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PONDY PAPERS IN ECOLOGY

MODELLING TREE ARCHITECTURE AND FOREST DYNAMICS A RESEARCH PROJECT IN THE DENSE MOIST EVERGREEN FORESTS OF THE WESTERN GHATS (SOUTH INDIA)

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Modelling tree architecture and forest dynamics

A research project in the dense moist evergreen forests of the Western Ghats (South India)

François Houllier, Yves Caraglio, Muriel Durand

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Abstract

This working paper presents a research programme which aims at modelling the dynamics of the dense moist evergreen forests of the Western Ghats (India) from analysing, modelling and simulating tree architecture.

The paper first reviews various approaches to modelling the dynamics of heterogeneous forests, either temperate or tropical: demographic matrix models, distance-dependent tree growth models, gap models, cellular automata and multi-agent systems. The advantages and drawbacks of the architectural approach are then discussed.

The proposed study site is then briefly presented and a programme is outlined: selection of some species which are both frequent and representative of the different forest strata, sampling strategy and measurements, methods used for modelling and computer simulation.

The preliminary results obtained since the project was started in early 1995 are then briefly reviewed; a more detailed account will soon be published in another paper of this series.

Key words: rain forest, architecture, forest dynamics, silvigenesis, modelling, growth.

Résumé

Ce document de travail présente un programme de recherche qui vise à modéliser la dynamique des forêts denses humides des Ghats occidentaux (Inde) à partir de l'analyse, de la modélisation et de la simulation de l'architecture des arbres.

Le document passe d'abord en revue diverses approches de modélisation des forêts hétérogènes, tempérées ou tropicales : modèles démographiques, modèles d'arbre dépendant des distances, modèles de trouées, automates cellulaires et systèmes multi-agents. D présente ainsi les avantages et les inconvénients d'une approche architecturale.

Le site d'étude est ensuite rapidement décrit. Puis, un programme de travail est proposé : choix de quelques espèces à la fois fréquentes et représentatives des diverses strates, échantillonnage et mesures, méthodes d'analyse des données et de simulation.

Un bref bilan des résultats acquis depuis le début du projet en 1995 est présenté ; il sera complété par un prochain document de travail de cette série.

Mots-clés : forêt dense humide, architecture, dynamique forestière, sylvigenèse, modélisation, croissance.

Introduction

In July 1993, the CNRS[1] Interdisciplinary Research Programme on Environment and the GIS Silvolab[2] organised a workshop in Kourou, French Guyana, on "Modelling the dynamics of tropical forests: scales, uses and biodiversity"[3]. The objective was to bring together ecologists, forest biometricians, modellers, computer scientists and mathematicians in order to explore the scientific interest, both theoretical and applied, as well as the feasibility of new approaches to modelling the functioning and dynamics of these forests (Houllier & Millier 1995).

As other activities since undertaken — on cellular automatons *(e.g.* studies initiated by the *Laboratoire de biométrie, génétique et biologie des populations*, CNRS-UMR 5558, at Lyon I University) and multi-agent systems (MAS; *e.g.* studies carried out in Kourou by the Forest Department of CIRAD in collaboration with the *Laboratoire forme et intelligence artificielle* at Paris VI University) —, the present project is a follow-up of this workshop: it was discussed in late 1994 and actually started in early 1995.

The aim of this paper is: (*i*) to review the scientific context of this project, especially to discuss whether and how a quantitative architectural approach will contribute to our understanding of tropical forest dynamics; *(ii)* to state the objectives, rationale and methods of the project; *(iii)* to briefly report on its progress (see Durand *et al.* (1995) and Durand (1996) for more details on preliminary results).

Situation of the problem

There are high stakes, environmental, social, economic and scientific, at improving our understanding of the silvigenetic processes in dense moist evergreen forests and modelling their dynamics (Pavé 1995). Hence, these forests play a key role in global biosphere processes and harbour a large number of species, animals and plants, a lot

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[1] CNRS: *Centre national de la recherche scientiflque.*

[2] Silvolab is a scientific group based in Kourou and Cayenne (French Guyana), which associates CIRAD *(Centre international de recherche agronomique pour le développement),* CNRS, ENGREF *(École nationale du génie rural, des eaux et forêts),* INRA *(Institut national de la recherché agronomique),* ONF *(Office national des forêts)* and ORSTOM *(Institut français de recherché scientifique pour le développement en coopération).*

[3] Most of the papers presented at this workshop were published in a special issue of *Revue d'Écologie (Terre, Vie)* (1995).

of them being still unknown. They also provide various products, timber and non timber (the so-called "minor forest products" in India), and are thus a resource not only for wood industries but also for rural communities. Whatever the viewpoint — conservation of biodiversity, global biogeochemical cycles, economic development or preservation of local communities —, the rapid shrinking of "natural" tropical forest areas has become a major global concern.

The development of management methods that are ecologically, socially and economically sustainable has thus emerged as a major issue. Such methods should take many factors and aspects into account, from different disciplines and at different scales. For example, it is now recognised that the perennial character of these forests has to be ensured to satisfy the needs of the local people, *i.e.*, forest management cannot be an integral conservation leaving the people out of the forests (Gadgil 1993). Among other elements that are thus required, a better knowledge and understanding of the dynamics of the forests — whether "natural" or "disturbed"[4], managed or unmanaged — is clearly important. However, the structural heterogeneity and species diversity of tropical forests, especially of the dense evergreen rain forests, make it a difficult, but exciting, task to decipher and model the ecological mechanisms in play: we are still far from possessing every knowledge and methods that are required[5].

No doubt there is a qualitative theory of the dynamics of heterogeneous forests, which is articulated around three principles (Oldeman 1983):

- A static description of forest structure: this could be considered as a mosaic (Aubréville 1938) made up of small homogeneous units called eco-units by Oldeman.
- A dynamic principle of stand renewal: these eco-units have a cyclic succession dynamics maintained by *chablis* (Oldeman 1990; Durrieu de Madron 1993; Moravie 1995).
- A morphological characterisation of trees associated with the sequence of growth stages: the eco-units pass through phases that are expressed in tree morphology (height-diameter ratio) and architecture (presence of reiterations, metamorphosis), which help distinguish trees of the "past", "present" and "future" (Hallé *et al.* 1978).

However, this theory hardly takes into account other silvigenetic processes such as "silvigenesis by substitution" (Loffeier 1989; Pascal 1995). Moreover, although it has inspired many attempts at quantitative modelling, *e.g.* gap models by

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[4]These words being quoted because of their highly subjective connotation and because the more we study these forests, the more we become aware of the very fact that nature and disturbance are relative concepts and that most forests, if not all, bear the imprints of human activities.

[5]Most of the problems raised here would also be valid for other heterogeneous forest stands, temperate and tropical. Nevertheless, the dense moist evergreen forests, with their high emergent trees, (shrinking) vastness and unique ambience, have an exemplary, or even symbolic, character in this domain.

Botkin (1993) and Shugart (1984) and the works of Koop (1989), it has not (yet) actually resulted in a quantitative approach which can be compared to empirical data obtained from long-term permanent plots.

On the other hand, several difficulties are encountered while considering quantitative approaches to the dynamics of heterogeneous stands:

- Classical experimental methods, of the "agronomic" or Fisherian type, to put it briefly, can rarely be applied and are not effective because of the inherent difficulty in defining and delimiting homogeneous experimental units which can be treated distinctly for purposes of statistical comparison. The results already obtained in such experiments are certainly useful — for example, they give the intensity and duration of the response of trees and stands to moderate harvesting (Schmitt & Bariteau 1990)— but the cost of these experiments is very high while providing little information on the ecological processes which are in play.
- Forest biometric growth and yield theories propounded for homogeneous forests (Houllier 1992) are not useful because they are based on the notion of an average tree, a notion rendered ineffective by the structural and species diversity of dense moist forests.
- Lastly, most of the models developed, including some which are certainly good aids for the understanding and management of forest dynamics — gap models *{e.g.* Shugart 1984) or demographic matrix models *(e.g.* Buongiorno & Michie 1980) — ignore the spatial dimensions of the phenomena: for example, neither the regulation of demographic processes by density-dependence nor seed dispersal mechanisms are represented.

However, since a few years, there has been a strong revival of methods and approaches with the development of: *(i)* demographic models with (groups of) several species and density-dependent regulations (Buongiorno *et al.* 1995); *(ii)* gap models which include some ecophysiological principles (Bossel & Krieger 1991); *(iii)* descriptive models of mosaic functioning based on cellular automatons (Wissel 1991; Auger 1995)[6]; (*iv*) individual models which describe the tree-to-tree competition (Gourlet-Fleury 1992[a] 1992[b]) and can be integrated in multi-agent systems[7] (Ferber 1995) or cellular automatons (Goreaud 1995; Pascal *et al*. 1995; Franc 1996).

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[6] See also the preliminary works of Bouton (1994), Croc (1994) and Lespargot (1994).

[7] See also the ongoing works of Dario Caruso (DEA at LAFORIA, Paris VI University in 1994) and Sylvie Gourlet-Fleury's Ph.D. thesis (CIRAD, Kourou).

Aim of the project

This project explores a path different from those just cited, a path which was initiated in the tropical forests and then developed successfully for trees in temperate regions: the qualitative analysis and quantitative modelling of tree architecture (Hallé *et al.* 1978, Reffye (de) *et al.* 1989)[8]. It is based on three methodological postulates:

- The dense moist forests are composed of highly heterogeneous stands. Therefore the approach should be centred on individual growth, while distinguishing species according to their ecological behaviour, development strategy and morphology.
- The collective dynamics of the stand should be seen as the result of the spatial coupling of individual or local growth phenomena, especially through competition processes; *i.e.*, we should accurately represent individuals in the space.
- The morphology of trees and the space they occupy should be viewed as indi cators of their developmental stage, as well as factors which condition their later growth. Hence it is necessary to describe tree architecture, the manner in which it develops and depends on local growth conditions, and how it modifies the envi ronment of the neighbouring trees.

The long term perspective of this project is thus to obtain a three dimensional (3D) representation of the different types of silvigenesis and to simulate the functioning of a plot in a dense moist forest, either undisturbed or moderately and selectively exploited *(i.e.*, where harvesting does not greatly alter the structure of the stand). As a medium-term project, *i.e.*, within 2-3 years, an attempt will be made to demonstrate the feasibility of this approach by representing the dynamics of a cluster of trees (about 0.1 ha) belonging to some of the most common species of the low-elevation dipterocarp moist evergreen forests in the Western Ghats (in the south-west of the Indian peninsula).

The proposed approach is based on the quantitative methods developed at CIRAD-AMAP[9] to describe, measure, analyse and simulate tree architecture (Reffye (de) *et al.* 1989, 1991, 1993). However, it does not mean that this approach should

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[8]A consequence (anecdotal) of this project would thus be to bring back to the tropical fold, quantitative methods developed in recent years in temperate milieus, but whose qualitative foundations were originally elaborated from observations of tropical trees!

[9]AMAP: *Atelier de modélisation de l'architecture des plantes.*

replace other promising ones undertaken elsewhere, especially cellular automatons and multi-agent systems. Rather, our aim is at exploring a complementary path which enables representing the morphology of trees, the way they occupy the space and the manner in which their local interactions determine the silvigenesis[10].

[10] In some ways, this approach constitutes an extension of MAS (Ferber & de Reffye, pers. comm.), because it means deducing the collective dynamics from the simulation of the behaviour of individuals, *i.e.*, trees, which can be viewed as objects and grouped into classes *(e.g.* species or functional groups of species are such classes).

Methodological context: models and theories of the dynamics of heterogeneous forest stands

Existing models

In order to bring out the potential of the architectural approach proposed here, the strengths and weaknesses of some existing models will be reviewed laying special emphasis on those which were conceived and/or applied with a view to describing or predicting the dynamics of heterogeneous stands (see also Collinet 1993; Vanclay 1994; Houllier 1995). To simplify, these models can be divided into two classes based on two criteria (Table 1): (*i*) level of description envisaged: global (stand, mosaic) or local (tree, gap); *(ii)* expected application: understanding of the functioning or management aid (global models for planning and local models for silviculture).

Table 1. Types of models used to describe the dynamics of heterogeneous forests.

Level / Objective	*Global*	*Local*
Functioning	Renewal of the mosaic Cellular automaton	Succession in gaps Gap models
Management	Planning Matrix models	Silviculture Tree models

A demographic and global approach: matrix models

This approach is based on the description of three important demographic processes: growth, mortality and regeneration (or recruitment if only trees above a minimum census-size are considered). The variables which characterise the system are thus the numbers of trees in size classes and/or groups of species. The original mathematical form of this class of models is simple, *i.e.*, matrix models which can be considered either as deterministic compartment models (at the stand level) or as stochastic Markov chains (at the tree level).

Recourse to size class is justified because of: *(i)* the irrelevance of age for trees growing in heterogeneous environments where it is the opportunity *(e.g.* death of a neighbouring tree, local availability of light or other resources) as much as the age which determines tree growth; *(ii)* the practical difficulty, or even impossibility, in measuring the age of trees in evergreen forests in the absence of clearly defined annual growth rings; *(iii)* the relative ease of measuring the diameter (or girth) of trees. Moreover, the preference to define the size class from diameter at breast height rather than height is based on the convenience with which measurements can be recorded, rather than on the ecological relevance of one or the other variable[11]. Furthermore, the choice of limits for size classes is not independent of the time step that is used (Houllier 1986).

The first demographic models were developed in temperate monospecific but heterogeneous formations (Usher 1966; Bosch 1971). These were unregulated linear models whose mathematical properties evoked keen interest: in general, they exhibit a unique asymptotic exponential behaviour characterised by a stable size-structure and a multiplication rate (Usher 1969; Houllier & Lebreton 1986; Houllier *et al.* 1989)[12].

These models were later adapted to mixed stands *(e.g.* see Buongiorno & Michie 1980). They however posed two kinds of problems which are still not fully resolved: (*i*) regulation of demographic processes by density-dependence, and other consequences of the spatial coupling of local dynamics; *(ii)* interaction among species and their incorporation (or not) into functional groups:

- It soon became necessary to introduce regulations which take into account the influence of density on regeneration or recruitment (Buongiorno & Michie 1980), and then on mortality and growth (Buongiorno *et al.* 1995). Favrichon (1995) applied this approach to the permanent plots monitored by CIRAD in Paracou (French Guyana). However, the mathematical properties of these models are not easy to study as they are beyond the scope of linear models. Their analysis becomes more complicated if medium-distance spatial coupling *(e.g.* seed dispersal) is intro duced: it then comes to diffusion-reaction models and cellular automatons (Murray 1993, Croc 1994), whose properties are still to be studied.
- The grouping of species into functional groups is gradually appearing as a necessity: on the one hand, the mixing of species in the heart of a single undifferentiated group leads to considerable bias (Favrichon 1995); on the other hand, it is necessary to limit the complexity of models. It therefore means taking the differences

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[11] Favouring ecological relevance would lead to prefer height to diameter, for height and crown play a key role in the partitioning of the light resource in multi-species uneven-aged stands.

[12] Though appealing and providing some insights in the trends of the population dynamics, these mathematical properties were also an indicator of the ill-conception of the early forest matrix-models, for an exponential steady-state regime is highly unlikely for tree populations growing in a fixed-area forest (except, may be, in the case of a generalised dieback!).

in the growth behaviour and strategy of the species into consideration —differences which are expressed at the level of demographic processes — and to work out a compromise between the representation of species diversity and the necessary simplification of the reality (Vanclay 1991; Favrichon 1994). However, the properties of most of these multi-specific models are still to be analysed and such studies usually rely upon simulation rather than on an analytical approach.

Dynamics of the forest mosaic: gap models and cellular automatons

A second approach based on the dual idea of forest mosaic and silvigenetic cycle led to the broad family of gap models. Their basic principle is to simulate the dynamics of a generic element of the mosaic, an eco-unit (Oldeman 1983), which is supposed to be independent of its surroundings. Two categories of models have emerged based on this approach: (*i*) gap models *stricto sensu*, where the succession is described locally, *i.e.*, within a moderate sized gap, about 0.01 to 0.10 ha (Bossel & Krieger 1991; Botkin 1993; Shugart 1984); *(ii)* transition matrix models, which can simulate the evolution of the mosaic (Riéra *et al.* submitted). However, as soon as the spatial dimension of the phenomena and the existence of couplings and relationships among the different elements of the mosaic are acknowledged, the same difficulties as mentioned earlier are encountered.

First, Shugart & West (1979) observed that gap models worked more or less well depending on the unit area studied: when it is too small or too big, competition phenomena are poorly described (either exaggerated or smoothed) and the model's predictions are not very good. This becomes more complicated if it is supposed that the spatial interactions are not simply within the modelled unit *(e.g.* competition for light), but also between the various gaps and units (*e.g.* propagation of *chablis*, seed dispersal, middle range competition).

This naturally leads to cellular automatons of the kind developed by Wissel (1991) for European beeches: from an initial state (bare land after mortality), every element of the mosaic (in this case, a quadrat of a few ares) goes through various stages of a deterministic silvigenetic cycle, from the installation of seedlings (colonisation and regeneration being dependent on the surrounding units) to mature beech highforest, until mortality, the latter being probabilistic and dependent on the immediate environment. This very simple model, where spatial coupling is expressed at the level of regeneration and mortality processes but not at the level of growth processes, enables the simulation of collective behaviour *(e.g.* presence of large gaps initiated by the death of a few trees) and also to demonstrate that the concepts of equilibrium and stability which are often cited when discussing heterogeneous

natural forests are undoubtedly meaningless in areas less than several dozen of hectares, or even a hundred, hectares[13].

The individual approach: empirical tree growth models and multi-agent systems

In the 60s and 70s, a third school of thought was developed in temperate forests before being applied to tropical forests. It was mostly the work of North American mensurationists and based on the double choice: *(i)* of the tree as the elementary unit whose behaviour should be modelled, and *(ii)* of growth as the main process of dynamics. This approach analyses tree growth in function of: site quality, tree development stage or size, and neighbourhood of the tree as characterised by various density- and competition-indices. The canonical structure of these models is of the type: "increment = potential x reducer" (Leary 1979), the potential resulting from the combination of site quality and tree size, and the reducer being expressed as a function of competition (Leary & Holdaway 1979).

Among the models thus developed may be cited those of Courbaud *et al.* (1993) (height growth of Norway spruce in mountain heterogeneous stands) and Gourlet-Fleury & Montpied (1995) (diameter growth in dense equatorial rain forests). Contrary to the generally accepted idea, these tree models — either distance-dependent or distance-independent (Houllier 1986) — were often developed for heterogeneous (in terms of both structure and composition) formations[14]. Some of the problems encountered with the individual approach are:

- the need to have as many sub-models as species (see earlier remarks on functional groups in matrix models);
- the difficulty in defining competition indices adapted to irregular structures (asymmetric competition) and mixed forest (species reacting in different ways to competition and influencing their neighbours in different ways);
- the difficulty in defining the "zone of influence" of individuals, a zone which varies according to the limiting factors (water, mineral elements, light, space);
- the lack of a temporal reference system, which would enable a strict ordering and comparison of the development stages of different individuals; the most important

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[13] It must be remembered that the stands studied by Wissel are relatively simple as regards their composition (diverse broad-leaved trees in the first stages of succession, and later on beeches). Generalisation of such a model to more diversified stands such as those encountered in tropical zones would certainly result in a much larger area. Also his model is supposed to operate under (spatial) homogeneous and (temporal) stable ecological conditions *(e.g.* soil, climate).

[14] See the works of USDA Forest Service in The Rockies (Wykoff *et al.* 1982) and Great Lakes (Belcher *et al.* 1982) regions, and the more recent model developed by Pretzsch (1992) for mixed spruce, beech and fir temperate forests.

consequence being that it is difficult to estimate the "potential" and "reducer" separately (see above; Vanclay 1994);

- the frequent paucity of data on the morphological characters most directly dependent on competition: there is generally very little information on height or crown size, though light is usually considered as the key factor in heterogeneous stands;
- the necessity to integrate processes other than growth alone because mortality and regeneration contribute to modifying the competitive conditions (see Ek & Monserud (1974) for a model integrating these various processes).

The most recent developments in this domain are of two kinds: less complex models thanks to the aggregation of species within functional groups (see above); use of modern computer methods, especially multi-agent systems, which make the best use of object-oriented programming techniques and software. It must be noted that the once oft cited material problem of the computation power (in terms of memory and/or speed), is now resolved (at least if the model is restricted to the minimum canonical description of trees, (*i. e.*, diameter at breast height).

Why an architectural approach?

Most models of the dynamics of heterogeneous stands which are currently available or being developed (see above) provide scant information on the morphology of trees and the manner in which they occupy the space. Whether they are stand demographic, tree competition models, or cellular automatons, the variable studied is generally, implicitly or explicitly, the diameter at breast height (rarely the total height). These three approaches have the tremendous advantage of enabling the simulation of the dynamics of large plots and, at least in the first case, to develop simple tools for aiding forest management and planning. The last two also make it possible to simulate spatial coupling of local cyclic dynamics (dissemination and germination, growth and mortality, succession stages), describe the mosaic and its evolution, and also study the link between the local heterogeneity of the stands and their global stability.

However, it seems that these approaches should be complemented by models which are more local, but which also take the tree morphology into consideration. Here are some examples which suggest the potential of such an approach:

- Most empirical biometric competition indices have a low predictive value in heterogeneous stands, but taking the light interception of tree crowns into account (*e.g.* using Dawkins' code) greatly improves the predictive value, at least for some species (Favrichon 1991; Gourlet-Fleury 1992b).
- The "gap models" already developed integrate, more or less clearly, the information on the global morphology of the tree: for example, they include height-diameter allometry and equations that are utilised to predict the foliar mass at

different levels of the canopy. This helps to take a better account of some ecological processes (attenuation of light, varying tolerance of species to shade) and control the qualitative behaviour of the model.

- Bernard Riéra (pers. comm.) interprets the structural differences observed between the moist evergreen forests of French Guyana and the Western Ghats through differences in the architecture (less number of species having wide spreading crowns — pertaining to Troll's model —, and more species with small leaves in India) and regime of seed dispersal (very few zoochorous species in India).
- The "empty spaces" may be markers of competition phenomena ("timidity of tree crowns") and at the same time, favoured places for certain activities *(e.g.* displacement of some animal species; Puig 1995; Charles-Dominique 1995).
- In homogeneous forests, the paradigm around which a number of modern timber-oriented growth and yield models are built places the role of height growth and crown development[15] in the forefront *(e.g.* Mitchell 1975; Houllier *et al.* 1993; Deleuze & Houllier 1995): site and age determine height growth, setting the pace of crown extension, which is itself modulated by the intensity of competition (not only for space and light, but also for water and mineral elements), girth increment (at breast height) being the ultimate result of these various processes.

The architectural approach developed by European botanists since a century, and later systematised in tropical forests (Hallé & Oldeman 1970; Barthélémy *et al.* 1989), has now led to a comprehensive and consistent body of botanical, statistical, mathematical and computer methods (Reffye (de) *et al.* 1989, 1991) which help not only to analyse, quantify and simulate the morphology and 3D growth of a single plant, but also to take into account competition for various resources (space, light, water) among neighbouring plants and to simulate the dynamics of a group of inter-acting individuals (Reffye (de.) *et al.* 1995).

[15] Root development is often omitted because of practical difficulties to observe and monitor root system.

Materials and Methods

Low-elevation evergreen dipterocarp forests of South India

Forest composition, structure and dynamics

The low-elevation dense moist evergreen forests of the Western Ghats (Southwest India) have been studied by the French Institute of Pondicherry since many years (Pascal 1988). These studies, mainly carried out in a permanent station near the village of Uppangala (Karnataka), have helped to: (*i*) refine the knowledge on their ecology, structure, composition and diversity (Loffeier 1988; Derouet 1994; Gimaret 1995); *(ii)* estimate the rate of their reconstitution after selective logging (Loffeier 1989; Cousin & Voyez 1993; Laborde 1994); *(iii)* describe their spatial structure, both horizontal and vertical, and characterise the silvigenetic mechanisms in play (Loffeier 1989; Pélissier 1995; Pascal & Pélissier 1996).

These heterogeneous forests have a fairly high species diversity (about 50-60 species per hectare and 100 species in a 28-ha compartment)[16], but a small number of species constitute the framework of this diversity (Pascal & Pélissier 1996), a feature which certainly facilitates the study of their dynamics. Moreover, these 4 to 6 species, which represent more than 50% of the basal area and number of stems per ha, exhibit distinct functions and behaviour. In the permanent station near Uppangala, these species are:

- *Dipterocarpus indicus* (Dipterocarpaceae): an emergent species which can exceed 40 metres;
- *Vateria indica* (Dipterocarpaceae): a very common species with a large number of dominant canopy trees which can attain heights of 40 metres;
- *Mesua ferrea* (Clusiaceae): trees of this species can reach the upper canopy with a maximum height of 30-40 metres;

[16] These forests are thus less rich in tree species than their South East Asian or South American counterparts.

- *Myristica dactyloides* and *Knema attenuata* (Myristicaceae): two lower canopy species with similar morphology and ecology, rarely growing higher than 25-30 metres; and
- *Humboldtia brunonis* (Fabaceae): a very common shade-tolerant species of the understorey, which rarely exceed 10-15 metres.

To this list we may add *Macaranga peltata* (Euphorbiaceae), a light-demanding pioneer species which does not grow beyond 15 m and colonises the gaps created by natural *chablis* or exploitation, as soon as they occupy an area of about 100 m^2.

In these forests, silvigenesis is dominated by at least two complementary modes of occupation of space (Loffeier 1989; Pascal 1995).

- "Silvigenesis by *chablis"*, which takes place in gaps caused by exploitation or by the natural fall of emergent or dominant trees: succession mechanisms then become preponderant. Such gaps, although present (Chandrasekhara & Ramakrishnan 1994), are rare in these forests mainly because emergents occupy a lesser area than in homologous forests in South America (Riéra pers. comm.). However, the role of cyclones, in terms of frequency as well as their impact on the vegetation, remains to be assessed.
- "Silvigenesis by substitution", which is observed when a dominant standing tree dies and a nearby tree, which was till then subordinate to the dead tree, takes the latter's place and occupies most of the liberated space. This process, which is more subtle than *chablis*, sometimes results in a peculiar organisation of the canopy, the so-called "soap bubbles structure" (Pascal 1995): each crown looking like a bubble which expands till the empty spaces around it (created by the death of standing trees) are filled up.

In both these situations, the manner in which the trees occupy the space and interact (interception of light and shade tolerance, mechanical contact with neighbouring crowns) plays an important role. Another important spatial feature emerging from Pélissier's study (1995) is the role of topography in silvigenetic processes: *chablis* mostly occur on the steep slopes or near ridges, while substitution seems to prevail on gentle slopes and plateaux. A good description of tree architecture, including 3D geometry, would thus be useful.

Forest management

These forests are managed by the State (Kamataka, Kerala and Tamil Nadu) Forest Departments. When not converted into agroforests or agricultural lands (due to strong human pressure), they have been, for the most part, subjected to selective felling in order to extract the best logs of economically important timber species (for structural uses and peeling).

By itself, moderate selective exploitation does not greatly modify the composition of the stand which can later get reconstituted gradually (Loffeier 1989). In

fact, it is the too frequent repetition of such felling and the consequences of the opening up of the forest to exploitation routes (easier access to the forest and increase in human pressure) which are the greatest danger for the survival of these forests whose area has been dramatically shrinking since more than a century. In the late 80s, a ban was thus imposed on felling in all "natural" State Forests in the Western Ghats, which is still in force.

Site and species

Study site

Since a decade, the French Institute of Pondicherry has been monitoring a permanent experimental station in the Kadamakal Reserve Forest (Coorg District, Karnataka), near the village of Uppangala (see Élouard *et al.* (1996) for a general presentation). The studies are focused on two 28 ha-forest compartments: a compartment which experienced selective felling in the late 70s, and a compartment which was never harvested[17].

The general data on tree size and morphology (height, diameter, crown dimensions) in these plots were recorded several times. In 1993 and 1994, a monthly survey of the phenology was also carried out in a sub-sample of about 500 trees of varying dimensions: observations on flowering, fruiting and growth "flushes" in more than 50 species (Aravajy 1995).

Species selected

For this project, the aim is to focus on some species which constitute the framework of the stand but, at the same time, exhibit diverse morphologies, roles and ecological behaviours (see above). After preliminary observations, the following species were retained: *Dipterocarpus indicus*, *Vateria indica*, *Knema attenuata*[18] and *Humboldtia brunonis*, along with *Macaranga peltata*. The choice of a small number of species which are simultaneously typical and frequent helps reduce the amount of work, at the same time ensuring a good representation of the functional diversity. Hence it avoids, at least at the beginning, the need to define functional groups.

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[17] According to the working plan, it was due to be selectively felled in the late 80s, but "escaped" exploitation thanks to the ban on felling.

[18] *Myristica dactyloides*, despite its botanical and ecological proximity to *Knema attenuata* and being more common among trees exceeding a girth of 30 cm, has not been retained because there are only a few seedlings and saplings. Hence, the systematic collection of *Myristica* fruits (used for dyeing) — over about 30 years and until the installation of this permanent station in this "undisturbed" forest — has most probably led to the quasi absence of regeneration.

Sampling, measurements and analyses

The architecture of these species is described in two ways: the first is mainly qualitative, characterising the whole sequence of the development stages of the tree, from seedlings to over mature and senescent trees; in the second, which is quantitative, the emphasis is on measuring and modelling the architectural development and its response to variations of the ecological conditions.

Qualitative description

The objective is to determine the development sequence of each of the selected species. The picture thus obtained defines the main architectural stages and the different stages in the structural evolution of the growth units.

First, we search and sample individuals which have attained varied stages of development and are in distinct competitive situations. The development stages studied are preliminarily defined on morphological bases (seedling, branched sapling, edification of the trunk, crown development, reiteration, *etc.),* which, more or less, correspond to given heights for a given species and in a precise context. The actual development stages, which vary according to the species studied, become clearer after the architectural analyses have been carried out.

The absence of distinct morphological markers (such as annual growth units delimited by bud-scars), as well as the irregular elongation phases (non-synchronous elongation of axes in the same individual) in some of the selected species necessitates: *(i)* recourse to phenological data acquired in 1993-94; *(ii)* monitoring tree growth in detail; and *(iii)* adapting the methods developed by CIRAD-AMAP.

Static observations

The method is based on the morphological description of the plant's axes, *i.e.*, their own characteristics as well as their topological and geometrical arrangement. Recognition of morphological entities such as internodes and growth units in the case of plants with rhythmic growth is the basis for understanding the construction, in both space and time, of plant architecture. It is mainly the knowledge of the similarities between the structural markers (cataphylls, branching, *etc.)* and elongation phases of the stem which enables the distinction of growth units, and hence to propose hypotheses on the chronology of the different events taking place during the plant's growth. This primary relationship between growth dynamics and the resulting architecture can be further established from growth records.

Growth monitoring

This kind of study involves observing the organisation of new elements of the plant at regular intervals. The aim is to demonstrate the similarities between certain mor-

phological criteria and elongation phases (Caraglio & Barthélémy 1997), as well as the duration and number of these elongation phases in a vegetative cycle. The time step chosen determines the sharpness of the observations and hence the precision of conclusions on growth dynamics. In the Western Ghats, the strong climatic contrast between the dry and wet seasons has to be compared to the succession regime of the elongation phases.

This study, although very constraining, usually gives satisfactory results for plants where all the axes show simultaneous growth phases. However, it is quite different for plants whose axes do not have synchronous growth. This asynchronism, which may be observed in different individuals of the same species as well as in the same individual, has been observed in at least three of the species selected. The growing zones of a certain number of species sampled at different stages should therefore be mapped. Regular markings made during the dry and monsoon periods complemented by recordings describing the environment (slope, light, *etc.)* should enable the postulation of hypotheses as well as new approaches to this phenomenon and its evolution during the growth sequence.

Architectural unit and reiteration

The first stage, indispensable for a global understanding of plant architecture, is to demonstrate and describe the architectural unit, the symbolic structure representing the expression of a branching system for a given species, when it has reached the maximum level of hierarchical differentiation. Once this elementary structural unit is recognised — in the majority of cases it corresponds to the phase of trunk edification in trees and/or the expression of flowering —, the construction of the tree crown and, more generally, reiteration phenomena can be taken up (Oldeman 1974). These phenomena correspond to the duplication of the elementary architecture and are often associated with the setting of the main branches.

These reiterated structures (also called reiterated complexes or reiterates) are located and described, and then compared with the structure of growth units and architectural unit in order to understand the various differentiation stages which accompany the growth phases (Barthélémy *et al.* 1997). In fact, from a very hierarchical structure where the main axis is dominant, there is often a very rapid "explosion" of the initial structure till a polyarchic organisation is obtained around several axes (Edelin 1993). The change in branching pattern (location, intensity) is a very important element in architectural description: in fact, an impoverishment in the branching pattern is often observed during growth, as also profound changes in the localisation of its expression (Sanoja 1992).

Evolution of the tree crown and growth sequence

As a first step, the analysis of the later evolution of the crown — an analysis which is often difficult for practical reasons (reduced visibility, limited accessibility to the

forest canopy) — can be made by studying trees at the edge of gaps or along pathways. Once the general evolution is understood, it can be further refined by a partial sampling of the trees in the forest. The wide variability found among crowns requires a detailed analysis of their ageing phases (Loup 1994). This stage of development, recently studied in detail in temperate and tropical forests (Drenou 1994), is essential for a better understanding of the acquisition and maintenance of the social status of a tree. It is also important in the perspective of analysing the diametric growth of tree trunks and studying the interactions among individuals.

Measurements and quantitative analyses

Sampling is essentially on the first stages of development. Competition is evaluated mainly with reference to illumination, the light factor having a strong influence on the final architecture (Nicolini & Caraglio 1995) and stem growth (Courbaud *et al.* 1993). Individuals in the undisturbed compartment where the cover is generally regular and dense are distinguished from those found in the once harvested compartment where the cover is less dense (on the average) and also more irregular. This sampling strategy, however, does not provide information on the earlier environment of the trees, whereas it could have conditioned their present architecture (in the case of medium and large sized trees), nor is it possible to know the exact age of the trees, which may lead to difficulties in some quantitative analyses.

Young trees

The choice of working mainly on young trees is justified for two reasons: (*i*) practical: easy access, facility of taking measurements, protected and fairly well defined environment, large number of individuals; and *(ii)* biological: the establishment phase is a favoured stage from three viewpoints, namely the speed of structural evolution, the degree of variability in terms of functioning, and because it is a phase which influences the later stages of development.

For each stage of development, about forty individuals are sampled. Measurements of axes of orders 1 to 4 (when the last is present) include recording:

- the number of nodes per growth unit (GU), distinguishing leaves with a limb from cataphylls;
- diameter and length of GU, as well as the total length and median width of leaves (in order to estimate their area);
- location (by node number) of lateral branches.

Beside these "standard" descriptions of morphological analysis, other phenomena such as apical mortality are also envisaged.

Big trees

For trees which have already attained an advanced stage of development, measurements are made for a smaller number of samples (for reasons of availability and size[19]). Even if the results thus obtained are not accurate and precise, they will help evaluate the general trends in the structural evolution of the GU. Importance is given to: (*i*) sampling and measuring the successive GUs along a branch in order to define the notion of drift (Reffye (de) *et al.* 1991); and *(ii)* measuring the mortality of branches along the trunk in order to appreciate and determine the evolution of the live crown at the time of stem edification as well as during the organisation of the crown. As regards the location and description of complex reiterates, local samplings *(e.g.* cutting and measuring a branch) should provide an idea of the evolution of growth parameters.

Description of ecological conditions

Tree growth is influenced by several factors which are difficult to control in quasi-natural heterogeneous formations. In this project, the emphasis is mainly on describing the influence of light. We proceed in two ways: (*i*) stratifying the sampling of trees in function of the average local conditions assessed in a subjective manner — "shade", "semi-shade" and "light" situations will thus be distinguished; *(ii)* using hemispherical photographs to assess the light conditions in a quantitative manner and then processing the pictures with the help of analytical tools available in micro-computers (Courbaud pers. comm.).

Relationships between individual architecture and structure of the stand

A good description of the growth of young trees of the understorey from the seedling stage up to a height of about ten metres is the first essential step for understanding and predicting the evolution of the forest structure. An attempt is made to establish a structural profile of the understorey using architectural information. The inventory of the "undisturbed" compartment is therefore completed by measuring the heights and describing the architectural stage of each tree, at least for the five selected species.

Statistical analysis and modelling[20]

Statistical analysis of architectural parameters will be carried out with the AMAPmod software (Guédon 1997; Guédon & Costes 1997), which enables the estimation of parameters characterising the probability distribution function of appearance,

[19] Moreover, the different parts of a plant have a tendency to express similar functioning when the structure is old.

[20] This stage of the project is just starting in 1996: thus, the use of the future tense.

survival and elongation of meristems in function of their position on the tree, development stage of the individual and environmental conditions. One important objective in this project will be to distinguish those traits which are inherent to the species from those that are due to local competitive conditions, particularly light.

Variations in the distribution of the number of internodes per GU will first be described by isolating the internal gradients[21] and external factors *(e.g.* influence of light). These distributions will be fitted according to classical laws and mixture of laws: Poisson's binomial, negative binomial, exponential (Jaeger & Reffye (de) 1992).

The probabilities of the death of meristems, particularly apical meristem, and the branching of nodes along various growth units will then be estimated. For the latter, the models used are Markov's chains which enable the description of the alternation of branched and unbranched nodes along growth units (Guédon 1995).

The study of the influence of external factors on plant growth poses two kinds of problems which are at the core of the project: (*i*) although it will be possible to distinguish between contrasting environmental conditions *(e.g.* shade *vs.* light), it will be difficult to measure gradual variations in the light factor and hence to model the associated plant's reaction; *(ii)* the consequences of accessing the canopy are often characterised by brutal changes in behaviour *(i.e.,* metamorphosis and reiterations) which can easily be observed and qualitatively described, but are more difficult to quantify.

Leaf morphology will be the subject of an allometric study. The leaf area will first be predicted from their dimensions; its variations will then be studied in function of their position on the tree (order of branching, position of the GU and location within the GU). It should then be possible to study the global leaf surface of the tree and split it according to the order of branching and/or level in the tree. This will nevertheless require that a new method is developed to describe and somehow measure the many subcrowns (or crownlets) that are formed in ageing trees.

Biometric data (thickness of axes, length of growth units) and girth measurements recorded in Uppangala since 1990 will be used to explore the relationship between leaf surface and secondary growth. We will try specially to assess a reasonable order of magnitude of the parameters used in allocation models for wood growth along the stem (Reffye (de) *et al.* 1995). However, it must be remembered that, in the absence of accurate increment measurements along the stem (except at breast height) and branches, this study can only be preliminary in nature, and that it will not be possible to precisely and directly estimate these relationships.

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[21] These gradients are of different kinds: base effect (*i.e.*, smaller growth units at the base of the tree), drift (*i.e.*, "ageing" of the GUs along the same axis), jumps in physiological age (or in vigour) between bearing and borne axes, acrotony, *etc.*

Simulations

Computer simulations of forest dynamics will be made with the AMAPpara software (Blaise 1991) which enables the representation of architectural growth and wood production of trees belonging to different species and located in the space, in function of their own architecture and environmental conditions. The objective of these simulations will be to test if this approach (based on the analysis of architectural growth and some of its environmental regulations) can account for different kinds of silvigenesis and predict the local evolution of the stands.

In its present version, the mode of functioning of the AMAPpara is schematically as follows (Blaise & Reffye (de) 1994; Reffye (de) *et al.* 1995):

- each species is characterised by parameters which take into consideration its topological and geometrical architectural development, and its reactions to competi tion;
- every tree is located in the 3D space and belongs to a species (or to a functional group of species);
- the appearance, elongation and death of meristems are simulated "in parallel", *i.e.*, simultaneously, in a probabilistic manner in function of the parameters of each species;
- the "voxel"[22] technique is used to describe the degree of filling up of the space by trunks, branches and leaves; it is further linked to techniques that simulate the radiative transfer through the canopy in order to estimate the amount of light received at any point (for example, at the level of a given meristem);
- the functioning of meristems is altered by local competition: spreading of branches being limited by neighbouring trees (if the voxel is already occupied) and reduced in function of light availability;
- woody growth (stem and branches) is then simulated by simple allocation rules which take into consideration the geometry and topology of the paths from the assimilating system to the roots. The efficiency of photosynthesis can also be regulated by the amount of water available for each tree and the quantity of light received at the level of leaves.

Most of the technical computer problems have been solved and simulations carried out in simple cases are able to account for the effects of competition for different resources (Reffye (de) *et al.* 1995, Reffye (de) *et al.* 1997). It was especially necessary to develop methods for simplifying the architecture, while respecting the major trends in the individual functioning of the tree (foliar mass, allocation of woody growth) and the collective functioning of the stand (aerial competition).

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[22] Voxels are small cubes resulting from the three dimensional discretisation of space: they generalise the pixels in 3D.

However, methods for *in situ* measurements still remain to be developed in order to estimate the parameters characterising the environmental regulations of tree architecture. Some effects of competition have been studied, such as competition (by contact) between branches of neighbouring trees (Masotti *et al.* 1995), but the study and simulation of axis reorientation and growth inhibition due to physical obstruction or indirect effects (shade, competition for water) require setting up new protocols which would take into account the sensitivity of species and their mode of development.

For technical reasons (memory, time for calculations), the simulations will be carried out in a unit containing about 100 trees (around 0.1 ha). The emphasis will be on representing the stand dynamics from different initial configurations in terms of spatial structure (horizontal and vertical) — *e.g.* closed high forest with a scattered low understorey, multi-layered stand, opening surrounded by tall trees —, species composition and disturbance — *e.g.* brutal elimination of one or more individuals. As for all simulations of forest dynamics, one of the difficulties encountered will be the definition of the initial conditions: the latter are indeed the output of previous dynamic processes, which are precisely those which we would like to model and simulate.

Progress of operations (by mid-1996)

Qualitative and quantitative studies began in 1995 with several field surveys before and after the monsoon. For convenience of sampling and gradual organisation of the work, measurements are not carried out simultaneously for the five species.

The basic architectural elements have already been identified for the selected species, but *Macaranga peltata*. The description of the architectural unit of *Vateria indica* and *Knema attenuata* has been completed (Durand 1997), but only outlined for *Dipterocarpus indicus* and *Humboldtia brunonis.*

Young trees were located and marked at the beginning of 1995 for monitoring of growth (observation started after the 1995 monsoon, and were continued in 1996):

- 95 branched or unbranched saplings of *Vateria indica,*
- 35 of *Knema attenuata,*
- 36 of *Dipterocarpus indicus,*
- and 40 of *Humboldtia brunonis.*

Similar observations will be initiated in late 1996 for *Macaranga peltata.*

As for older and larger trees, the description and analysis of their tree crown is difficult, so that both trees standing outside the Uppangala permanent station and felled trees *(e.g.* recent *chablis*[23]*)* have been selected and measured.

Quantitative measurements of young trees of *Vateria indica* under three different light conditions began in 1995 —shade (36 individuals), semi-shade (30) and light (15)[24] — and under two conditions for *Knema attenuata* — shade (40 individuals) and semi-shade (19). A preliminary analysis of *Vateria indica* shows that the frequency of death of the apical meristem increases when light availability decreases (Durand *et al.* 1996).

The main difficulty for analysing these data is that the age of the trees is unknown: we are thus obliged to compare trees of the same size but different ages. Once the qualitative analysis and architectural studies are completed, these measurements will be extended to other species and other growth stages.

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[23] Due to the ban on felling in the Western Ghats, we cannot observe recently harvested trees. However, two big trees of *Vateria indica* which fell naturally during the 1995 monsoon were described in November 1995.

[24] Despite careful prospecting, it was not possible to find more young trees of *Vateria indica* growing in full sunlight in the Uppangala station. However, as this species is sometimes planted on roadsides, it will certainly be possible to find young trees growing under such conditions.

In early 1996, a partial survey of *Vateria indica* (more than 300 trees) and *Knema attenuata* (more than 200 trees) was carried out in the "undisturbed" compartment: their architectural stage of development (4 classes), the relative amount of vertical and lateral light received by the crowns (4 classes each) and detailed Dawkins class (13 classes) were observed, with the aim at relating these data with those of girth, height and girth increment data collected since 1990[25].

Such a study will be completed for other individuals of these species as well as for *Dipterocarpus indicus.*

[25] Preliminary results on *Vateria indica* show that: (*i*) as expected, tree size, architectural stage of development, vertical position in forest stand and light availability are correlated, making it difficult to discriminate which factors predominantly determine tree growth; (*ii*) *Vateria indica* is highly variable and sensitive to its local environment; (*iii*) the best predictor of diameter increment is the detailed Dawkins class that combines light availability and the vertical position of the tree.

Expected results and perspectives

The first step is to describe the growth sequence of a few species of dense moist forests, the quantitative aspects being better assessed for the initial stages of development. The originality in these works lies in the fact that the two aspects, quantitative and qualitative, will be studied in heterogeneous formations — in contrast to numerous former studies, mainly qualitative, carried out in tropical forests or to the recent quantitative studies conducted in temperate homogeneous forests (plantations).

Another originality of our approach stems from the study of the influence of some ecological factors *(i.e.,* aerial competition, light) on architectural growth. As mentioned earlier, preliminary observations on *Vateria indica* tend to show that the monopodial or sympodial character of the stem and elongation of growth units depend on light conditions (Durand *et al.* 1995). Such phenomena are expected, but have not been well documented until now. Their study opens the door to the more general investigation of the mechanisms regulating aerial architecture.

The development of a computer programme which simulates 3-D tree growth and integrates structural information besides classical biometric data, should enable the development of a management-oriented tool and also improve the organisation of our qualitative and quantitative knowledge on forest dynamics:

- This simulator will provide the elements for answering questions like "what happens locally *(i.e.,* in a few ares) if selective felling is practised?": its applications to management would thus concern silviculture more than planning[26].
- Collection of botanical and ecological data will enable not only a better understanding of the functioning of trees and silvigenetic mechanisms (at the level of the stand), but will also help identify the lacunae in these data.
- The 3D-representation and visualisation of silvigenesis under "undisturbed" or moderately "disturbed" conditions, complemented by predicting the wood production, will be useful for training and popularisation.
- Comparison of this approach with the cellular automaton developed by Moravie (1995[b]) should also provide some interesting methodological insights: for example, is it necessary to describe crown morphology in detail in order to assess inter-tree competition and simulate stem growth at breast height?.

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[26] For planning, other kinds of models, which are less detailed, are more relevant (see the paragraph titled "Existing models").

At a later stage, it would be interesting *(i)* to extend the study to other less common species, and (*ii*) to carry out a comparative study in another dense moist evergreen forest where stand physiognomy and tree morphology are different, for example, in other (more diverse) dipterocarp forests in South East Asia, or in the radically different forests in South America.

Another perspective (in agroforestry) would be to analyse the architecture and simulate the growth of shade giving species in under-cover coffee plantations established in the semi-evergreen and moist deciduous forests of the Western Ghats since nearly two hundred years[27,28]. The aim would then be to predict the evolution of the forest cover and light conditions on the ground because these are the important factors for the yield of coffee plants.

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[27] See "Asphalt in the jungle: dynamics of natural systems and human activities resulting from the development of road network (Coorg District, South India, XIII-XX centuries)", a research proposal submitted in 1995 to CNRS-P1R *Environnement, Vie & Sociétés* by the French Institute.

[28] In fact, the first works on quantitative modelling of plant architecture at CIRAD started on coffee (see de Reffye's paper *"Travaux sur le caféier"*, CIRAD, *Centre de recherches de Montpellier).*

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