddots & & 0 \\ \ddots & 1 - b_{si} - m_{si} & \\ & b_{si} & \ddots \\ 0 & & \ddots \end{bmatrix}$$

where m_{si} is the probability for a tree of species group *s* in diameter class *i* to die between time steps *t* and $t + \Delta t$, and b_{si} is the probability for a tree of species group *s* in diameter class *i* to stay alive and move up to the next diameter class between time steps *t* and $t + \Delta t$. So $1 - b_{si} - m_{si}$ is the probability for a tree of species group *s* in diameter class *i* to stay alive and remain in the same class.

The matrix model is density-dependent, which means that the transition probabilities m_{si} and b_{si} are functions of a stand attribute, namely the cumulative basal area *B*. The relationships are linear:

$$b_{si} = \alpha_{s0} + \alpha_{s1}\overline{D}_i + \alpha_{s2}\overline{D}_i^2 + \alpha_{s3}B/B_0 \qquad [3]$$

$$m_{si} = \beta_{s0} + \beta_{s1}\overline{D}_i + \beta_{s2}\overline{D}_i^2$$

where $\overline{D}_i$ is the average diameter of the i^{th} class, and B_0 is a reference basal area that equals the basal area of an undisturbed stand. In a similar way, the recruitment flux r_{s1} or its log transform depends linearly on *B* or on the total number of trees *Y*:

$$r_{s1} \text{ or } \ln(r_{s1}) = \delta_{s0} + \delta_{s1}(B/B_0 \text{ or } Y/Y_0)$$

where Y_0 is the number of trees of an undisturbed stand.

The matrix relationship [2] that is valid for one species group can be extended to the whole stand by concatenating the vector y_s into a single vector $Y = [y_1 \ldots y_5]'$ that describes the whole stand. The temporal evolution of *Y* is given again by Equation [2], replacing y_s by *Y*, r_s by $R = [r_1 \ldots r_5]'$, and the transition matrix A_s by a block diagonal matrix whose diagonal elements are the A_s. The model is not equivalent to five independent matrix models as the species groups interact through the stand characteristics:

$$Y = 1'Y$$

$$B = [\bar{B}_{1,1} \ldots \bar{B}_{5,11}]Y$$

where 1 is the unity vector of length 55 and $\bar{B}_{si}$ is the average basal area of the i^{th} diameter class of species group *s*.

The matrix model can be performed in a deterministic way when computing [2], or it can be performed in a stochastic way following the Markov chain interpretation of the Usher matrix. The developed form of [2] is indeed:

$$y_{si}(t + \Delta t) = F_{s,i-1 \to i}(t) + F_{s,i \to i}(t) \qquad [4]$$

where $F_{s,i-1 \to i} = b_{s,i-1}y_{s,i-1}$ is the flux of individuals growing up from diameter class $i - 1$ to class *i*, and $F_{s,i \to i} = (1 - b_{si} - m_{si})y_{si}$ is the flux of individuals that remain in diameter class *i*. We also note $F_{s,i \to \text{death}} = m_{si}y_{si}$ the flux of individuals that die in diameter class *i*. In the stochastic formulation of the matrix model, the vector $(F_{s,i \to i+1}, F_{s,i \to i}, F_{s,i \to \text{death}})$ follows a multinomial law with parameters $(y_{si}, b_{si}, 1 - b_{si} - m_{si}, m_{si})$.

2.2.2. Hybrid model

The hybrid model is a mix of a matrix model for trees smaller than 40 cm DBH and of an individual-based model for trees greater than 40 cm DBH, that is: the diameter distribution for $D \leq 40$ cm is modelled by a matrix model, and the flow of trees that grow outside the last diameter class of this restricted matrix model constitutes the recruitment flux for an individual-based model.

Matrix component. The matrix component for small trees is actually identical to the restriction to the first six classes of the matrix model defined in the previous section.

Individual-based component. The individual-based component for big trees relies on a growth equation that depends on the cumulative basal area of the plot:

$$\Delta_t D = (a_{s0} + a_{s1}\ B/B_0)\Delta t \qquad [5]$$

where the parameters a_{s0} and a_{s1} are specific to each of the five species groups of the matrix model, and B_0 is again the basal area of an undisturbed 1.5625 ha sub-plot. This growth equation is complemented by a mortality rate that depends on diameter only.

Connection between the two components. Three conditions are required at the diameter threshold of 40 cm to ensure the continuity of the diameter distribution:

1. Recruited big trees in the individual-based component have a diameter of 40 cm exactly.
2. The flux of individuals is continuous at $D = 40$ cm, which means that the number of recruited big trees of species group *s* in the individual-based component between time steps *t* and $t + \Delta t$ equals $b_{s6}y_{s6}$.
3. The diameter growth rate is continuous at $D = 40$ cm, which implies:

$$b_{s6}\,\frac{\Delta}{\Delta t} = \frac{\Delta_t D}{\Delta t} \qquad [6]$$

where $\Delta = 5$ cm is the width of the diameter classes.

Confronting [5] with [3] shows that, in our case, the third continuity condition [6] can be rewritten:

$$a_{s0} = \frac{\Delta}{\Delta t}(\alpha_{s0} + \alpha_{s1}\overline{D}_6 + \alpha_{s2}\overline{D}_6^2)$$

$$a_{s1} = \frac{\Delta}{\Delta t}\ \alpha_{s3}$$

which means that the growth curve of the individual-based component is completely specified by the matrix component.

2.3. Model characteristics: summary

Table 1 summarizes the broad characteristics of the models. More details about the models, in particular the values of the parameters, the way parameters are estimated from the Paracou dataset, the quality of the adjustment of the equations to the data, the computer implementation of the models, or the way species groups were obtained, may be obtained: from Gourlet-Fleury (1998, 1997, 1999), Gourlet-Fleury and Houllier (2000), Gourlet-Fleury and Montpied (1995) for SELVA; from Favrichon (1994, 1995, 1998a,b) for the matrix model; from Picard (1999), Picard et al. (2001), Picard and Franc (2001), Picard et al. (2002) for the hybrid model or for the model derived from gap models. More details about the growth process also figure in Chapter 4, this Part.

2.4. Comparing models

The model predictions may be confronted with the observations in two ways: on one hand, one can focus on the steady state to see if the characteristics of an undisturbed stand are well reproduced by the model; on the other hand, the dynamics after a disturbance may be the main concern, to see, for instance, if the reaction of the stand to an opening of its canopy is well accounted for by the model. We shall first compare the four models concerning their ability to predict the steady state. As a reference for the steady state, the 12 plots of Paracou in 1984 will be used. Then, the four models will be compared on the basis of their ability to predict the dynamics after a disturbance. Hence, the treated plots will be taken as the reference. To compare two models, one is forced to align on the less detailed model. So we will mainly compare diameter distributions, total basal area or the total number of trees. Incidentally, SELVA and the model derived from gap models will also be compared on the basis of their ability to predict the spatial pattern of the trees.

In what follows, all variables are estimated at the plot scale (6.25 ha), and then scaled to 1 ha. As the matrix and the hybrid models work at the scale of a quarter of a plot (1.5625 ha), four model runs are necessary to simulate one plot. Hence, when we say that 12 simulations have been performed with the matrix or the hybrid models, this means that the model was run 12 × 4 = 48 times.

Table 1
Characteristics of the four models built at Paracou

	SELVA	*Model derived from gap model*	*Matrix model*	*Hybrid model*
Level of stand description	Tree	Tree	Distribution	Distribution and tree
Tree characteristics	*D*	*D, H*	*D*, species group	*D*, species group
Species description	No	No	5 groups	5 groups
Tree interactions	Space-dependent	Space-dependent	Space-independent	Space-independent
Size of neighbourhood	2,827 m^2	50 m^2	1.5625 ha	1.5625 ha
Stochastic dynamics	Yes	Yes	Possible	Yes
Dynamics out of steady state	Yes	No	Yes	Yes
Quality of adjustment to data*	23% (6 parameters) or 41.6% (65 parameters)**	5.8% (4 parameters)	–	–

* It represents the percentage of variance of the diameter increments explained by the growth equation of the model.
** Depending on the number of species groups (one “grey” species or 15 species groups).

2.5. Shifting from one model to another

Models may be confronted by comparing their predictions. Another approach consists of deriving rules to shift from one model to another and to see whether these rules are realistic (Franc et al., 1999). Two rules are necessary: one to shift from space-dependent interactions to space-independent interactions, and a second to shift from the individual-based level of description to the distribution-based level.

The first link is achieved through a mean-field approximation that consists of taking the spatial average of the space-dependent competition index, or letting the size of the neighbourhood tend to infinity (Pacala and Deutschman, 1995; Pacala and Levin, 1997). More precisely, let $L(x,q)$ be a space-dependent competition index that depends on the tree characteristics x (e.g. diameter, height) and on its spatial coordinates q. Let $U_h(.,q)$ be a bidimensional kernel smoother with bandwidth h such that $U_0(.,q)$ is the Dirac distribution at q. Then the spatial average of L at the scale h is:

$$\bar{L}_h(x,q) = \iint U_h(s,q)L(x,s)\,\mathrm{d}s$$

and the mean-field approximation corresponds to the limit $h \to \infty$.

The shift from the individual-based level to the distribution-based level, which corresponds to an aggregation operation following the aggregation theory (Iwasa et al., 1987; Ritchie and Hann, 1997), may be achieved in two ways (Picard and Franc, 2001). First, when tree interactions are space-independent, Liouville's approach may be used; this consists in establishing a conservation law in any volume of the phase space (Evans, 1998; Gardiner, 1985). The approach is very similar to that used in fluid mechanics, provided that the flow of fluid particles in the physical space is replaced by a flow of trees that "move" along the diameter (or height) axis. It brings a scalar conservation partial differential equation on the diameter distribution, that is a non-linear integro-differential equation (Hara, 1988; Hara and Wyszomirski, 1994; Kohyama, 1989, 1991; Suzuki and Umemura, 1974; Yokozawa and Hara, 1992). When tree interactions are disregarded, this equation simplifies to Liouville's equation (if the individual growth curve is deterministic) or to the Fokker–Planck equation (if the individual growth curve is stochastic). Second, when tree interactions are space-dependent, the moment equations may be derived (Bolker and Pacala, 1997, 1999; Bolker et al., 2000; Dieckmann et al., 1997; Levin and Pacala, 1997; Pacala and Deutschman, 1995; Pacala and Levin, 1997). This consists in sequentially deriving the evolution laws of the moments of the dynamical point process that corresponds to the tree-based model.

So far, these formal links between the different types of models have been derived only for the gap-like model.

3. Results

3.1. Steady state

Fig. 1 shows the discrepancy between the diameter distribution on the 12 Paracou plots in 1984 (taking into account all species) and its stationary counterpart as predicted by each model. The discrepancy is quantified as a percentage of the number of trees in the 11 diameter classes of the matrix model. The discrepancy between each of the 12 Paracou plots and their average also gives an idea of what natural fluctuations may be. The predicted distributions are computed as an average over 12 simulations, except for the matrix model whose deterministic formulation is used.

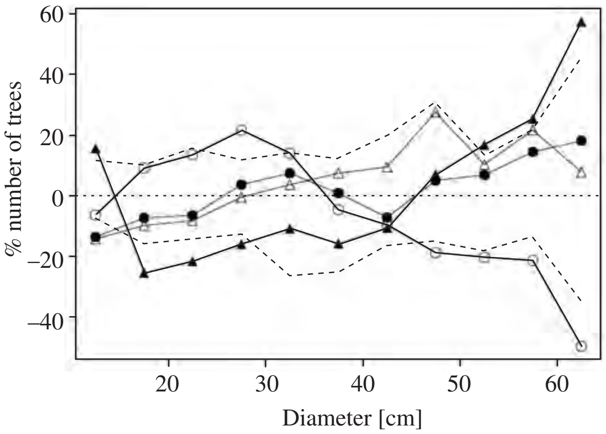


Fig. 1. Gap (in % of the number of trees in each diameter class) between the diameter distribution on the Paracou plots in 1984 and the predicted distribution: ● matrix model; Δ: hybrid model; ▲: SELVA; o: model derived from gap models. …. envelopes (maximum and minimum) of the 12 Paracou plots.

Thus, both the matrix and the hybrid models tend to underestimate the number of trees in the first diameter class. Moreover, the hybrid model tends to overestimate the number of big trees (≥55 cm). SELVA underestimates the number of small trees (15–25 cm) and overestimates the number of big trees (≥50 cm). As for the model derived from gap models, it overestimates the number of medium-sized trees (25–35 cm) and underestimates the number of big trees (≥45 cm).

At a coarser level of stand description, total basal area and the total number of trees may be predicted by the models and confronted with field observation. Results, derived from the 12 Paracou plots in 1984 or from 12 simulations with a given model (the stochastic formulation of the matrix model is used) are shown in Fig. 2.

Let us look first at the total number of trees. The matrix and the hybrid models underestimate it. More strikingly, they both significantly underestimate its variability. SELVA also underestimates the number of trees and its variability, but to a much lesser extent. The results are not shown for the model derived from gap models as the number of trees is, by construction, kept constant in this model. As for total basal area, the matrix and the hybrid model reproduce the Paracou characteristics quite well, in terms of both its average level and its variability. SELVA performs even better in this respect. The model derived from gap models, however, underestimates the basal area.

The space-dependent models (SELVA and the model derived from gap models) may also be compared concerning their ability to reproduce the spatial pattern of trees. All species confounded, the spatial pattern of trees at Paracou in 1984 exhibits regularity over short distances (<10 m) and clustering over medium distances (about 40 m) (Mercier, 1997; Picard, 1999; Picard et al., 2001). The model derived from gap models reproduces the regularity under 10 m, but does not reproduce the clusters around 40 m. On the contrary, SELVA reproduces the 40 m clusters, but does not reproduce the 10 m regularity.

3.2. Treated plots

We now turn to treated plots to assess whether the models are able to predict the dynamics of a plot after a disturbance. Two treatments, namely treatments 1 and 3, are illustrated in Figs. 3 and 4 that show the observed evolution from 1984 to 1997 and the predicted evolution from 1988 to 2038.

SELVA correctly reproduces the evolution of plot 9 (treatment 1), in terms both of basal area and number of trees (Fig. 3, top). On the contrary, the matrix model and the hybrid model (whose predictions are actually very close to those of the matrix model) are less convincing for plot 9: the total number of trees seems to reach its stationary value too fast, and the basal area tends to be overestimated.

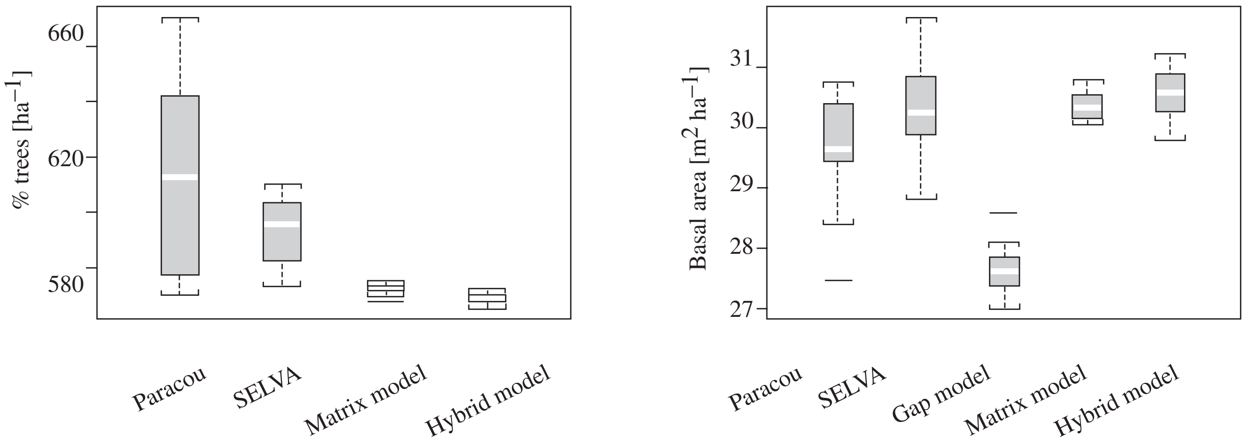


Fig. 2. Total number of trees and total basal area on the 12 Paracou plots in 1984 and as predicted by the models at steady state. The stochastic formulation of the matrix model was used for these simulations. Each boxplot summarises the distribution of the number of trees or of the basal area over 12 replicates. The boxplot at the left represents the Paracou data; the other boxplots represent model predictions.

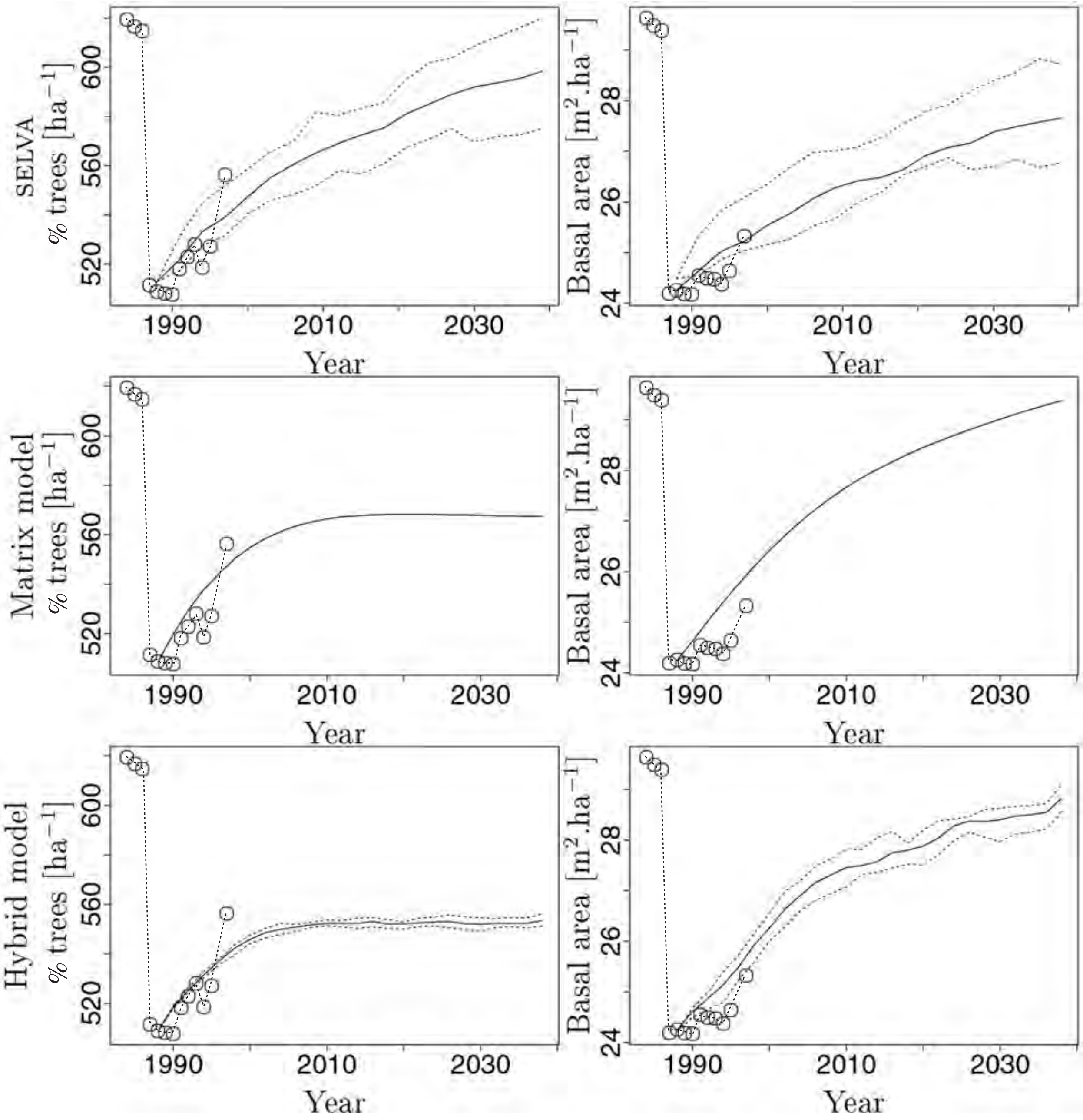


Fig. 3. Predicted (—) and observed (o) evolution of plot 9 of Paracou that underwent treatment 1: — average evolution over 12 simulations (SELVA, hybrid model) or deterministic evolution (matrix model); …. envelopes of the 12 simulations.

For plot 8 that underwent treatment 3, the tendencies are reversed: SELVA predicts a basal area and a total number of trees that increase too slowly to fit the observed dynamics. The matrix (or the hybrid) model provides a better fit, except for the number of trees in 1997 which is strongly underestimated. The evolution predicted by the matrix model does not lie precisely on the observed trajectory, but rather seems to be parallel to it. A reason for this discrepancy could be the delayed death (sometimes more than 2 years after poisoning) of the poisoned trees. Indeed, the matrix model takes as the initial state the plot as it was in 1988, considering as "healthy" those trees that are actually dying because they have been poisoned. The

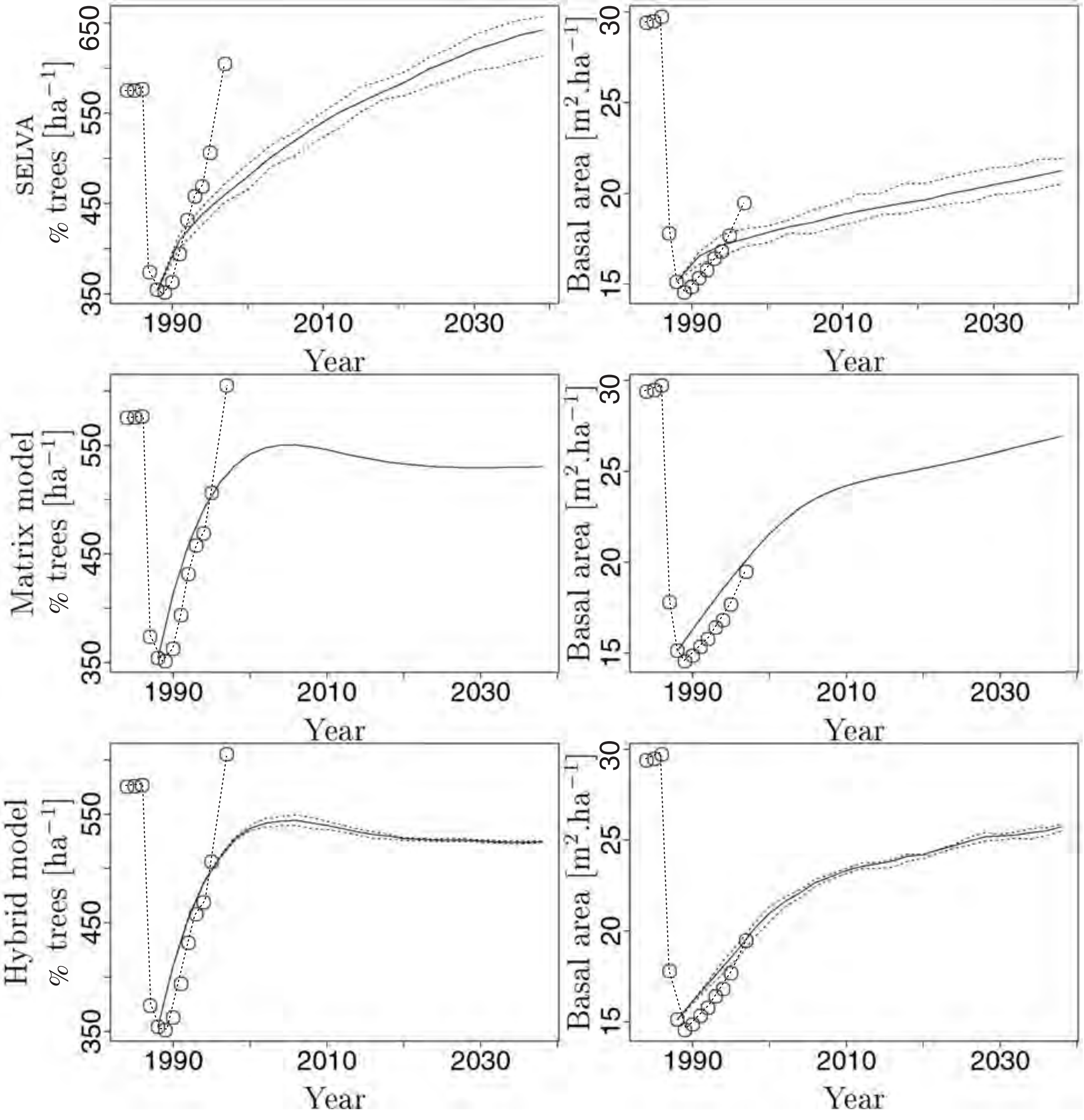


Fig. 4. Predicted (—) and observed (o) evolution of plot 8 of Paracou that underwent treatment 3: — average evolution over 12 simulations (SELVA, hybrid model) or deterministic evolution (matrix model); …. envelopes of the 12 simulations.

model is thus unable to reproduce the decrease in both basal area and number of trees that occurred between 1988 and 1990.

Generally speaking, SELVA produces slower dynamics than the matrix or the hybrid model: the number of trees or the basal area following a disturbance increases more slowly in SELVA than in the distribution-based model. The time to reach the stationary state also seems to be longer for SELVA than for the matrix model. However, the time to reach the stationary state is difficult to assess because (i) it depends, of course, on the starting point; (ii) the stationary state is very gradually reached at the end, so that the limit between the stationary state and transients is uncertain (the limit is all the more uncertain for stochastic models where stochastic fluctuations can mask the trend). Nevertheless, starting from an empty plot, it takes about 250 years using the matrix model, and about 300 years using SELVA to reach the stationary state.

3.3. Validity of the formal links between models

The mean-field approximation and the conservation law have been applied to the model derived from gap models only, thus yielding an individual-based space-independent model, a distribution-based space-dependent model, and a distribution-based space-independent model (Fig. 5). The formal links are consistent, in the sense that the same distribution-based space-independent model is obtained from the individual-based space-dependent model by first applying the mean-field approximation and then the conservation law, or first applying the moment equations and then the mean-field approximation.

In the space-independent case, the distribution-based model turns out to be equivalent to its individual-based counterpart as soon as the number of trees in the plot is large enough. In the space-dependent case, the moment equations converge towards the individual-based model as the order of the moments tends to infinity (Fig. 5).

At each level of stand description, however, the mean-field approximation fails to conserve the properties of the model: the individual-based space-independent model yields predictions that are different from those of its space-dependent counterpart. Similarly, the distribution-based space-independent model that can be obtained from the moment equations by truncating them to the first order yields different predictions. However, the discrepancy between measured data and model predictions is of the same order whatever the model, so that the space-dependent model cannot be considered a better predictor than its space-independent counterpart.

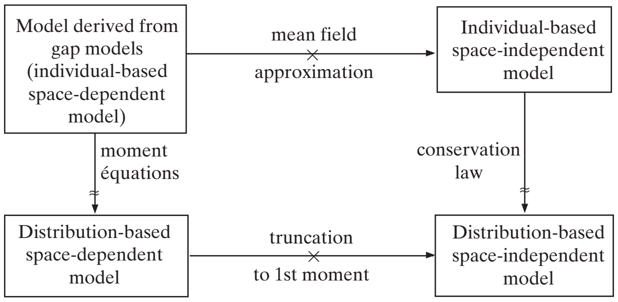


Fig. 5. Interrelations between the four types of models: × indicates that the shift yields an alteration of the model predictions; ≈ indicates that the shift conserves the model properties provided that an asymptotic condition is fulfilled.

4. Discussion

We shall first discuss the contribution of modelling at Paracou, its successes and the problems it raises with respect to research purposes. Then, the further developments required to address management purposes will be outlined.

4.1. Research purposes

So far, the four models that have been developed at Paracou have been mainly research tools. This is especially true for the model derived from gap models, which has been so simplified that it can account only for the stand stationary state. Models can serve first for quantitative tests of some hypothesis about the processes that drive the forest ecosystem, viz. recruitment, growth and mortality. They allow to check whether the three components together lead to realistic dynamics at the stand scale.

Relevant level of description. All the models yield rather realistic predictions, the model derived from gap models being the least efficient. In the stationary state, SELVA, which is the most detailed model, yields the best predictions at the stand level (total number of trees and cumulative basal area) but performs less well at the distribution level. The matrix model, on the contrary, makes better predictions at the distribution level, which is also its working level of description (Fig. 1). If we require that a model makes reliable predictions at the level at which it works, then SELVA or the model derived from gap models should predict where every tree will be at each point in time. This, of course, is nonsense. Thus, there is a gap in individual-based models between the level at which the model works and the level at which the model can be validated: only aggregate properties can be reliably predicted (Levin et al., 1997).

Individual-based models, however, enable scaling down to details such as seed dispersion around parent trees, light (or more generally any local) competition, treefall gap, etc., that would be impossible to reach with distribution-based models. If the equations that are independently calibrated for each of these detailed processes collapse in a complete model that makes reliable predictions of aggregate properties, then they can be accepted as sensible processes. The individual-based models thus remain relevant tools for testing hypotheses about detailed processes of forest dynamics.

Time scale. Our results show another general feature of models: they can make reliable predictions of the steady state, but may fail to account for the short-term dynamics after a disturbance. Figs. 3 and 4 show that SELVA tends to react to a disturbance more slowly than does the matrix model. It has been advocated that slower dynamics could be linked to space-dependent interactions (Pacala and Deutschman, 1995). Our results based on the formal links between the different types of models does not confirm this hypothesis: the four models in Fig. 5 take the same time to reach the stationary state. The relationship between the spatial scale and the time scale in a model rather remains an unsolved question (Bolker and Pacala, 1999). The partitioning of species into groups (pioneers in particular) also stands as an hypothesis that could explain faster dynamics.

The role of space. Another question of mathematical ecology that can be dealt with using the models at Paracou is the role of space. It has been advocated that space-dependent interactions have important implications for the maintenance of ecosystem function (Deutschman, 1996; Pacala and Deutschman, 1995; Tilman and Kareiva, 1997). These conclusions were derived from the comparison of a space-dependent model to its space-independent counterpart derived through the mean-field approximation. We observed in Section 3.3 that the mean-field approximation indeed alters the behaviour of the model.

This approach is, however, biased as soon as the space-dependent model is calibrated on real data and the space-independent model is derived from it. If the space-independent model is also calibrated on real data, it can then yield as reliable (or even better) predictions as the space-dependent model. Indeed at Paracou the matrix model performs at least as well as SELVA, and there is no evidence that spatial interactions are required to predict aggregate characteristics such as diameter distribution.

However, spatial interactions are quite obviously necessary when one is concerned with the spatial pattern of trees. The predictions of SELVA and of the model derived from gap models are quite complementary: SELVA predicts the aggregation at medium scale and the model derived from gap models predicts the regularity over short distances. These scales are directly related to the size of the tree neighbourhoods, as the range of tree interactions is 30 m in SELVA and 4 m on average in the model derived from gap models (Table 1). Thus, to simulate a spatial pattern that would reproduce the one observed at Paracou, it may be necessary to combine the medium-range competition index of SELVA and the short-range competition index of the model derived from gap models. This is currently being done in SYMFOR which relies both on a local (5 m radius) and on a non-local (30 m radius) competition index (Phillips et al., 2000b).

Hierarchy of models. Finally, models can be compared to see which is the closest to real measurements or, more interestingly, to obtain different points of view on a common “what if?” scenario. However, to understand the discrepancies between models, some formal links between them must be defined. So far, the mean-field approximation and the conservation law (Liouville’s approach) have been applied only to the model derived from gap models. It would be interesting to continue this work with SELVA, and then to derive formal links between partial differential equations (continuous distribution-based models) and matrix models (discrete distribution-based models).

Another approach relies on a mix of an individual-based and a distribution-based model, as in the hybrid model. Presently, the hybrid model adds little to the matrix model, as can be seen from Figs. 3 and 4. It could, however, be advantageous in situations where an explicit individual description is required for big trees (to model seed dispersion around parent trees, or logging when the minimum diameter for felling is greater than the greatest diameter class limit, etc.).

4.2. Further developments for management applications

Management plans in tropical forests still rely on simple hypotheses about forest dynamics: constant diameter growth, constant mortality rate, etc. Models can provide a finer description of these dynamics, but the level of details that they provide must comply with the manager's requirements.

Return time. A first variable of interest for the forest manager is the return time, that is the time necessary for the forest to recover its initial stem stock after exploitation. However, estimating the return time for a large area (several thousand hectares) with a model that can predict the dynamics of a few hectares is problematic.

A first solution consists of considering a real hectare plot as a random sample from the forest area. The plot can then be taken as the starting point, a logging operation is carried out or simulated, and then the model predicts the time necessary to come back to the starting point (provided that it does!). The spatial heterogeneity of the forest area will result in understocked plots with a longer return time, and overstocked plots with a shorter return time. The return time, then, is itself a random variable whose characteristics have to be estimated.

A quicker solution consists of considering a real plot as a random realisation of an ideal stationary state that is not observable but that can be predicted by the model. Then, the return time is estimated as the time necessary to reach the theoretical stationary state. This approach, however, has a major drawback: it supposes that the stationary state predicted by the model is correct. In particular for a stochastic model, the range of predicted variation around the average level in the stationary state should be consistent with the observed inter-plot variability. Fig. 2 shows that the models underestimate this variability, SELVA being the most valuable model in this respect.

One way to overcome this limitation could be to favour randomness in the models, e.g. through the Markov chain interpretation for matrix models. Indeed, equation [4] enables to compute the number y_i of trees in the i^{th} diameter class in either a deterministic or a stochastic manner. In the simulations that were performed, we used the deterministic formulation for the first 6 diameter classes (<40 cm DBH) and the stochastic formulation for the remaining five classes (≥40 cm DBH). By lowering this threshold, we could enhance the variability.

Felling cycle and minimum diameter for felling. In contrast to the return time, which is an intrinsic characteristic of forest dynamics, the felling cycle and the minimum diameter for felling are control parameters that are fixed by the manager. The models should then be a tool to evaluate some "what if?" scenarios, such as: what if the minimum diameter for felling is increased by 10 cm? What if the felling cycle is shortened by 10 years? This should eventually allow determination of an optimal and sustainable felling plan.

At present, there are two main limitations to assessing such "what if?" scenarios with the models: simulating an initial state of the plot and simulating realistic logging practices.

Initial state. All four models developed at Paracou can take any real plot of Paracou as the starting point. However, to test new scenarios (for instance, the influence of the initial diameter distribution), one may want to simulate initial plots. This can be done for the space-independent models.

For the space-dependent models, this remains a serious issue, as realistic tree spatial patterns should take into consideration the link between the diameter structure and the spatial structure (Hanus et al., 1998; Mercier, 1997; Pielou, 1960), as well as the specific spatial pattern of each tree species (see Chapter 1, this part). The simulation of an initial state of the plot (for a given diameter distribution, for instance) does not strictly speaking fall within the competence of a model of forest dynamics. However, it limits the range of investigation that can be carried out with the model. The SYMFOR developers, for instance, are currently designing procedures to generate artificial tree position data (Phillips et al., 2000b).

Logging practices. In the matrix model, logging operations can be modelled by replacing Equation [2] with:

$$y_s(t+\Delta t) = A_s(t)[y_s(t) - h_s(t)] + r_s(t)$$

where h_s is the vector of the number of harvested trees in each diameter class. The mortality rate may also be adjusted to account for those trees wounded during logging operations. However, some issues still remain: how to account for the trees that are destroyed by logging operations, that is, for a given number of harvested trees, how many trees should be removed? For a given logging intensity, how to select the number of trees to be removed in each diameter class?

SELVA, thanks to its recursive process for treefalls, can deal with felling damage. However, logging damage, which also includes skid trail damage, etc., is more intensive. In SELVA, there is also a problem (though not a serious one) of selecting the logged trees in a routine way. At present, this can be done only by hand, thus providing a tool for stem by stem silviculture.

So far, the consequences of logging have been assessed at Paracou on the basis of the real treated plots. A module for realistic logging operations remains to be developed for each model.

Species composition. The level of stand description used by the model conditions our perception of whether the stand is or is not in its stationary state. The four models defined at Paracou predict the tree diameters or their distribution. At a coarser level, we then can derive the total number of trees and the cumulative basal area. Returning to an initial basal area or to an initial diameter distribution does not ensure, however ,that the forest has returned to its initial state, as there may have been some readjustments between species. The species composition is thus a significative characteristic to assess the status of the stand.

Presently, only the matrix model provides some information on the species composition on the basis of five species groups. Species information has actually been taken into account in the growth component of SELVA by forming 15 species groups. For each group, a growth equation has been developed in a form similar to [1] (the Korf growth curve is replaced by a Gompertz curve for the average growth, and seven variants of the modification factor are used). However, as species information is not yet integrated into the mortality and recruitment components, SELVA can at present only be run in its "no species" configuration.

The level of specific detail which the modeller can reach is limited mainly by rare species that prevent parameters from being precisely estimated. To avoid this problem of rare species, a reasonably small number of species groups could be derived for each of the three components of the dynamics. A number of n species groups for recruitment, p groups for growth and q groups for mortality provides $n \times p \times q$ possibilities. Each species would then be characterised by a triplet that corresponds to the three groups through which it passes during its development.

5. Conclusion

Presently, the matrix model appears to be the most efficient tool for management purposes at Paracou. It predicts aggregate stand characteristics such as diameter distribution in a reliable way, can be either deterministic or stochastic, and requires little computing time. Some progress is still required to simulate realistic logging operations and, more dramatically, to account for species diversity.

The individual-based space-dependent model SELVA, however, remains a major tool for research purposes, as it allows scaling down to details and quantitative assessment of the relevance of some ecological processes. Its refinement will continue as our understanding of the ecosystem processes increases (Chapters 1 to 4, this part), with an emphasis on regeneration and description of species diversity.

Ideally, these two levels of stand description could be joined by formal links that would allow the forest manager to scale up and down, depending on the required level of details.

References

Alder D., 1995. Growth modelling for mixed tropical forests. Tropical Forestry Papers no. 30, Oxford Forestry Institute, University of Oxford, Oxford, UK.

Alder D., 1997. User-s guide for SIRENA II, a simulation model for the management of natural tropical forests. Manual, CODERSA (Comisión para Desarollo Forestal de San Carlos).

Bolker B.M., Pacala S.W., 1997. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. Theor. Popul. Biol. 52, 179–197.

Bolker B.M., Pacala S.W., 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. Am. Nat. 153, 575–602.

Bolker B.M., Pacala S.W., Levin S.A., 2000. Moment methods for stochastic processes in continuous space and time. In: Dieckmann U., Law R., Metz J.A.J. (Eds.), The Geometry of Ecological Interactions: Simplifying Spatial Complexity. Cambridge University Press, Cambridge, pp. 388–411.

Boscolo M., Vincent J.R., 1998. Promoting better logging practices in tropical forests: a simulation analysis of alternative regulations. Development Discussion Paper no. 652, The Harvard Institute for International Development, Harvard University, Cambridge, Massachusetts, USA.

Bossel H., Krieger H., 1991. Simulation model of natural tropical forest dynamics. Ecol. Model. 59, 37–71.

Buongiorno J., Dahir S., Lu H.C., Lin, C.R., 1994. Tree size diversity and economic returns in uneven-aged forest stands. Forest Sci. 40, 83–103.

Buongiorno J., Michie B.R., 1980. A matrix model of uneven-aged forest management. Forest Sci. 26, 609–625.

Buongiorno J., Peyron J.L., Houllier F., Bruciamacchie M., 1995. Growth and management of mixed-species, uneven-aged forests in the French Jura: implications for economic returns and tree diversity. Forest Sci. 41, 397–429.

Deutschman D.H., 1996. Scaling from trees to forests: the problem of relevant detail. PhD thesis, Cornell University, Ithaca, NY.

Dieckmann U., Herben T., Law R., 1997. Spatio-temporal processes in plant communities, Interim Report no. IR-97-026. International Institute for Applied Systems Analysis, Laxenburg, Austria.

Durrieu de Madron L., 1993. Chablis, mortalité et rôle des trouées dans la sylvigenèse, avant et après exploitation dans le dispositif d'étude sylvicole de Paracou, Guyane française, Thèse de doctorat, ENGREF, Paris.

Evans L.C., 1998. Partial differential equations. Graduate Series in Mathematics no. 19, American Mathematical Society, Providence, Rhode Island.

Favrichon V., 1994. Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise. Rev. Écol. (Terre et Vie) 49, 379–403.

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, Université Claude Bernard – Lyon I, Lyon.

Favrichon V., 1998a. Apports d'un modèle démographique plurispécifique pour l'étude des relations diversité/dynamique en forêt tropicale guyanaise. Ann. Sci. Forest 55, 655–669.

Favrichon V., 1998b. Modeling the dynamics and species composition of tropical mixed-species uneven-aged natural forest: effects of alternative cutting regimes. Forest Sci. 44, 113–124.

Franc A., Gourlet-Fleury S., Picard N., 1999. Introduction à la modélisation des forêts hétérogènes, ENGREF, Nancy.

Gardiner C.W., 1985. Handbook of Stochastic Methods for Physics, Chemistry and the Natural Sciences, second ed. Springer Series in Synergetics no. 13, Springer Verlag, Berlin, Germany.

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, Université Claude Bernard – Lyon I, Lyon, France, 2 volumes.

Gourlet-Fleury S., 1998. Indices de compétition en forêt dense tropicale humide: étude de cas sur le dispositif sylvicole expérimental de Paracou (Guyane française). Ann. Sci. Forest 55, 623–654.

Gourlet-Fleury S., 1999. Individual-based spatially explicit modelling of forest stands in French Guiana. In: Laumonier Y., King B., Legg C., Rennolls K. (Eds.). Data Management and Modelling Using Remote Sensing and GIS for Tropical Forest Land Inventory. Rodeo International Publishers Publishers, Jakarta, pp. 473–490.

Gourlet-Fleury S., Houllier F., 2000. Modelling diameter increment in a lowland evergreen rain forest in French Guiana. Forest Ecol. Manag. 131, 269–289.

Gourlet-Fleury S., Montpied P., 1995. Dynamique des peuplements denses forestiers en zone tropicale humide: ébauche d'un modèle d'arbre à Paracou (Guyane française). Rev. Écol. (Terre et Vie) 50, 283–302.

Hanus M.L., Hann D.W., Marshall D.D., 1998. Reconstructing the spatial pattern of trees from routine stand examination measurements. Forest Sci. 44, 125–133.

Hara T., 1988. Dynamics of size structure in plant populations. Trend. Ecol. Evol. 3, 129–133.

Hara T., Wyszomirski T., 1994. Competitive asymmetry reduces spatial effects on size–structure dynamics in plant populations. Ann. Bot. 73, 285–297.

Hawthorne W.D., Filer D., Turnbull D.J., 1999. Tree data management, mapping and the development of the TREMA software. Int. Forest Rev. 1, 87–96.

Iwasa Y., Andreasen V., Levin S.A., 1987. Aggregation in model ecosystems: I. Perfect aggregation. Ecol. Model. 37, 287–302.

Köhler P., Huth A., 1998. The effects of tree species grouping in tropical rainforest modelling: simulations with the individual-based model Formind. Ecol. Model. 109, 301–321.

Kohyama T., 1989. Simulation of the structural development of warm-temperate rain forest stands. Ann. Bot. 63, 625–634.

Kohyama T., 1991. Simulating stationary size distribution of trees in rain forests. Ann. Bot. 68, 173–180.

Levin S.A., Grenfell B., Hastings A., Perelson A.S., 1997. Mathematical and computational challenges in population biology and ecosystems science. Science 275, 334–343.

Levin S.A., Pacala S.W., 1997. Theories of simplification and scaling of spatially distributed processes. In: Tilman D., Kareiva P. (Eds.), Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions. Princeton University Press, Princeton, NJ, pp. 271–295.

McLeish M.J., 1999. Modelling alternative silvicultural practices within SYMFOR: setting the model and interpreting the results, SYMFOR Technical Note Series no. 2. Institute of Ecology and Resource management, University of Edinburgh, Edinburgh, UK.

Mercier F., 1997. Analyse et modélisation de la dynamique forestière guyanaise à l'aide de diagrammes de Voronoï, Thèse de doctorat, Université Claude Bernard – Lyon I.

Moravie M.A., 1999. Un modèle arbre dépendant des distances pour l'étude des relations entre la dynamique et la structure spatiale d'une forêt dense sempervirente, Thèse de doctorat, Université Claude Bernard – Lyon I, Lyon.

Munro D.D., 1974. Forest growth models: a prognosis. In: Fries J. (Ed.), Growth Models for Tree and Stand Simulation. Royal College of Forestry, Department of Forest Yield Research, Stockholm, Research Notes no. 30, pp. 7–21.

Oldeman R.A.A., 1974. L'architecture de la forêt guyanaise, Mémoire ORSTOM no. 73, ORSTOM, Paris, France.

Ong R., Kleine M., 1996. DIPSIM: a dipterocarp forest growth simulation model for Sabah, FRC Research Papers no. 2. Forestry Department, Sabah, Malaysia.

Pacala S.W., Deutschman D.H., 1995. Details that matter: the spatial distribution of individual trees maintains forest ecosystem function. Oikos 74, 357–365.

Pacala S.W., Levin S.A., 1997. Biologically generated spatial pattern and the coexistence of competing species. In: Tilman D., Kareiva P. (Eds.), Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions. Princeton University Press, Princeton, NJ, pp. 204–232.

Phillips P., McLeish M.J., Brash T., Herry Susanti F., Gadas S., Purnama B., et al., 2000a. The SYMFOR model: a general description, SYMFOR Technical Note Series no. 3. Institute of Ecology and Resource Management, University of Edinburgh, Edinburgh, UK.

Phillips P., McLeish M.J., van Gardingen P., 2000b. The SYMFOR model of natural forest processes: opening the black box, SYMFOR Technical Note Series no. 1. Institute of Ecology and Resource Management, University of Edinburgh, Edinburgh, UK.

Picard N., 1999. Passage d'un modèle individuel à un modèle de distribution de la dynamique forestière – Application à une forêt dense tropicale humide de Guyane française, Thèse de doctorat, ENGREF, Paris, France.

Picard N., Bar-Hen A., Franc A., 2001. Spatial pattern induced by asymmetric competition: a modelling approach. Nat. Resour. Model. 14, 147–175.

Picard N., Bar-Hen A., Franc A., 2002. Modeling forest dynamics with a combined matrix/individual-based model. Forest Sci. 48, 643–652.

Picard N., Franc A., 2001. Aggregation of an individual-based space-dependent model of forest dynamics into distribution-based and space-independent models. Ecol. Model. 145, 69–84.

Pielou E.C., 1960. A single mechanism to account for regular, random and aggregated populations. J. Ecol. 48, 575–584.

Riéra B., 1983. Chablis et cicatrisation en forêt guyanaise (piste de Saint Élie), Thèse de doctorat, Université Paul Sabatier, Toulouse.

Ritchie M.W., Hann D.W., 1997. Implications of disaggregation in forest growth and yield modeling. Forest Sci. 43, 223–233.

Shugart H.H., Hopkins M.S., Burgess I.P., Mortlock A.T., 1980. The development of a succession model for subtropical rain forest and its application to assess the effects of timber harvest at Wiangaree State Forest, New South Wales. J. Environ. Manag. 11, 243–265.

Suzuki T., Umemura T., 1974. Forest transition as a stochastic process. In: Fries J. (ed.), Growth Models for Tree and Stand Simulation. Royal College of Forestry, Department of Forest Yield Research, Stockholm, Research Notes no. 30, pp. 358–379.

Tiama 1999. Traitement des inventaires appliqué à la modélisation des aménagements, République du Cameroun, Ministère de l'environnement et des forêts, Direction des forêts - Agence canadienne de développement international – Tecsult Inc., Québec, manuel d'utilisation du logiciel.

Tilman D., Kareiva P. (Eds.), 1997. Spatial Ecology – The Role of Space in Population Dynamics and Interspecific Interactions. Monographs in Popluation Biology no. 30, Princeton University Press, Princeton, New Jersey.

Usher M.B., 1966. A matrix approach to the management of renewable resources, with special reference to the selection forests. J. Appl. Ecol. 3, 355–367.

Usher M.B., 1969. A matrix model for forest management. Biometrics 25, 309–315.

Vanclay J.K., 1989. A growth model for north Queensland rainforests. Forest Ecol. Manag. 27, 245–271.

Vanclay J.K., 1995. Growth models for tropical forests: a synthesis of models and methods. Forest Sci. 41, 7–42.

Wan Razali B.W.M., Rustagi K.P., 1988. Development of a generalized growth model for mixed tropical forests of peninsular Malaysia. In: Ek A.R., Shifley S.R., Burk T.E. (Eds.), Forest Growth Modelling and Prediction. USDA For. Serv., Nor. Cen. For. Exp. Sta., St. Paul, Minnesota, Gen. Tech. Rep. no. NC-120, vol. 1, pp. 167–174.

Yokozawa M., Hara T., 1992. A canopy photosynthesis model for the dynamics of size structure and self-thinning in plant populations. Ann. Bot. 70, 305–316.

Zeide B., 1993. Analysis of growth equations. Forest Sci. 39, 594–616.