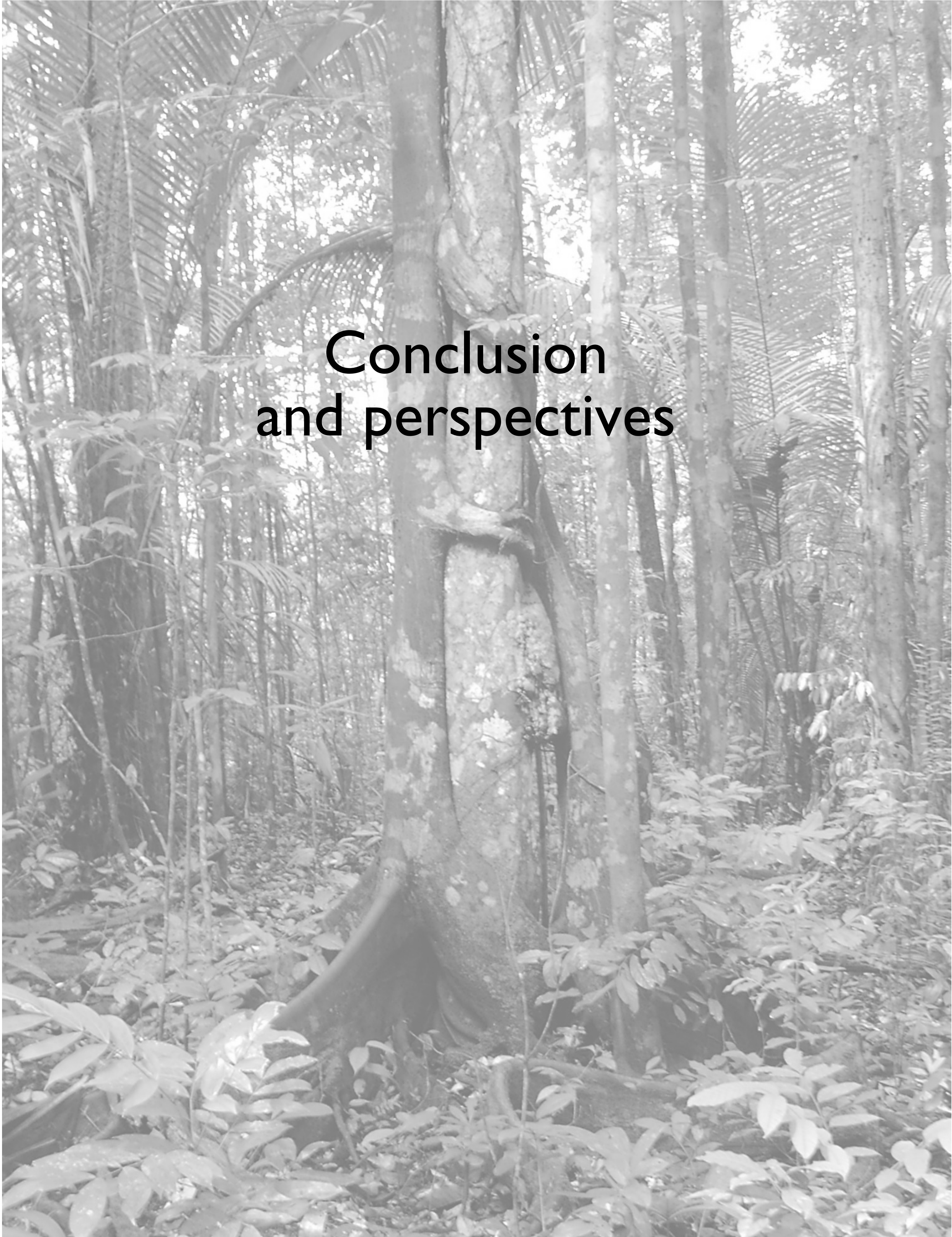
Conclusion and perspectives



Ecology and Management of a Neotropical Rainforest

Conclusion and perspectives

Marc Fuhr, Sylvie Gourlet-Fleury, Florent Ingrassia, Olivier Brunaux, Jean-Marc Guehl

The topics addressed throughout this volume deal mainly with the biological and ecological aspects of sustainable forest management, leaving aside the specific sociological and economical context of French Guiana, which cannot be easily extrapolated to other tropical regions. The chapters reflect several shifts in the concerns of the scientific communities working at Paracou since the beginning of the project. The Paracou experiment was aimed primarily at providing concrete answers to the National Forest Office (ONF), which manages most of the 80,600 km^2 of tropical rainforests that cover the department. The accumulation of data on the growth and demography of trees, and their analysis in order to feed models of forest dynamics, has shed considerable light on the potential of the forest as regards the quantity and species of timber that could, or could not, be recovered after logging for the first time. It also allowed to point out the existence of disturbance thresholds that cannot be exceeded without significant modification of the floristic composition and structure of the stands. In this sense, it can be said that the initiators of Paracou have fulfilled their objectives.

Over time, however, an awareness of the potential value of the genetic, specific and functional diversity of ecosystems both widened and constrained the objectives of management plans (Leslie, 1997, Mankin, 1998, Mengin-Lecreulx, 2000, Dutrève et al., 2001), and enlarged the set of questions addressed to researchers. This led several teams from INRA, MNHN, ENGREF, IRD, and more recently CNRS and the University of Lyon, in collaboration with CIRAD, to profit from the existence of a large area of more than 50,000 mapped and historically known trees to develop research programs dealing with:

- the regeneration potential and the temperament of the main tree species, on the basis of extensive surveys, and in situ and greenhouse experiments;
- the part played by animals in the dispersal of some specific species (pioneers vs large-seeded trees);
- the level, distribution and prediction of changes in the genetic diversity of several species which differ in their biological attributes;
- the affinities of tree species with specific soil characteristics, such as poorly drained soils;
- the mycorrhizal and atmospheric N_2-fixing status of most of the species at the site;
- the water-use efficiency of species and stands, in order to determine the part played by the Guiana rainforests in the water and carbon cycles.

As results accumulate, new hypotheses are formulated and intensive collaboration between teams is initiated, opening the way for more accurate predictions of the impact of disturbances on the various functions and services of the forest ecosystem, and not only timber production. In the following paragraphs, we will briefly summarise the main achievements of the activities carried out at Paracou from both the applied and the scientific standpoints, distinguishing: (i) the practical outcomes of use to forest managers, (ii) the way scientific activities are participating in the international debate on questions such as the mechanisms leading to high biodiversity and its maintenance, or the links between biodiversity and the biogeochemical/hydrological functioning of ecosystems. We will conclude by outlining the most urgent research needs for the immediate future, some of which have already given rise to new projects.

1. Practical outcomes for sustainable forest management

The results reported in this book are useful in two domains: 1) the management and silviculture in natural forests, at present of prime importance for French Guiana, and 2) the selection and silviculture of species which perform well in plantations, as well as species which can enhance secondary successions on degraded lands such as those left by gold mining. Applications in this latter domain are more modest, as they concern less than 100 hectares compared to the more than 1,300,000 hectares that will soon be under management in the coastal part of the department. However, these applications should also be of interest for neighbouring countries where wood production and soil restoration are more critical issues than in French Guiana.

1.1. Management and silvicultural rules in natural forests

1.1.1. Setting felling cycles on a wise basis

As emphasised in Chapter 5, Part IV, after logging, primary forests under management for timber production will probably recover neither their structure nor their floristic composition within a period of time consistent with the time scale of managers (less than 100 years). This is because the volume extracted at first cut has accumulated over several hundreds of years and concerns mainly species belonging to the late stages of succession.

In Paracou, 10 trees/ha with a DBH ≥ 50 or 60 cm, belonging to about 60 species, were extracted, yielding a mean volume of 50 m^3/ha. Such an extraction volume can be locally reached in the typical managed forests of French Guiana, but extraction is most often in the range of 10 to 20 m^3/ha, corresponding to 2 to 4 trees/ha. Models built on data sets accumulated since 1984 show that a minimum recovery of 75 to 85% of the number of valuable trees above the diameter cutting limit (DCL) can be expected within 40 years, and 80 to 90% within 50 years. These trees will probably be smaller than in the previously undisturbed forest, and the floristic composition will differ from the initial composition, a shift being observed towards fast-growing species. Possible problems will arise with two valuable species, *Sextonia rubra* Mez (Lauraceae) and *Caryocar glabrum* (Aublet) Persoon (Caryocaraceae). These species are characterised by an U-shape diameter distribution and by low diameter increment rates, and they do not regenerate abundantly. Models predict the recovery of less than 30% of the number of trees above DCL within 50 years, and the long-lasting loss of large trees could have an important impact on the population dynamics of these species. This should justify the adoption of specific silvicultural rules in order to preserve their future (see below).

Lengthening felling cycles far beyond 50 years in order to recover 100% of the initial stock of valuable trees is not recommended for two reasons: first, while waiting to obtain more trees, natural mortality can cause the loss of trees ready to be extracted (the balance can well be zero), and second, the opening of the forest by logging stimulates the growth of the remaining trees during 6 to 20 years. As logging is generally the only silvicultural operation occurring within the felling cycle, it should not be postponed too long.

1.1.2. Limiting forest openings and adapting thinning rules

The results presented in Chapters 4 and 5, Part IV, show that opening the stands has desirable as well as undesirable consequences. It stimulates the growth of remaining trees and the recruitment of new trees for several years, yet it also increases mortality rates by creating imbalance around canopy gaps. When opening is too great (e.g. the most severe treatment at the Paracou site, T3), growth reaches a maximum which is shared by a diminishing number of undamaged valuable trees; in the meanwhile, the stands are invaded by fast growing non valuable species.

We estimate that the intensity of disturbance reached in the logging+poison-girdling T2 treatment at Paracou, that is, elimination of 1/3 of the initial basal area (from 30m^2/ha to 20m^2/ha) should not be exceeded in the managed forests of French Guiana. An immediate loss of 5 m^2/ha, possibly repeated every 15 years in the course of a 45 year felling cycle, appears an optimal solution in order to maintain the high growth rate observed following logging (× 1.5 compared to an undisturbed forest) while avoiding a significant species shift in the stands.

Where repeated thinnings appear economically viable during the felling cycle, caution is required as concerns the intensity, as previously stated, but also to the thinning modalities. At Paracou, logging in T2 and T3 was completed by refinement through the systematic elimination of non desirable species above 40 cm DBH. While experimentally fruitful and technically simple to implement, this rule is probably not ideal, as (i) it can be useless when the stands are too poorly stocked with future crop trees; (ii) it can have long-term consequences on biodiversity, and (iii) it limits the possibilities of adaptation to changes in market demand. Liberation directed at future crop trees should be favoured, and possibly completed or replaced by refinement over limited areas when the density of valuable trees is high and justifies it.

1.1.3. Logging as the first silvicultural operation

1.1.3.1. Adopting reduced impact logging (RIL)

Most often, logging is and will be the only intervention in the stands during the felling cycle. In addition to avoiding the lengthening of felling cycles, as previously said, it is particularly important to profit from the opening to stimulate the number of future crop trees. This implies preserving them from damage during logging operations; for the forestry profession today, there is a real stake in reducing the impact of logging in French Guiana.

1.1.3.2. Preserving seed-bearers, key and value-laden species

As explained in Chapter 1, Part III, logging can induce lower effective population sizes and disturbance in pollination mechanisms, even if this was not clearly demonstrated at Paracou, except for *Carapa procera* DC. (Meliaceae). However, the sizes of the disturbed areas in Paracou may not be adapted to a correct evaluation of the long-term consequences of logging on the mating systems of the species studied, and large-scale experiments inside managed forests are still needed to confirm these findings. In the meanwhile, managers of the National Forest Office have adopted "caution" rules in order to preserve several categories of trees:

- future crop trees[1], potentially seed-bearers, chosen among the major species of commercial interest[2], between 35 cm DBH and the diameter cutting limit (DCL): 1 to 2 trees per ha (of exploitable area) are preserved, with a mean spacing of 100 m. *Sextonia rubra,* which shows a marked U-shaped diameter structure, is systematically preserved.
- Potential key resource species, i.e. seed-eaten species whose fruiting period does not match with the fruiting period of most of the others, such as *Goupia glabra* Aubl. (Celastraceae) and *Bagassa guianensis* Aubl. (Moraceae). For these species, 10 crop trees of diameter greater than DCL are preserved for every 300 ha (mean size of a plot in a managed forest), as well as all the future crop trees.
- Extremely valuable species such as *Aniba rosaeodora* Ducke (Lauraceae) are completely preserved, when recognised.

The stake for researchers is now to provide new information to help in deciding if these empirical rules can guarantee the long-term survival of commercial species.

1.1.3.3. Establishing new rules

Among the critical and still unsolved problems, let us mention two: (i) species such as *Sextonia rubra* or *Caryocar glabrum*, previously pointed out as sensitive due to their unbalanced diameter class structure and low regeneration level. More reflection is needed concerning a possible ban on their extraction after first logging; (ii) clumped species, such as *Dicorynia guianensis*, the most heavily extracted in French Guiana. Although, on a mean basis, logging extracts only 2 to 4 trees/ha, it can cause local levels of elimination and disturbance comparable to Paracou treatment T3 due to the aggregated spatial pattern of trees. In such cases, the future crop trees are particularly endangered as they neighbour the exploitable ones. Depending on the temperament of the species and the structure of the clumps (some are overstocked and need to be opened to favour the recruitment of conspecific trees), rules based on a minimum distance between two crop trees could be implemented and tested.

[1] Which diameter is large enough to reach the diameter cutting limit within the current felling cycle and which qualities make it harvestable at the next cycle.

[2] Those species are, at present: *Dicorynia guianensis* Amshoff (Caesalpiniaceae), *Manilkara bidentata* (A. DC.) A. Chev. (Sapotaceae), *Qualea rosea* Aubl. (Vochysiaceae), *Ruizterania albiflora* (Warm.) Marc.-Berti (Vochysiaceae), *Sextonia rubra* Mez (Lauraceae), *Vouacapoua americana* Aubl. (Caesalpiniaceae), *Goupia glabra* Aubl. (Celastraceae), *Peltogyne venosa* (Vahl) Bentham (Caesalpiniaceae), and various "precious woods" (*Cedrela odorata* L., Meliaceae, *Brosimum guianense* (Aubl.) Huber, Moraceae, *Brosimum rubescens* Taub., Moraceae, *Bocoa prouacensis* Aubl., Caesalpiniaceae, *Euplassa pinnata* (Lam) Johnston, Proteaceae, *Zygia racemosa* (Ducke) Barneby & Grimes, Mimosaceae, *Paramachaerium ormosioides* (Ducke) Ducke et *P. schomburgkii* (Benth.) Ducke, Fabaceae, *Swartzia panacoco* (Aubl.) Cowan, Caesalpiniaceae, *Dendrobangia boliviana* Rusby, Icacinaceae).

1.2. Plantation and rehabilitation or restoration of bare lands

The results presented in Chapter 4, Part II, show that the biomass increment of *Dicorynia guianensis* seedlings is dependent on their mycorrhizal status. Within the context of a common ONF/INRA/CIRAD project aimed at developing technical means for the plantation of native species, several trials on this species are underway to compare the effects of growing seedlings either with sand+forest soil, with soil taken inside clumps of *D. guianensis,* or with a specific *D. guianensis* root crush enriched soil. It is hoped that more general results from ongoing research will help design a growing number of large-scale experiments on a sound basis.

In addition to plantations, several years ago the National Forest Office launched, with the help of CIRAD-Forêt, experiments concerning land reforestation in areas degraded by gold mining. Those experiments are based on the use of the Australian N_2-fixing species *Acacia mangium* Willd. (Mimosaceae), highly growth efficient on very poor soils. The identification of native species able to fix atmospheric N_2, as presented in Chapter 5, Part II, opens the way to abandoning such exotics in favour of local species. Real scale experiments have started in the context of an ONF/CIRAD-Forêt/INRA/CNRS project, with the following species: *Inga thibaudiana* DC. (Mimosaceae), *Inga pezizifera* Benth. (Mimosaceae), *Inga cayennensis* Sagot ex Benth. (Mimosaceae), *Tachigali melinonii* (Harms) Zarucchi & Herend. (Caesalpiniaceae) and *Diplotropis purpurea* (A. Rich.) Amshoff (Papilionaceae).

2. An original contribution to tropical rainforest ecology

Paracou has offered an incomparable context for the development of research programmes in ecology. The questions addressed by the different teams relate to two main scientific issues: (1) the mechanisms underlying the maintenance of high biodiversity at local scale, and (2) the relationships between biodiversity and ecosystem functioning (hydrological and biogeochemical cycles).

2.1. Mechanisms underlying the maintenance of high biodiversity at local scale

2.1.1. Specific and functional diversity

At the scale of a site like Paracou, three theories are commonly evoked to explain the high specific diversity observed (546 woody species ≥ 2 cm DBH have been recognised over 5 ha, see Part I):

- the niche diversification theory and its derivatives such as the "intermediate disturbance hypothesis" (Grime, 1973, Connell, 1978) explain, either in equilibrium or in non-equilibrium communities, that species are all the more numerous in the same place as the spectrum of available resources is large and the species are fitted, through their ecological behaviour, to this spectrum.
- The Janzen-Connell model hypothesises that trees tend to put away conspecific juveniles through parasitism and predation mechanisms, thus allowing other species to settle in their neighbourhood (Janzen, 1970, Connell, 1971).
- The "community drift model" or "recruitment limitation hypothesis" (Hubbell, 2001) argues that all individuals are ecologically equivalent, whatever the species. This neutral theory states that differences between traits that we know really differ from species to species – birth, growth and death rates, habitat preferences, dispersal abilities – can be neglected. What only matters is to be at the right place at the right time.

The results obtained in Paracou can be discussed in terms of mechanisms related to these three theories:

- early studies of the light responses of different species under greenhouse conditions (Chapter 1, Part II) and in situ (Chapter 3, Part IV) show that temperaments are contrasted and species are not equivalent in their reactions to light, as it has been demonstrated for different rainforests (e.g. Swaine and Whitmore, 1988, for a review). The validity of the intermediate disturbance hypothesis was stated in a recent study on transects settled in 10 plots of the site (see Part I), by Molino and Sabatier (2001).
- The existence of complex spatial patterns in species with short distances of dispersion, such as *Dicorynia guianensis*, *Eperua falcata* Aubl. (Caesalpiniaceae) or *Vouacapoua americana* Aubl. (Caesalpiniaceae) (see Chapter 1, Part IV and recent work on the subject at Paracou: Chevolot, 2001, Traissac et al., submitted), can be explained by distance and/or density

dependence, in a way consistent with the Janzen-Connell theory.

- Nevertheless, several works carried out in Paracou resulted in grouping the many species present into a limited number of groups for which the behaviours, regarding different processes, appear homogeneous to some extent (e.g. ecological temperaments in Favrichon, 1994; diameter increments, see Chapter 4, Part IV; height/diameter relationships in Collinet, 1997; water use efficiency, see Chapter 2, Part II or Bonal et al., 2000; seed sizes and dissemination syndromes, Sabatier and Molino, unpublished data), although considerable variation still exists for the different variables within the different groups of species. Strong tendencies exist for the pioneer species, short-lived and long-lived, as well as for the shade-tolerant species of the understorey, to be systematically grouped into the same classes whatever the process under study. The "community drift model" could thus be at work at the scale of specific species groups.

Establishing the relative importance of the different mechanisms underlying the significant local diversity at Paracou is the subject of ongoing interdisciplinary work. It is important to carry out such approaches in contrasting ecological conditions: this will hopefully help demonstrate, for example, that in some forests such as those encountered in the Barro Colorado Islands, the dominance of one particular group of species (heliophilic species in that case) makes the "recruitment limitation hypothesis" a sufficient theory to explain the local species diversity (Hubbell et al., 1999, Molino and Sabatier, 2001, Sheil and Burslem, in press).

Ecophysiological approaches at tree community level have led to the characterisation of an unexpectedly high interspecific functional diversity both for leaf gas exchange (CO_2 and H_2O) traits (Chapter 2, Part II) and for nitrogen acquisition traits (Chapter 5, Part II), allowing the distinction of functional types of species for the different traits. A further relevant step in these approaches would now be to consider the spatial distributions of the different functional types with the ultimate aim of characterising spatial structures (or the absence of structure), possibly reflecting niche complementarity.

2.1.2. Genetic diversity

As stated in Chapter 2, Part III, it is hypothesised that, in tropical forest ecosystems where numerous species exhibiting a wide range of biological traits coexist, there must be a great variety of genetic diversity levels; the stake for researchers is to build a general predictive model of this diversity.

The hypothesis was confirmed on 10 of the species present at the Paracou site. Among a set of life-history and demographic traits examined, only the size of the specific distribution area showed a positive relationship with the level of within-population diversity, while no clear trend was found for floral phenology, identity of the pollinators or seed dispersal type. A tendency was found for aggregated spatial patterns, and thus reduced gene flow, to be negatively correlated with diversity.

Ongoing studies on a greater number of species and at wider geographical ranges (French Guiana and Guiana Shield) will help clarify and complete the first results.

2.2. Links between biodiversity and ecosystem functioning

Studies at Paracou have encompassed the original attempts at ecosystem-level functional integration by taking into account the functional diversity among tree species. Scaling up from tree to ecosystem was carried out for symbiotic N_2 fixation (Chapter 4, Part II), providing a preliminary picture of the different terms of the ecosystem-level N_2 balance and its modulation by soil properties. A similar exercise was performed for canopy carbon isotope discrimination (Chapter 3, Part II), a parameter used in global carbon cycle modelling (Bonal et al., 2000). These tools must now be further developed and used to assess landscape – or regional – level gradients in ecosystem function.

3. Needs for the near future

Most debates focus today on the sustainable character of forest management, simultaneously considering as many functions as possible. In order to simulate the effects of various logging scenarios on two important functions: timber production and biodiversity (specific, functional, genetic) preservation, the development and improvement of forest dynamics models remain a crucial issue.

Making use of the huge data bank collected on the dynamics of the stands at Paracou, a major modelling program has been conducted since 1992, the principal results of which are presented and discussed in

Chapter 6, Part IV. Among the scientific or technical bottlenecks identified, two are of particular importance.

3.1. Improved description of the regeneration processes

While encouraging results were obtained in growth modelling (see Chapter 4, Part IV) and description of the mortality phenomena, several key problems remain concerning regeneration. At present, only the recruitment is modelled (probability for a new tree to appear above the 10 cm DBH threshold), and specific behaviours are not taken into account, because, for the great majority of species, this event is too rare to be correctly described (Chapter 6, Part IV). A more detailed account of the regeneration processes (seed production, dissemination, survival and growth of juveniles) in dynamics models is crucial for at least two reasons:

- forest managers are interested in the floristic composition of the stock of timber trees they will recover at the end of the felling cycle. If only one felling cycle is simulated with a dynamics model, the knowledge of the population's diameter structure in the stand, at the beginning of the cycle, is sufficiently informative to predict the final composition of the upper diameter class (above DCL): most often, the smaller trees (10 to 15 cm DBH) will not have enough time to reach these classes within the cycle. However, if simulations are to be undertaken for two or more cycles, it will be necessary to describe the arrival of new individuals, which will play a more important part as time goes by.
- Investigations on the long-term effects of logging on genetic diversity requires the establishment of direct links between new trees appearing in the stands and their parents. Modelling the recruitment above 10 cm DBH, when possible for the species studied (enough individuals), is useless as too much time has passed and too many events have occurred between seed dissemination from a mother tree and recruitment: the diameter threshold is too high.

More generally, the increasing need to take into account the medium and long-term impacts of human interventions on all aspects of biodiversity makes it necessary to keep track in the models of species or species groups over long periods of time, and thus to be able to describe how disturbances influence the early stages of their lives.

A significant effort has been made since 1999, through various projects and theses, to describe the regeneration strategies of several important species, with two objectives: (i) to identify and model the variety of behaviours that exist in the forest, and (ii) to look for relationships between these behaviours and biological traits in order to "assign" a strategy to each species of the forest. Most of the teams operating at Paracou are involved in these projects.

3.2 Ability to extrapolate the Paracou results to other sites

The results acquired at Paracou help foresters of the National Forest Office define management and silvicultural rules inside an area of about 1,300,000 ha of forests spreading along the coast from the Maroni to the Oyapock rivers. The sensitive point is that these forests encounter a great variety of geological and rainfall conditions, and little is known about the representativity of the forest dynamics characteristics studied at Paracou.

To gain insight into the effects of these two major environmental factors on forest dynamics, the National Forest Office, together with CIRAD-Forêt and IRD, in 2001 started a "Permanent Sample Plots" project aiming at duplicating the Paracou site, on a reduced scale, in several managed forests showing contrasted environmental conditions. By the end of 2004, nine sites located on four types of geological substrate (Caribbean granite and migmatite, schists, volcanic rocks, white sands) and two levels of annual rainfall (between 2500 and 3500 mm, more than 3500 mm) will provide new data and help relativise the knowledge already gained at Paracou. At the same time, a thorough examination of the soil/growth relationships has started at the Paracou site, thanks to the involvement of pedologists from ENGREF and CIRAD-Forêt. This will hopefully help reduce the remaining residual variability of the growth models developed so far (see Chapter 4, Part IV), that is to quantify the soil effect on this important component of the stand dynamics. An improved understanding of these relationships will help extrapolate the models to other sites.

The experiment which started in 1982 at Paracou has become, over time, a real scientific adventure, gathering at the same site multi-disciplinary teams from all the scientific organisations working in France on ecological matters. As questions multiply, a growing number of people have become involved and new scientific programs are organised. The most recent has resulted in the settlement of an “eddy-flux tower” (direct assessment of ecosystem-level CO_2 and H_2O fluxes) near the undisturbed plot P15, around which several new scientific teams will start working on carbon and water cycles from 2004 on, combining approaches at the global ecosystem scale and at the scale of the different ecosystem components and transformations.

This makes Paracou a particularly interesting place, where the considerable efforts and the amount of data accumulated should lead to significant progress in our knowledge in the near future.

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Colour Plates

Part I / Chapter 1 – Experimental Plots: Key Features (p. 3)

Sylvie Gourlet-Fleury, Benoit Ferry, Jean-François Molino, Pascal Petronelli, Laurent Schmitt

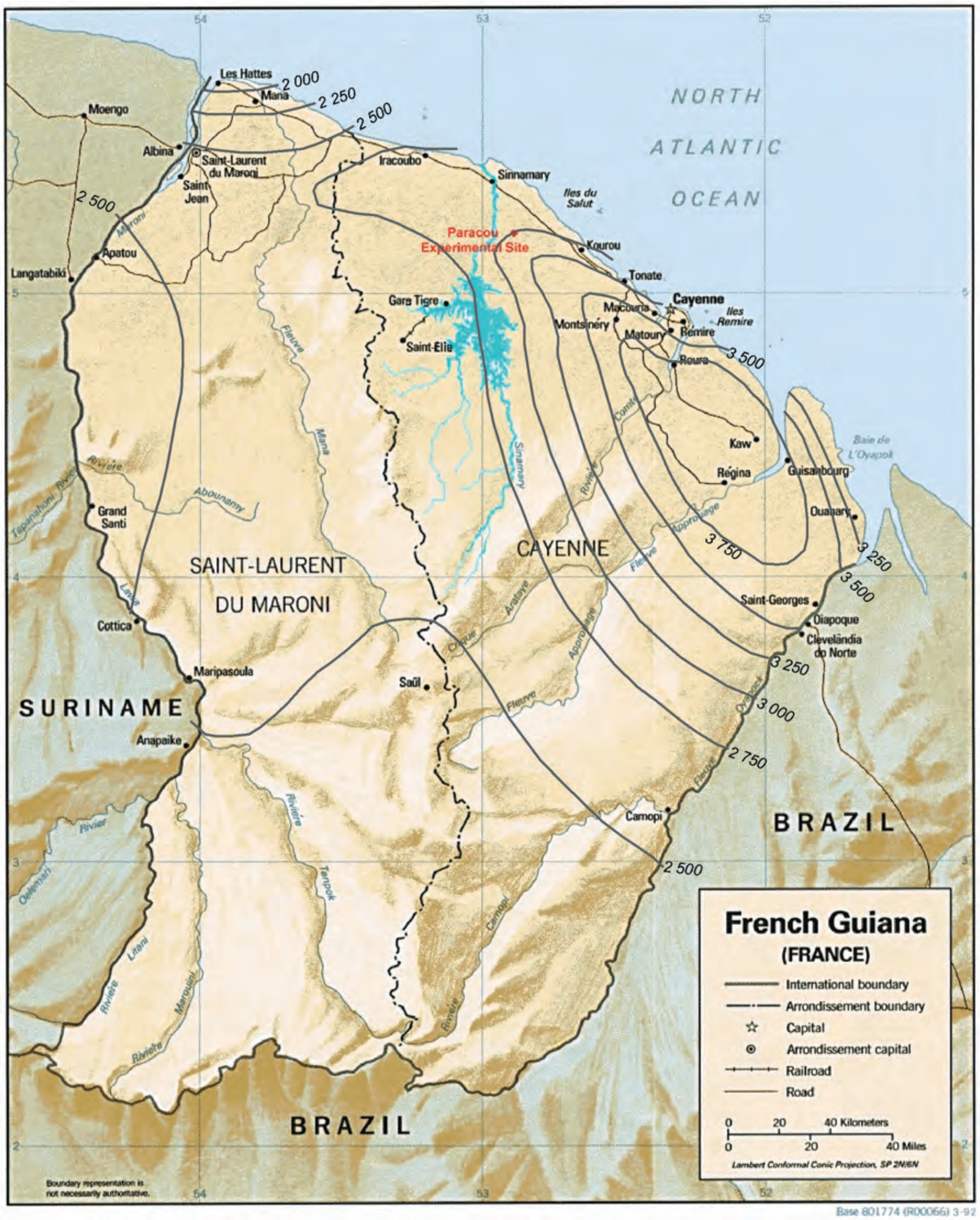

Fig. 1. General map of French Guiana, isohyets and location of the Paracou site. Map adapted from the file available at http://www.lib.utexas.edu/maps/americas/french_guiana.gif.

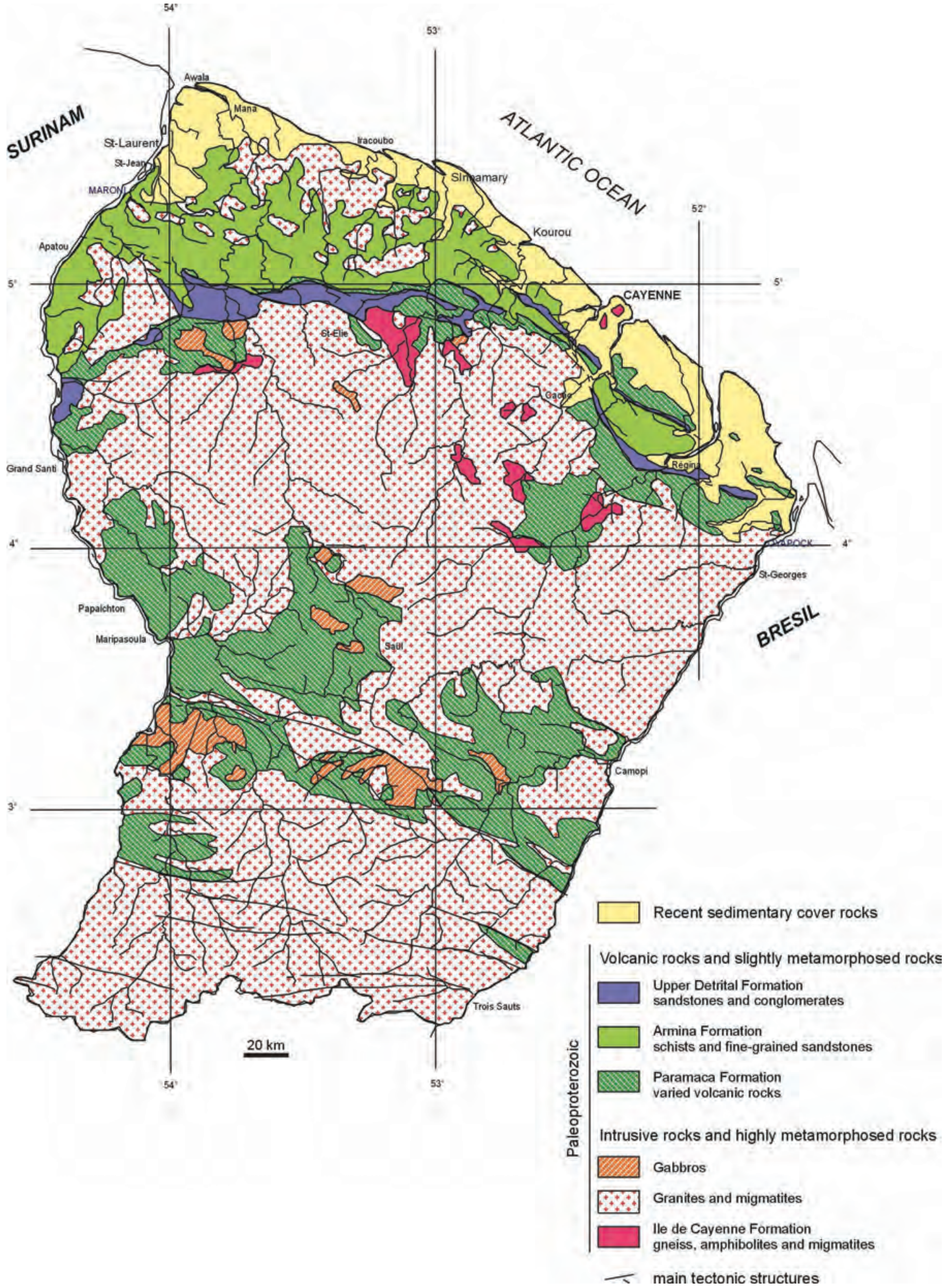

Fig. 3. Geology of French Guiana. From BRGM, adapted by Paget (1999).

Part IV / Chapter 3 – Natural regeneration of selected tropical rain forest tree species of French Guiana: established seedlings and saplings during the period 1986–1995 (p. 204)

Judy M. Rankin-de Mérona, Pierre Montpied

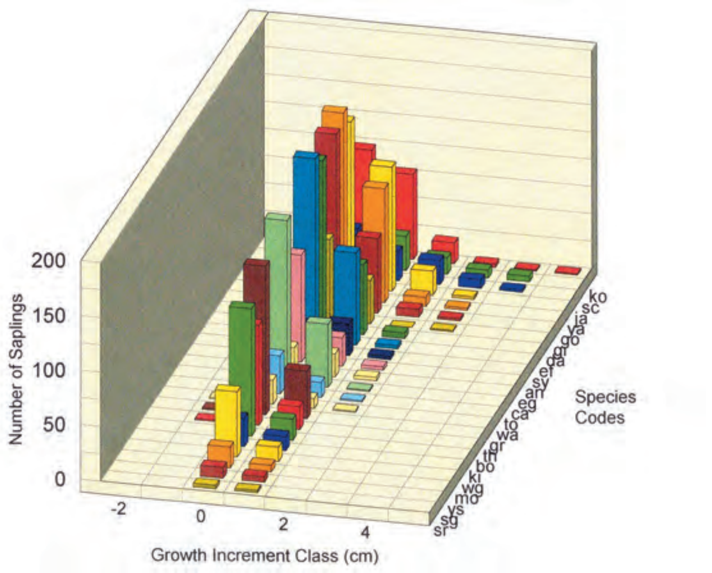

Fig. 5. Sapling diameter increments of 23 tree species by 1 cm diameter classes and by species for all treatments and ordered by decreasing increments as observed in 1995.