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**A PATCH-MODEL FOR MANAGED TROPICAL LOWLAND
RAIN FORESTS IN COSTA RICA**

By

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Dissertation for the
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**Tropical Agricultural Research and Higher Education Center
(CATIE)**

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To the memory of my mother

Abstract

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The gap modeling approach was used to develop a simulation model for *Pentaclethra* forests of the Central American Atlantic Moist ecoregion. The model uses empirically estimated functions fitted from a eight-years field data. These functions include diameter growth, height functions, and the effects of crown exposure and form on diameter increment. Volume functions were obtained from local literature. Ecologically estimated parameters were obtained for those procedures not directly fitted from field data. Trial and error procedure was used to calibrate the desired model output level. The model was tested and evaluated comparing long-term simulations with the presently known characteristics of *Pentaclethra* forest. Ecologically estimated parameters were evaluated for sensitivity. The resulting model called **Gavilán**, after the Spanish name of *Pentaclethra maculosa*, the most abundant species, could represent most of the dynamic characteristics of *Pentaclethra* forest. The use of species growth rate and position of the adult size on the mature forest strata for diameter increment functions produced a modeling efficiency of 0.39. These species groups were also used to estimate growth mortality and recruitment parameters to give a more realistic approach. Initial species abundance and gap opening are used together with species regeneration guild to estimate the probability of a species to establish. The model maintained the characteristics of *Pentaclethra* forest over a simulation period of 400 years, starting from an observed plot after logging. Ecological parameters were moderately sensitive, and a variation of 20% of the initial value produced between 6 and 25% in the model output. The model was used to estimate the cutting cycles when the silvicultural treatment of liberation was applied. This was found to be between 15 and 35 years with a sustainable yield of about $20 \text{ m}^3 \cdot \text{ha}^{-1}$ in each harvesting. After 200 years of successively logging in a 20 years periodicity the forest structure, the species richness and diversity were maintained. These findings suggest that forest management of *Pentaclethra* forests could be done in an ecologically sustainable way if logging intensity and silvicultural treatments are maintained within reasonable limits.

Keywords: Gap models, growth and yield models, *Pentaclethra* forest, *Pentaclethra maculosa*, tropical rain forest, Costa Rica

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1 Introduction

Predicting structure, composition, diversity, and timber yields, and how these aspects of forest stands dynamics are affected by human interventions, such as harvesting and silvicultural treatments, in tropical rain forests (TRF) is highly desirable. The answer to this question would help decision making regarding management of these forests, which is an urgent task for conservation of these ecosystems (Clark and Clark 1999). Lack of resource data and complexity of TRF has reduced the capacity for such predictions, especially in comparison with even-aged plantations (Vanclay 1991 b, 1994, Alder 1995). Although adequate data for characterising the dynamics of these systems is scarce and the existing long-term data sets come from observation plots designed for different objectives or mensuration methods have changed over time (Sheil 1995) it is notorious the effort existing to approach this question. Among these approaches, forest growth and yield models are the most important advances in this area (Vanclay 1994, 1995). However, apart from being timber-oriented, most of the models are empirical and do not address ecological aspects of the forest, as it would be desirable for an ecologically sound and sustainable forest management. On the other hand, most of the existing models in TRF are in experimental sites, where research is taking place such as the Southeast Asia (Bossel and Krieger 1994, Liu and Ashton 1995, Ong and Kleine 1995), Ghana, Brazil and Costa Rica (Alder 1995, 1997, Alder and Silva 2000).

Growth and yield models have been used to simulate conditions that could be difficult or costly to create in reality. Questions like "What is going to be the future composition of the stand?", "How much timber volume can be harvested without destroying the economic and ecological value of the stand?", "How is growth of trees of commercial species affected by silvicultural treatments applied at certain intensity?", and others, would be difficult to answer quick and cost effectively without a model (Schneider 1992). Most of these questions have been asked since decades (for example Canonizado 1978) and few of them have been correctly answered. These and other questions are pertinent particularly

nowadays when information on sustainability of forests is required for timber certification (Prabhu *et al.* 1996). For forest management planning purposes, only a model can respond promptly most of the questions. Among the current modelling techniques used to simulate forest growth, two procedures are usually used according to the background principles applied. Statistically based, or empirical techniques - commonly used in forestry for timber yields prediction - and ecological process-based techniques, commonly used among ecological modelling community to estimate biomass productivity and carbon balance. Alder (1995) classify models using dichotomy between empirical-process, deterministic-stochastic, aggregated-disaggregated, spatial-non spatial, among others. His discussion is oriented towards the model selection procedure depending on available data and model objectives.

Process models are based on ecological theories and require data of the eco-physiology of the elements of the system being modelled (Landsberg 1986, Botkin 1993, Pacala *et al.* 1996, Valentine 1999). In these models, forests are usually represented by a single compartment of carbon container or primary producers in an ecosystem or biome. If timber yield is the modelling objective, the allocation of carbon within the stem compartment as well as wood density should be modelled. Little work has been done in tree-compartment carbon allocation in the tropics and if any it has been done in monospecific plantations (e.g. Marku Kanninen personal communication). Empirical models do not seek necessarily to represent biological processes and could be build with relatively easy-to-measure data, such as forest inventories where only stem diameters and some times heights are measured. These models usually produce good predictions for timber yields under the conditions set for the model.

Empirical and process-based approaches are complementary and neither model alone can be simultaneously general, precise and realistic as is needed for a good model (Levins 1966, 1993, Botkin 1993). A model is required to be general so that it can be portable and be used in a wider context and a variety of conditions. It should also be precise so that it can predict values close to the observed ones and should be realistic so that it can simulate the

ecosystem behaviour and response to disturbance. All these characteristics are required, but they have trade-off and the modeller should decide what to focus depending on the modelling objectives. The historic development of the two modelling categories has shown that process models require a large amount of costly data, and the final utility of the model is often limited to scientific uses, and is not suitable for use in predictions of outcomes required in common forestry practices. On the other hand, empirical models are thought to have reached their maximum development process with good predictions but lacking ecological adequacy (Amateis 1994). Intermediate models incorporating biological processes and empirical procedures have been developed to bring the biological knowledge to the management practices.

Gap models are ecological models that include demography (recruitment and mortality) providing information on individual tree growth and forest succession. The development of gap-based modelling technique (Botkin *et al.* 1972, Shugart 1984, Botkin 1993) provided an important historic landmark in forestry. Since the publication of the first gap model, tens of derivatives have been published and the initial assumptions have been improved in most of the cases, as data on ecosystem functioning and processes became available (Shugart 1998). Being so flexible, gap-models have been applied for several purposes and their popularity is due to their simplified ecological principles and a flexible structure that allow model development as data become available. Models such as SORTIE (Pacala *et al.* 1996), for instance, represent a great advance on the way of realistic representation of ecologically based models descending from gap models. This evolution, however, was made reality in part because of the extensive research programs in temperate regions, the criticism of the earlier models, and the low species richness in temperate forests compared to the tropics, among others. Earlier applications of gap models in the tropics were to study effects of hurricanes in forest succession in Puerto Rico (Doyle 1981) and to study eucalyptus forest succession and fire response in Australia (Shugart and Noble, 1981). Bossel and Krieger (1994) made another significant impulse on tropical forest modelling by developing a gap-model for managed stands in Sabah. Their model, FORMIX2, is among the pioneers in gap-model use for tropical rain forests for timber production. It simulates different logging

techniques and different intensities of silvicultural treatments. The model treats species within five groups depending on the position of mature tree in the forest stratum. Liu and Ashton (1995) used an approach similar to that used in FORMIX2, but relatively simple, and developed a gap model (HYBRID) in which the authors have put together gap-based functions to simulate forest stand growth as a function of environmental factors and empirical functions to simulate mortality and regeneration. The resulting model predicts timber yields and forest succession processes. Ong and Kleine (1995) also used a similar approach and produced DIPSIM, which is more of a silvicultural model than an ecological model, but provided a useful framework for model development. DIPSIM uses empirical growth functions developed for each of 20 species growth groups, and simulate logging operations but do not include silvicultural treatments.

Because of ecological specificities and differences in the initial database used to develop the aforementioned patch-models, although some are in TRF, these models cannot be used directly in other regions such as Central American Atlantic Moist Forest Ecoregion (CAAMFE). Differences in data used for model development and modelling objectives make it unsuitable to directly use the framework developed for these models. Presently, a cohort model, SIRENA2 (Alder 1997), is being evaluated for Central American lowland rain forest. This model was designed to predict changes in forest stands under silvicultural interventions and gives important silvicultural information. Vanclay (1995), while not stating explicitly, suggests that individual tree models could represent more realistically the selective logging and silvicultural treatments in TRF than whole stand or aggregated models.

Within CAAMFE, lays a forest type, ranging from Nicaragua through Costa Rica and Northern Panama, floristically dominated by the canopy legume tree *Pentaclethra macroloba*. This forest type, denominated *Pentaclethra* forest by Finegan and Camacho (1999), has been degraded for several purposes mainly agriculture and livestock and it has been considered endangered so that its wise management is urgent (see Finegan and Camacho, 1999). The Tropical Agricultural Research and Higher Education Centre

(CATIE) in Costa Rica is conducting long-term forest management experiments in these forests with the objective of understanding forest dynamics, and to test and evaluate ecologically sound and economically sound management practices. Formal experiments have been established since 1988 using forestry permanent sample plots methodology (Synnott 1979, Alder and Synnott 1992). The experiments include logging and silvicultural treatments such as refinement/liberation and shelterwood. Detailed description of the site and the experiments may be found in Finegan and Camacho (1999). Preliminary data analyses have shown effects of silvicultural interventions on tree growth rate, regeneration and mortality, identified growth patterns and habits of individual species, and species diversity, among other patterns (Finegan and Sabogal 1988, Manta 1989, Siteo 1992, Quiros and Finegan 1994, Delgado 1995, Finegan *et al.* 1999, Finegan and Camacho 1999). These data and information from other published or non-published sources on the same or similar forest type were used in this study to develop a growth model for these forests.

The purpose of this research was to develop a gap-model for the *Pentaclethra*-forest using data commonly collected in forestry permanent sample plots. The model was based on gap dynamics principles (Botkin 1993, Shugart 1998) and one site in Costa Rica, where all tree (DBH \geq 10 cm) have been identified to species and studies on growth patterns have been carried out (Finegan and Camacho 1999, Finegan *et al.* 1999). The model was designed to take a list of individual trees, species-specific parameters, and site characteristics as input from which future stand conditions such as tree numbers, diameter distributions, species composition, basal area, and volume are predicted. The model allows simulation of undisturbed forest stands as well as selective logging operations and silvicultural treatments. Potential uses for the model are timber production planning, evaluation of silvicultural management plans, and research on forest dynamics in *Pentaclethra*-forests.

1.1 Problem statement

Forest managers need to understand the consequences of forest management practices and forestry researchers should provide the bases of forest dynamics (growth, mortality and

regeneration) and tree species successional processes required to understand the effects of logging and silvicultural treatments in changing environmental conditions. Understanding these dynamics will enable forest managers to evaluate different forest management plans, not only from the point of view of timber production, but also from the point of view of forest protection and sustainable use of forest resources. Models that can simulate forest dynamics based on ecological principles, predicting timber yields, and allowing selective logging and silvicultural treatments is an ideal tool to perform this task. This thesis, which is part of a larger research project, had the goal to develop a patch-based model to simulate dynamics of undisturbed or silviculturally managed forest stands. Lack of data limited the development of a fully ecologically based model. However, the approach presented here aims to generate new insights, and test hypotheses concerning forest dynamic processes and forest management sustainability while guiding data collection procedures by identifying knowledge gaps.

1.2 Objectives

General Objective

To assess the adequacy of a patch-model to simulate forest stand dynamics, and predict timber yield in managed *Pentaclethra*-forests, in Central America.

Specific objectives

- i) Build the model environment: select conceptual basis, group species according to growth patterns, estimate parameters by species group, build the user-interface using a general programming language.
- ii) Evaluate the model against the observed patterns: does the model represent the currently known *Pentaclethra*-forests dynamics?
- iii) Use the model to evaluate logging and silvicultural treatments: what is the function and effect of logging and silvicultural treatments?

1.3 Significance

This research proposal is part of a larger research project being carried out by CATIE in Central America on sustainable use of tropical lowland rain forests. One of CATIE's priority research lines, *Development of Technologies for the Sustainable Management of Natural Forests and their Biodiversity*, has predicted an output which is defined as the "understanding of stand dynamics of tropical forests". The general objective defined to address this output is "to broaden and deepen knowledge of the growth, commercial yield and natural regeneration" (Campos *et al.* 1997, CATIE 1995).

2 Background and literature review on modelling growth and yield of tropical rain forests

2.1 Basic aspects of forest productivity

Ecologically speaking, productivity is the rate at which radiant energy is used by producers to form organic substances as food for consumers (Microsoft Bookshelf 1996). In forest ecosystems in particular, productivity is understood as the rate at which trees accumulate biomass. Because traditional forestry is specifically oriented to wood production, forest productivity could be expressed as the rate of wood volume accumulation. The terms growth and yield, have been particularly used in forestry to mean the rate of wood volume accumulation and the amount of wood volume utilisable at the time of harvest respectively (Knuchel cited by Alder and Synnott 1992). In this section, productivity is used interchangeably with growth and the forestry definition is used in all the cases unless explicitly indicated. Although growth could be used for the rate of change in individual trees or forest stand diameter, height, or basal area, these parameters are highly correlated to stem volume and the meaning of growth in this case could be generalised as the rate of change of tree or stand dimensions.

From the ecological to the forestry definition of productivity, there is an exclusion of several organisms that are present in forest stands but not traditionally observed or measured in traditional forestry practices. Ecosystem managers have criticised this exclusion since the excluded organisms may have an important role in forestry as the trees themselves (David 1997). Decomposing microorganisms for instance, have an important role in nutrient recycling and returning of dead matter to available nutrients for plants and other living forms. However, because in this study the traditional forestry approach is used and timber production, tree growth rates, and wood volume estimation are the main focus, there are no further references of other forest organisms but trees.

2.1.1 Forest growth and yield mensuration

Forest inventories and permanent sample plots are some of the most important and old means of measuring forest growth and yield (Alder and Synnott 1992). The techniques were developed to provide information of forest stocking. During forest inventories and permanent sample plots assessment, trees are generally measured for stem diameter and because of difficulties measuring heights only a small sample are taken for height mensurations. These procedures are still valid today although several other techniques including remote sensing, are used to assess forest stocking. Change in forest wood volume is monitored by successive forest inventories with the aim to provide planing information for the timber industry. The information so collected is generally summarised in volume tables, giving a relation between the age of the stand and the timber volume. Tables of volume became more complicated when they had to include several variables such as species, site conditions, apart from the age of the stand. The use of volume functions and the development of computer technology have been replacing gradually the tables of volume and presently volume could be estimated by means of complex volume functions using several variables.

Although the volume mensurations provided by forest mensuration techniques offer useful information on wood stocking, their precision is low mainly due to the difficulty measuring the tree heights. The stem analysis technique, which consists in measuring growth rings (in diameter and height), provides a highly precise method to obtain diameter and total height of trees in all their life span. The information so collected is analysed as function of site conditions and climate factors. This technique provided very useful information of growth and yield of temperate forest plantations and some tropical forest plantations. However, in tropical lowland rain forests, where hundreds of species coexist in the same area, and each tree grows in particular and varying conditions, and trees of different ages grow on the same stand simultaneously, the deliquescent form of branching of tropical trees, and the absence of growth rings in most of tropical species, the stem analysis technique does not produce similarly accurate results in these forests (Borman and Berlyn 1981). Moreover, it would be required a large amount of trees to be cut down and analysed and several assumptions

would be required to estimate the competition status of each tree in the past periods where no information of stand density would be available. The cost of this method, among others, is its destructive nature, which is not desirable in research areas where other ecological studies ought to be carried. Montés *et al.* (2000) describe a non-destructive method for estimating above ground forest biomass, however, it requires that complete trees be represented in a photography which is not feasible in closed forest stands such as TRF.

By knowing the growth rates and the wood stocking of forest stands, foresters decide when it is more profitable to harvest. In plantation forests, this is usually the period in which the stand growth rate begins to decline and the amount of accumulated wood does not increase significantly. In uneven aged forest stands, this period is generally defined according to logging intensity, as the period required to restock the harvested volume (Whitmore 1990, de Graaf 1986). The period between two consecutive loggings in uneven aged forests is called cutting cycle.

2.1.2 Cutting cycles

The period between two consecutive logging operations is called cutting cycle and, in the case of forest monocyclic silvicultural systems, it is equalled to the period that trees need to grow to the harvestable size. In TRF where logging is selective and only part of the mature trees is removed (as required for sustainable forest management – see Alder and Synnott 1992) the cutting cycle is the period in which the forest stand needs to re-stock the harvested timber and it is generally less than the time trees take to mature – the rotation age (Whitmore 1990). The difference between monocyclic and polycyclic silvicultural system is based on the number of logging operations within one rotation of trees. In polycyclic systems, more than one logging is applied within a single rotation age, and the next logging is guaranteed by trees already established in the forest stand.

The characteristics of polycyclic silvicultural systems, in which selective logging is applied, and potential crop trees are present in the forest stand, require that certain care be taken to

cause least damaged on the future crop. Whitmore (1990) suggests that the amount of damage to the remnant stand does not depend on the volume but the number of trees extracted in a proportion of one tree smashed and another tree damaged for every tree logged (but see Alder 1995 and Vanclay 1994).

In Suriname, de Graaf (1986) describes a series of experiments where monocyclic systems with 60-80 years were expected to produce high quality timber. However, because of the length and costs of monocyclic systems, they are not encouraged if sustainable production is required. On the other hand, de Graaf (1986) expressed his doubt regarding the effect of the final logging on the following regrowth. He suggests that the final logging would be drastic and could lead to deterioration of the recovering capacity of the forest stand.

Polycyclic systems have been reported as the best alternative for tropical forest management and several silvicultural systems have been developed in different regions (Lamprecht 1990) depending on the management objectives and the abundance of commercial species. With the polycyclic systems, the cutting cycles are shorter and sustainable yields could be obtained if logging intensity is maintained within the forest production capacity. In the CELOS silvicultural system for instance, the logging is kept on $20 \text{ m}^3 \cdot \text{ha}^{-1}$ in 20 years cutting cycles, which balances the annual volume increment of $2 \text{ m}^3 \cdot \text{ha}^{-1}$ (de Graaf 1986). Silva *et al.* 1995 estimated a cutting cycle of 30-35 years for a logging intensity of $75 \text{ m}^3 \cdot \text{ha}^{-1}$ without silvicultural treatment in the Brazilian Amazon forest.

Quiros and Finegan (1994), using a polycyclic silvicultural system at Tirimbina, with a logging intensity of $10 \text{ m}^3 \cdot \text{ha}^{-1}$ followed by a silvicultural treatment, estimated a 20-year cutting cycle. These authors estimated the cutting cycle considering that the number of potential crop trees in the diameter class ($50 \leq \text{dbh} \leq 59.9 \text{ cm}$) after logging in the study area was higher than the minimum number of trees required to ensure future logging. They also considered the $0.5 \text{ cm} \cdot \text{yr}^{-1}$ median diameter increment estimated by Siteo (1992) for fast and slow growing species in the same area as enough for trees in the size class $50 \leq \text{dbh} \leq 59.9 \text{ cm}$ to reach the minimum cutting diameter of 60 cm. The Costa Rican standards for forest management (CNCF 1999) do not indicate the cutting cycle (as it

differs from one site to another and the logging intensity) but states that in disturbed forests, logging shall not be applied until 15 years have elapsed since the last intervention.

Assessing growth and yield, as well as evaluating logging practices and silvicultural options are among the requirements and tasks of forest planning (de Graaf 1986). Because tropical rain forests are complex and several silvicultural systems could be applied, it is usual to set experiments to evaluate the effects of logging and silvicultural treatments. Information generated from these experiments is later concentrated in growth and yield models, in which virtual experiments could be applied and guide decision-making. The role of growth and yield models in forestry is well established and it is recognised as the central point in all the process of long-term data collection and silvicultural experiments (Alder and Synnott 1992). The forest model presented in this study is an example of this practice. It is constructed on a decade of data from logged and silviculturally treated experimental permanent sample plots. The background and the conceptual basis of the model are presented in Section 4.1 while ecological evaluation and silvicultural experiments are presented on Section 4.2.

2.2 The development of concepts in modelling growth of tropical rain forest

Forest growth and yield models have been used since the eighteenth century when Germans developed the first growth and yield tables for coniferous forests. These tables were simple and had only one predicting variable: the stand volume as function of age. This helped the management process of European forests for several decades. Then, tables were improved to incorporate other variables like diameter, height, and site conditions to respond to the requirements of diversified sites and stand conditions (Philip 1983).

Since the middle of the twentieth century when computer technology became popular, new developments have been registered in the field of growth and yield modelling. Yield tables, although considered good forest management tools, were gradually replaced by regression equations with a considerable number of variables. From the sixties up to date, several

growth and yield models have been produced and have assisted forest managers in decision-making (Vanclay 1994, 1995).

Modelling techniques have been developed in temperate forest plantations, and it has been reported as a difficult task to produce an accurate model for tropical rain forests (TRF) because of their complexity. The first attempts to modelling growth and yield of TRF were made during the early 70's using plantation forest techniques. Since then, models have been developed to predict growth and yield of TRF in several parts of the tropics and a significant improvement on modelling strategy and accuracy has been registered (Vanclay 1994, Alder 1995).

Tree species diversity and low abundance of most of tree species has been particularly pointed to as one of the major limitations to modelling accuracy in TRF (Clark and Clark 1999, Finegan *et al.* 1999). Species may differ in growth patterns, mortality and recruitment rates, and respond differently to changes in environmental conditions. Modelling tropical rain forests can not realistically be done by using average stand characteristics, such as stand density, mean height, and diameter distribution, if the purpose is to understand ecological aspects of forest dynamics. Botkin (1993) sustains that to produce output at a certain hierarchical level, the model should work at the immediate lower (more detailed) level. On the other hand, modelling each species individually is not practical as most of the species are rare and their abundance is not enough for a significant sample for modelling individual species. Modelling individual species will also result in an unmanageable number of equations and interactions. A compromise is usually adopted and several species that have common habits are grouped and modelled together. This approach has been recommended as the best option to model tropical rain forests (Vanclay 1991a, Alder 1995). However, silvicultural modellers tend to group species according to their merchantability as merchantable and non-merchantable, which does not reflect the real behaviour of species in the ecosystem (see Vanclay 1994). Merchantability of a certain species is function of market structure and has no direct relation with ecological characteristics. Some classifications based on light requirements for regeneration, such as light demanders and

shade tolerants have been proposed, but these have been criticised because establishment requirements are probably not determinant for future growth rates and patterns (Clark and Clark 1991). Vanclay (1991 a) and Alder (1995) grouped species according to growth rate and observed maximum size (diameter) in North Queensland and Brazilian Amazon respectively. Finegan and Camacho (1999) grouped species according to growth rate and adult size position in northern Costa Rica. These procedures could be enhanced if more species-specific data is obtained. A better species grouping, including growth rate and pattern, wood density, and maximum height, could be the basis for improvement of species classification criterion to model tropical rain forests. These strategies used for modelling are still in their development phase since there are still few institutions developing growth models for TRF.

Textbooks on growth modelling for TRF were not available up to the publications of *Modelling Forest Growth and Yield: applications to mixed tropical forests* by Jerry Vanclay in 1994, and *Growth Modelling for Mixed Tropical Forests* by Denis Alder in 1995. These textbooks bring an up-to-date summary of the development of modelling tropical mixed forests and discuss the strategies for selecting growth models as well as the methods to build some of these models for management purposes. These two textbooks emphasise empirical models as the main modelling processes for management purposes. Also of great help, but not specific for tropical regions, is the issue number 69 of the *Forest Ecology and Management*, which constitutes the proceedings of a conference on "*Process versus empirical growth modelling in forestry*". A large collection of papers with different points of view is presented. Process models, empirical models and hybrid models are discussed, more specifically on how they can be used for management purposes and how practical they are in terms of flexibility, precision, easy management and data availability. The general impression of the papers is that while empirical models have advanced many steps in their development and have been widely used for forest management purposes, they seem to have reached the limits of their development. On the other hand, process based models do not meet properly the requirements for management, but provide an useful tool for hypotheses testing, based on biological and physical principles, about growing processes

and the affects of environmental factors (Amateis 1994). Some recommendations state the need for taking the advantage of each modelling technique and join them into a single model. Liu and Ashton (1995) and Bossel and Krieger (1994) presented HYBRID and FORMIX2 growth models respectively, which are hybrid of ecological and silvicultural models using empirical functions together with process based functions. These models seem well structured and have future for hybrid approaches to be used for management purposes. Other relevant references on forest modelling techniques, not specific for tropical rain forests, but worth mentioning here are Reichle 1981, Botkin 1993 and Shugart 1998. These textbooks describe forest modelling from an ecological point of view with emphasis to temperate ecosystems. The thoughts and the framework presented in these textbooks are general and if well interpreted, may be used in TRF.

2.3 Definition and classification of forest growth models

A model is defined as a graphical or mathematical representation of a reality that can not simply be described or observed (Jeffers 1982). The main purpose of growth models in forestry is to simulate the future state of a stand given the present state and site conditions, and silvicultural interventions. A good model for forest management must not only describe accurately the future state of the stand but also provide information about a series of alternatives for timber harvesting and silvicultural treatments intensities (Vanclay 1994).

A forest stand level growth model, using the same level input, can be described in a simple way as a function of gross growth, mortality and in-growth (recruitment) and represented as $nG = gG - M + R$ (Alder and Synnott 1992), where nG is the net growth, gG is the gross growth, M is the mortality and R is the recruitment. If silvicultural interventions (silvicultural treatments - ST and logging - H) are considered, the respective variables must be added to the right side of the equation. Logging and silvicultural treatments are a special case of mortality and some times may be incorporated in the mortality components, however separating natural mortality from human disturbances is preferable. Each term of the equation above can be a complicated sub-model described by multiple variables. For

instance, Jerry Vanclay devoted journal articles to present regeneration and recruitment (Vanclay 1992) and selection harvesting Vanclay (1989 b). All components of the model are designed to interact together and produce a harmonious and consistent model.

Silvicultural treatments and logging, for instance, affect the other model components by reducing the stand volume and basal area, and by enhancing recruitment and increasing gross growth. Within each model component, there could be complex interactions, such as those represented by among tree interaction effect on growth. These interactions are commonly represented by competition indices, which may differ according to the level of aggregation of the model. Competition indices can be included implicitly within the general growth function as one of the growth factors, such as the regression function fitted by Ong and Kleine (1995) which includes stand basal area and overtopping basal area as factors. Alternatively, competition indices could be set separated from the species optimum growth as multipliers or growth modifiers as it is commonly done in gap modelling techniques (e.g. Botkin 1993). The subsequent sections describe in detail the components of a forest growth model.

The modelling strategy is the summation of procedures used to build the component sub-models. That is why there are many classes of models, some with more and others with less detail according to the objective, data availability and modeller's ability. Alder (1995) presents a general classification of forest growth models according to aggregation level, stochasticity, and the conceptual basis.

Aggregation level in forest growth models refers to the entity used as the elemental subject of the simulation. Highly disaggregated models simulate each individual tree in the forest stand using tree characteristics, while highly aggregated models simulate entire stands using stand average conditions. Output of an individual tree model could be aggregated to give average stand conditions, but output of forest stand models could not be dissociated in their respective trees. There is a large variety of models in between the two extremes of aggregation. Cohort models (Vanclay 1989 a, Alder 1995, Alder and Silva 2000) are a special case of intermediary aggregation level where trees of similar size (cohort) are

simulated together using average cohort characteristics. The level of aggregation, in this case, is determined by the size of the cohort, so that the smaller the cohort the model approaches the level of individual tree and the larger the cohort, the model approaches forest stand model.

Stochastic or probabilistic models produce random output that may differ even using the same input basis. This is used to represent the natural variation in which processes not well understood are left to randomly varying factors. A single estimate from a stochastic model with Monte Carlo output is of little use and a whole set of estimates is necessary to provide information on the variability of the predictions. A mean or median and the variance should be determined after a series of estimates. This approach, although it imitates more closely the natural situation, it is not preferred for management purposes because of the variability of the results which can turn decision making more difficult. However, for research purposes, it can be used with success if good interpretation is provided (Alder 1995). Runs of deterministic models always yield the same results if considering the same input basis and the results express the mean growth rate. Whole-stand forest growth models for management purposes are commonly constructed on deterministic basis.

Forest growth models could be based on biological principles or empirical principles. Empirical models are commonly concerned with function fitting to data using statistical or mathematical principles such as goodness of fit, distribution of residues, and level of significance. Parameters fitted by this procedure alone do not necessarily represent biological processes. These models, in forestry, are a consequence of data collection techniques mainly derived from forestry inventories such as the permanent sample plots (Alder and Synnott 1992), which is the main source of data for forest growth models. Models based on biological principles seek to represent organism or ecosystem components and rates of energy or matter flow among components. Data collection, in this case, is guided by the need of knowing the component interactions, the nature and rate of energy flow among them, which results in forest growth.

2.4 Tree growth models

Commonly, tree growth for timber yield estimations, is expressed in terms of diameter (e.g. Vanclay 1991a) or basal area growth (e.g. Ong and Kleine 1995). Diameter is the main determinant of basal area, it is strongly related to timber volume, and is relatively easy to measure, hence the preference of expressing tree growth in terms of either diameter or basal area growth. Diameter growth can be calculated in many ways depending on data availability and model objectives. These techniques are discussed in the next subsections where distinction is made between empirical and process-based (biological) procedures.

2.4.1 Empirical approaches

Empirical growth models are based on long-term field data observations (continuous inventories or permanent sample plots), generally fitted to non-biological growth functions using regression techniques. For practical reasons, foresters have been using empirical models for management purposes. In one hand because it could be assumed that what has been observed in the forest in the long-term is likely to happen again if the stand conditions do not change significantly. On the other hand, it is relatively easy to ignore the biological processes, such as photosynthesis and respiration, involved in tree growth and fit the rate of change in stem size as function of initial size. When environment changes occur slowly the first assumption can be considered true, but if long-term simulations are considered, environmental changes may be more evident and worth to be considered (Shugart 1998). The assumption of non-changing environment has been useful for forest management purposes where simulations commonly done for relatively short periods. Vanclay (1994) and Alder (1995) discuss some of the most common empirical management oriented forest models and their assumptions.

In spite of their usefulness, empirical models have some disadvantages. They are limited to the range of data collection, so that extrapolations should be done with care. They do not explain the process being modelled in the sense that biological processes are not used as

basis for model building. For empirical models, diameter or basal area growth is calculated as mean annual difference between two measurements. Then, diameter growth functions are fitted by regressing growth on tree-specific and site-specific variables. The commonly used tree-specific variable is initial diameter and some times crown form and position are included. Site-specific variables may include site quality (e.g. current stand basal area, past stand volume, dominant height, and soil properties), competition indices, slope and others.

Many general functions can be used for diameter growth prediction. Vanclay (1994) discusses several of them from which Alder (1995) recognised three commonly used (Table 2.1).

Table 2.1 Empirical functions commonly used to estimate tree growth in tropical rain forests

Function type	Example	
Quadratic	$DI = a + b.DBH + c.DBH^2$	(2.1)
Power-Exponential	$BAI = a.TBA^b.exp(c.TBA)$	(2.2)
Modified Beta	$DI = a.(D_{max} - DBH)^b.DBH^c$	(2.3)

DI is diameter increment ($cm.yr^{-1}$), BAI is basal area increment ($cm^2.yr^{-1}$), DBH is diameter at breast height (cm), TBA is the tree basal area at the reference height (cm^2) and D_{max} is the maximum diameter attained by the species (cm) and a, b, c are regression coefficients.

The quadratic function can be easily fitted by general regression methods. It must be used with care especially in the tropics where few data can fit a wrong equation leading to an ascending growth function without limit. It must be clear, that this equation is valid only for coefficients $b > 0, c < 0$ with an a -coefficient positive and close to zero. The power-exponential is used in its basal area version rather than diameter. The coefficients of the equation are obtained after applying the logarithm in each side of the equation and use of linear regression ($\ln(BAI) = \alpha + b.\ln(TBA) + c.TBA$). Coefficient a is obtained by $\exp(\alpha)$. Provided c coefficient is negative, the predicted increment will tend to zero, as TBA

becomes larger. The b coefficient should be positive, giving zero increments for trees of zero basal area. The modified Beta function has the advantage that can be fitted with few data and is constrained by a maximum diameter (D_{max}) which once reached, the diameter increment tends to zero.

Modifiers can be added to the basic equations to express tree-specific or site-specific constraints. Vanclay (1989 a) used the modified Beta function with a modifier derived from stand basal area, site quality, and soil parent material. Ong and Kleine (1995) used the power-exponential equation enhanced with site quality, stand basal area and overtopping basal area. The latter authors defined site quality as a dummy variable (1 for good sites and 0 for poor sites). The overtopping basal area was defined as the basal area of the neighbouring trees with a diameter greater than the subject tree, which together with the subject tree basal area expresses the competition index.

A general structure of an empirical forest growth model is presented in Figure 2.1. The parallelograms represent data and the dashed arrows represent information transfer. Information transfer is made via equations such as the ones presented earlier in this section.

2.4.2 Biological approaches

Biological approaches derive from system dynamics, a discipline of engineering that has been brought to ecosystem analysis during the second half of the twentieth century (Odum 1971). Box-and-arrow diagrams are used to represent biological processes and energy flow. This procedure impelled the development of global bio-geo-chemistry and food webs models (Shugart 1998). Figure 2.2 represents a classical box and arrow diagram of a process-based model for a forest ecosystem dynamics adapted and simplified from Gardner and Mankin (1981). In this diagram, each box represents a compartment of carbon storage and the arrows represent carbon or energy fluxes.

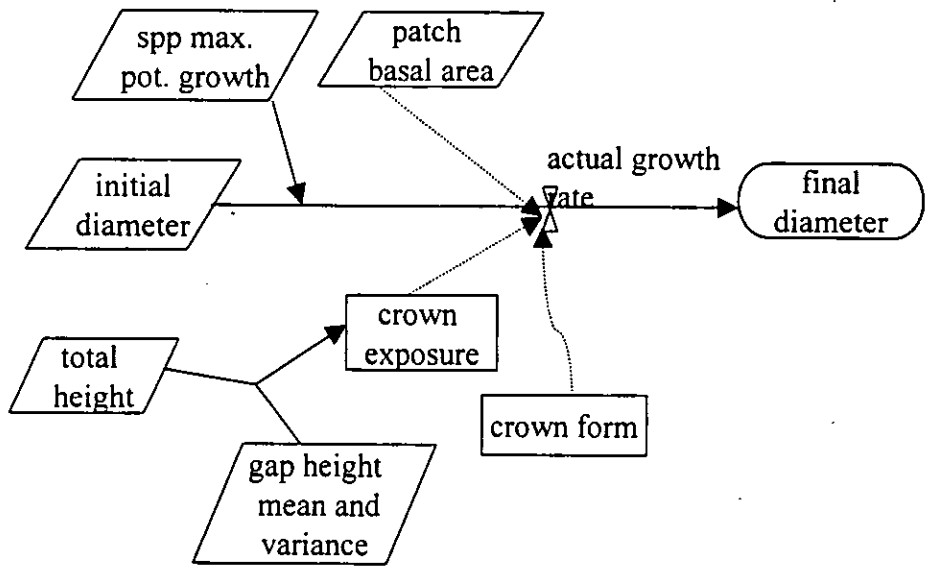


Figure 2.1. Flux diagram of an empirical model

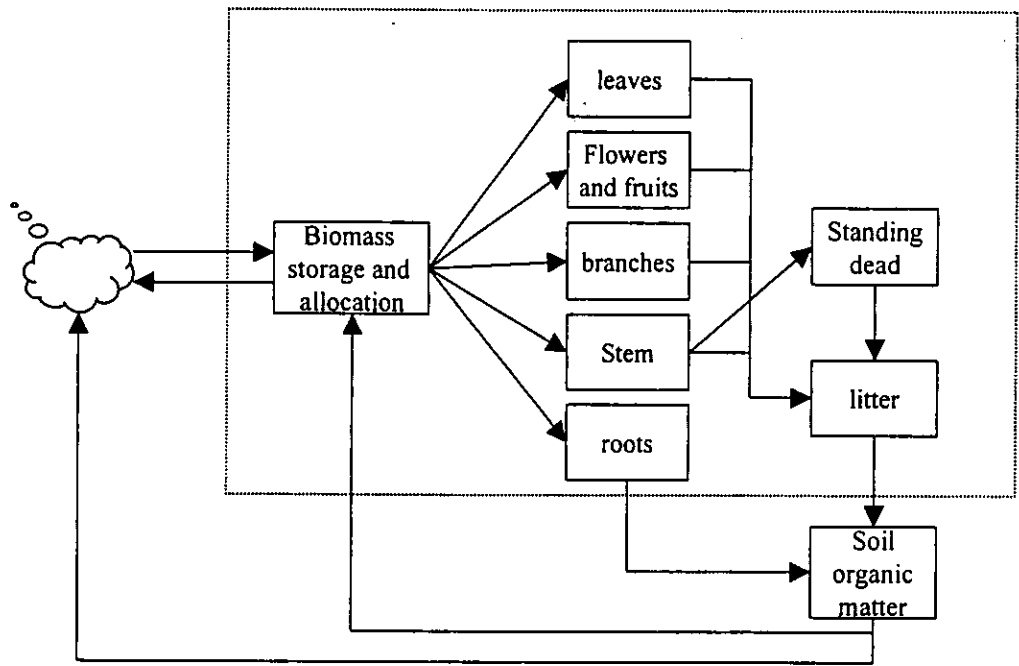


Figure 2.2. Flux diagram of a process based model. Adapted from Gadner and Mankin 1981.

Compartment models can represent complicated biological processes. The main task on building compartment models is to identify the compartments of interest, flow directions, flux rates between compartments, and initial state of the compartments. Presently there are software platforms developed to facilitate compartment model building. Examples include STELLA, one of platforms that enable building complex models without the need of writing computer code (Deaton and Winebrake 1999) and TIME ZERO which is based on a simplified computer language to define the model structure. Compartment models may not be adequate to represent individual tree-level models for mixed forests. Material and energy fluxes for instance, tree uptakes of water and soil nutrients and their further allocation through the organs would be difficult to measure in practice.

Process-based models may be used to simulate growth rates based on carbon and energy balance using functions that estimate the efficiency of energy use (Valentine 1999). This method has the advantage of predicting growth based on biophysical processes occurring in the trees such as photosynthesis, respiration, structure maintenance, and so on. Process-based models are meant to simulate biological processes and state of chemical elements or biomass within the system in relation to the surrounding environment. They respond more to scientific questions than to forest management questions (Parton *et al.* 1992). How environmental changes affect forest dynamics and carbon balance status are some of the main questions to which process-based models can suggest answers. The type of data used for these models is the limiting factor to their use for management purposes. Photosynthesis and respiration as well as biomass allocation through tree components for each species are among the required and most difficult-to-get data. If environmental changes are to be simulated, then the effects of different factors such as water, soil chemical elements, and atmosphere components should also be evaluated.

Long-term data have been collected for forest management purposes on silvicultural parameters especially stem size and quality, but few biological information like leaf area, photosynthesis, respiration and carbon allocation. However, Amateis (1994) suggest that it is becoming necessary to incorporate some physiological principles in management oriented

models to express the biological processes being modelled. As a matter of fact, there are some forest growth models such as those described by Landsberg (1986) and Pacala *et al.* (1996) which are mainly process based models but seek usage for management purposes. Sustainability criteria and indicators required for monitoring forest management activities (Prabhu *et al.* 1996) may be evaluated by including biological processes in a forest management model.

Theoretically, the basic growth equation could be expressed as $nG = P - R - L$, where nG is the net growth, P is the amount of photosynthate produced in the period, R is the respiration loss during the period and L is the litter-fall. This general function, however, considers a tree or a forest (depending on the level of aggregation) as a carbon container and does not specify where the photosynthate are stored within parts of the component such as stems, leaves, roots, and bark. Thus, this general function could be used unchanged if modelling objectives are food webs or regional biogeochemical cycles where there is no interest in knowing the part of the tree where carbon has been stored. However, because the parts of the tree have different properties, such as the decomposition rate, it is generally required the information of the biomass allocation so that the nutrient and energy cycling could be understood in a finer level. Parton *et al.* (1992) for instance, need biomass allocation information to simulate forest ecosystem nutrient cycling and dynamics of biomass. Bossell and Krieger (1994) used this basic equation, mixed with pipe model theory and transition matrix algebra to base their forest management growth model.

Applied biological approaches, such as in gap-model theory described below, use photosynthesis functions based on light use efficiency, species tolerance level and total radiation received by the crown. Light reduction through the inner part of the crown is calculated by an exponential function of the crown density and the incident light in the top of the crown (Botkin 1993). Leaf area is calculated as an allometric function of dbh (Botkin 1993) for each species (Desanker and Prentice 1994) or species group (Bossell and Krieger 1994). The photosynthetic efficiency is estimated from the level of species light

requirement (Botkin 1993). Respiration and litter fall are estimated as functions of tree size and site factors.

The Bertalanffy growth equation (Bertalanffy 1968) expresses the simplest form of biological-based growth functions. Its basic principle is that, the growth of an organism in a given period of time (dY/dt) could be expressed as allometric function of its mass Y as [$dY/dt = b_1 Y^\alpha - b_2 Y^\gamma$], where α and γ are constants of anabolism and catabolism respectively, b_1 and b_2 are regression coefficients. This equation was originally developed for animal growth studies. Some adaptations were suggested for its application in plant growth and the resulting equation is known as the Chapman-Richard equation (Shifley and Brand 1984, Haefner 1996). The problem with this equation is that the anabolism and catabolism constants are highly correlated, giving problems in the fitting process. If α and γ are correlated an infinite set of solutions is obtained. On the other hand, tree mass is not all living mass, so that, it can not be correlated directly with tree mass growth using that equation, but only the living parts (sapwood, leaves, fine roots and fine branches). Modification of this equation for an $\alpha=1$, have been considered more useful and several models have been produced on this basis. Vanclay (1994) presents some of these equations applied for whole stand basal area increment and individual-tree diameter increment. The maximum size attainable by species is used in the modified Bertalanffy equations so that it can be constrained by a maximum tree size or stand basal area. The general modified equation, constrained by the maximum size is given as [$dY/dt = bY(1 - Y/Y_{max})$], which is a well-known logistic equation (see e.g. Odum, 1971).

The theoretical equations presented above are usually adapted to express growth processes based on tree size so that basal area or diameter is the explanatory variable. This is assuming that anabolism and catabolism will be depending on these variables directly. However, some times diameter is not a good predictor for leaf area. The relationship between leaf area and stem diameter has been a matter of research and the main findings are that in plantations of coniferous species the relationship is good, however, sapwood area has a closer relation to leaf area (Snell and Brown 1978). In broadleaf species, on the other

hand, this relationship is reported to be weak. The current sapwood area, which is only a part of the whole sapwood, is more closely correlated to leaf area (Rogers and Hinckley 1979).

The relationship between sapwood and leaf area is the basis of the pipe model theory. This theory states that tree stems and branches can be considered as unit pipes each supporting a proportional unit amount of photosynthetic organs (Shinozaki *et al.* 1964 cited by Shugart 1998). This theory has been largely used to relate sapwood and crown dimensions (area or volume) in temperate forests (Ryan 1989, Kaufmann and Troendle 1981, Rogers and Hinckley 1979, O'Hara and Valappil 1995). However, there are a few experiments in the tropics using this theory. Some of the assumptions taken into account in temperate even aged monospecific forests are not easily applicable in tropical rain forests, where hundreds of broadleaf species in varied sizes occur simultaneously. First, the fact that dbh and total sapwood area does not present a good relationship with crown dimensions complicates somehow the data collection process, since sapwood has to be divided into current and not active. Second, it is assumed that trees not experiencing competition have symmetric crowns. This helps to calculate the potential photosynthesis for some species (Smith 1994) but there is no account for competition effect, which is the most common situation in tropical mixed forests. No references were found confirming crown symmetry on trees not facing competition in tropical forests although it appears reasonable. Third, the method is destructive, which is not desirable in case of permanent sample plots. Thus, other ways to estimate leaf area in tropical forests must be found. Experimental determination is crucial for development of process-based models.

Morataya (1996) determined experimentally the relationship between sapwood area and crown dimensions in *Tectona grandis* and *Gmelina arborea* plantations in Costa Rica and found significant correlation with coefficients of determination (r^2) of 0.79 for both species considered separately. Morataya had to cut down the trees and measure the leaf weight and sapwood. Nygren *et al.* (1993) refer to a non-destructive method for evaluating sapwood – leaf area relationship, but it is only applicable where trees are periodically pruned

like in agroforestry systems, and the branches can be used in place of the main stem. They used the method and found a good relationship, with correlation coefficient ($r=0.90$) between leaf area and branch sapwood in *Erythrina poeppigiana* in an agroforestry system in Turrialba, Costa Rica. The method used to determine the stem or sapwood relation with leaf area seems to work well in tropical broadleaf plantations, where trees are relatively evenly distributed in space and only one species is under consideration. However, the destructive character of the data collection procedure makes it difficult in situations that are more complex like in tropical rain forests, where trees are distributed unevenly and several species are present. Neighbouring trees may affect crown form and species diversity poses another sampling problem discussed in later sections.

As an alternative way to get the relation stem size – leaf area, Smith (1994) used an empirical equation to predict crown volume for growth modelling in coniferous plantations. He measured crown projection (four corners), stem height and total height as well as the tree Cartesian coordinates. With these data, he used an empirical equation considering the potential crown size (that of a tree not experiencing competition) and the effect of neighbouring trees (if there were any overlap). This is a good approach for monospecific plantations where trees are of the same age and the effects of the neighbouring trees tend to be reciprocal. To be used in tropical mixed forests, this alternative should also include the crown position concept that describes the amount of light “seen” by a given tree crown. Another approach used to deal with crown characteristics and photosynthesis rate in forest trees is the use of the light extinction equation (or light penetration) which estimates the leaf density above the observation point. This approach does not give directly the individual tree crown characteristics but may give the relative amount of crown in each forest layer. Koop and Sterck (1994) studied light penetration functions in a tropical rain forest in French Guyana based on that, light has been reported as determining tree growth. They used hemispheric photographs and measured light penetration directly in the field trying to get a correlation between measured light and use of hemispheric photos scanning method. The point here is that they projected crowns on every measuring point, and their conclusion was that the model they developed (SILVISTAR) did not respond well. The reasons indicated as

the main causes were the inaccuracies in measuring tree height and crown projections especially those of overlapped ones. The other reason mentioned was that of the steep slope terrain, where trees located at large distances might shade, at certain times of the day, trees in the lower position. If good results were found in this experiment, the resulting equation would be useful as one of gap models input: the exponential light reduction equation.

2.4.3 Gap-dynamics approaches

Gap models are ecological models that represent a forest stand as a mosaic of patches (may be of the same or different size). Individual-trees are simulated for diameter growth and demography (regeneration and mortality) are simulated to produce new individuals and eliminate some other individuals following general, but applicable, principles of competition. The general formulation of gap models is based on empirical relations that can be translated into tree growth. The characteristics and the basic principles of gap models make them classify between biological and empirical. *Gap*, in the context of gap modelling, is defined as an area equivalent to the neighbourhood that can be affected by a big tree (Botkin 1993). The size of a gap depends on the average forest height (van der Meer *et al.* 1994). It should not be confounded between “gap” as an opening in a forest stand with patch, a small piece of land – not necessarily open. To avoid this potential confusion in terms, it is some times preferable to use “patch-model” instead of “gap-model”.

In gap models, individual-tree volume growth is defined as the potential growth reduced by limiting environmental factors. The potential growth is commonly estimated by using an asymptotic function, generally called fundamental growth equation, which depends on leaf area (LA), the amount of living non-photosynthetic tissue (D.H) and the maximum size (D_{max} and H_{max}) attained by the species. Botkin *et al.* (1972), Botkin (1993) and Shugart (1998) present the mathematical and logical derivation of the fundamental growth function starting with the theoretical function indicated below (2.4) in which volume increment $\delta(D^2H)$ is expressed as function of the maximum intrinsic net assimilation rate of the species (R), the tree leaf area (LA) and current size (D – stem diameter and H – total height) constrained by species maximum size.

$$\delta(D^2H) = R \cdot LA \cdot \left(1 - \frac{D \cdot H}{D_{\max} H_{\max}}\right) \quad (2.4)$$

Note that D^2H is also called gross volumetric production index. The other factors of volume are fixed values, so this index can be used to express volume growth. The right hand side term inside parenthesis expresses the maintenance cost while the term $(R \cdot LA)$ expresses the photosynthesis. From this basic equation, a series of assumptions are considered for practical reasons. Some of these assumptions are based on ecological theories such as the pipe model theory and others. Dimension analysis is required for each species or each species group to make the equation practical. Some of these data were available in temperate forests and assisted the birth of JABOWA (Botkin *et al.* 1972), the first gap model. Since then, data collection have been stimulated mainly in temperate forests and most of the initial assumptions have been reviewed and improved (see for instance Pacala *et al.* 1996). Following, there are some of the assumptions considered to make the fundamental growth equation more practical. The first assumption is that leaf area is proportional to leaf weight (W), which is function of tree diameter (D). This assumption is supported in part by the pipe model theory, in which, the amount of leaves supported by a tree is proportional to the vascular area of the respective stem. The resulting function found by Botkin (1993) [$W=C \cdot D^2$] and assumed by other gap modellers is simple and easy to work with. It is clear that it is not the resulting equation that is important but the way to find a relation between leaf area (which is difficult to measure) and diameter. The second assumption relates diameter to tree height. Botkin (1993) experimented with about 20 different types of equation before taking the quadratic. At La Selva, Lieberman *et al.* 1995 used a simplified equation to relate diameter to height [$H=5.5 \cdot D^{2/3}$]. They do not discuss the origin of this equation but it can be assumed as result of their observations. Measuring height is another difficult task in tropical rain forests, but this must be done so that an equation relating height to diameter should be obtained. Considering the first two

assumptions and deriving the equation so that it can be expressed in terms of diameter increment, other constants and coefficients are produced. For the case considered by Botkin (1993), other assumptions were considered giving a biological meaning to the coefficients and an easy way to get them. Some of these assumptions considered are that maximum height, and maximum diameter are attained at the same time. In fact, assumptions must be made according to the available data and the knowledge of the functioning of the system.

The final potential growth function thus derived, with quadratic height function is equation 2.5 and derivation details could be found in Botkin (1993).

$$\delta D = \frac{g \cdot D \left(1 - \frac{D \cdot H}{D_{\max} H_{\max}} \right)}{2a + 3bD - 4cD^2} \quad (2.5)$$

The effect of environmental factors on individual tree growth can be expressed in several different ways. Haefner (1996) presents five multiple controlling factors procedures and discusses their respective consequences to the simulated (growth) rates. The multiplicative effect results if we consider existence of interaction among the considered factors. It is represented by multiplying all effects of the considered factors by the maximum growth rate. The resulting effect is an unrealistically low growth rate if several factors are being considered. Haefner also explains the arithmetic and harmonic mean as well as the additive procedures that can be used depending on each situation. The Leibig's law of the minimum, which states that the factor in least supply limits the plant growth, assumes that there are no interactions among limiting factors. Then, the plant responds to each factor independently, but responds to all of them simultaneously. Botkin (1993) argues that, if this is true, then each environmental response function must be obtained separately from single regression so that the effect of each factor can be isolated in a single equation. Following this, he developed a set of different equations depending on the environmental factors considered. Available light, temperature, soil humidity, soil nitrogen content and the basal area a plot can support are the environmental factors considered by Botkin (1993). It should be noted that the procedure to use for multiple factors effect depends on each situation considered

and the modeller should experiment with the available procedures to find out which is more convenient for each case. In tropical lowlands some factors like temperature, soil humidity, and the sun angle do not vary significantly through the year and may be considered constant (see Lamprecht 1990) and not limiting factors to tree growth. Several studies have shown that light availability at the canopy is one of the most important factors in tropical rain forests (Clark and Clark 1999, Finegan *et al.* 1999) so that it is analysed here with some detail.

Light availability in gap models is estimated using the Lambert-Beer Law, a negative exponential function for light extinction:

$$AL(h) = AL_0 \cdot e^{-k \int LA(h) dh} \quad (2.7)$$

$AL(h)$ is the available light at height h inside forest canopy. AL_0 is the available light at the top of the canopy, k is the light extinction coefficient and LA is the shading leaf area.

Taking into account some assumptions, this equation can be made easier to apply.

- i) all the leaves of a tree are concentrated at the top of the tree
- ii) the leaves of a tree, shades all the leaves of a shorter tree
- iii) no single leaf of a taller tree is shaded by a leaf of a shorter tree

If we re-consider the relationship between leaf area and leaf weight (see above in this section) and taking into account the three assumptions above, then, we can estimate the factor under integral sign. The value of k is obtained experimentally by measuring the light intensity at different depths of the forest canopy. Information available on the literature (e.g. Lamprecht 1990 and Whitmore 1990) can be used if no data is available locally. The value of AL_0 can be obtained from meteorological stations, but Botkin (1993) normalised it to the

unit (1) and he found it not differing from observed values. Apart from this, he considered two different equations for light availability according to the species shade tolerance so that light compensation point is higher for shade intolerant species and, under lower light intensity, only shade tolerant species can grow.

Later gap models (Desanker and Prentice, 1994; Bossel and Krieger, 1994) have some modifications to the assumptions above. An equation is used to express the vertical variation of the crown and use observed values of available light on tree canopy. This approach can be used if an accord is reached on the diameter to leaf weight relationship. However, attention must be drawn relatively to the effect of topography as noted by Koop and Sterck (1994) that trees can be shaded by trees on the top hills out of the considered neighbourhood. Competition among trees is implicitly incorporated in the shading effect of the neighbouring trees. This is assuming that competition for light is the most important competition factor.

Due to their flexibility, gap-modelling techniques have been used to simulate forest dynamics in a variety of ecosystems and purposes. Their quasi-biological nature and versatility confer on them more reliability for ecosystem analysis than that of the classical empirical models. Several models have been developed under this umbrella and analyses described as functional and robust (Doyle 1981, Smith *et al.* 1992, Botkin 1993, Desanker and Prentice 1994). A compromise must be taken and a decision must be taken regarding the procedure to get the leaf area or crown characteristics. It is obvious that a precise and cost effective method is not currently available and one of the existing approaches must be used. Crown size projection (Smith 1994) and light penetration functions (Koop and Sterck 1994) are two of the approaches that can be used in this study. Direct mensurations or use of photographs can be implemented with some degree of confidence. In both cases it is determinant that tree heights are precisely measured apart from crown sizes.

Lieberman *et al.* 1995 used an allometric function to estimate tree height in a tropical rain forest in Costa Rica ($\text{Height} = 5.5 * \text{DBH}^{2/3}$). Botkin (1993) used a quadratic function of total

tree height on diameter ($\text{Height} = a \cdot \text{DBH}^2 + b \cdot \text{DBH} + 137$) and also assumed that leaf area is proportional to leaf weight and this can be estimated from a quadratic function of dbh ($\text{Leaf Weight} = \text{Const.} \cdot \text{DBH}^2$). These examples show the use of some allometric functions that can also be developed in this study to be used in model development. The Lieberman and his colleagues' example is from a quasi-similar forest type as the one to be used for this study. Botkin (1993) exemplifies the use of these relationships on model development. In fact, if a model is to be drawn, some assumptions should be considered and improved as experimental results and data become available.

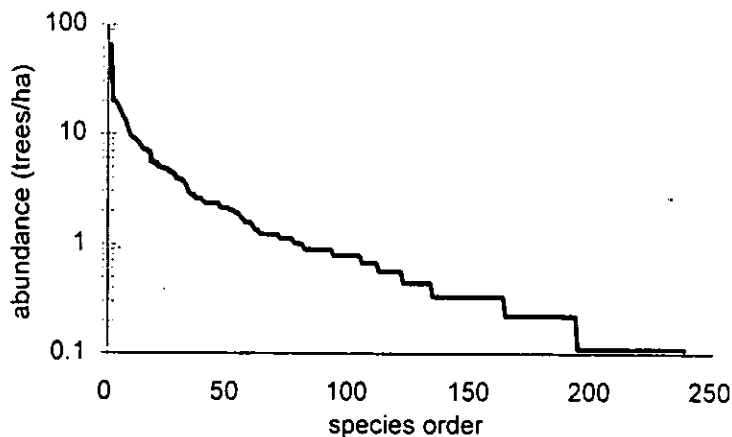


Figure 2.3 Species rank abundance distribution at La Tirimbina for trees dbh ≥ 10 cm.

2.5 Species aggregation

In tropical forests where hundreds of species occur simultaneously, the success of any modelling activity will greatly depend on the modeller's level of understanding species biology. This could be inferred from the effort spent in several other models to find species-specific parameters (Vanclay 1991a, Alder 1995). Species composition, diversity and stand structure result from the interaction among individuals of a given species, and the individuals of another species given the conditions of the surrounding biotic and abiotic environment. One of the major efforts in modelling tropical forests has been applied in understanding patterns governing tree species regeneration, growth, and mortality but the

low abundance of most of tropical species greatly limited the present status of knowledge (Vanclay 1991a, Alder 1995). At Tirimbina, for instance, more than 100 of the 250 species have abundance of less than one tree.ha⁻¹ (Figure 2.3).

Several approaches have been presented to deal with species diversity in modelling (Swaine and Whitmore 1988, Vanclay 1991 a, Alder 1995). Grouping species according to a certain characteristic of interest is desirable. Timber merchantability, diameter-increment functions, and light requirements for regeneration and recruitment are some of the criteria used to group species (Vanclay 1989b, Alder 1995, Ong and Kleine 1995). Bossel and Krieger (1994) grouped species according to the position of the adult individuals in the forest stratum. Their five groups included emergent, main canopy, understory, small trees and herb/shrubs. This grouping resulted from aggregating species characteristics including wood density, photosensitivity parameters, and leaf-proportional energy use efficiency, among others. Vanclay (1991 a), working in forests of North Queensland, Australia, identified 41 species groups based on dbh increment regression functions. He found no relation between these groups and species regeneration guild. Within the same group there were light demanding species together with shade tolerants. Even species of the same genera resulted in different groups. As an example, Vanclay mentions 15 species of *Syzygium*, which were classified within 13 different groups.

Some times, single-criteria grouping is not enough to represent all the desired species characteristics for modelling, and multiple-criteria has been applied. Swaine and Whitmore (1988) suggested grouping TRF tree species into ecological guilds and maximum size (total height) for ecological purposes. Favrichon (1998) grouped species according to shade tolerance and height range occupied by adult tree. Finegan *et al.* (1999) used the median and the quartiles of dbh increment and the height range occupied by the adult tree as criteria for grouping species at Tirimbina. They found that the criteria used for grouping made significant contribution to the identification of growth patterns of more than one hundred forest species. The broad patterns among the species are meaningful, however, more understory and middle storey species were classified in very slow and slow growth groups

while more canopy and emergent species were classified in fast and very fast growth. Because Finegan *et al.* (1999) grouped species within treatments, there were species classified in different groups according to the treatment.

2.6 Recruitment

Recruitment is the process by which a set of trees reaches a specified minimum mensuration size in a given period and area. Commonly a dbh of 10 cm is used as minimum mensuration size, and recruits are those trees that during observations, or simulation, reach this limit (Vanclay 1994, Alder 1995). Recruitment represents the process of natural regeneration in which trees establish in the forest stand. Natural regeneration is complex and numerous factors affect its dynamics (Whitmore 1990). Modelling regeneration is simplified by modelling only those trees that reach the minimum considered dbh. This is not to underestimate the processes that take place from seed germination until recruitment, but for an individual tree simulation model, this would demand an elevated amount of computer resources while not increasing the understanding of the processes of interest (this is considering growth and yield as the processes of interest) (Vanclay 1994). Some modellers have, however, modelled regeneration from seed dispersal (Bossel and Krieger 1994) in tropical forests, but the common practice is to model recruitment from a larger size (e.g. 10-cm dbh) (Vanclay 1992, Alder 1995, Ong and Kleine 1995).

Modelling recruitment requires answering some questions depending on the level of aggregation. In disaggregated models of mixed-species forests, questions like “will be there any recruitment at all, in a given year?”; “how many trees will be recruited?”; and “what species will be recruited among the known species pool?” ought to be asked (Alder 1995). This approach is made by Botkin (1993) for JABOWA, but includes a fourth question which is pertinent for individual trees model: “what is the size (height, diameter, and leaf area) of the new recruits?” The last question is pertinent in highly disaggregated models where individual tree information is required. The initial question regarding occurrence or

not of regeneration in a given year can be stated as "are there conditions for establishment of any of species considered in the species pool?" To give answer to this question the knowledge of species requirements for establishment is needed. The degree of disturbance, that results in canopy openings, is among the most important factors to be considered for tree species establishment.

Saenz *et al.* (1999), studying growth and survival of seven tree species at La Tirimbina, Northern Costa Rica, found significant correlation between light availability (canopy openings) and growth of non established individuals (seedlings and saplings). These findings suggest that saplings growing in canopy openings are likely to reach recruitment size faster than those growing in closed canopy. Alder (1995) and Ong and Kleine (1995) fitted linear equations relating number of recruits to degree of disturbance (basal area or number of trees removed) and found the best fits during the years just after disturbance. The correlation between disturbance level and number of recruits seems coherent with theory that canopy openings will create conditions for light to reach lower heights of the forest and nutrients will be made available for trees to establish. In tropical rain forests, light availability has been reported as the most important factor for tree establishment and growth (Clark and Clark 1999). Alder (1995) found a good relationship ($r^2=0.62$) between number of recruits (N) and basal area (BA) removed in a harvesting operation and recruitment five years later, using a simple linear equation ($N = a + b*BA$). The positive a intercept was not considered significantly different from zero and the b -coefficient was positive and different from zero. The fact that the intercept was near zero means that under closed stand condition, the recruitment will be low. Ong and Kleine (1995) used the current stand density (basal area) to predict the number of recruits for different groups of species considered. The general finding in these studies is that it is relatively easy to fit recruitment functions to pioneer, light-demanding species rather than non-pioneer, shade-tolerant species (Alder 1995, Ong and Kleine 1995). The reason for this is that pioneers are more likely to establish in well-defined microsites such as logging gaps than in any other forest area and that non-pioneers establishment is not particularly affected by gap opening (Whitmore 1990). Vanclay (1992) estimated the probability for species (species were

grouped into eight regeneration groups) to be recruited as function of stand basal area, soil conditions, silvicultural treatment, and presence of the species in the stand ($\text{dbh} \geq 10\text{cm}$).

Alder (1995) considers the recruitment modelling process as a two-step approach. In the first step, the total number of recruits, irrespective of species, is empirically determined, and in the second step, the recruits are distributed stochastically through species (individuals or groups) using probabilities of a species to establish. Desanker and Prentice (1994) estimated the probability that a species would establish as function of its light requirements. If the light in the considered gap is between the light compensation point and the tolerance level, the species would establish. Then, saplings are generated with initial dimensions of 1.3 m height, 1 cm dbh and an attribute to the leaf area index. Bossel and Krieger (1994) simulated regeneration from the seed dispersal phase and seedlings are incorporated into the model according to the species group light and temperature requirement. In all the cases mentioned above the patch conditions will dictate the probability for a species to establish. If several species can establish, stochastic processes will take place to find which species is going to establish. The size of individual recruits can be either determined as Desanker and Prentice did, or stochastically assign a reasonable initial size according to an empirical recruits initial diameter distribution.

Vanclay (1989a, 1992) and Alder (1995) present relevant studies in recruitment of tropical forest species. They use dynamic approaches where species abundance or dominance is taken into account. Vanclay (1992) simulated recruitment as function of stand basal area, site quality, and species basal area as proportion of stand basal area. The proportion of species basal area in the existing stand ($\text{dbh} \geq 10\text{-cm dbh}$) gives the probability for a species, or species group, to be recruited. If a species could be recruited, then the number of recruits of that species is estimated as function of stand basal area, site quality and species abundance ($\text{dbh} \geq 10\text{-cm dbh}$). Alder (1995), after estimating the amount of recruits as function of past disturbance (logging and silvicultural treatments), assigned trees to species in the same proportion as that of observed recruits. Alder (1995) used the observed recruits as the species pool. Simulated recruits species were assigned according to the proportion of

observed number of recruits during the study period. In both studies, Vanclay (1992) and Alder (1995), the recruitment procedure can reproduce the situation observed in the field if simulation period is equal or less than the period of observations. Rare species, which may not have been observed in the recruit's pool during the observation period, would not be allowed to establish during the simulation, which may not be realistic if simulation is run for large periods.

2.7 Mortality

Mortality is the proportion of trees that die during the study period. It varies with time and space and is affected by many factors, including rare and infrequent events such as hurricanes, droughts, and fires (Alder 1995). Because of the high variability in mortality, large periods of observations are required to capture the characteristic mortality of a given site (Vanclay 1994). Mortality is among the most challenging processes to understand among stand dynamic processes, and several approaches have been developed to deal with this matter (Hawkes 2000). The way mortality is modelled varies greatly with the aggregation level of the model. Highly aggregated models such as whole stand models can treat mortality by assigning a constant rate of mortality. If the model is highly disaggregated, such as in individual tree models, a constant mortality rate should be enhanced by a procedure to assign individual trees to die every simulated period (Vanclay 1994). Studies in several tropical forests have shown that mortality is around 1-3% annually, with no variation among tree size class for trees ≥ 10 cm, but trees with very low growth rates showed higher mortality than those with high growth rates (Mervart 1972, Lieberman *et al.* 1985, Lieberman and Lieberman 1987, Swaine *et al.* 1987, Vanclay 1994, Alder 1995, Finegan *et al.* 1999). Modelling mortality in disaggregated models is commonly done stochastically by estimating a probability for a tree to die in a given period (Botkin *et al.* 1972, Botkin 1993, Vanclay 1994, Alder 1995, Ong and Kleine 1995). The main difference in modelling mortality is on the factors considered to estimate the mortality probability and the definition of the causes of mortality.

Vanclay (1994) simplified the modelling of mortality process and considered two types of mortality according to their nature as catastrophic and regular. He considered regular mortality, the one caused by senescence, competition, pests, diseases, or weather phenomena. Catastrophic refers to death caused by abnormal conditions like storms, hurricanes, wildfires and other factors that occur irregularly. However, because of the high annual variability of mortality, the difference between regular and catastrophic mortality may sometimes be difficult to discern and the distinction between the two may be controversial.

In his model for North Queensland (Vanclay 1989 a) considered only regular mortality and used a logistic function to estimate the annual mortality probability as function of stand basal area, and dbh. Vanclay's approach of modelling mortality is used in other growth models of tropical forests, differing in the set of predictor variables used to estimate the annual probability (e.g. Alder 1995, Ong and Kleine 1995).

Botkin (1993) considers two main categories of mortality, but in a different way from that of Vanclay. The first cause of mortality is the one that can not be explained by the factors explicitly considered, called inherent risk of death. It is independent of age or tree size, exponentially distributed, and it is function of the species maximum age [$M_i = 1(1 - \epsilon_i)^{\text{MaxAge}_i}$] where ϵ_i is the annual probability of death for i -th species. The second category of mortality is competition-induced (density-dependent), set for trees growing under a given threshold. This approach has been adopted by other gap models and Botkin (1993) expressed his surprise that after two decades little had been done to change the structure and even the arbitrary parameters set for the mortality procedure in earlier gap models.

Hawkes (2000) reviewed 61 woody plant (trees and shrubs) mortality algorithms used in different modelling techniques among empirical, process, and gap models. Her conclusion was that algorithms methodologically operable and theoretically sound are difficult to develop, so that mortality must be modelled by consensus. Realistic modelling of mortality requires knowledge not only of the causes of mortality, but their variability as well.

Lieberman and Lieberman (1987) studied an undisturbed *Pentaclethra*-forest at La Selva, about 7 Km West of Tirimbina, and classified it as among the most dynamic tropical forests studied then. They indicated high rainfall, saturated soil, strong winds and steep topography as the main contributing factors. Aguirre (1999) found, in a logged and silviculturally treated *Pentaclethra*-forest at Corinto, that the greater proportion of deaths was density-independent and due to disturbance. Most large dead trees die for this reason and an important proportion of small trees die damaged and destroyed by falling large trees. Recognition of this important cause of density-independent mortality led to rejection, in this study, of the terms "intrinsic" or "inherent" mortality, used by Botkin (1993).

Mortality is among the most important process particularly in individual tree models. Stage and Renner (cited by Vanclay, 1995) reported about 80% of the variability in volume predictions as caused by uncertainties in mortality estimates in temperate forests. In fact, the presence or absence of an individual tree in a stand may make the difference especially if the tree is large. The death of a big tree has the following consequences in a model: (a) its basal area is removed from the stand basal area accounts; (b) the remaining trees have more space and resources for growth; (c) new recruits are more likely to establish; and (d) remaining trees have less density-dependent death probability in the next period. The consequence of these effects is that a good growth equation is not an indicator of a good model if mortality can not be predicted with certain level of accuracy. Vanclay (1989) considers the development of an individual model for TRF infeasible because of the difficulty to predict mortality. However, this is not to discourage the development of individual tree growth models for TRF.

Mortality is generally expressed in terms of percentage of dead trees over initial number of trees using linear or logarithmic function (Lieberman *et al.* 1985, Sheil and May 1996). These functions are used when field data is available and a description of the system is required. However, in modelling, where predictions of mortality are required, mortality is calculated using logistic regression functions of the general form

$$P_{\text{mort}} = (1 + e^{f(x)})^{-1} \quad (2.7)$$

with $f(x)$ as a linear function of several explanatory variables (Vanclay 1994). Explanatory variables can be stand density (basal area or volume) mean stand diameter (Ong and Kleine 1995), crown exposure (Alder 1995) or any other variable which may affect the survival of trees. Equation 2.7 does not always fit well to empirical data and other methods must be found to estimate mortality. For instance, Ong and Kleine (1995) were able to fit the equation for pioneer species in a Dipterocarp forest but did not succeed to fit it for non-pioneers. Desanker and Prentice (1994) used negative exponential equations expressed as function of tree status and the amount of light received by the crown, to predict mortality in their gap model.

Studies in TRF show that apart from trees dying as result of competition and others by the density-independent mortality, others exist that die smashed under big tree fall or broken pulled by a liana tied to a falling tree (Lieberman *et al.* 1985; Aguirre 1999, Finegan and Camacho 1999). This tree falling pattern would result in large gap formation. Because falling large trees could damage and kill smaller trees in a distance proportional to their total height, it would require that a gap-model using small patches (say 10x10 m) take into account the effect of tree fall into the neighbour patches. On the other hand, slow growing trees not always result from competition effects so that a threshold to define "slow growth" should be clearly defined. There are species which characteristically grow slowly such as the understorey species of the *Pentaclethra* forest in Central America, *Capparis pittieri* which presented median growth between 0-1 mm.yr⁻¹ (diameter growth estimations of six years) (Finegan *et al.* 1999). Finegan *et al.* (1999) for instance, found that only trees with negative or null increments had significantly higher mortality rates.

2.8 Logging and silvicultural treatments

Silviculture is the manipulation of the forest to favour certain species and thereby, to enhance its value to man. More commonly, manipulations are to favour timber species

(Graaf 1986, Whitmore 1990). There is a variety of silvicultural treatments and the selection of one depends mainly on the forest structure, species composition, merchantability, and management objectives. There is no single silvicultural treatment that can be prescribed for all forest types, or for all stands in the same forest type.

Timber extraction is one of the main objectives of tropical silviculture (Whitmore 1990). Polycyclic silvicultural systems are commonly used in tropical forests (de Graaf 1986, Lamprecht 1990, Whitmore 1990) to minimise canopy opening as required for sustainable forest management of uneven aged TRF (Prabhu *et al.* 1996). Polycyclic silvicultural systems are based on repeated removal of selected trees in a continuing series of felling cycle, whose length is less than the time it takes the trees to mature (Whitmore 1990).

Polycyclic silvicultural systems consist mainly of selective removal of trees either by logging or silvicultural treatment. In a logging operation, mature trees, over a specified cutting diameter, are harvested. Because there are hundreds of tree species within a forest stand and not all are accepted in timber markets, species are generally classified according to the timber market requirements. The classification nomenclature could vary from one region to another, but commonly it incorporates the value of timber. The Costa Rican Forest Chamber, for instance, uses the terms “desirable” for highly valuable timber such as that of *Swietenia macrophylla*, “acceptable” for merchantable, but with less value than desirable species, such as *Pentaclethra macroloba*, and non-commercial for species which timber is not accepted in local markets. Minimum diameter allowed to cut is established on base of species growth characteristics (e.g. Vanclay 1989 b) and is normally specified by species group within local forest legislation. Non timber forest products have revealed to be important for a sustainable management but harvesting of these products are rarely modelled in growth and yield models. There will be no more reference to non-timber forest products in this review and all harvesting are referred to timber only.

Modelling harvesting practices requires knowledge of the harvesting regime (by cutting cycle or by stocking), minimum cutting diameter and other variables like the number (or

percent) of trees to be left as mother trees or reserves. The logistic equation is generally used to predict the probability of a tree to be harvested or damaged by a logging operation. Vanclay (1989 b) used such an equation with species, tree size, and time since last harvesting as explanatory variables for selecting logging trees in Northern Queensland forests. Stem quality indicator such as that developed by Hutchinson (1987) for logs used for sawn timber, could also be included in predicting functions to estimate whether a tree will be logged or not. Ong and Kleine (1995) described a method used for Malaysian Dipterocarp forests. They take into account economic restrictions by evaluating the stocking before a logging operation, slope restrictions and tree size limits (lower and upper dbh limits). Once all restrictions are overcome, all mature trees are logged. The consequences of logging operation are expressed in terms of damage caused to remnant stand, by assessing different levels of injuries to crown and stem. Whitmore (1990) estimated that the amount of damage is function of the number of trees felled, while other authors (Alder 1995, Vanclay 1994b) used logged basal area, and terrain slope to estimate the amount of damage to remnant stand. Jonkers (1987) and FAO (1997) present some of the most detailed studies on damage caused by logging operation in tropical forests, however their results are not directly applicable to an individual tree model. Their response variable is the remnant stand damaged basal area of commercial species only. They do not provide information for non-commercial species damage, and damage is not classified into stem size, as is required for an individual tree model. Inglis *et al.* (1997) give information of the proportion of number of damaged stems but did not give detail of its distribution per size class. Kopelman (1990) studied logging damage at La Tirimbina and his results include all species (including non-merchantable) and each of his three damage categories is presented by stem size class.

Tropical forest simulation models rarely include silvicultural treatments. The North Queensland forest simulation model (Vanclay 1989b, 1992, 1994), and the Sabah Dipterocarp forest simulation model (Ong and Kleine, 1995), which were designed for forest management, and have been comprehensively described in the references above, do not include silvicultural treatments. Alder (1995) describes briefly the simulation of silvicultural treatments for cohort models as conceptually similar to a logging operation.

This view may be true for a cohort model and does not necessarily apply to an individual tree model. The difference is that while a cohort model simulates at an aggregated level and silvicultural treatments may be represented by a proportional reduction in number of trees or basal area of a given cohort, individual tree models need the exact indication of each particular tree that requires liberation and the tree that could be removed. Favrichon (1998) transition matrix model also simulates silvicultural treatments but does not describe in detail the procedure used.

In forest stand models, it is enough to specify the average volume to extract per area or a proportion of the total volume or basal area (either to be logged or to be left) without going through tree selection process. For individual-tree models, the exact tree to be harvested should be precisely selected from the current tree list. During a logging operation, the remaining trees could be damaged by falling logged trees or during skidding operations. Similarly, damaged trees could be selected according to tree size, topography, logging intensity and type of machinery used. The probability for a tree to be damaged in a logging operation may be estimated by fitting the logistic equation to individual tree data using maximum likelihood estimation. Vanclay (1989b) used tree size (diameter), topographic slope, basal area removed as explanatory variables to estimate the probability for a tree to be logged or to be damaged in a logging operation.

Silvicultural treatment is a kind of selectively reduce stems on the stand where trees not belonging to presently commercial species will be reduced to provide growth space for commercial species. Trees of commercial species could be removed depending on their stem form, health condition, and competition level within the neighbourhood. The silvicultural treatment of liberation applied at Tirimbina research site by the Unit of Natural Forest Management of CATIE for instance considered two steps after potential crop trees have been selected. The first step consisted in removal of competing trees of non commercial species, and the second step if two or more potential crop trees were competing, remove the one with less commercial value (Quiros and Finegan 1994). Depending on the process used to apply the silvicultural treatment (girdling or cutting

down), the damage to the remnant stand will be different. Treatment by cutting down trees will have an immediate effect on the stand as logging causing damage and gap opening. The effect of girdling will not be evident at the date of application but will take time to bring trees do death.

2.9 Model evaluation

One of the most important phases in model building is its testing against observed data or against theoretical principles. Model testing and evaluation are as important as the model conceptualisation itself. Because a model is an abstraction and a simplification of nature, its usefulness should be assessed by comparing model output with the nature being modelled. A thorough model evaluation is a complex process and would consist of several steps but should include qualitative and quantitative methods (Vanclay and Skovsgaard 1997). It is important to have the model objectives in mind when testing a model, since no model is expected to represent all the nature but the parts for which the model was defined to represent (Mankin *et al.* s.d.). Qualitative model evaluation could consist in testing whether the equations used represent the processes being modelled (Vanclay and Skovsgaard 1997). A more simple qualitative evaluation could consist in visual comparisons of simulated output with observed results. If a specialist in the system being modelled could not distinguish between simulated and observed, then the model is passed (Haefner 1996). Quantitative model testing consists of using numerical and statistical methods to compare the model output with observed data. Among the classical methods for model evaluation there is testing of statistical assumptions such as that the errors associated with the prediction should be normal, independent, and randomly distributed with zero mean and unknown variance. Vanclay and Skovsgaard (1997) stated that in forestry, model testing has been carried out in two steps, namely verification and validation. Verification consisting of the testing of the model using the data used to build the model while validation is done with data other than that used in model development.

The meaning of “verification” and “validation” are discussed in ecosystem modelling literature (Botkin 1993, Haefner 1996, Mankin *et al.* s.d.) and have been described as inappropriate for some reasons for an ecosystem model evaluation. Verification was redefined as the confirmation of the computer code and data used in the model to see if it represents what the modeller had in mind. Validation was redefined as the comparison of simulated results against nature to test whether the model is true or not. These terms are used in other scientific disciplines with different meanings: a model is valid if it is logically correct, and is verified if it is true. These meanings do not fit well in ecological modelling where the truth is not known in the strict sense of the word. The truth in ecology is no more than the representation of our perception of the ecosystem functions and in most of the cases it is limited by measuring instruments, time scales of observed data and complexity of the system. Therefore, it is not possible to prove a model true if we can not accurately assess the truth. Based on this discussion the terms “evaluation” and “testing” are currently more acceptable (Botkin 1993, Haefner 1996, Mankin *et al.* s.d). During model testing and evaluation questions like “is the model stable in the long term?” and “ does the model react as expected?” among others particularly concerning modelling objectives should be answered (Jorgensen 1997).

Mankin *et al.* (s.d.) discuss the validity and usefulness of an ecological model according to its ability to represent the modelled system properties and conclude that ecosystem models could only be invalid-useful since no model could represent all the ecosystem properties (condition to invalidate the model) but only parts of it (condition for usefulness). Then, the model could be assessed according to its “adequacy”, which is measured by the fraction of the system that is correctly modelled and “reliability”, which is the fraction of the model output that is correct. These authors also suggest that some of the modelling objectives could be attained without validation (comparison of model simulation with nature) if models are developed with purposes other than predicting system behaviour. The model objective could be guiding research and data collection. They also suggest that systematising a concept in the form of a model is the most valuable contribution which modelling can offer to ecology.

Evaluating a forest growth model is limited by data constraint and some authors have used the short-term observed data to compare with model simulations (Alder and Silva 2000), long term simulations compared with undisturbed forest stand (Bossel and Krieger 1994) or both (Favrichon 1998). Vanclay and Skovsgaard (1997) describe the real difficulty in obtaining independent data in TRF and the difficulty of having a model validated, in the strict sense of the word. These authors indicate some models that despite their popularity and acceptance in modelling and management failed the rigorous test of validation. The classical example of a non-validated model is the discrete population growth logistic model, which produces chaos under given range of parameters (Hilborn and Mangel 1997, Jorgensen 1997). Although models may not be adequately validated or tested, they could be helpful in testing new hypothesis and increase the understanding of the phenomenon being modelled (Mankin *et al.* s.d.). Vanclay and Skovsgaard (1997) presented some general guides for forest growth model evaluation and discuss applicability of the procedures. These authors discuss several techniques to deal with this situation, among splitting the data set in two parts so that one subset can be used to develop the model and the other to evaluate the model, and use of bootstrap, and jack-knife methods for more robust parameter estimation. The problem with splitting data for model building and testing is that generally, data are limiting in most of the cases, and splitting may weaken the power of parameter estimation and non-important variables may be included in the model. On the other hand, using all data for model development in detriment of evaluation is also of no use at all because there is no way to find out whether the model produces what it is meant to produce. Bootstrap and jack-knife procedures are alternative methods to deal with this data limitation.

Model evaluation should consider the logic and the bio-logic of the components. This means each step of model building should be evaluated and discussed in the light of biological theories. If the model uses biological equations, then the meaning of the coefficients should be discussed taking into account their magnitude and sign. After integrating, all components of the model should be evaluated by experienced foresters as a

whole and field observations should be compared with predictions of the model. Graphical and analytical procedures can be used although analytical methods appear to be difficult when the integrated model has feedback loops and several equations (Vanclay and Skovsgaard 1997).

The model could be evaluated for statistical properties, that is, if statistical assumptions are satisfied (Vanclay and Skovsgaard 1997). Graphical methods are commonly used to evaluate error (residual) distributions. Transformations may be performed to satisfy statistical requirements. Statistical tests are also required to check the model precision. The simplest statistical test of model performance is a regression of observed on predicted data with a null hypothesis that the slope is 1.0 and zero intercept. Another technique also used is the evaluation of a statistic called modelling efficiency (equation 2.8).

$$EF = 1 - \frac{\sum (y_i - \hat{y})^2}{\sum (y_i - \bar{y})^2} \quad (2.8)$$

This statistic provides a simple index of performance on relative scale where 1 indicates a perfect fit, 0 means that the model is not better than the mean and negative values indicate a poor model (Vanclay and Skovsgaard 1997). Ong and Kleine (1995) for instance, used this function to evaluate DIPSIM. This statistic can be incorporated as the objective function in parameter optimisation routines like Simplex (Nelder and Mead 1965) for model construction to find the best set of parameters.

Sensitivity analysis consists of checking the model response to parameter changes (equation 2.9) (Soares *et al.* 1995).

$$S_p = \frac{\partial y / y}{\partial p / p} \quad (2.9)$$

This test produces information on the robustness of the model. Models that are not sensitive to parameter change are called robust while those that produce big changes in output with little parameter change are called sensitive. A model is required to be robust within a certain range of parameter change. If sensitivity analysis is to be performed, a decision should be taken on which parameters should be tested. A common forest growth model has several parameters so that not all parameters and their combinations can be tested.

The great emphasis in Vanclay and Skovsgaard (1997) is that model evaluation should concentrate in four points: (1) logic and bio-logic, (2) statistical fit and properties of the selected functions on data, (3) characteristics and distribution of residuals, and (4) sensitivity analysis. In all phases of model evaluation it should be borne in mind that, model evaluation should reveal where future data collection and model revision efforts may be more useful. The model should be questioned about biological principles as well as statistical requirements. The modelling assumptions adopted "because they are more feasible" but not biologically or statistically sound should be avoided and replaced as soon as data and information become available.

2.10 Standards and criteria for model selection

Selection of a model is the most important preliminary stage for model development. Alder (1995) states that data availability and objectives of the model define model selection. This is true considering that most of the time we require a model to respond to certain questions and the data to be used in local archives or to be taken from the literature is limiting.

Considering this limitation, Alder (1995) presents a diagram for model selection according to data availability and modelling objectives. Since there are many modelling criteria, and several modelling strategies could be adopted for the same objective, selecting one may be a complicated process in which available data, modelling objectives, and site related publications should be carefully reviewed. Because there are several modelling approaches, the final model to be developed would result from several interaction processes of trial and error. Botkin (1993) and Alder (1995) present the standards and criteria for model selection.

They use different terminology but the concepts are equivalent. Botkin's terminology is used here for comprehensiveness but Alder's will be used for specific aspects not referred to by Botkin.

Botkin (1993) describes three criteria for model selection, which have to be defined before a model can be designed. These criteria are realism, generality, and accuracy. Realism is how the model outputs are comparable to the observations in terms of qualitative shape of the output curves. The generality criterion refers to the range of applicability of the model, that is, the area extent of the forest type or types to be covered by the model. Accuracy refers to how quantitatively the outputs differ from the observed values. In fact, realism expresses the quality of a model while accuracy expresses the quantitative value of a model. To build a model, these criteria should be defined at the beginning taking into account that not all but two criteria could be achieved by a model. After choosing the criteria to be prioritised, some procedures must be defined to be the base of the model:

a) *Choose variables of interest*

Define the output required from the model. Depending on the objective of the model, the common output requested from a forest model are biomass (total or by species), merchantable timber, and individual tree characteristics.

b) *Choose the structure level and conceptual basis*

Define the output level desired and the model working level. Botkin describes ten ecological levels that can be considered, ranging from cellular phenomena through individual trees, populations and ecosystems to the biosphere level.

Alder, from the point of view of modelling forest management, describes the structure level in terms of aggregation of the forest elements. He classifies as highly aggregated models those that operate on whole-stand statistics without considering individual trees or groups of trees or species. At the other extreme, he considers highly disaggregated models those that operate on individual trees with all the

detailed information of species, size, and sometimes the spatial location (see Section 2.2). Conceptual basis refers to the principles on which the model should stand. Conceptually, models may be process-based or empirical. Process-based or biological models use energy and matter flux as the principle of functioning while empirical ones use statistical principles and easy of data collection.

c) *Choose the generality criterion*

Determine the range of phenomena the model is required to simulate. A general model also requires a data set covering the area of study. If the generality criterion is chosen for a large area, then description of functioning of the system in that region must be available to express the characteristics. For instance, *Pentaclethra forest* may be defined as the generality criterion.

d) *Determine the goal of the model*

Determine whether the goal is realism or accuracy. If the model is to be used for management, a certain level of accuracy is desirable for sound decision making. However, if the objective of the model is to understand the ecosystem dynamics and data availability is limiting, realism should be the most appropriate decision.

Among other aspect pertinent to forest modelling referred to by Alder (1995) is the requirement to define if the model output is deterministic or stochastic. Deterministic models are preferable in all the cases (research and management) for their easy interpretation. Nevertheless, it is difficult to find a complex of functions that can deterministically and accurately simulate natural ecosystems, especially when working at the individual tree level. In this case, stochastic functions may be used to predict the future condition of the forest stand. When dealing with individual trees, for instance, the commonly available information for mortality is the percentage of the whole-stand death rate. The question of which particular tree is going to die in a given period remains unanswered. Part of this question may be answered knowing the factors that affect tree mortality but the intrinsic mortality, which can not be explained by any of these factors, is

to be left to randomness. When good interpretation is done to stochastic model output, then, it may be of great use in research.

3 Materials and methods

An extensive literature review was presented in Chapter 2 with the aim to provide the necessary background on modelling tropical rain forests. This information was used in the selection of the conceptual basis of the model as well as the model development and testing. Among the existing modelling strategies, gap-modelling strategy was selected because of its ability to represent the main forest stand dynamics driving forces such as gap formation and species light requirements for regeneration and establishment among others. Section 4.1 presents details of model development starting from function selection and parameter estimation from field data, to selection of the ecological parameters considered relevant in *Pentaclethra* forests. Section 4.2 is dedicated mainly to model testing and evaluation. The model was run starting with real forest data and several aspects of forest dynamics were evaluated. Finally, when the model was found to be representing most of the characteristics of interest in *Pentaclethra* forest dynamics, it was used to evaluate the effects of silvicultural treatments on the remnant forest stand. Species richness and diversity, diameter distribution, and cutting cycles were among the aspects evaluated.

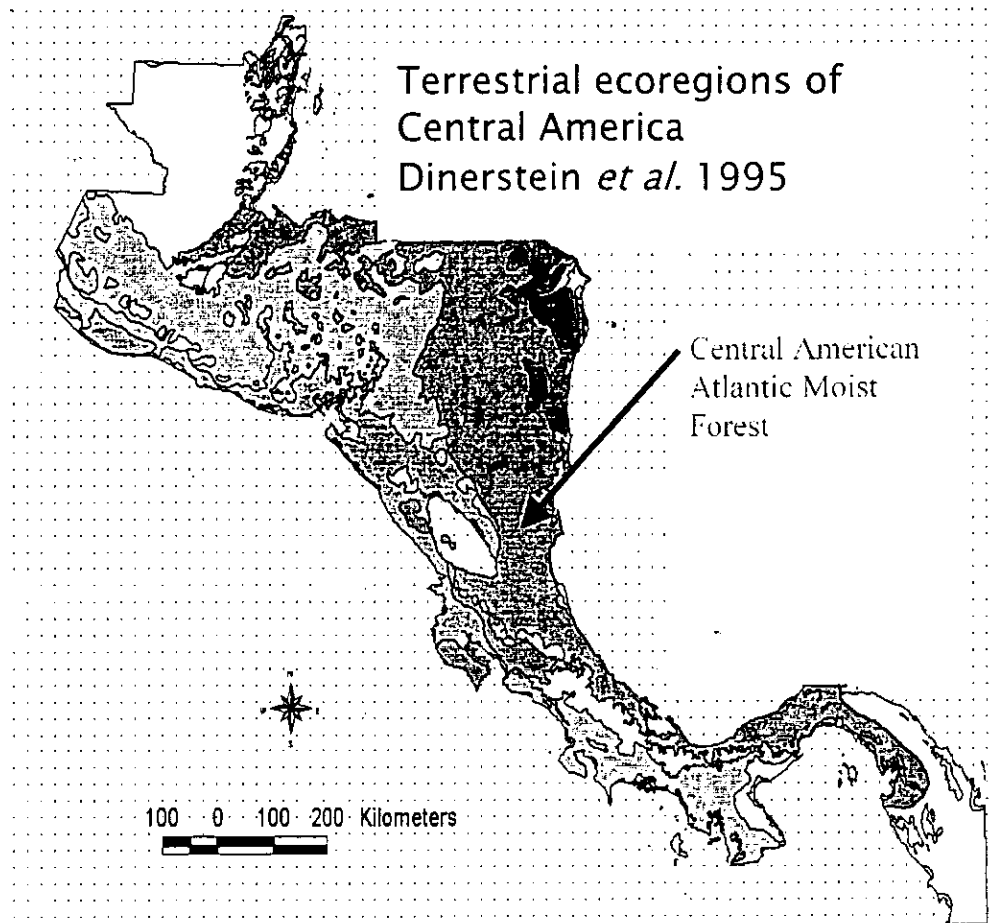


Figure 3.1 Location of the Central American Atlantic Moist Forest Ecoregion (CAAMFE) and the study sites

3.1 Site description

The model was developed for *Pentaclethra* forests of Central America (**Figure 3.1**). In this section, there is a summary of the ecological characteristics and forest dynamics in four *Pentaclethra*-forest research sites, one of which (Tirimbina) was used for model development. The other three sites are Corinto (Costa Rica), La Lupe and Los Filos (Nicaragua) (Finegan and Camacho 1999, Finegan *et al.* 1999, Castillo 1997, Mejía 1994).

Table 3.1. Description of the four research sites in *Pentaclethra* forest, used as the base for Gavilan model development and testing.

Site	Tirimbina	Corinto	Filos	Lupe
Geographical Location	Northern Costa Rica, 10°24' N and 84°06' W, bnh-T	Northern Costa Rica, 10°13' N and 83°53' W	Southern Nicaragua, Rio San Juan , Gran Reserva Biologica Indio-Maiz buffer zone. 84°45'W and 11°10'N	
Altitude (masl)	160-220	235-345	100-200	100-200
Precipitation (mm)	3,800	4,000	3,000	3,500
Topography	Low hills dissected by water streams, with steep slopes 0-30%	Plain to undulated, with steep slopes 0-40%	Generally flat, with some low hills	Undulated, with slopes 10-40%, dissected by water streams
Temperature (°C)	24.5	23.0	25	25
Observation period	1988-98	1988-98	1992-97	1990-97
Plots (plot area)*	9 (100mx100m)	9 (100mx100m)	8 (100mx100m)	6 (100mx100m)
Logging year	1989-90	1991	1992	Not logged
Treatment year	1990	1992	Not treated	1991-92

* Number of plots and (effective plot area).

Forest stand at each of the four research sites indicated above was described for changes in stand density, structure, species composition, diversity, mortality, recruitment, and growth rates. The geographical location and general description of the sites is presented in Table 3.1. All study sites fall within the *Pentaclethra* forest (Finegan and Camacho 1999) which is part of the Central American Atlantic Moist Forest Ecoregion (Dinerstein *et al.* 1995). The forests of this region are fragmented as consequence of the extension of the agricultural frontier. The study sites are located within buffer zones of conservation areas, where remainders of primary and secondary forests are mixed with pastures and agriculture fields (Finegan and Camacho 1999). The soils are highly weathered, acid, and infertile (Mata 1997, Finegan and Camacho 1999, Mejía 1994).

The sites have been measured for five to ten years between 1988 and 1998 using forestry permanent sample plots mensuration procedures (Alder and Synnott 1992). One-hectare (100m x 100m) plots were used and all stems (trees, tree ferns, and palms but not lianas) with DBH (diameter at breast height) ≥ 10 cm were measured. The observation period is short relative to the longevity of the trees in these forests but conclusions concerning forest stand dynamics of the observed period and other *Pentaclethra* forests could be drawn. This information, as well as from other *Pentaclethra* forests (e.g., Brandani *et al.* 1988, Lieberman *et al.* 1985, Lieberman and Lieberman 1987, McDade *et al.* 1994) and tropical rain forest in general (Swaine 1989, Whitmore 1990), was used to discuss the results obtained from simulation scenarios.

All the results were averaged by area (e.g. trees ha^{-1} , basal area in $\text{m}^2 \cdot \text{ha}^{-1}$). For those years where the period between the previous mensuration and the actual mensuration is more than one year the number of recruits and the number of dead trees were averaged to produce the corresponding annual values. The number of dead trees only considers those identified as natural mortality. Trees killed by harvesting, harvesting damage and silvicultural treatment were not counted as natural mortality.

In general, the considered study sites present similar stand density, structure, and species composition. show the general tendency through the period of direct measurements in stand density, recruitment and mortality rates, species richness and diversity. The four forest stands have average densities (trees $DBH \geq 10$ cm) before intervention ranging from 400 to 500 ha^{-1} and basal area between 20-28 $m^2 \cdot ha^{-1}$ (Figure 3.2). Logging and silvicultural treatments were the major causes of annual variations within the same site. Differences in plots measured each year do not constitute an important source of annual variation in stand density. The figures observed in these areas are close to those found in an undisturbed *Pentaclethra* forest at La Selva (Lieberman and Lieberman 1987) and other neotropical lowland rain forests (Swaine *et al.* 1987). Natural mortality is highly variable from one year to another (Figure 3.2), which is typical for 1-ha plots (Lieberman and Lieberman 1985). Logging and silvicultural treatments may have increased significantly the number of dead trees and reduced the basal area. Tirimbina and Corinto, for instance, increased three fold the number of dead trees per hectare a year or two after logging. Most of the trees could have been directly damaged by falling trees or machinery, or trees that die as consequence of abrupt canopy opening. Alder (1995) reported an increased mortality after logging, which he attributed to excessive canopy opening and increased susceptibility for damaged trees to fungal infections. However, the general tendency is 5-15 $tree \cdot ha^{-1}$ dead annually (Figure 3.2 a) which means 1-3% annual mortality rate (logarithmic model) falls within the range observed in tropical forests (Swaine *et al.* 1987). Lieberman *et al.* (1985) found varying mortality rates (1.8-2.2%, logarithmic model) among plots in the old growth undisturbed *Pentaclethra* forest at La Selva in a 13-year observation period.

The number of recruits is equally variable from one year to another within the same site with 5-30 $recruits \cdot ha^{-1}$ (1-6% annual recruitment) (Figure 3.2 b). Logging and silvicultural treatments seem to stimulate recruitment. In fact, the average number of recruits doubled after logging at Tirimbina and Corinto. The balance between mortality and recruitment suggests stability in the number of trees for Corinto, but not at La Lupe and Los Filos, while at Tirimbina there is an increase in the number of recruits after intervention (Figure 3.2 c). The high mortality originated after silvicultural intervention is compensated by a

proportional number of recruits. Years of negative balance (Recruitment-Mortality) tend to be followed by years of positive balance. At Los Filos and La Lupe there were no years of negative balance, which is less variable compared to Tirimbina and Corinto.

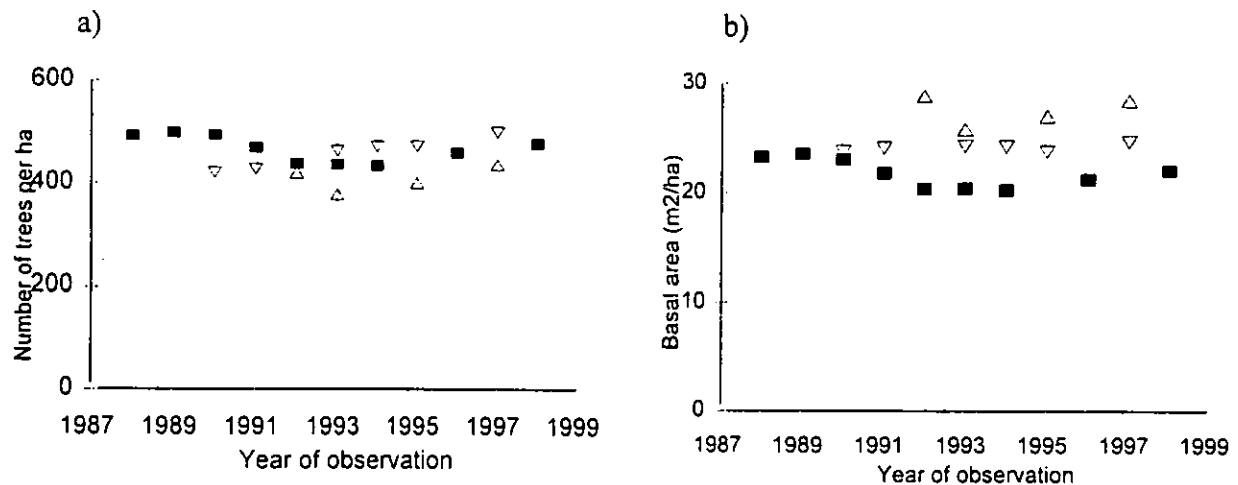
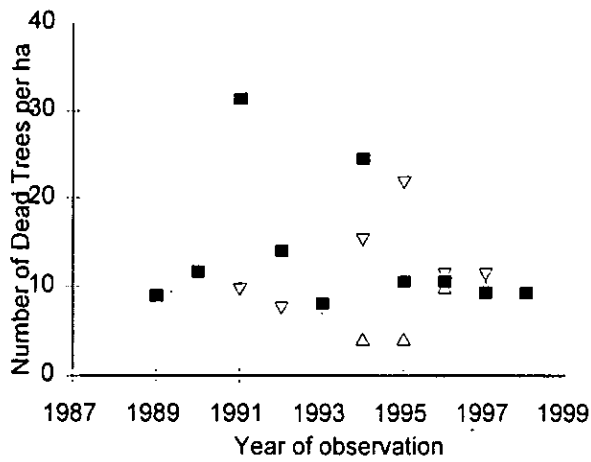


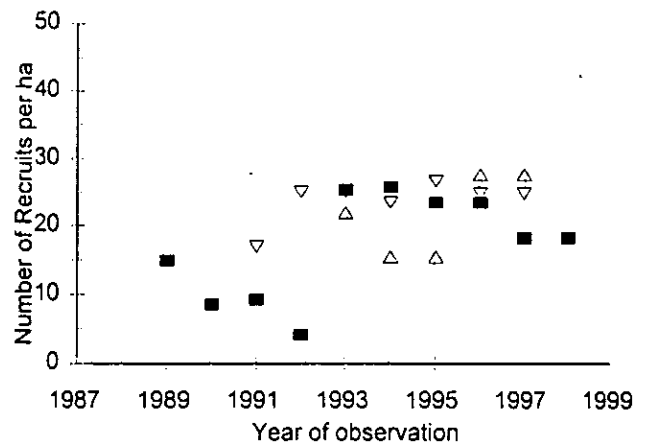
Figure 3.2 Forest stand density in four *Pentaclethra* forests in the Central American Atlantic Moist Forest in the period 1988-1998 for trees $dbh \geq 10$ cm. a) Number of trees; b) Basal Area ($m^2 \cdot ha^{-1}$). Tirimbina (■), Corinto (○), La Lupe (▽), and Los Filos (Δ).

The Nicaragua sites were not evaluated for species richness and diversity because species identification needs to be completed. Tirimbina and Corinto averaged 90-103 species per hectare and 3.8-4.3 of Shannon diversity index respectively (Figure 3.3 a-b). Lieberman and Lieberman (1987) found species richness varying from 96-107 species per hectare at La Selva undisturbed forest, which is comparable to Tirimbina and Corinto. *Pentaclethra maculosa* is the most dominant species in all sites comprising between 11.0 and 25.5% of the total number of trees. Palms, such as *Welfia georgii*, *Socratea exorrhiza*, and *Euterpe precatoria* are among the most dominant species comprising up to 10% of the total number of trees. The most abundant species vary from one site to another, but among the 15 dominant species at the initial mensuration, there are some common species in all sites

a) Mortality



b) Recruitment



c) Balance (recruits - deaths)

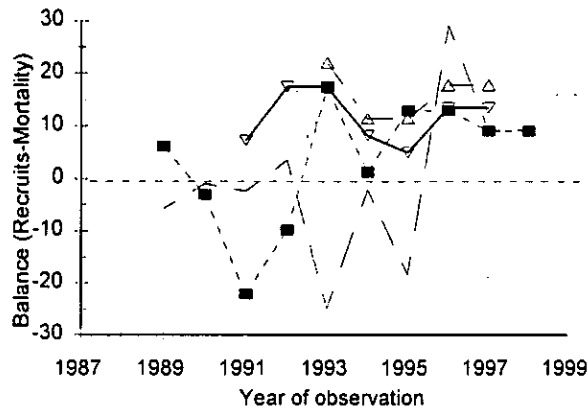


Figure 3.3. Forest stand dynamics (Mortality and Recruitment) in four *Pentaclethra*-forests in Central American Atlantic Moist Forest in the period 1988-1998 for trees DBH ≥ 10 cm. A - Number of dead trees; B - Number of recruits; C - Balance (Recruitment-Mortality). Tirimbina (■), Corinto (○), La Lupe (▽), and Los Filos (△).

besides *Pentaclethra macroloba*. These include the canopy species *Carapa guianensis*, the intermediate species *Dendropanax arboreus*, and *Protium spp.* (Figure 3.3 c-f). At La Lupe and Los Filos, several species remain to be identified or have been identified only to the botanical family. At Tirimbina, most of the species not identified at the first mensuration have been fully identified by the last mensuration. By the 1996 mensuration, there were less than ten individual trees, out of 4000, without identification to species or genus, though all have families. The most abundant species at the beginning of the study maintain their rank position in the last mensuration. The species relative abundance did not vary significantly during the study period, although at Corinto it could be clearly identified the effect of logging expressed by reduction of the abundance of merchantable species *Carapa guianensis*, *Minquartia guianensis*, and *Dendropanax arboreus* (Figure 3.3 d). Species composition in all the four sites is similar to the description of La Selva undisturbed forest stand where *Pentaclethra macroloba* accounted for 13.7% of the stems ($dbh \geq 10$ cm) and palms (*Welfia georgii* and *Iriartea deltoidea*) as well as the canopy *Carapa guianensis* were among the most abundant species (Lieberman and Lieberman 1987).

The diameter distribution shows the classical reverse-J in all sites with no significant differences between the initial and final observation period (Figure 3.4 a-d). La Lupe and Los Filos lower diameter classes increased substantially from the initial to the final observation period as high recruitment was registered during the study period. The Liocourt ratio ($=NDC_{i+1}/NDC_i$) (Vanclay 1994) varies from 0.2 to 0.7 with higher values in the intermediate size classes (Figure 3.4 e). The Liocourt ratio is an indicator of the structure and the regeneration capacity of the forest stand. Its theoretical value is about 0.5 and constant among diameter classes, but Vanclay (1994) found that in TRF this could vary around the expected theoretical value.

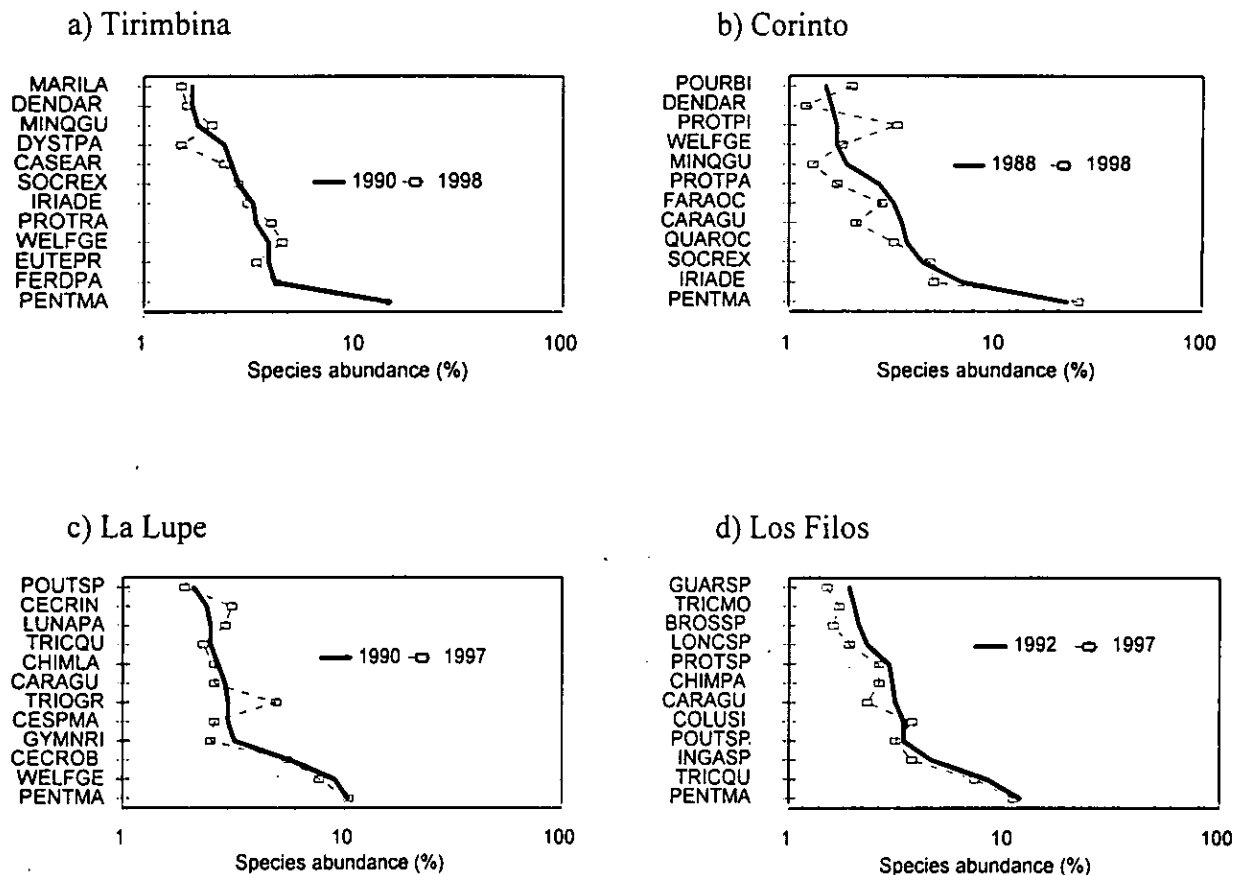


Figure 3.4 Tree species composition and diversity in four *Pentaclethra* forests of the Central American Atlantic Moist Forest in the period 1988-1998 for trees dbh \geq 10 cm.

Finegan and Camacho (1999) studied the dynamics of Tirimbina in the period between 1988 and 1996 including the effects of silvicultural treatments on diameter increment. They found median diameter increment of 3.0 mm.yr⁻¹ for all trees but commercial and potential crop trees growing faster with median diameter increment between 5-6 mm.yr⁻¹. In general, there were no significant differences between treatments between the period 1990-1993, however, commercial species and potential crop trees grew faster in silviculturally treated plots during period 1993-1996. For the period 1993-1998, the median diameter increment of potential crop trees (10 \leq dbh $<$ 40 cm) of treated plots was double of the control plots

(Finegan *et al.* 1999). Mejía (1994) found mean diameter increments between 2.3 and 6.9 mm for all species at La Lupe but commercial species grew faster compared to the all species. There was no clear tendency of diameter increment in relation to the initial dbh but Camacho (in prep.) found a positive relation between the median diameter increment and the initial dbh for trees until dbh class < 70 cm at Corinto. Camacho (in prep.) also found that understorey species grew slower than canopy trees. Finegan *et al.* (1999) and Camacho (in prep.) aggregated species according to growth rates in five growth groups between very fast and very slow growing. They found pioneers and non-pioneers sharing the groups, so that although very fast growing species were pioneers, there were some pioneers found in very slow growing groups.

3.2 Model development

3.2.1 Species aggregation

In this study, a procedure similar to that used by Finegan *et al.* (1999), with some modifications, was used. The purpose of species aggregating in this study was to group together species with similar growth potential. Because potential growth is more related to the maximum dbh increment, and Finegan *et al.* (1999) found that the first quartile of the observed diameter increment in a six-year period was the least important of the parameters used in the analysis. In this study, the median and third quartile of dbh increment of the period 1990-1998 were the only variables used. In order to have species assigned to a single group, and hence, derive a single set of parameters for a species, the effect of silvicultural treatment was not included in grouping criteria. The first step for each species aggregation consisted of classification into growth rate categories. Species with total number of trees $3 < N < 70$ individuals were used in a clustering procedure by the growth characteristics, namely the median and third quartile. Student's t^2 statistic (SAS 1989) suggested six groups as providing maximum grouping effect. However, for biological significance and nomenclature, five growth groups denominated by Finegan *et al.* (1999) as (i) very slow growing (ii) slow growing (iii) moderate growing (iv) fast growing and (v) very fast

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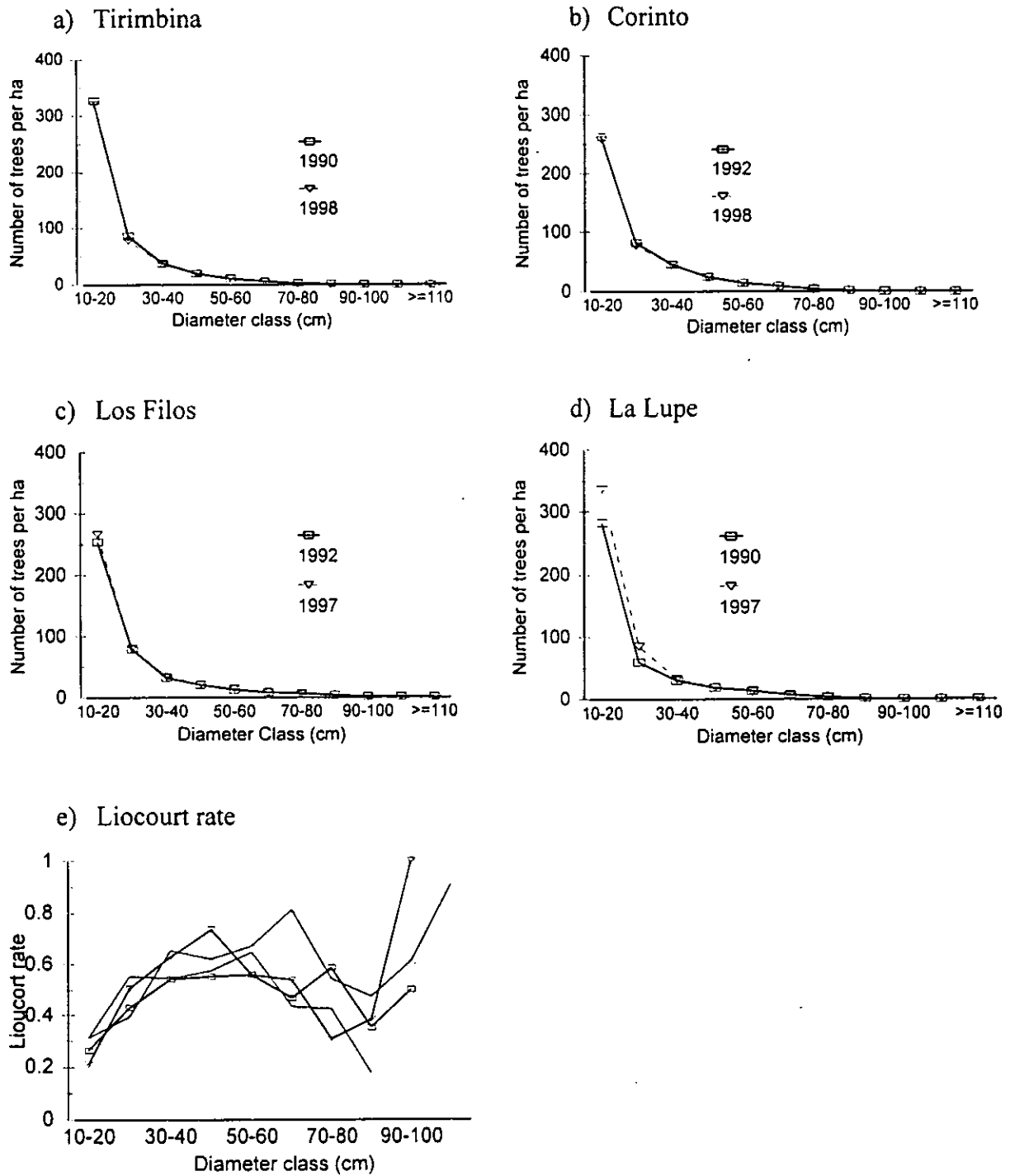


Figure 3.5 Diameter distribution in four *Pentaclethra*-dominated tropical rain forests in Central American Atlantic Moist Forest in the period 1988-1998 for trees DBH ≥ 10 cm. Diameter distribution for all species at the first and the last year of observation at a) Tirimbina, b) Corinto, c) Los Filos, and d) La Lupe; e - Lioucourt rate ($=NDC_{i+1}/NDC_i$) at the beginning of observations.

growing, were used. Abundant species, *Pentaclethra macroloba*, *Protium ravenii*, *Ferdinandusa panamensis*, and *Minquartia guianensis*, each with more than 70 individuals, and well represented along their respective range of size classes were considered to be enough to stand by themselves as individual species. Species with less than 3 individuals, but with at least one individual, were later assigned into the resulting growth groups using the discriminant procedure and the observed diameter increment.

The second step consisted in subdivision by species adult position in the forest stratum. Previous studies showed that species occupying different forest strata represented different growth patterns (Finegan *et al.* 1999) so that species in growth groups were a posteriori divided according to this criteria. Meaningful adult positions were defined by these authors as (i) understorey, (ii) intermediate, (iii) subcanopy and (iv) canopy.

3.2.2 Diameter growth estimation

Diameter increment functions

Dbh increment could be estimated by Botkin's (1993) fundamental function, or by Moore's (1989) growth function, or by a logistic population type function (Table 3.2). The first two functions are very similar in form but Moore's is considered as having better biological interpretation and is considered an evolution of Botkin's fundamental growth (Bugmann *et al.* 1995). These equations predict the potential diameter increment and further, reduced by a set of considered factors. The diameter increment functions have been enhanced to allow power functions for estimating height. The considered reducing factors in this case are tree crown exposure, crown form, and patch density.

Table 3.2 Diameter increment functions used in Gavilan 1.0

Function name	Function form
Logistic-type function	$dD = dD_{\max} \left(1 - \frac{D}{D_{\max}} \right) * \min(f(\text{crownform}, \text{crown exposure})) \quad (3.1)$
Fundamental growth function (Botkin 1993)	$dD = \frac{g_s D \left(1 - \frac{DH}{D_{\max} H_{\max}} \right)}{2a_s + 3b_s D - 4c_s D^2} * \min(f(\text{crownform}, \text{crown exposure})) \quad (3.2)$
Modified fundamental growth function (Moore 1989)	$dD = \frac{g_s D \left(1 - \frac{H}{H_{\max}} \right)}{2a_s + 3b_s D - 4c_s D^2} * \min(f(\text{crownform}, \text{crown exposure})) \quad (3.3)$
Exponential function	$dD = e^{(b_0 + b_1 D + b_2 D_{\max} + b_3 g_s + b_4 CF + b_5 CE)} - \alpha \quad (3.4)$

Diameter increment (dD) is estimated as function of current tree characteristics (dbh - D , total height - H , crown form - CF , and crown exposure - CE), species group properties (maximum dbh - D_{\max} , maximum potential growth - G , and maximum height - H_{\max}). Botkin's, Moore's, and logistic-type functions were selected because of their theoretical background while the exponential was selected because of simplicity in parameter estimation and statistical fit.

The maximum potential dbh increment (G) was estimated from field observations by fixing the dbh at which maximum increment was observed to two thirds of the maximum dbh and using the observed maximum dbh increment, maximum dbh, and maximum total height. Maximum height (H_{\max}) corresponds to the tree with the observed maximum dbh within species group. Parameters a , b , and c in Botkin's and Moore's functions are height function coefficients for species or species group and could be fitted separately (see Height Functions below). Maximum dbh was estimated from the field mensurations by species or species group (as defined in species grouping Section above) in all mensuration periods.

Because no big trees were observed in the study area and it is believed that the maximum observed diameter is generally lower than the expected maximum size (Clark and Clark 1999, Aguirre 1999) the maximum observed diameter was increased by 20 cm to allow trees to grow more than the observed size.

Competition effect and tree characteristics limitations

Once potential growth is estimated, the actual simulated growth is finally obtained by multiplying the optimum growth by a reducing factor. The considered reducing factors account for inter-tree within patch competition and tree specific characteristics. Three factors could be selected to reduce optimum growth, namely patch density, crown form, and crown exposure. The selection of factors used as growth modifiers was based on data availability, and consists of data traditionally collected in permanent sample plots for forestry studies (Alder and Synnott 1992). The factors considered in this study were found in previous studies, to be correlated with dbh increment (Siteo 1992, Finegan *et al.* 1999). Other gap models use other factors depending on what was found to be important in the region for which the model was designed. The factors normally considered include light availability, leaf area, potential basal area, site quality (which includes temperature, wilt factor, soil moisture, and nitrogen) (Botkin 1993, Shugart 1998, Urban 1993). These factors were not all adopted literally because of the differences in the measuring methods – for instance leaf area is represented in **Gavilan** by crown form while light availability is represented by crown exposure – and lack of significance in the region for which the model was designed – for example nitrogen availability, soil moisture, and growth degree days, which are not considered limiting factors in the study area (Vitousek and Denslow 1986, Lamprecht 1990).

The effect of each factor is evaluated by functions giving result in the range 0.0-1.0, where 1.0 means no effect, and zero the maximum effect. Exponential, Power, Weibull, Richard-Chapman, and Blumberg equations (Haefner 1996), in order of function complexity, are among the growth modifier functions that could be selected. Single or multiple factors can

be selected to reduce growth. In case where two or three factors are selected, then a selection could be made of the multiple effect among additive, minimum, multiplicative, and average effects. Parameters for these functions may be estimated by using an iterative parameter search procedure (Press *et al.* 1989) provided with the model. The procedure searches for the parameter combination that gives the least sum of square of error (SSE) of the simulated versus observed dbh increment, according to the following equation:

$$SSE = \sum_{i=1}^n (y_i - \hat{y}_i)^2 \quad (3.5)$$

During this procedure, recruitment and mortality were set to the observed data (not modelled) to avoid the random variation of these processes and the effect that could result on growth parameters. The effect of growth factors could also be evaluated by other tools external to the model (e.g. see Sit and Poulin-Constello 1994) and later incorporate the parameters into the model.

Diameter increment functions were evaluated by comparing graphically the simulated and observed growth curves, and statistically by means of the modelling efficiency estimator (Equation 2.8) and linear regression of observed on simulated diameter increment (see Section 2.9). Eight-year simulations, starting from 1990 forest conditions were used to compare with the observed diameter increment of the period 1990-1998.

Height functions

The total height could be estimated by quadratic or power functions depending on which function best fits the data. These two equations were included in the model because Lieberman *et al.* (1995) used a power function for total height estimation at La Selva, while the quadratic function fits well to Tirimbina data and is usually tied with the diameter growth function in gap models (Botkin 1993, Shugart 1998). An asymptotic function is described by Bugmann *et al.* (1995) as being more realistic than the quadratic and several gap models have already adopted it. The quadratic function, however, could represent well

the range of observed data and is easy to fit. In this study, the maximum height, the one observed in the field, was used so that fitting asymptotic function was not experimented. Quadratic and power functions were experimented with all species groups from Tirimbina using general linear regression (SAS Institute, 1989).

Volume functions

The Costa Rican Forest Service (MIRENEN 1994) has published two commercial timber volume (V_c) equations to be used in Atlantic lowland forests, for *Pentaclethra macroloba* and all other species as follows:

$$V_c = 0.000248 * D^{1.81847} * HC^{0.64862} \quad (3.6)$$

$$\text{Log}V_c = (2.03986 * \text{Log}D) + (0.779 * \text{Log}HC) - 4.07682 \quad (3.7)$$

These equations were adopted in the model for commercial volume estimation. The source (MIRENEN 1994) does not provide the definition of "commercial height" (HC). In order to use these functions, commercial height was defined, for the purpose of this model, as the distance in meters from the base of the tree until the base of the crown, which could be estimated as a proportion of the total height. Total stem volume is estimated by the following general function:

$$V_t = BA * H * FF \quad (3.8)$$

where BA is basal area (m^2), HT is total height (m) and FF is a unitless form factor ($0 < FF < 1$) that accounts for tree diameter reduction with height.

Crown form and exposure effect

Crown form and exposure are among the most important growth-modifying factors and previous studies have shown this factor to be correlated with dbh increment in tropical rain

forests in general (Alder and Synnott 1992) and at the Tirimbina in particular (Siteo 1992, Finegan *et al.* 1999). Both variables vary with time, silvicultural treatments, and the relative size of neighbouring trees. The model considers variation in crown form resulting from logging or tree fall damage. Crown exposure is considered with more detail. Considering that tree crown exposure is dynamic as neighbour trees die or new recruits are incorporated, then a way to simulate these changes dynamically is needed. To address this problem, a procedure that evaluates the mean and standard deviation of the total height in each patch was used. It was hypothesised that crown exposure is correlated with the standard distance (sd_{ij}) from the total height of the subject tree (ht_{ij}) to the patch mean height (hm_j), calculating standard) distance as

$$sd_{ij} = \frac{(ht_{ij} - hm_j)}{std_j} \quad (3.9)$$

where i is the subject tree subscript, j the patch subscriptor, and std_j is the standard deviation of the tree heights in patch j .

This seems reasonable since crown exposure evaluation is generally estimated visually by comparing the subject tree crown position, which depends on the subject tree's total height, and the total height of the neighbouring trees. To test this hypothesis, a logistic function (Equation 3.10, Neter *et al.* 1996) was fitted.

$$P(Y_i = k | x_i) = \pi_k = \frac{\exp(\beta_{0_k} + \beta_1 x_i)}{1 + \exp(\beta_{0_k} + \beta_1 x_i)} \quad (3.10)$$

Here, $x_i = sd_{ij}$, π_k is the probability that tree i located in patch j with sd_{ij} will be classified into crown class k , and β_i are regression coefficients.

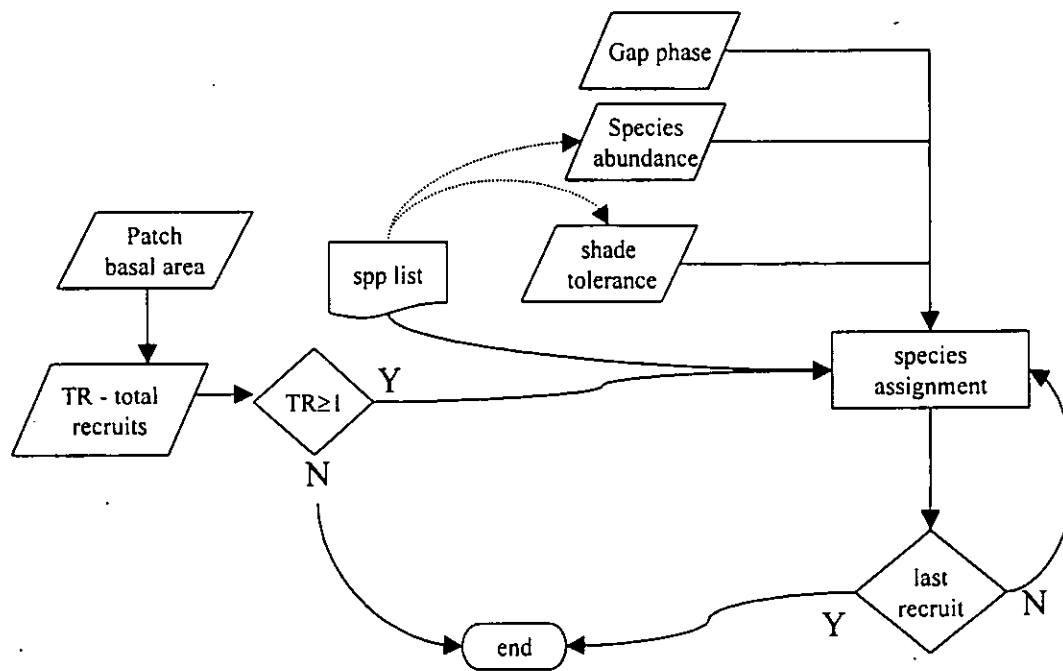


Figure 3.6 Diagram of recruitment procedure used in Gavilan model.

3.2.3 Recruitment

In this study recruitment is simulated dynamically in two stages where, initially, the number of recruits is estimated as function of disturbance level and secondly, the recruits are assigned to species (Figure 3.6). The first stage evaluates the patch density (basal area), and patch gap phase, as indicator of patch openness. Observed post-logging and silvicultural treatment regeneration patterns in the study area suggests that, as is to be expected, in open areas, such as tree fall gaps and abandoned roads, the regeneration be dominated by light demanding species while in closed areas the regeneration is less abundant and is dominated by shade tolerants (Cabrelli 1992, Diaz 1995, Guariguata and Dupuy 1997). Based on this pattern, different probabilities for species to establish were estimated depending on ecological guild. Pioneer species were set to have higher probability to establish in gaps and less in closed forest areas and vice-versa for non-pioneer species. The second stage consists of assigning species to the recruits. Species relative abundance within regeneration guild is used to represent the probability of the species to establish once it is known that its

regeneration guild is to be recruited. Because species abundance varies with time, it could be reviewed and updated during simulation in predefined periods to allow dynamics of forest stand composition. The initial dbh of recruits is set to a random value between the minimum dbh considered (10 cm) and the maximum dbh observed for recruits following the observed distribution of dbh of recruits in 1-cm dbh classes (Figure 3.7). Stem form, and crown form are set according to the pattern observed in the study site and were not allowed to change during the simulation period unless damage has occurred that could cause a stem or a crown to be reclassified.

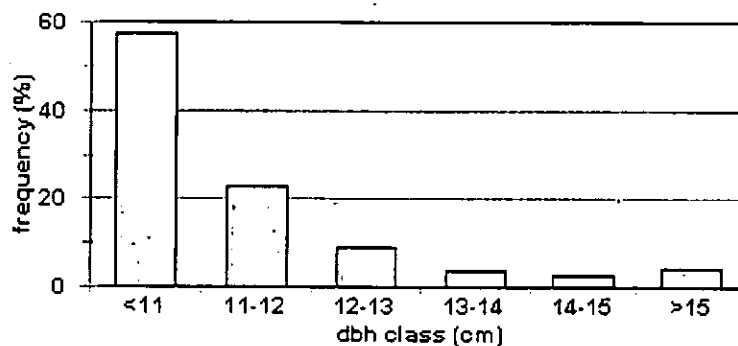


Figure 3.7 Recruits initial dbh distribution pattern at Tirimbina.

Recruits used for this plot were observed during the period 1990 - 1998 in all 9 plots ($N=1283$).

For species assignment, Vanclay's (1992) procedure was enhanced to allow species not observed among recruits and even those species not currently existing in the study plots, but present in the neighbour forest, to establish. At Tirimbina, for instance, despite the silvicultural interventions, which could have eliminated some species from the stand ($\text{dbh} \geq 10$ cm), the number of new species not observed at the beginning of the study is higher than that of species that disappeared in the period (UMBN unpublished data). To accomplish this task, first a "disturbance gap" was defined as one of the simulation patches in which a large, logged or naturally falling tree has caused severe damage (see Section

3.2.6). In the forest, this is generally where skidders go through to collect the log, and damage to standing trees and soil exposure is more likely, and the areas where a naturally falling tree has pulled neighbour trees down (Lieberman *et al.* 1985, Whitmore 1990). A patch would remain in gap phase for a given number of years before closing again. Denslow (1987) suggests that two years are enough for gaps to close and restore closed forest stand environmental conditions. Secondly, pioneers were defined as light demanding species that have higher probability to establish in gaps than in non disturbed forest (Swaine and Whitmore 1988). As consequence of these definitions, all patches that do not meet the disturbance gap are non-gaps and those species not meeting pioneers definitions are non-pioneers. Thus, species are assigned by checking if the patch is currently in a gap phase and use the corresponding probabilities to define if a pioneer or a non-pioneer species is to be recruited. Finally, the species relative abundance within regeneration guild is used as the probability for a species to be recruited.

3.2.4 Mortality

Five causes of mortality were defined in **Gavilan**. The first is the density-independent mortality as that defined in Botkin (1993) as intrinsic mortality. It is constant and can affect all trees independent of age, size or growth rate. This mortality cause includes most of the unexplained and unpredictable mortality causes. A second cause of mortality is derived from what Botkin (1993) termed competition-induced mortality. Several studies support (e.g. Lieberman and Lieberman 1987, Swaine *et al.* 1987, Vanclay 1995, Finegan *et al.* 1999) that while slow growing trees have higher probability to die, there are slow growing species, such as those of understorey, that could maintain their slow growing rates for many years. Based on this fact, the growth threshold, under which trees will face competition induced mortality, was established as a percentage of species maximum potential growth rates in opposition to an absolute growth threshold for all species that could result in high and disproportionate mortality for understorey species. Mortality so defined affects relatively slow growing trees, but could not be generalised as competition-induced mortality since trees reaching maximum size will also present slow growth rates. Thus, this is defined

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as competition-induced mortality for small trees but senescence-induced mortality for big trees. The third mortality cause is tree fall damage. When a tree is logged or dies for natural causes, as indicated previously, it could cause damage to neighbouring trees. Although this mortality is density-independent, it is treated separately from the density-independent mortality described above, because it is considered within predictable causes of mortality. Small trees are more prone to be smashed by a falling large tree and lianas could pull down other trees in the neighbourhood (Lieberman *et al.* 1985). In a managed forest, logging and silvicultural treatments are important causes of mortality, and in **Gavilan**, they constitute the fourth and fifth causes of mortality. Logging and silvicultural treatments are performed according to forest structure and species composition and rules established by national or international laws (see Logging and Silvicultural Treatments sections below). Silviculturally treated trees are assumed not to be cut as in a logging operation but girdled or poisoned so that the tree does not necessarily die immediately but its annual mortality probability increases. This procedure gives chance for trees to survive the treatment as observed in the field (personal observation).

Two parameters are used in **Gavilan** for natural mortality estimation. First, the density-independent mortality parameter expressed by the proportion of trees that could survive to species maximum age. Second, the joint competition- and senescence-induced mortality parameter expressed by the proportional dbh-increment threshold below which trees will face additional mortality. This parameter was set by species adult position in order to allow higher probability for understorey species to survive than canopy species. These parameters crystallise a large variety of mortality causes. For instance, Aguirre (1999) found several types of natural disturbance, including uprooting as consequence of wind blow, slope and soil conditions, which are accounted here by the density-independent mortality factor. The values of mortality parameters were set by trial and error procedure to fit the mortality rate and stand density known from *Pentaclethra* forests. In Section 4.2.2 there is a discussion and evaluation of the significance and sensitivity of mortality parameters.

3.2.5 Gap formation and duration

The model identifies the gap formation event as when a tree falls within a given patch. This was implemented as a tentative way to identify a gap when a tree falls and causes severe damage in the patch. Gap formation procedure follows the same procedure as logging damage effect: the number of damaged trees is linearly proportional to the size (basal area) of falling tree and the severity of the damage is inversely proportional to the size of the damaged tree. The bigger the tree the higher the possibility of it forming a gap and the smaller the tree the higher the possibility of being smashed by a falling tree. Based on this, which is of general belief (Brandani *et al.* 1988, Shugart 1998), we set the parameters to produce a similar tendency within acceptable limits. Once the gap has been formed it should recover its non-gap characteristics after a given period. The model does not evaluate gap size and quality but recognises a patch in which the gap was formed.

The gap formation frequency is controlled mainly by the mortality parameters (Section 3.2.4) and the parameters used to estimate the number of trees damaged and killed by a falling one. Presently the model uses the same parameters for naturally falling as well as logged trees. This is assuming a logging impact similar to a natural disturbance, however, non-improved logging techniques may have higher impact compared to natural disturbances (Jonkers 1987, Kopelman 1990).

3.2.6 Logging and silvicultural treatments

Gavilan simulates logging and silvicultural treatments based on sustainable tropical forest management principles (Prabhu *et al.* 1996) in general, and Costa Rican forest management sustainability standards (CNCF 1999). Silvicultural groups were defined as those that have similar treatment for silvicultural purposes. These groups include merchantable species, non-merchantable species, and protected species. The Costa Rican Forest Chamber (s.d.) classifies species according to timber quality as desirable (highly valuable timber, such as *Swietenia macrophylla* and *Cedrela odorata*, which are preferred in a silvicultural activity) and acceptable (merchantable timber, but not as valuable as desirables, such as

Pentaclethra macroloba and *Jacaranda copaia*), species in these categories are treated differently in silvicultural operations. Because of *Pentaclethra macroloba* abundance and dominance it is treated as separate silvicultural group. Usually, protected species are rare or endangered species protected by local legislation (MINAE 1997) such as *Sclerolobium costaricense*, or by international conventions (IUCN 1997).

The logging simulator consists of a diagram of decision making to select trees that could be harvested, while considering the restrictions of the proportions of trees to be left for mother trees, the proportion of basal area and volume allowed to harvest, protected, and rare species. The method for selecting trees for logging depends on three main aspects. First, the timber market requirements, which dictates the species and log sizes that could be sold. The Hutchinson's (1987) stem form classification, in which a harvestable log is the one with actual dbh higher than the minimum dbh cut and at least 4-m of good, healthy, and undamaged stem was used. Second, the ecological limitations, commonly expressed in local forest legislation in terms of proportions of trees or basal area that should be left after a logging operation, to guaranty a low impact harvesting and to protect rare or endangered species. This is to comply with the sustainability criteria as expressed by Costa Rican standards (CNCF 1999) and the minimised impact to biodiversity of the forest ecosystem criteria of sustainable management of tropical forests (Prabhu *et al.* 1996). Third, the minimum economic cut defined as the minimum timber volume per hectare, which yield an economically viable harvesting operation in a particular stand.

The logging criteria used in this study is similar to that defined by Ong and Kleine (1995) in terms of number of trees per hectare. The selection of trees for logging begins with the selection of the silvicultural groups specifying the minimum dbh allowed to cut, the stem form and the proportion of harvestable basal area that should be left on the remnant forest. When all parameters are set and harvestable trees are listed based on the specifications, the stocking assessment takes place to determine if currently harvestable timber is over the minimum economic cut (defined as the timber value that balances cost of the the logging operation). If all the conditions are met, the logging operation takes place. All harvestable

trees of the simulated area are listed, and bigger trees are logged first, until the allowable logging limits are met. The logging procedure used in this study differs from Ong and Kleine (1995) in that in this study, not all mature trees are harvested, but ecological aspects could be considered to protect rare and endangered species as well as maintenance of a minimum stand density. The number of damaged trees resulting from a logging operation is estimated as a linear function of harvested basal area so that higher logging intensity will cause more damage than lower logging intensity (Alder 1995, Vanclay 1994). Damaged trees are randomly selected from the patch where trees have been felled and the neighbouring patches following a user-provided frequency distribution of damage by dbh size class. The Kopelman's (1990) damage categories were adapted to include the part of the trees damaged, in addition to the damage severity. Three damage categories were defined as (i) killed; (ii) injured stem; and (iii) injured crown. The injured categories result in worsening of the current level of stem or crown form and the severity of the damage is expressed as the amount of change in crown or stem form levels.

Gavilan simulates different silvicultural treatments including liberation and refinement. The silvicultural treatment of liberation consists of elimination of trees that prevent an adequate light reception by potential crop trees (PCT). Tree elimination is commonly done by girdling alone or enhanced with poisoning of shading, undesirable trees in the neighbourhood of desirable potential crop trees (Hutchinson 1987). The method of selection of trees for treatment depends on the type of treatment considered and intensity. Trees are considered within silvicultural groups (see above) and two groups of trees are defined according to whether they are to be liberated by the treatment or are to be girdled. Potential crop trees, defined as trees of species of interest, commonly merchantable, with at least four meters of clean and straight stem, but not satisfying minimum harvestable size, compose the group of trees to be liberated. The group of trees to be girdled is mainly composed by non-merchantable species but could also include trees of merchantable species not included in PCT due to tortuous or damaged stem, severely bad crown form, or damaged crown.

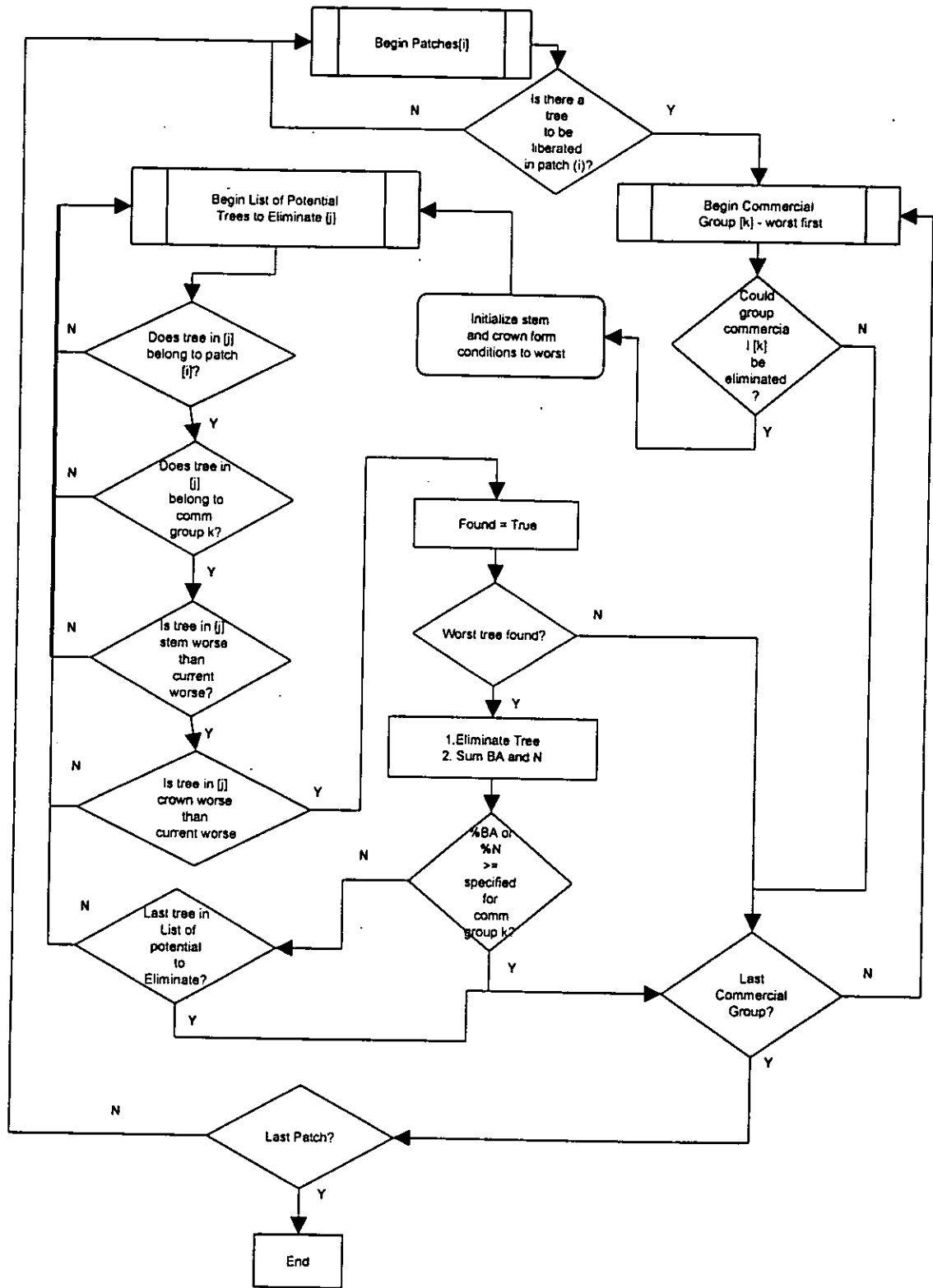


Figure 3.8 Silvicultural Treatment Flux Diagram of the Gavilan model

As in logging operations, protected and rare species can be explicitly protected from being removed by establishing the amounts of permissible proportion of trees to cut or totally inhibit their elimination.

The silvicultural treatment module operates in three stages at a patch level (Figure 3.8). The first consists of searching for PCT according to the specifications set by the user. The second checks if there is at least one PCT in a patch before applying a treatment. If a PCT was found in a patch, the model searches for potential trees that could be girdled to benefit PCT. A decision could be taken by the user to apply treatment in a patch where there is no PCT. The third stage is the treatment itself, which consists of selecting trees to be girdled while not surpassing the limits established for each silvicultural group. For non-commercial species, the biggest trees are eliminated first and for merchantable species the worse (damaged or tortuous stem and poor crown form) are eliminated first. Potential trees to be eliminated are "girdled" in this sequence until the limits of treatment intensity are reached. Trees eliminated by the treatment do not die immediately, since the model assumes a low impact treatment that consists of girdling undesired trees. These trees increase their annual mortality probability and the case is taken over by the mortality process. This gives a non-zero probability for few trees to survive the girdling and some to have a delayed death. Trees dying this way are considered to have minimal damage to the remnant forest stand and no treatment-associated damage is considered. Treatment schedule could be set as a post-logging operation or totally independent of logging operation into a fixed periodicity.

3.3 Model testing and evaluation

The model was evaluated qualitatively and quantitatively at individual tree, population, and community level. The qualitative evaluation was done graphically by comparing the simulated distribution patterns of diameter growth, species composition, equilibrium stand density, and mortality and recruitment rates, with those known from *Pentaclethra* forests and other tropical rain forests. Quantitative evaluation includes statistical testing of differences in distribution patterns and central tendency measures.

3.3.1 Non-disturbance scenario and steady state

The model was run for 400 years with data observed at Tirimbina using Monte Carlo procedure (Sokal and Rohlf 1995) with 20 repetitions without disturbance. Unless specified, one-hectare logged and refined plot (Plot-1) was used to obtain the initial stand conditions for simulation starting from year 1996 without further disturbance. The initial forest stand conditions were those of Plot-1 in 1996 (after logging) with 305 stems ha^{-1} , basal area $19 \text{ m}^2 \cdot \text{ha}^{-1}$, 98 species, *Pentaclethra macroloba* with abundance of 14% of total number of stems, followed by *Welfia georgii*, *Lonchocarpus oliganthus*, *Warszewiczia coccinea*, and *Miquartia guianensis*, all accounting for 15% of the total number of stems. The growth functions and parameters used for the simulation in this study, were obtained from the nine 1-hectare plots of Tirimbina using jack-knife procedure (Sokal and Rohlf 1995), in which one plot were excluded each time, and the estimated parameters averaged. One-ha plot is used to allow long-term simulation, which is not easy with all the nine plots simultaneously due to computer memory requirements. Preliminary simulations using each plot separately and starting at different observation periods revealed similar tendencies in terms of steady state stand density, mortality and recruitment rates, as well as species composition. Based on these preliminary analysis, Plot-1 was randomly selected to perform long-term simulations used to evaluate the ecological adequacy of the model with undisturbed long-term simulations, but the three control plots (Plots 2,4 and 8) were used to simulate the effect of silvicultural interventions. The results presented in this study could be considered representative of the site. Diameter distribution, species composition, and diversity were evaluated over the simulation period. The discussion of the results is done based not only on the observed patterns at Tirimbina but also at other three sites, at Corinto, in Costa Rica, and La Lupe and Los Filos, in Nicaragua, totalling 23.0 ha. With this simulation, it is expected to represent what would the forest stand look like in the following four hundred years and observe that the principles of TRF dynamics are not severely violated. The idea is that if the model could sustain these principles for this simulation period, then useful simulations could be performed.

Table 3.3. Qualitative model evaluation criteria used to test the **Gavilan** model adequacy. The values of the ranges suggested in this table were observed in neotropical lowland forests (33-500 masl) in Barro Colorado Island, La Selva, and Puerto Rico where minimum measured DBH was 100 mm (see Swaine *et al.* 1987).

Criteria	Indicator
1. Number of trees	Number of trees in the simulated long-term should maintain within known limits. This is about 400-600 trees.ha ⁻¹ (Swaine et al 1987)
2. Basal area	Basal area of the forest stand in the simulated long-term should maintain within observed limits. This value is about 25-38 m ² .ha ⁻¹ (Swaine et al 1987)
3. Mortality	The number, percentage, distribution and causes of mortality in the simulated long-term should correspond to those known in local forests. Mortality rates should be constant among size classes. Observed annual mortality rates are between 1-3%.yr ⁻¹ (Swaine et al 1987, Lieberman et al 1985)
4. Recruitment	The number, species composition, frequency of recruits in the simulated long-term resembles that of known local forests. The recruitment rate is usually stated as being close to the mortality rate (see point 3).
5. Species composition	Species composition in the simulated long-term resembles that of known local forests. Check the proportion of pioneer/non-pioneers, adult sizes, palms, <i>Pentaclethra</i> . Species composition varies from one site to another, however, in <i>Pentaclethra</i> dominated forest the most common species tend to be the same. What could be difficult to conclude is whether <i>Pentaclethra</i> will continue to dominate in the long term (see Swaine 1989).
6. Number of species	The number of species in the simulated long-term forest stand should maintain close to those of known local forests. The number of species is between 70-142 species.ha ⁻¹ (Swaine et al 1987)
7. Diversity indices	Check if there is no decrease in species diversity. <i>Pentaclethra</i> forests are highly diverse and 4-5 Shannon diversity index was found (dbh≥10cm) (this study) and 96-107 species ha ⁻¹ were found in old growth forests (Lieberman et al 1985)
8. Crown exposure distribution	Crown exposure distribution should be close to known distribution pattern in local forests
9. Structure (diameter distribution)	The distribution of trees by size class (dbh) should be the traditional reverse J. A formal test of the reverse J distribution could be performed by using the Liocourt rate (Vanclay 1994), which is estimated to be around 0.5.
10. Diameter growth rates and distribution	Growth rates variability among species, trees (even within the same species and size class), within tree auto-correlation, and rightward skewed distribution should be evident in all the simulated periods. The ranges should be compared with locally observed data.

Table 3.3 presents the criteria used to evaluate the principles of forest dynamics in the tropics at the individual, population, and community level. Although knowledge of TRF species composition dynamics is limited and few sites have been monitored and described for long periods (Swaine 1989, Swaine *et al.* 1987, Lieberman and Lieberman 1987, Clark 1994, Finegan and Camacho 1999), in this study, it was assumed that the initial forest species composition at Tirimbina silviculturally managed forest were close to those of the steady state (primary undisturbed forest). This assumption is based on the widespread of *Pentaclethra* forest and the references about its dynamic (e.g. Lieberman and Lieberman 1987, Mejia 1994). Considering this, no substantial changes in species composition were expected in a simulation without heavy disturbance. Infrequent events such as catastrophic fires, drought, and windstorms, which may not happen within a century in the area of Central America where *Pentaclethra* forest is found (Hubel and Foster 1986 b), are indicated as the most important factors that could produce permanent and significant changes in species composition (Swaine 1989). In addition, non-changing climate scenario is implicit in the simulations presented in this study.

3.3.2 Ecological-based parameter evaluation

The model uses statistically estimated and ecologically based parameters. Statistically estimated parameters were fitted from field observed data mainly from Tirimbina. Ecologically based parameters are those that could not directly be estimated by fitting field observations because longer observation periods are required (e.g. mortality) or data are unavailable (e.g. gap formation and duration), but could be "guessed" based on theory and knowledge of TRF dynamics. Among these parameters are the period in years that a patch remains in gap phase after its formation, the probability for a pioneer species to establish in a non-gap patch, mortality and recruitment parameters, among others (Table 3.4). These ecologically based parameters were qualitatively evaluated, to find their effect on the model response in comparison to ecological theory. The base line scenario parameters were "fitted" in base of their effect on the simulated results. For instance, the mortality and

recruitment parameters were fitted to produce mortality rate and forest stand density within the range of values indicated in Table 3.3.

Table 3.4 Ecologically based parameters used in Gavilan and the values set as the baseline scenario.

Parameter name	Symbol	Value
<i>Parameter to estimate the number of recruits as linear function of patch basal area</i>	<i>a</i> – intercept	<i>a</i> =1.35
	<i>b</i> - slope	<i>b</i> =-0.6
<i>Density independent mortality parameter, as the proportion of trees reaching maximum longevity</i>	<i>dim</i>	4%
<i>Number of years a patch stays in gap-phase after gap formation</i>	<i>T_g</i>	2 years
<i>Probability of a pioneer to establish in a gap</i>	<i>P_{gp}</i>	0.9
<i>Probability for a species not present at the beginning of simulation to establish</i>	<i>P_{nb}</i>	0.3

The actual values of the parameters were defined arbitrary but to produce an output in terms of stand density, mortality and recruitment rates, species composition, gap formation rate, and to attain the equilibrium within the range observed in *Pentaclethra* forests.

The simulations were executed under the base line scenario, defined as the set of parameters that produced an acceptable (according to existing information of *Pentaclethra* forest – see Table 3.3) simulated equilibrium of the forest stand in the long term. The values of ecologically based parameters considered for the base line scenario are presented in Table 3.4. Statistically estimated parameters including those of height function and diameter increment were presented in Section 4.1. The initial forest stand conditions for simulations in this section were those of plot 1 in 1996 as described in Section 3.3.1.

To further assess the importance and sensitivity of the ecological parameters, some of the base line parameters were changed by $\pm 20\%$ and the model output evaluated the same aspects as in the base line scenario simulation. Sensitivity analysis was performed by varying one parameter each time while fixing the others as defined on the base line scenario values. If the statistic $S_p = (\delta y / y) / (\delta p / p)$, where y is the response variable (e.g. basal area or

volume) and p is the parameter being evaluated (Soares *et al.* 1995), is high, the parameter is highly sensitive. The proportion of change in model output measures the parameter importance. Parameter changes that produce little change in model output are robust and could be representing well-estimated parameters, while parameter changes that produce substantial changes in model output deserve more investigation and should be treated with care.

3.3.3 Recovery capacity of the forest after disturbance

The capacity to return to stability after disturbance was evaluated using the baseline parameters but with a heavy logging, in which all harvestable trees (mature trees, dbh ≥ 50 cm, of commercial species) were logged. A thinning silvicultural treatment was applied two years after logging removing trees of non-commercial species and tortuous and damaged trees of commercial species $20 \leq \text{dbh} \leq 80$ cm. The intervention was applied once at year 20 (logging) and 22 (silvicultural treatment), and the forest was left to recover until year 200. The accumulated effect of logging and silvicultural treatment on stand density reduction was 52% of the initial basal area and 26% of the initial number of trees. Heavier intensities were experimented until 60% of the initial basal area to find the response of the stand dynamics after disturbance. The simulated intensity of intervention is within the intensity of 40-60% of the initial basal area, indicated in the literature (Dawkins 1958, Baur 1964, de Graaf 1986) for the forest to respond the intervention. The initial forest conditions for the evaluation of recovering capacity, as well as for evaluation of logging and silvicultural treatments indicated below, are those of the three control (logged but not treated) plots at Tirimbina in 1996.

The period in which the forest returned to its steady state in stand density (number of trees per hectare), basal area, and species composition was evaluated and discussed as the recovering capacity of the forest stand. In this study, steady state was defined as the stable condition that does not change over time or in which change in one direction is continually

balanced by change in another. In practice, it was estimated as the period in which changes in stand density and basal area were close to zero.

3.4 Applications of the model

3.4.1 Ecological implications of logging and silvicultural treatments

A simulation with logging and silvicultural treatment intervention was used to evaluate the effects of silvicultural interventions on ecological sustainability of the forest stand. Log-and-leave and log-and-treat systems are compared to evaluate the role of silvicultural treatments in forest management as they were perceived by the model. Because of the uncountable possibilities of combinations of logging intensities and schedules, and silvicultural treatments, a simulated undisturbed forest was compared with two scenarios, one with heavy and other with light logging intensity. The low-intensity logging schedule was defined according to local experiences (Quiros and Finegan 1994) with logging periodicity of 20 years with the minimum diameter cut of 60 cm for all merchantable species and a logging intensity of about $20 \text{ m}^3 \cdot \text{ha}^{-1}$. The simulated ecological limitations were set to harvest only 90% of the harvestable trees and the economic logging limit, under which yield does not cover logging costs, to $5 \text{ m}^3 \cdot \text{ha}^{-1}$ (Quiros and Finegan 1994). Fully protected species were those defined in current Costa Rican legislation (MINAE 1997), which form a specific silvicultural group within the model. Within the experimental plots at Tirimbina, only one species, *Sclerolobium costaricense*, was found. No species were protected on base of low abundance, but maximum terrain slope limit for cutting was established at 60% (Quiros and Finegan 1994).

The heavy intervention scenario was created by simulating an uncommon heavy logging operation and a silvicultural intervention two years after logging. In the logging operation, all trees $\text{dbh} \geq 50$ cm of commercial species were harvested - the ecological and economic restrictions were set off. The silvicultural treatment of refinement removed trees $20 \leq \text{dbh} \leq 80$ cm with intensity no more than 60% of the patch basal area. Bigger trees of

non-commercial species were removed first and deformed trees of commercial species were last to be removed if necessary.

Silvicultural treatments were scheduled two years after logging operation. Potential crop trees (PCT) were defined as those of merchantable species with good stem (Hutchinson's stem form category 2 – see Hutchinson 1987), good crown (Dawkins' crown form categories 1-3 – see Alder and Synnott, 1992 for crown form categories), and $10 \leq \text{dbh} < 60$ cm. Potential trees to be removed by treatment were defined as all non-commercial species (palms and protected species excluded), and trees of acceptable species and *Pentaclethra macroloba* with poor stem form (Hutchinson's stem form categories 3-5) and poor crown (Dawkins' crown form 4-5) and $20 \leq \text{dbh} < 80$ cm. In all cases no more than 40% of total basal area could be removed in any patch to maintain the overall desirable treatment intensity.

To simulate the effect of successive logging and silvicultural operations on forest stand, logging was scheduled for 20-years cutting cycle as indicated in the light logging intensity above. The silvicultural treatment of liberation was applied two years after logging as explained above.

3.4.2 Estimating cutting cycles

To estimate cutting cycles, the undisturbed and the low logging intensity scenario described above were used. The resulting simulated volume table (simulation time and volume of commercial species) was used to estimate the approximate time in which accumulated volume amounts to the planned logging intensity of $20 \text{ m}^3 \cdot \text{ha}^{-1}$. This period was defined as the cutting cycle in this study. Because of the annual variation in volume, the simulated average volume curve was initially fitted to a third degree polynomial function ($V_c = \beta_0 + \beta_1 X + \beta_2 X^2 + \beta_3 X^3$, where X is simulation time) to capture the long-term trend in volume increment. The first derivative of that function was used to estimate the volume increment for each period.

After silvicultural treatment, volume increment is high and decreases with time. Generally, when the increment becomes insignificant it is time for logging, if stock is enough, or for a silvicultural treatment to stimulate increment. De Graaf (1996) for instance, applied a second treatment eight years after the first silvicultural treatment to stimulate volume increment. In this study, a second treatment was not applied because it was not considered necessary. The volume of commercial species described by the third degree function above includes all tree sizes and stem forms. With the conditions set for the simulations in this study the volume of harvestable trees in the steady state was about 15% of the total volume of commercial species while the remaining percentage is comprised by potential crop trees and trees with damaged or tortuous stems. Using the information above, the cutting cycle was estimated for a logging intensity of $20 \text{ m}^3 \cdot \text{ha}^{-1}$, taking into account the 20-years cutting cycle and the required restrictions to protect endangered species. Quiros and Finegan (1994) using low abundance species and slope restrictions at Tirimbina logged an average of $10 \text{ m}^3 \cdot \text{ha}^{-1}$.

4 Results and discussion

4.1 Model development

4.1.1 Species Grouping

The pairwise comparisons between growth groups resulting from the clustering procedure were all statistically different ($\alpha = 0.05$). The discriminant procedure applied to the same set of species to confirm the clustering procedure found less than 5% of the species misclassified. The least square distance were between very-slow and slow growing species and most of the misclassified species were in these groups, however statistically different at $\alpha = 0.05$. More than a half of the total number of species and all of understorey species were classified among very slow and slow growing group. The used grouping procedure resulted in 135 species used to found the growth groups and 88 being assigned to existing groups. Fifty species without growth information in the study area were assigned to the existing groups according to existing information in *Pentaclethra* forests (eg. Lieberman and Lieberman 1987), or existence of species of the same genera in the groups already formed, in this order. Where none of these rules could apply, species were set to the default groups as very slow growth for understorey species and slow for all other adult size position (see Table 4.1). *Pentaclethra macroloba*, *Miquartia guianensis*, *Protium ravenii*, and *Ferdinandusa panamensis* were not used to build up the groups since they stand by themselves, but were included in Table 4.1 using discriminant procedure, just for comparison with the resultant species groups.

The resulting groups are similar to those obtained by Finegan *et al.* (1999), however some species moved from one group to the adjacent. Species that were classified in different groups when treatments were considered (Finegan *et al.* 1999) were classified into the highest class by the analysis carried out in this study. For instance, *Casearia arborea*, which was classified slow-growing in control plots but moderate-growing in treated plots (Finegan *et al.* 1999), was classified into moderate growing by the analysis presented in this study. As stated by Finegan *et al.* (1999), the fast growing trees of the population are the ones that make the difference in species classification using diameter increment median, first and third quartiles as grouping criteria. Species of silvicultural interest, those benefited by the silvicultural treatment at Tirimbina, presented higher growth rates in treated plots resulting in significance of the silvicultural treatments for species grouping (Finegan *et al.* 1999).

The grouping strategy used in this study resulted in 26 groups, of which six were represented by single species (Table 4.1). These groups were then used to derive species-specific data such as maximum growth rate, maximum dbh, and maximum age. Group- and species-specific parameters (depending if species was within a group or standing by itself) were used for purposes of dbh growth estimation and for annual mortality rate. Individual species information, such as regeneration guild and merchantability, which were not used to form the species group, were used for recruitment and silvicultural interventions respectively.

4.1.2 Description and structure of the model

4.1.2.1 Model selection

The idea of “deepening the knowledge of the growth, commercial yield and natural regeneration” envisaged by CATIE’s research program (Campos *et al.* 1997) suggests the use of process models, which in principle try to find biological facts (and their relation to the environment) affecting biomass production and its allocation through the whole plant

system. Comparing existing process based models, it is clear that they are built in simple ecosystems like even aged forest plantations (Perttunen, *et al.*, 1998, Amateis 1994). Attempts to use this approach in mixed tropical forests have always faced with lack of data. A long way is still to be constructed to build process-based models for TRF. Some attempts have already been made on this way using intermediate approaches like the gap-modelling techniques.

Gap models have been used to simulate several aspects of tropical forest stand dynamics, particularly the effect of climate change, the effect of hurricanes, effect of forest fire, and the effect of drought on biomass production (Doyle 1981, Shugart and Noble 1981, Desanker and Prentice 1994). Gap models were originally developed to evaluate forest successions, structure, composition, and the effect of environmental factors on biomass production of tree species or functional groups (Shugart 1984). That property is used in **Gavilan** to simulate stand dynamics in naturally or silviculturally disturbed forests. Few studies have attempted to model timber production using gap models. Doyle (1981) developed a gap model for a Puerto Rican "tabonuco" forest to evaluate biomass production in a forest affected by hurricanes. Desanker and Prentice (1994) developed a gap model for miombo woodlands of Central and Southern Africa to evaluate biomass production in changing environment conditions. Neither study includes human intervention such as silvicultural treatments or logging. Bossel and Krieger (1994) used a hybrid gap-matrix approach model to simulate timber production in South East Asia but do not evaluate silvicultural interventions. Vanclay (1995) recognises that gap-models have not been used to predict timber yield but are used to evaluate concepts of ecology, however, he suggests that single tree non-spatial models, which include gap-models, may offer an efficient alternative for yield forecasting. It was therefore suggested that an enhancement of gap-model for yield predictions could present an efficient alternative to estimate timber yields and silvicultural interventions while evaluating ecological concepts. However, most of the data, such as species identification, and long-term repeated mensurations covering species life history, used in gap models may not be available in tropical forest ecosystems, so that

the enhancement of a gap model for timber production evaluation in tropical forests will often be limited by data availability (Vanclay 1991 b).

In the process of designing **Gavilan**, some of the properties of gap models, such as those of effect of climate and soil nutrients, were excluded, but the concept of the gap as a "neighbourhood" and the diameter increment function and mortality functions were preserved and enhanced where required. For example, diameter growth could be simulated by using Botkins' (1993) or Moore's (1989) function. Day length was excluded as unnecessary in the tropics where it does not vary significantly. Lamprecht (1990) describe a daylight variation of ± 1.5 hours by the tropic lines, and no variation at all in the equatorial line. Temperate forest gap models use nitrogen availability among the driving variables (Botkin 1993), yet, Vitousek and Denslow (1986) reported nitrogen as a non-limiting factor in undisturbed *Pentaclethra* forests at la Selva, just 7 Km West of the area of study. The model enhancement consisted mainly of connecting silvicultural intervention modules, which are commonly found only in empirical forest growth and yield models (Vanclay 1994, Alder 1995, Ong and Kleine 1995). In addition, the recruitment and mortality procedures were adapted to reflect the reality of the observed data with particular emphasis on species recruitment dynamics and the causes of mortality. A light competition index was estimated from individual tree total height in relation to the average height within the neighbourhood. This was an alternative to the visually estimated crown exposure index with five categories (Alder and Synnott 1992).

Gavilan focuses on forest dynamics, namely forest structure, mortality, recruitment, growth patterns, and species composition, as these factors directly affect timber production in tropical forests (Favrichon 1998). Special attention was concentrated on growth and recruitment processes considering the complexity of the structure and species composition typical of a tropical forest stand. Routines for simulation of logging and silvicultural treatments were designed according to the conditions and common practices in tropical forests (Vanclay 1994, Alder 1995, FAO 1997, CNCF 1999) as well as those typical in *Pentaclethra* forests. The grouping of species based on observed growth patterns and the

height range reached by adult trees was the first step in model development. The model also intends to evaluate forest management criteria and indicators required for a sound ecological management practice (Prabhu *et al.* 1996). The model was designed to perform stochastic simulations. It is expected that this be the first phase of the model that should eventually include processes like climate change, soil fertility, and economic factors. In this study, the description of the model and discuss the consequences of its usage and its particularities were presented.

The model presented in this study should not under any circumstances, be viewed as the final product or the "best" model compared to existing ones like SIRENA2 (Alder 1997) since other models use different conceptual basis and were designed for different purposes which may differ from those of **Gavilan**. Its main purpose is to stimulate investigation on a new direction of model development. The idea of "patch model" presented here is an alternative to find a transition between silvicultural and process-based models. **Gavilan** is an individual tree model, developed using both deterministic and stochastic functions, according to data availability and current knowledge of *Pentaclethra* forest ecosystem functioning. The idea of this kind of model is to make it open for further "evolution" so that it can be improved as research produces more information on ecosystem behaviour. It was not feasible in this study to present all existing modelling techniques although some of them may also be applicable to the present situation. It is assumed that the literature review presented in earlier sections has provided the necessary information to justify the selection of this modelling approach. Further information on other modelling techniques may be obtained from the references mentioned earlier such as Vanclay (1994) and Alder (1995).

The model was developed to work at the individual tree level and needs information of the initial forest stand conditions to start a simulation. If one run is made, the current initial stand conditions are used, but when stochastic simulation is carried out, the initial conditions are used for the first run and the statistics of the initial conditions (species abundance, dbh, stem form, and crown form distribution) are used to generate random initial stand conditions. The term 'patch' is used in this study with the meaning of neighbourhood in which every other tree within it may affect all the trees in the

neighbourhood (Botkin 1993). This is preferred over “gap”, traditionally used to describe a piece of forestland with open canopy (Swaine and Whitmore 1988). Thus, patch-model is used in place of gap-model. The model does not assume relations between neighbour patches for growth, and regeneration but tree falling (harvested or naturally) may cause damage in neighbour patches. The simulations presented in this study used 20x20 m patches aggregated in 100x100-m plots but this is not fixed by the model and could be changed for other patch sizes as required. The adoption of the patch size used in this study was based on estimated tree mean total heights, which is more than 18 m (Figure 4.1) and that in the study area 20x20 m subplots are used for easy location of trees and constitute the measurement and sampling unit.

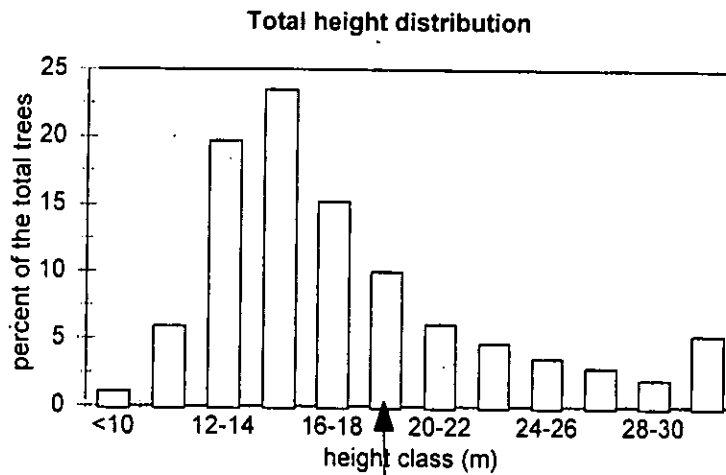


Figure 4.1 Individual tree height distribution frequency for trees dbh \geq 10cm at Tirimbina.

The arrow indicated the position of the plot mean height. Trees on the right hand side of the mean height are expected to have higher crown exposure than those on the left-hand side.

Several patches and many years could be simulated at once and the limit depends on the computer capacity. The predefined time step is one year and the model does not account for within year variation. The study area did not seem to have important seasonal variation either in terms of temperature or precipitation (Lieberman and Lieberman 1987).

4.1.2.2 Input requirements

Input data set consists of a list of trees present in the initial stand. The list of trees includes a unique identification number, consisting of the number of the plot, patch, and stem number, a species code, an initial dbh, and stem form class (using Hutchinson's 1987 five-level scale). In addition, the list of species, which should include not only the species present in the initial stand but also the surrounding areas. Species-specific information such as the variables used for growth, regeneration, and silvicultural procedures should be included in the list of species. Their definition and values for Tirimbina are presented in Annex 1. The usage of these parameters is described in detail in the next sections (growth, recruitment, mortality, logging, and silviculture modules).

To simulate silvicultural experiments, topographic and intervention schedule data are required. The silvicultural schedule should define the type of silvicultural intervention, periodicity and intensity, as well as the ecological, and economic restrictions. Ecological restrictions could be expressed in terms of maximum slope limit where logging could be carried out, and rare species protection directives, while economic restrictions simply specify the minimum volume under which logging operation is not economically attractive. Information on the logging damage intensity, expressed as the number of damaged trees, type, and severity of damage as well as its distribution by tree size class is required to simulate the effect of logging damage. Varying the intensity of damage can simulate traditional and improved logging techniques.

4.1.2.3 Model output

The model outputs consist of plots, tables and lists with the most common stand dynamics variables, including recruitment and mortality rates, species abundance, diameter distribution, basal area and volume tables, growth patterns and statistics (descriptive statistics of diameter growth, comparisons of observed versus simulated growth, residual analysis), and yield tables. Unprocessed raw data produced by the model runs can also be saved in ASCII or database format and exported to statistical packages for specific analysis.

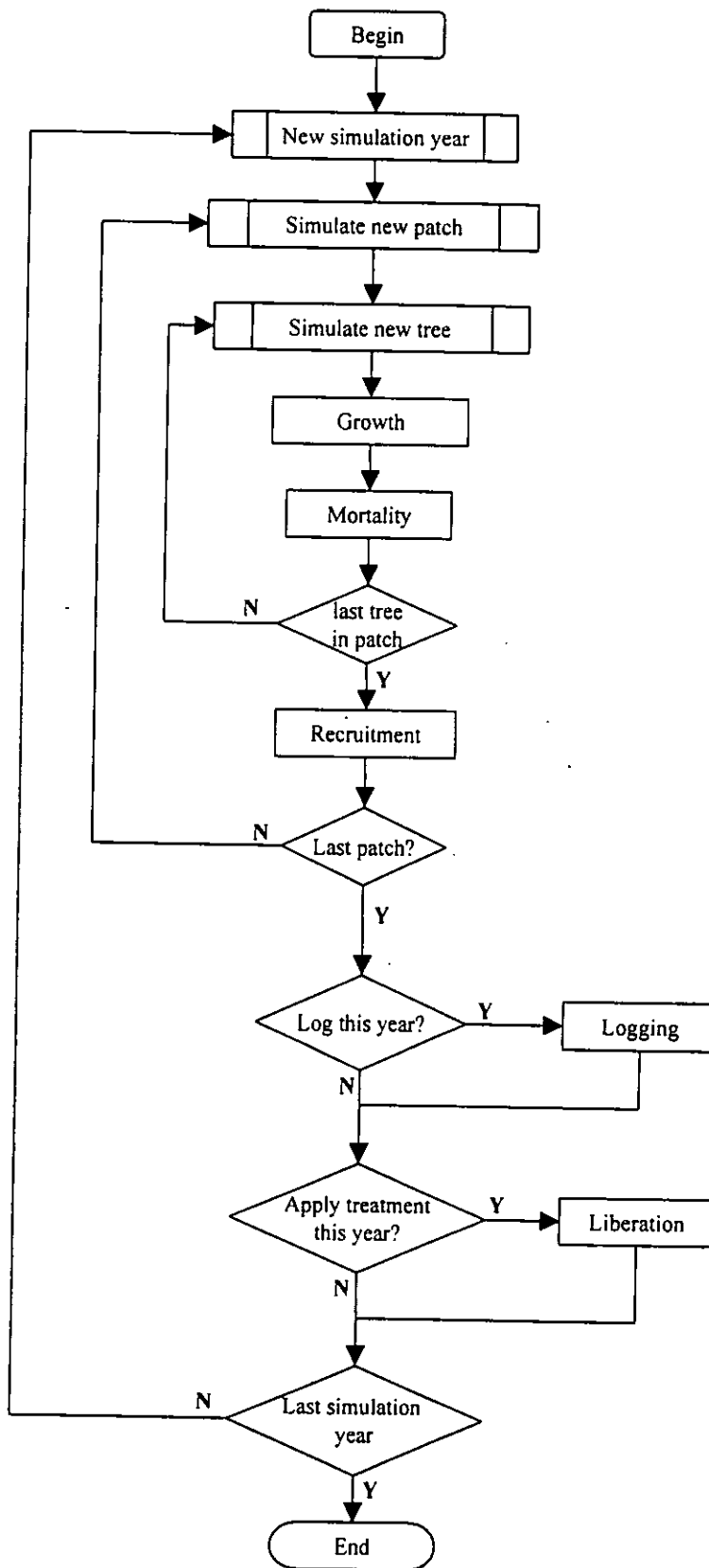


Figure 4.2 Gavilan model simulator flux diagram

4.1.3 Structure of the model

The structure of the model is similar to that of conventional forest models for timber harvesting (Alder 1995, Ong and Kleine 1995). The main components of the model are growth, recruitment, mortality, logging, and silvicultural treatment modules. Figure 4.2 presents the model structure and flux diagram and the following sections describe in more depth each of the modules.

4.1.3.1 Diameter increment

The growth trajectories (Figure 4.3.) provided by Lieberman and Lieberman's (1985 a) simulation method (the cloud of lines), were produced with eight years growth data from Tirimbina for comparison with curves produced by the logistic growth function (dark lines) used in **Gavilan**. Fast and very fast growing canopy species plots suggest trees of these species never die by senescence. Trees die while their growth rates are still high, which suggest vigour of the trees. These results are similar to those obtained from La Selva by Lieberman and Lieberman (1987) who found that slow growing species survived periods over ten years, while shade intolerant species maintained high growth rates over all the 13-year study period, and Clark and Clark (1999) who found no decrease in diameter increment for trees close to the maximum observed diameter.

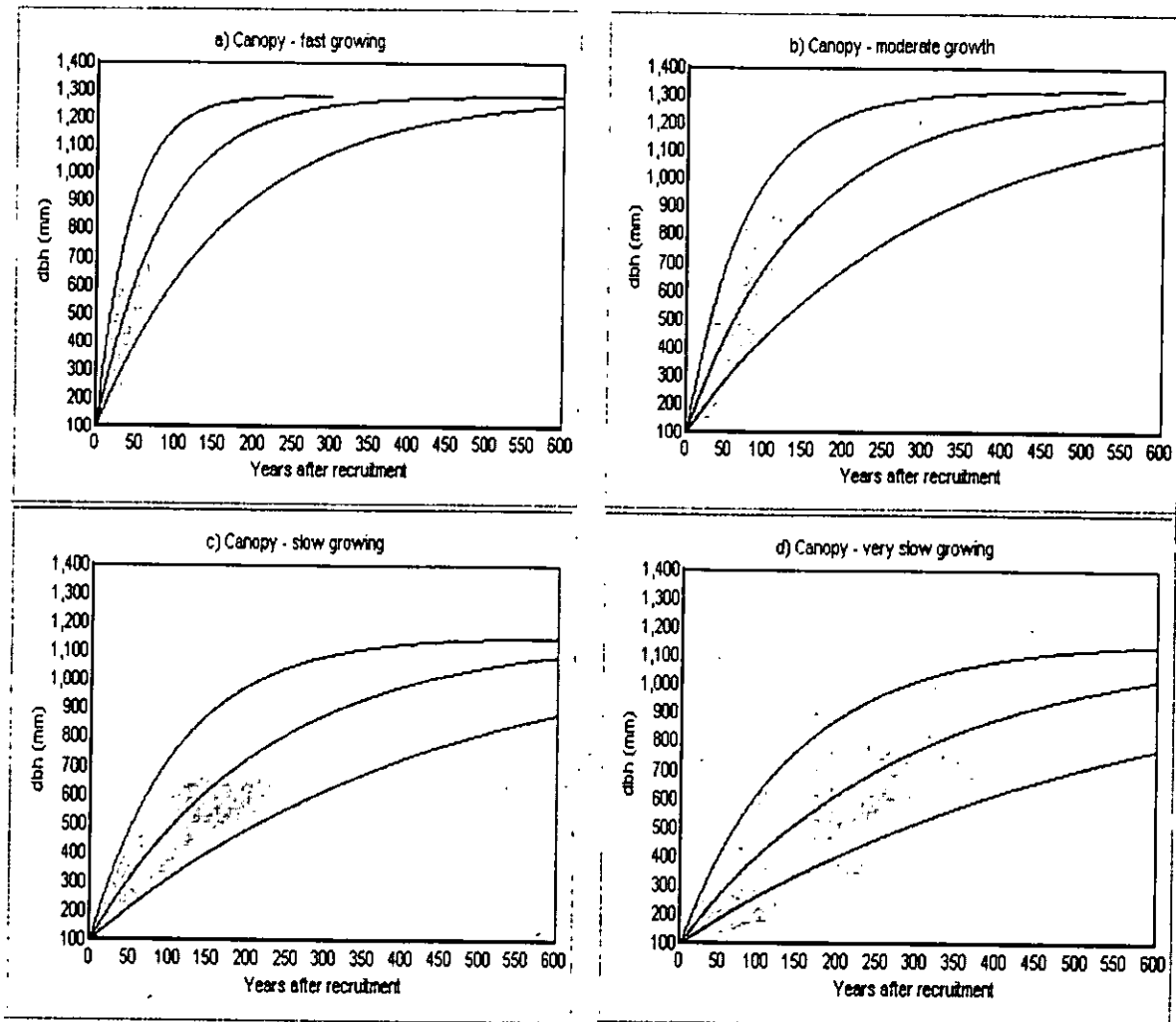


Figure 4.3. Diameter growth trajectories resulting from Lieberman and Lieberman (1987) simulation procedure (the cloud of 200 curves in gray) and growth curves produced by Logistic diameter increment function (the 3 dark lines) of which the leftmost curve is the maximum potential growth, the middle and the rightmost curves represent 50 and 75% reduction in growth potential.

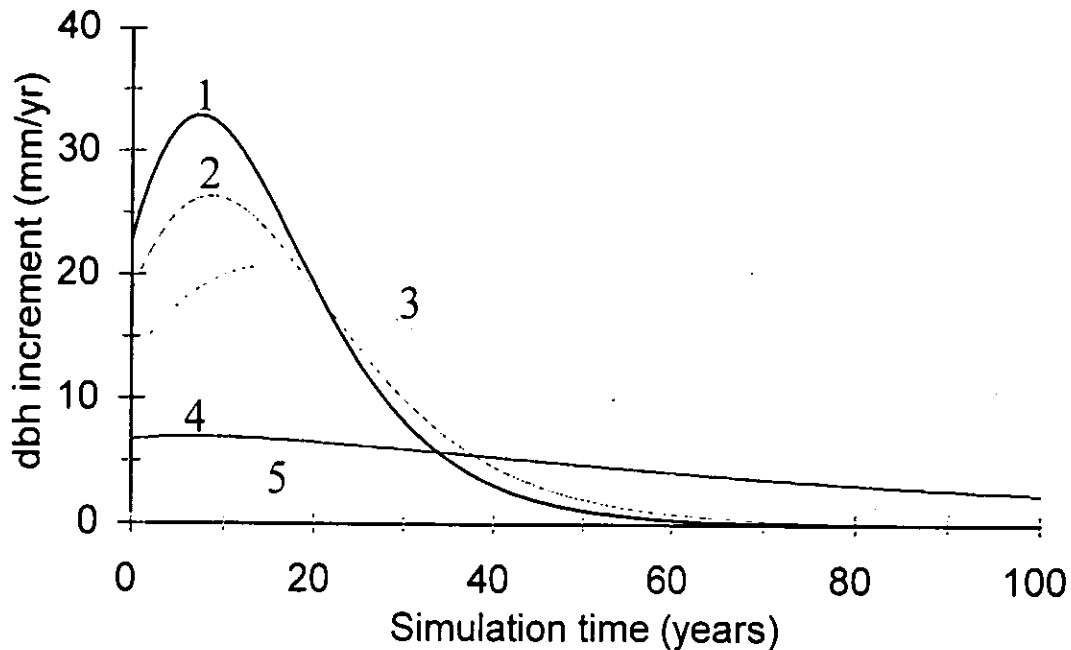


Figure 4.4 Diameter growth curves for canopy species using Botkin's (1993) fundamental growth function.

1- very fast grow, *Goethalsia meiantha*; 2 – fast grow, *Simarouba amara*; 3 – moderate grow, *Tapirira guianensis*; 4 – slow grow, *Minquartia guianensis*; and 5 – very slow grow, *Brosimum lactescens*

Figure 4.4. presents diameter increment curves obtained by Botkin fundamental growth function for selected canopy species. *Goethalsia meiantha* and *Simarouba amara* are used as examples of very-fast and fast growing species respectively and their being pioneers is not the case here, because other pioneer species, such as *Abarema macradenia* and *Ceiba pentandra* were found in slow and very slow growing groups. The height of the curve is proportional to species potential growth, and the maximum size (dbh and height) defines the steepness of the curve after maximum growth rate has been attained. The effect of difference in potential growth could be seen for *Tapirira guianensis* and *Minquartia guianensis*, which have the same maximum size, but differ in potential growth rate. The

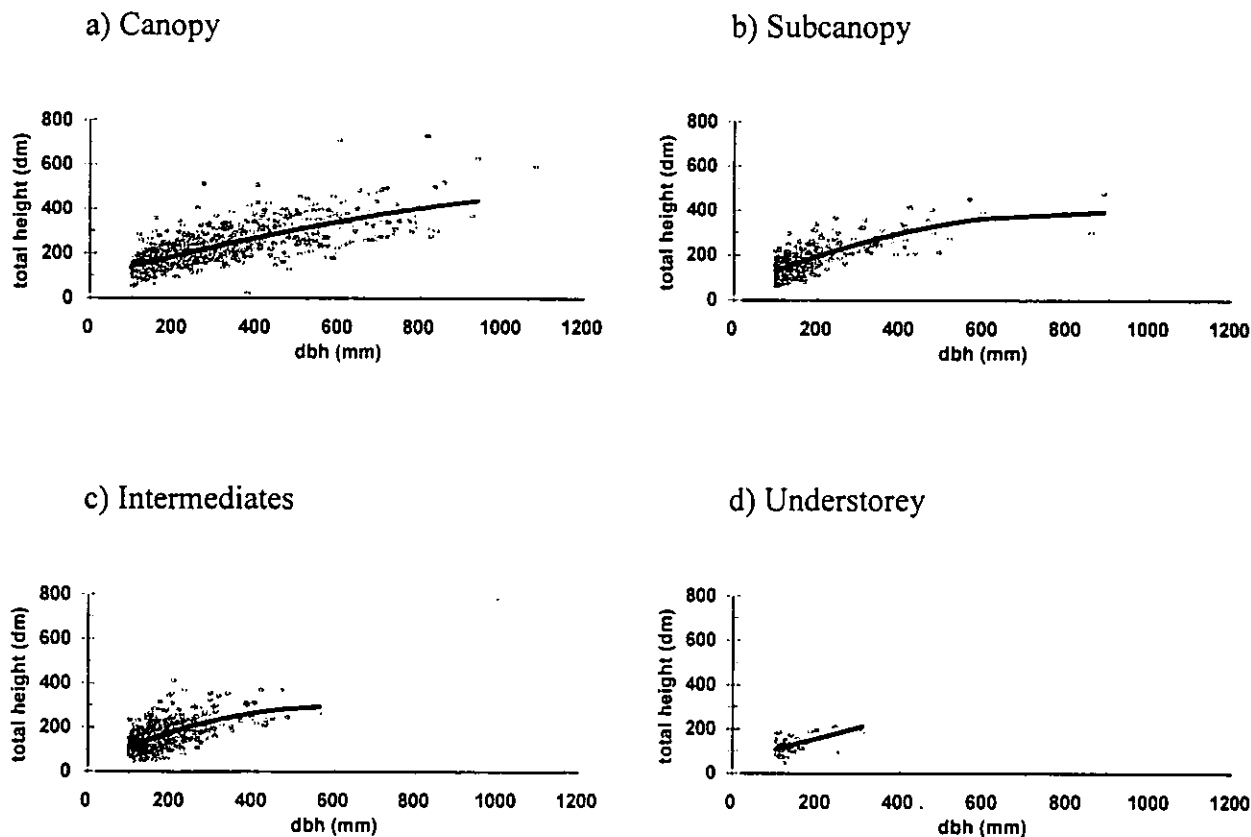


Figure 4.5. Total height functions for La Tirimbina fitted by group of adult size position in the forest stratum. The best fit was obtained with quadratic function for all adult position groups but understorey fitted well with linear function.

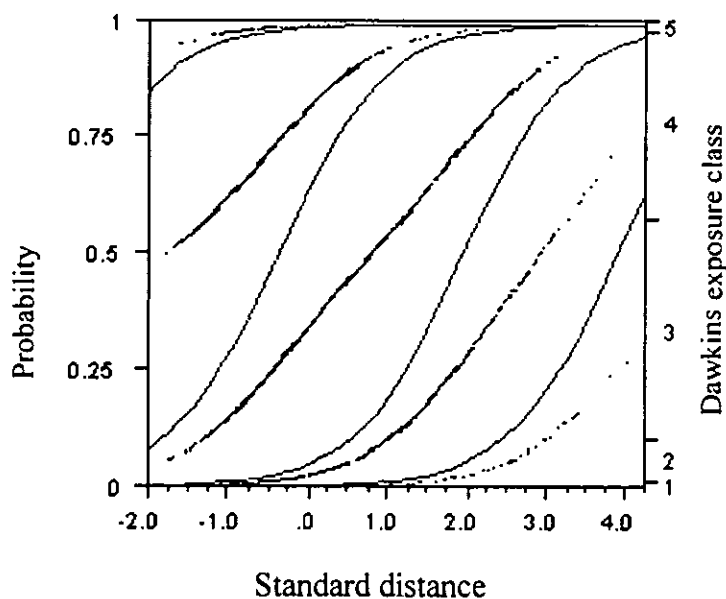


Figure 4.6. Logistic function fitted to Dawkins crown exposure on standard distance from the subject tree total height (sd_{ij}) to patch j mean height. The solid lines represent the regression estimates of between exposure class probability limits. The dashed lines show how the standard distance is related to the probability for a tree to be classified in a given crown exposition class. Regression parameters: $\beta_0' = [-5.905 \ -2.985 \ 0.547 \ 4.702]$, $\beta_1 = 1.512$ (see function on the text). All parameters are significantly different from zero (Prob < 0.0001).

effect of competition and other growth modifiers is similar to a decrease in the potential growth rate. Trees facing competition grow slower than do non-competing trees.

The quadratic, and some times linear function fitted better to diameter to height relationship (Figure 4.5, and Table 4.2.). Siteo *et al.* (1999) also found a better fit with the quadratic function at Corinto, one of CATIE's natural forest management research sites. All parameters and all functions are significant ($\alpha=0.05$). The regression residual plots were checked and no departures from normality and randomness were observed. Although there are differences in growth habits and form among palms (Rich 1986), these differences were not considered in this study, just to reduce the model complexity, and it is suggested in this study that this will not constitute the major source of error in forest characterisation.

Table 4.2 Parameters for the quadratic function used for tree total height estimation at La Tirimbina.

Adult size	Growth rate	<i>a</i>	<i>b</i>	<i>c</i>	N	R ²	Significance
Understorey	very slow	41.69	0.604	0	76	0.28	*
	Slow	139.29	-0.046	0	8		ns
Intermediate	Very slow	53.22	0.547	0	427	0.40	*
	Slow	84.58	0.411	0	116	0.46	*
	Moderate	59.91	0.839	-0.00078	175	0.36	*
	Fast	-0.72	1.436	-0.00165	38	0.56	*
	Very fast	-91.12	2.528	-0.00399	34	0.51	*
Subcanopy	Very slow	53.58	0.626	0	57	0.74	*
	Slow	32.16	1.033	-0.00008	75	0.75	*
	Moderate	21.15	1.134	-0.00126	108	0.63	*
	Fast	126.00	0.432	0	6	0.82	*
Canopy	Very slow	47.94	0.819	-0.00060	113	0.64	*
	Slow	117.41	0.408	0	105	0.55	*
	Moderate	104.43	0.421	0	114	0.61	*
	Fast	105.47	0.485	0	86	0.65	*
	Very fast	44.54	0.549	0	9	-	ns
Canopy	Pentaclethra	93.66	0.495	-0.00008	360	0.54	*
	Ferdinandusa	67.78	0.668	0	46	0.33	*
Canopy	Minuartia	60.76	0.558	0	58	0.66	*
	Protium	75.68	0.514	0	122	0.37	*
Unclassified	Unidentified	195.25	0.072	0	3	-	ns
	Palms	375.97	-3.719	0.01433	367	0.20	*

The hypothesis that crown exposure is correlated with the standard distance from the total height of the subject tree to the mean height of the respective patch, was tested using 225 patches (20x20 m), with 4197 trees for which crown exposure was evaluated using H.C. Dawkins five-point-scale (Alder and Synnott 1992). Total height was estimated with the quadratic function with the parameters provided in Table 4.2.

The individual tree standard distance from its total height to the patch mean height was found to be correlated with crown exposure (Spearman $r_s = -0.54$ and Pearson's is $r = -0.59$) suggesting that a certain estimation of the crown exposition could be performed with the help of the standard distance (sd_{ij}). The regression plot and coefficients are presented in Figure 4.6. The score test for the proportional odds assumption produced a Chi-square = 22.99 and $P < 0.0001$; all intercepts are significant at 1%. Sixty five percent of the predicted probabilities were concordant with the observed response, while 12% were discordant and the remaining 23% were tied. This corroborated the hypothesis that the higher the sd_{ij} or ($ht_{ij} > hm_j$) the higher the probability for the tree to be classified as emergent and vice-versa (Figure 4.6). This function and the maximum likelihood criteria are used to estimate the Dawkins class of tree crown exposure required for forest management purposes, but the standard distance (sd_{ij}) itself is used to represent the crown exposure effect in the dbh increment function.

The values of crown form and the standard distance estimated as indicated above were used as reducing factors in diameter growth function. The respective parameters were estimated separately (one effect each time) by growth group for Logistic, Botkin and Moore diameter growth functions using non-linear data fit on data from Tirimbina (Table 4.3 and Table 4.4). The effect of each parameter was expressed by exponential function. Each growth function (Equations 3.1-3.4) was evaluated preliminary, by fitting crown form and exposure parameters to the ungrouped set of trees. The statistical significance, residual distribution, and the range of the simulated diameter increment produced by each function were evaluated.

Table 4.3. Parameters of crown exposure effect using exponential function estimated by growth group at Tirimbina. The growth groups were defined in Section 4.1.1. The exponential function is $Y=ae^{bx}$, where x is the standard distance of the tree heights to patch mean height (see Section 3.2.2. Equation 3.9), and y is equivalent to the crown exposure effect on diameter increment.

Group	N	Logistic		Botkin		Moore	
		a	b	a	b	a	b
Understorey very slow	98	0.353*	0.888*	-	-	-	-
Understorey slow	7	1.093	0.631	0.400	0.302	0.376	0.285
Intermediate very slow	703	0.277*	0.228	0.151*	-0.004	0.199*	0.099
Intermediate slow	160	0.474*	0.325*	0.282*	-0.011	0.347*	0.090
Intermediate moderate	216	0.400*	0.348*	0.211*	0.256*	0.230*	0.255*
Intermediate fast	46	0.528*	0.067	0.237*	0.077	0.266*	0.067
Intermediate very fast	39	0.714*	0.135	0.266*	0.209*	0.291*	0.184*
Subcanopy very slow	76	0.230*	-0.023	0.146*	-0.183	0.180*	-0.067
Subcanopy slow	101	0.418*	0.091	0.252*	0.022	0.290*	0.069
Subcanopy moderate	151	0.471*	0.196*	0.222*	0.185*	0.247*	0.171*
Subcanopy fast	7	0.575*	0.341	0.418*	-0.033	0.482*	0.095
Canopy very slow	206	0.338*	0.254*	0.145*	0.222*	0.193*	0.215*
Canopy slow	178	0.524*	0.074	0.460*	-0.234	0.521*	-0.150
Canopy moderate	210	0.453*	0.191*	0.378*	0.017	0.431*	0.077
Canopy fast	137	0.435*	0.208*	0.363*	0.044	0.410*	0.100*
Canopy very fast	10	1.416	3.614	0.574	3.330	0.854*	3.468
<i>Pentaclethra maculoba</i>	545	0.557*	0.092*	0.403*	-0.104	0.464*	-0.035
<i>Ferdinandusa panamensis</i>	163	0.517*	0.189	0.234*	-0.038	0.315*	0.060
<i>Minuartia guianensis</i>	81	0.374*	0.147	0.231*	0.033	0.285*	0.092
<i>Protium ravenii</i>	154	0.558*	0.412*	0.284*	0.167	0.375*	0.258
Unidentified	5	1.268	-0.882	2.439	-5.511	2.186	-4.540

Table 4.4 Parameters of crown form effect using exponential function estimated for each growth group at Tirimbina. The growth groups were defined in Section 4.1.1. The exponential function is $Y = ae^{bx}$, where x is the Dawkins crown form, $a = 1.0$. The response value, y is the magnitude of the crown form effect on diameter growth rate and varies from 0.0 to 1.0 expressing maximum and minimum effect respectively.

Group	Logistic	Botkin	Moore
	<i>b</i>	<i>b</i>	<i>B</i>
Understorey very slow	-0.522*	-	-
Understorey slow	-0.123	-0.381*	-0.399*
Intermediate very slow	-0.498*	-0.667*	-0.587*
Intermediate slow	-0.336*	-0.483*	-0.415*
Intermediate moderate	-0.366*	-0.638*	-0.599*
Intermediate fast	-0.268*	-0.661*	-0.601*
Intermediate very fast	-0.131*	-0.585*	-0.543*
Subcanopy very slow	-0.518*	-0.680*	-0.608*
Subcanopy slow	-0.288*	-0.511*	-0.434*
Subcanopy moderate	-0.301*	-0.614*	-0.564*
Subcanopy fast	-0.164	-0.385*	-0.285*
Canopy very slow	-0.391*	-0.632*	-0.596*
Canopy slow	-0.248*	-0.366*	-0.288*
Canopy moderate	-0.296*	-0.399*	-0.234*
Canopy fast	-0.299*	-0.437*	-0.350*
Canopy very fast	-0.849*	-1.176*	-1.033*
<i>Pentaclethra macroloba</i>	-0.193*	-0.381*	-0.296*
<i>Ferdinandusa panamensis</i>	-0.289*	-0.570*	-0.462*
<i>Minuartia guianensis</i>	-0.413*	-0.608*	-0.519*
<i>Protium ravenii</i>	-0.279*	-0.483*	-0.395*
Unidentified	-0.059	-0.206	-0.177

The exponential function presented the highest regression coefficient ($r^2=0.38$) with the randomly distributed residual, however, the function was discarded because the maximum simulated diameter increment (19.5 mm.yr^{-1}) was lower than the observed (40.0 mm.yr^{-1}). The Moore and Botkin functions were able to predict the observed maximum diameter increment, with regression coefficient of $r^2=0.31$, but the residual was not randomly distributed. These functions predicted overestimated slow growing trees and underestimated fast growing trees. The logistic-type function presented a regression coefficient of $r^2=0.34$ and randomly distributed residual, but relatively lower maximum simulated diameter increment (35.0 mm.yr^{-1}). The logistic-type function was then selected for the simulations presented in this study, unless explicitly indicated, because of its biological basis, statistical significance, and simplicity.

The crown form and the height standard distance effects on diameter growth effects were presented on Table 4.3 and Table 4.4. It seems that the crown form in general, has a significant effect on diameter growth for all species groups. This is reasonable considering that the photosynthetic ability of any species, independent of its ecological characteristics, will be affected by its leaf area. The same is not valid for height standard distance (which is the equivalent of crown position or light competition level), which although presented a significant effect in the ungrouped set of trees, did not show significance for some of the species growth groups. All tested functions are consistent with the significance of this parameter and there is no general pattern in either species adult size or growth speed on light competition effect significance. However, it could be expected very slow and slow growing trees not to react significantly to competition effects. These species, generally maintain slow growth rates even if light conditions are good and survive long periods even if growing slowly (Finegan and Camacho 1999, Clark and Clark 1999). On the other hand, fast growing species were expected to be more affected by light competition and show statistical significance, however, intermediate and subcanopy moderate growing and canopy very fast growing species do not show significant (at 5% level) effect of light competition level with diameter increment. Canopy very fast growing species were represented by few

(10) trees which grow in similar light competition condition (Figure 4.7), which may have contributed to the lack of significance. Subcanopy fast growing species were represented by seven trees only, but occupying a broader range of light competition species conditions, however, this light competition index was not found significant. Other factors, such as diameter size or crown form, could be interacting affecting the actual significance of this parameter.

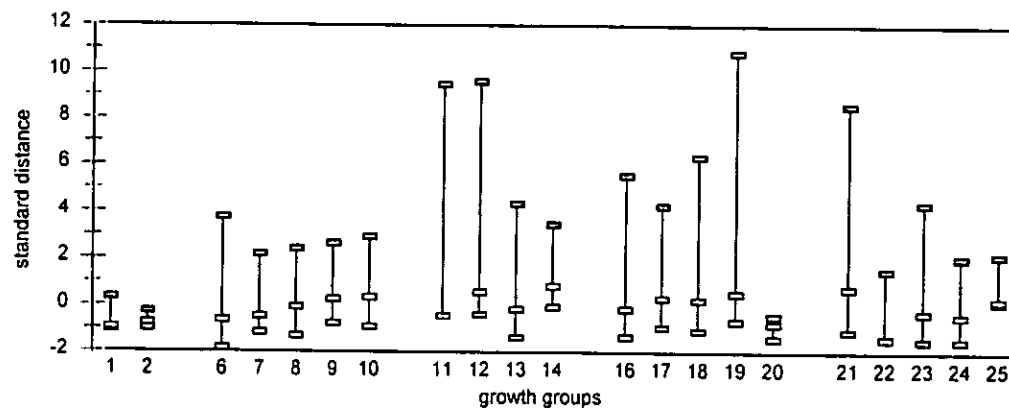


Figure 4.7 Light competition index expressed as the total tree height standard distance to patch mean height.

Range (maximum and minimum values) and median of the standard distances of all trees ($dbh \geq 10$ cm) by growth group in 1996 at Tirimbina. The number of trees in each group is the same indicated in Table 3.3. Growth groups: 1-2: Understorey (very slow and slow growing respectively); Intermediates: 6-very slow, 7-slow, 8-moderate, 9-fast, 10-very fast; Subcanopy: 11-very slow, 12-slow, 13-moderate, 14-fast; Canopy: 16-very slow, 17-slow, 18-moderate, 19-fast, 20-very fast; Species standing by themselves: 21-*Pentaclethra maculosa*, 22-*Ferdinandusa panamensis*, 23-*Miquartia guianensis*, 24-*Protium ravenii*; 25-Unidentified species.

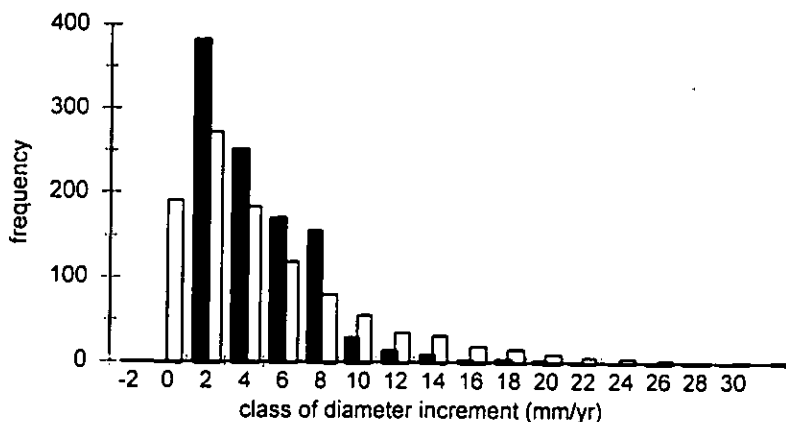


Figure 4.8 Absolute frequency distribution of the observed (open bars) and simulated (closed bars) diameter increment.

The observed increments are annual diameter increments from 1990 to 1998 in the nine 1-ha plots. The simulated increments were estimated in eight-year simulation starting with the nine-one hectare plots at year 1990 conditions. Recruitment and mortality were set off and observed dead trees and recruited trees were removed or included in the simulation at the respective year respectively.

4.1.4 Diameter increment

The simulated stand median diameter growth (annual growth of all trees during 8 years, with mortality and recruitment set as observed) is 2.9 mm.yr^{-1} against 3.0 mm.yr^{-1} of the observed median diameter increment in the period 1990-98. Simulated growth rates vary from zero to 35 mm.yr^{-1} with most of the trees growing slowly and few growing fast (Figure 4.8). This pattern is similar to the observed in natural tropical forests where most of the trees grow in shade conditions (adults of understorey species and juveniles of canopy and dominant tree species). The descriptive statistics of the simulated diameter increment reveal that canopy species, in general, grow faster (median 5.5 mm.yr^{-1}) than all adult sizes and the understorey trees grow the slowest (2 mm.yr^{-1}). The model simulates higher growth rates for trees observed with slow growth and lower growth rates for trees observed with high growth rates.

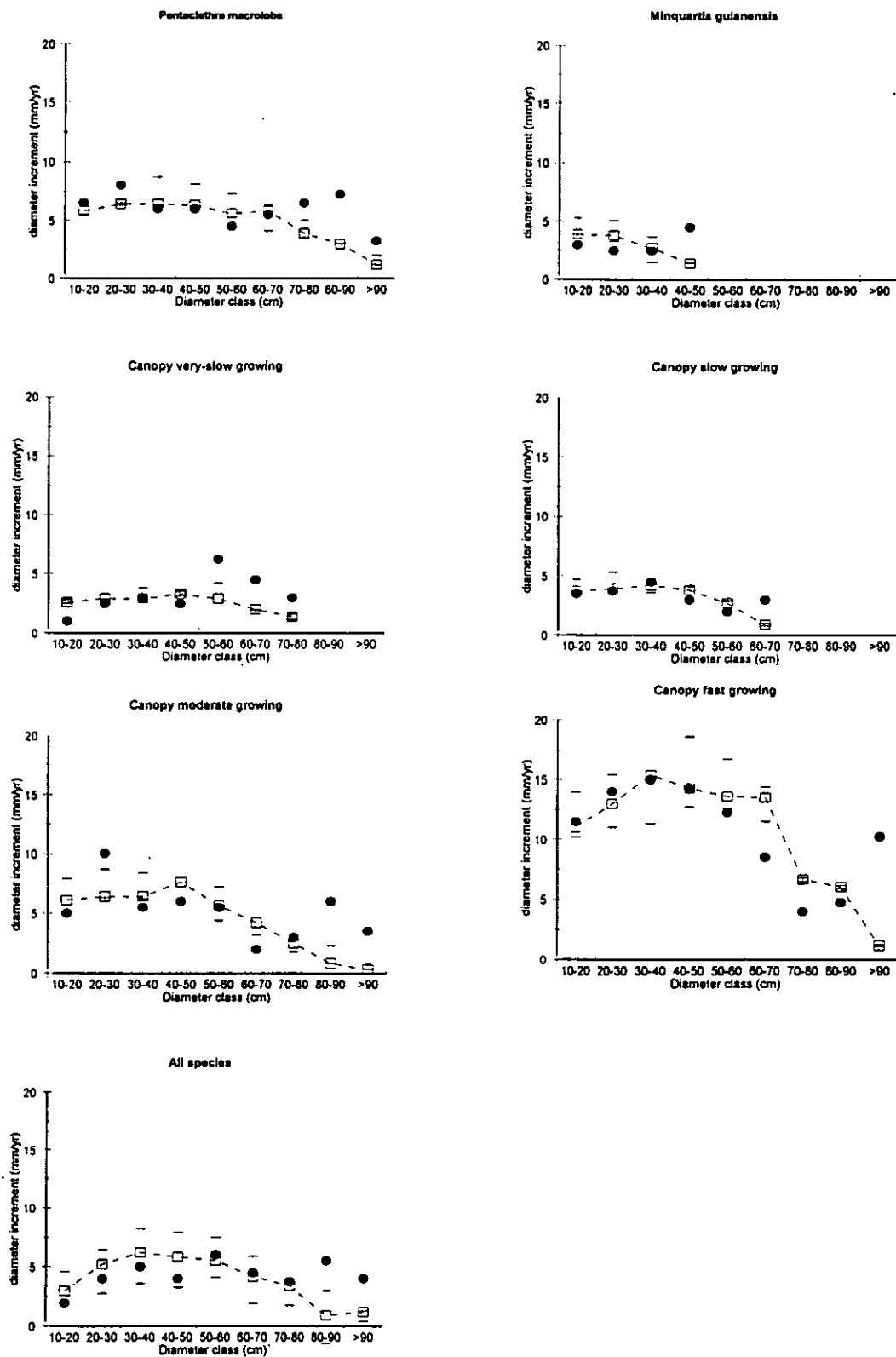


Figure 4.9 Observed versus simulated diameter growth medians per size class, using the 8 years (1990-98) at Tirimbina. □ simulated median, ● observed median, — simulated first and third quartile. The statistical test of differences between observed and simulated median are given in Table 4.6.

The overall modelling efficiency EF (Equation 2.8) estimated with all trees that survived the observation period between 1990 and 1998, was 0.39, which is among reported values for TRF simulation models (see below, Alder 1997, Favrichon 1998, Gourlet-Fleury *et al.* 1999). The linear regression coefficient between observed and simulated growth ($y_i = a + b \hat{y}_i$) rates is $r^2 = 0.38$ with intercept $a=0.15$ and slope $b = 1.1$ which are not statistically different from intercept zero and slope 1.0 respectively ($P < 0.001$). These statistics suggest that the model represents a significant proportion of diameter increment of the trees being modelled.

Comparisons between simulated and observed growth medians by species and growth groups are presented in Figure 4.9 and Table 4.5 for selected species and adult position groups. As already stated, the general tendency is that the model captures part of the variability observed within each group, however, because there is a large variability in observed diameter increments, and there is no clear tendency within growth groups or species, the model predicts average conditions but does not capture the individual tree growth well. Medians of canopy (fast, moderate and slow growing) trees could be simulated more closely and in most of the cases the median one-way test did not found statistical differences between simulated and observed medians (Table 4.5). If all species are considered together, the simulated medians are higher in lower diameter classes but lower in higher diameter classes. The simulated diameter growth residuals do not vary with time and maintain a constant trend over the simulated period meaning that there is no simulation time-associated inflation of the predicting capacity of the model. The simulated growth patterns presented here are in general, similar to those observed in most tropical forests and at Tirimbina in particular. However, the model does not describe accurately the growth rates at individual tree level but does represent average conditions at the stand level and species group.

Table 4.5 Median one-way analysis to test differences between simulated and observed diameter increment medians.

Species or group	Statistic test	Diameter class (cm)								
		10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	>90
All Species	N	8152	2910	1321	841	357	140	112	39	30
	1 st Quartile	1.4 (0.5)	1.9 (1.0)	3.1 (2.0)	2.7 (1.0)	3.6 (2.0)	2.8 (1.0)	2.3 (1.3)	2.0 (4.0)	2.2 (2.0)
	Median	2.0 (2.0)	4.0 (4.0)	6.0 (5.0)	5.7 (4.0)	5.5 (6.0)	4.1 (4.5)	3.9 (3.8)	3.3 (6.0)	3.6 (4.0)
	3 rd Quartile	3.9 (5.0)	7.4 (9.0)	7.2 (10)	6.6 (9.0)	6.4 (10.5)	5.4 (9.0)	4.3 (8.5)	4.1 (8.0)	4.1 (8.5)
	χ^2	407.6	43.6	45.3	38.5	0.2	0.5	0.6	22.9	22.0
	Significance	***	***	***	***	NS	NS	NS	***	***
<i>Pentaclethra maculosa</i>	N	624	727	552	345	191	60	63	8	14
	1 st Quartile	7.9 (4.0)	7.5 (4.0)	6.7 (3.0)	6.0 (2.5)	5.4 (2.0)	4.3 (2.0)	3.8 (2.5)	3.0 (5.0)	2.1 (1.5)
	Median	8.0 (6.5)	7.7 (8.0)	7.0 (6.0)	6.5 (6.0)	5.7 (4.5)	5.3 (5.5)	4.1 (6.5)	3.4 (7.3)	2.2 (3.3)
	3 rd Quartile	8.1 (11.0)	7.9 (13.0)	7.4 (11.0)	7.0 (10.0)	6.3 (9.0)	5.7 (9.5)	4.3 (12.0)	3.4 (14.0)	2.6 (8.0)
	χ^2	38.7	103.2	0.74	2.1	3.8	1.2	9.9	15.0	5.0
	Significance	***	***	NS	NS	*	NS	**	***	*
<i>Minquartia guianensis</i>	N	179	127	42	4					
	1 st Quartile	2.5 (1.0)	2.1 (1.0)	1.6 (0.0)	1.6 (4.0)					
	Median	2.6 (3.0)	2.3 (2.5)	1.9 (2.5)	1.6 (4.5)					
	3 rd Quartile	2.9 (5.5)	2.9 (4.0)	2.6 (5.5)	1.6 (5.0)					
	χ^2	6.9	41.3	0.2	7.0					
	Significance	**	***	NS	**					
Canopy very slow growing	N	610	190	101	118	20	9	16		
	1 st Quartile	1.9 (0.0)	1.9 (1.0)	1.6 (0.5)	2.0 (0.5)	1.7 (5.0)	1.5 (4.5)	1.0 (2.0)		
	Median	2.0 (1.0)	2.0 (2.5)	1.8 (3.0)	2.1 (2.5)	2.0 (6.3)	1.5 (4.5)	1.2 (3.0)		
	3 rd Quartile	2.1 (3.0)	2.0 (5.0)	2.2 (5.5)	2.2 (4.5)	2.4 (13.0)	1.6 (7.5)	1.3 (7.5)		
	χ^2	274.9	3.9	0.5	5.8	15.0	10.3	20.5		
	Significance	***	*	NS	NS	***	**	***		
Canopy slow growing	N	287	154	90	81	36	24			
	1 st Quartile	4.3 (1.0)	3.9 (1.0)	3.6 (3.0)	3.6 (1.0)	3.3 (0.0)	1.9 (0.5)			
	Median	4.4 (3.5)	4.1 (3.8)	3.8 (4.5)	3.8 (3.0)	3.4 (2.0)	2.8 (3.0)			
	3 rd Quartile	4.6 (7.0)	4.4 (6.0)	4.1 (6.0)	3.9 (6.0)	3.6 (5.5)	2.9 (4.8)			
	χ^2	0.9	0.0	2.3	1.2	1.2	13.2			
	Significance	***	NS	NS	NS	NS	**			
Canopy moderate growing	N	355	183	116	88	42	32	21	11	8
	1 st Quartile	5.0 (2.0)	4.6 (6.0)	4.3 (2.0)	4.2 (2.3)	3.3 (0.5)	2.6 (0.0)	2.3 (1.0)	2.0 (4.0)	3.6 (0.0)
	Median	5.1 (5.0)	4.9 (10.0)	4.6 (5.0)	5.5 (6.0)	4.6 (5.5)	4.0 (2.0)	3.4 (3.0)	2.0 (6.0)	3.7 (3.5)
	3 rd Quartile	6.5 (8.5)	6.7 (12.0)	6.0 (11.0)	5.7 (12.0)	5.3 (12.0)	4.2 (9.5)	4.7 (3.0)	3.3 (7.5)	3.8 (4.0)
	χ^2	12.7	16.8	1.8	3.3	0.2	1.0	0.4	21.0	0.9
	Significance	**	***	NS	NS	NS	NS	NS	***	NS
Canopy fast growing	N	112	102	61	58	52	7	4	4	8
	1 st Quartile	10.5 (5.0)	10.0 (8.0)	8.9 (10.0)	9.8 (4.0)	9.6 (8.0)	9.1 (8.5)	6.2 (3.0)	5.8 (4.0)	4.2 (5.0)
	Median	10.9 (11.5)	10.4 (14.0)	11.4 (15.0)	10.9 (14.2)	10.4 (12.0)	11.1 (8.5)	6.3 (4.0)	5.9 (4.8)	4.4 (10.2)
	3 rd Quartile	11.6 (15.8)	12.4 (21.0)	12.3 (21.0)	11.8 (20.0)	12.4 (17.5)	11.5 (13.0)	6.4 (6.0)	6.1 (5.5)	4.5 (12.3)
	χ^2	0.04	0.0	0.8	0.0	0.6	0.3	1.7	7.0	15.0
	Significance	***	NS	NS	NS	NS	NS	NS	*	***

The resulting differences between simulated and observed diameter growth may be partly justified by the low capability of the model to predict the changes in micro environmental conditions such as soil conditions and health condition of the tree, which are not accounted in this model, and crown form, which is randomly set within the model. Light availability is estimated based in average patch conditions and the mean height for each tree. Considering that three of the six parameters used to estimate potential diameter increment (in Botkin and Moore functions) are those of the height function, we suggest that an important variability in diameter growth could be explained by increasing the accuracy of the height function. The current height functions could explain 24-70% of the height variability (Table 4.2). During model development, different growth functions were experimented but among the selected growth functions (see Section 4.1.4.1) there were no significant differences in modelling efficiency and the long-term simulated trend was not affected.

Other authors modelling tropical forests, at different levels of model aggregation and conceptual frameworks, faced problems estimating tree growth (diameter or basal area increment). Alder and Silva (2000), modelling Brazilian Amazon forests, found that their logarithmic growth function in general, underestimated small tree size (classes 20-30 cm) and overestimated large tree diameter increment. Alder (1997) used a regression function to estimate basal area increment as function of initial stand basal area for SIRENA in Central American forests. The regression coefficient was $r^2 = 0.09$, but justifies that this function was useful in showing that increment is relatively constant over a range of basal areas, and implies higher net per tree growth at lower stockings. In French Guyana, Favrichon (1998) found regression coefficients between $0.05 \leq r^2 \leq 0.22$, using a transition matrix model where five species groups of adult position and shade tolerance were considered separately, and Gourlet-Fleury *et al.* (1999) found a modelling efficiency $EF = 0.42$, using a spatially explicit individual tree model.

4.1.4.1 Recruitment

At Tirimbina, a positive relation between initial species abundance (in 1990) and the number of recruits in eight years period (1990-98) was found. A linear regression fitted to the number of recruits on initial species abundance ($\text{Recruits} = a + b * \text{Abundance}$) was highly significant ($N=278$, $r^2 = 0.68$, $P < 0.0001$). The positive non-zero intercept (95% confidence limit of the intercept $0.13 \leq a \leq 0.41$) supports that species not present at the beginning were recruited during the study period.

The hypothesis that recruits of pioneer and non-pioneer species have random crown exposure was rejected ($N=1209$, Likelihood ratio Chi-square = 222.128 and $P < 0.001$), which suggest pioneer species establishing in more open than closed canopy conditions. Literature (Denslow 1987, Whitmore 1989, 1990) and field observations support the fact that recruits of pioneer species have more probability to establish in more open conditions. Some aspects could, however be mentioned regarding recruitment procedure and species abundance and diversity. It was stated earlier that tropical forests have high species diversity, with many of the species presenting abundance less than one tree per hectare (Figure 2.3). This situation is maintained in the field over long periods despite that rare species could temporarily disappear from the plots ($\text{dbh} \geq 10\text{cm}$). It was hypothesised that this could be so because the species pool from where tropical forests could establish is actually higher than the current species composition known at a given short period of observations. With a species pool larger than presently observed species, rare species could go locally extinct and reappear later, and species not presently found at the beginning could establish.

Gap dynamics is very important in logged forests and is particularly recognised as one of the driving force of tropical forest dynamic (Swaine and Whitmore 1988, Whitmore 1990, Hubell and Foster 1986 a). The recognition of "regeneration patches", or regeneration microhabitats within a forest stand is a requirement to realistically simulate species composition in tropical forests. In this study, gap dynamics was approached by considering two important aspects indicated above, gap – non-gap, and pioneer – non-pioneer. The

discussion around the terminology “gap” and “pioneer” (Meer *et al.* 1994, Clark and Clark 1987, Brokaw and Schneider 1989, Lieberman *et al.* 1989, Whitmore 1989) provides interesting points of view about tropical forest ecology. The simplified definition was used although with the risks of using arbitrary, but justifiable, boundaries in species grouping and gap descriptions. Using the continuum concept of species light requirement for regeneration as suggested by Lieberman *et al.* (1989) would not necessarily produce a better model and would demand costly heavy work including the characterisation of species in the continuum of regeneration requirements. Note that even with so few classification levels difficulties recognising a gap as well as defining whether a species is pioneer or not still persist.

The values of recruitment parameters, those used to estimate the number of recruits and the probability for a species to establish, were set by trial and error procedure to fit the recruitment rate, species composition, and stand density known from tropical rain forests. Parameters estimated by trial and error are discussed and evaluated using sensitivity analysis techniques in Section 4.2.2

4.2 Evaluation of the ecological adequacy of the model

4.2.1 No disturbance scenario

4.2.1.1 Stand density

The output of this simulation was evaluated at the steady state, which was defined as the period in which there were no significant changes in stand density. This period was observed about 100 years after the beginning of the simulation (Figure 4.10). The average values indicated in this section refer to this period.

The initial stand density, after logging and silvicultural treatment, were below the equilibrium conditions of stand density. This explains the initial increase both in the number of trees and basal area until stand density becomes stabilised. The total number of trees after steady state was attained was between 450 and 500 ha^{-1} and the basal area levelled up at about $28 \text{ m}^2 \cdot \text{ha}^{-1}$ (Figure 4.10). These characteristics of stand density are within the known interval in neotropical lowland rain forests (see Table 3.3) and within the range observed in an undisturbed forest at La Selva, a *Pentaclethra* forest site, with stand basal area of $25\text{-}30 \text{ m}^2 \cdot \text{ha}^{-1}$ and $395\text{-}529 \text{ trees} \cdot \text{ha}^{-1}$ (Lieberman and Lieberman, 1987). Within the model, stand density is mainly affected by mortality and recruitment parameters as discussed below (see Section 4.2.1.2) below). The recruits should balance the deaths to maintain the steady state number of trees and basal area in the stand otherwise stand density would either increase up or will fall below observed lower limit of stand density in *Pentaclethra* forest (Table 3.3).

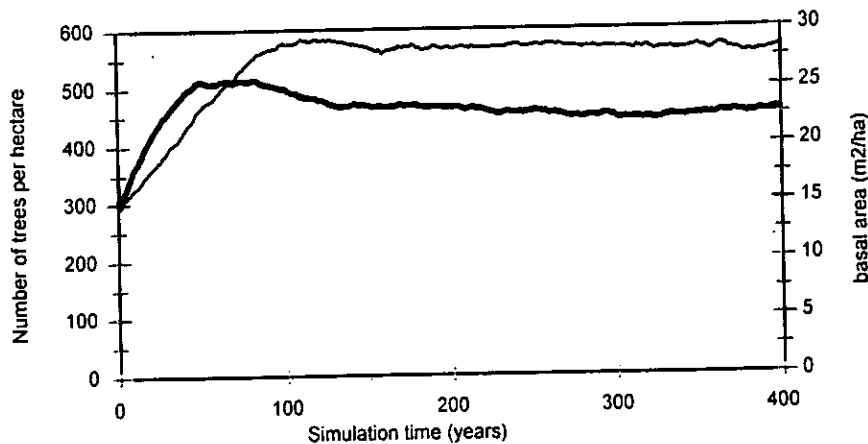


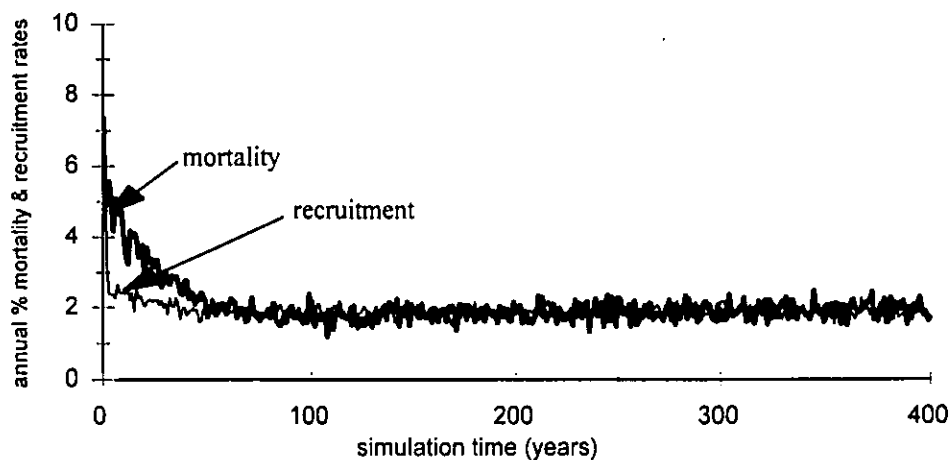
Figure 4.10 Non-disturbance scenario simulated stand density and basal area. Average curves of 20 Monte Carlo simulations using 1-ha logged and silviculturally treated plot of La Tirimbina. (—) number of trees per hectare, and (---) basal area $\text{m}^2 \cdot \text{ha}^{-1}$ at Tirimbina starting from year 1996.

4.2.1.2 Mortality and recruitment

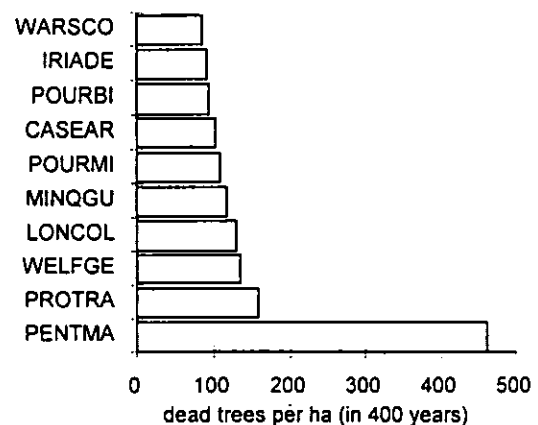
Annual mortality rate varies from one year to another but maintains a long-term trend of annual values between 1-3% (logarithmic model), which is about 6-10 dead trees.ha⁻¹.year⁻¹ (Figure 4.11a). The simulated average annual mortality rate is 1.9% for the 400 years. Peaks of particularly high mortality could be observed eventually as catastrophic events but do not characterise the mortality of the stand. In the four study sites reported above, mortality rates varied from one year to another and in general, particularly high mortality rates were associated to logging and silvicultural interventions. Lieberman and Lieberman (1987) found 1.80-2.24% annual mortality (logarithmic model) over a 13-year period in the undisturbed old growth forest of La Selva. The simulated mortality rates are within the observed range for neotropical rain forests (Table 3.3) and the *Pentaclethra* forests in particular (Section 0).

Most of the dead trees (80%) died due to density-independent factors, which are not explicitly modelled but aggregated under the single concept of density-independent mortality. This includes trees killed by wind throw, uprooted, and suddenly broken, and is an inverse function of species longevity. It is equally distributed among trees of different sizes and is independent of growth rates. Falling trees kill 7% of the dead trees, of which most of them are among small and suppressed trees. Trees so killed were among the slow growing ones probably because these are the ones that are under the canopy of large trees – the ones that fall and destroy them. The remaining proportion (20%) of dead trees was caused by competition and senescence, which affects relatively slow growing trees.

a) Percentage of annual mortality and recruitment



b) Commonly dead species



c) Commonly recruited species

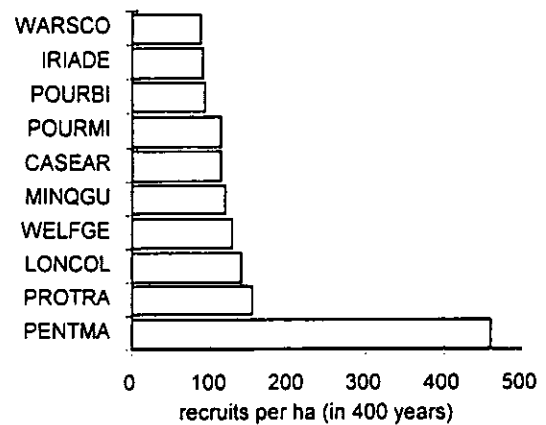


Figure 4.11. Non-disturbed scenario simulated annual mortality (---) and recruitment (—) percentage at Tirimbina starting from year 1996 using one-ha logged and silviculturally treated plot with 20 Monte Carlo repetitions; (b) the most commonly dead and recruited species during all the simulation period.

The species that made up the mortality were among the most abundant species at the beginning of the simulation (Figure 4.11 b). The distribution of the number of dead trees by size class shows a reverse-J similar to the structure of the forest. In general, small trees have higher mortality rate (2-3% for diameter classes 10-30 cm) than larger trees (0.5-1.0 % for diameter classes higher than 50 cm). This pattern is not necessarily the observed in the field, where no differences in mortality rates among tree size classes were observed (Mervart 1972, Lieberman *et al.* 1985a, Finegan *et al.* 1999). The model presents a higher mortality rate in smaller trees probably because of the additional mortality to smaller trees associated with large tree fall.

The simulated average number of recruits was about eight (range 5-15) $\text{ha}^{-1} \cdot \text{year}^{-1}$, with canopy and intermediate species (the most abundant groups in the forest stand) being the most common among recruits (Figure 4.11 c). This recruitment rate is comparable to the 6-10 recruits. $\text{ha}^{-1} \cdot \text{year}^{-1}$ found at La Selva by Lieberman and Lieberman (1987), however the latter figures are an average of 13 years, with no year-to-year censuses, and do not account for those recruits that did not survive the period. The 10 most commonly recruited species were present as the most abundant at the beginning of the simulation (Figure 4.11 c) given that the probability for species being recruited is proportional to initial species abundance (see Section 4.1.4.1).

In the model, recruitment is governed by several parameters and procedures. The number of recruits is stochastically estimated as a function of patch basal area. The recruits initial dbh is estimated from observed distribution pattern with 1-cm diameter class. The initial dbh is independent of life form or regeneration guild so that trees, palms, pioneers and non-pioneers get their initial dbh from the same distribution (Section 4.1.4.1).

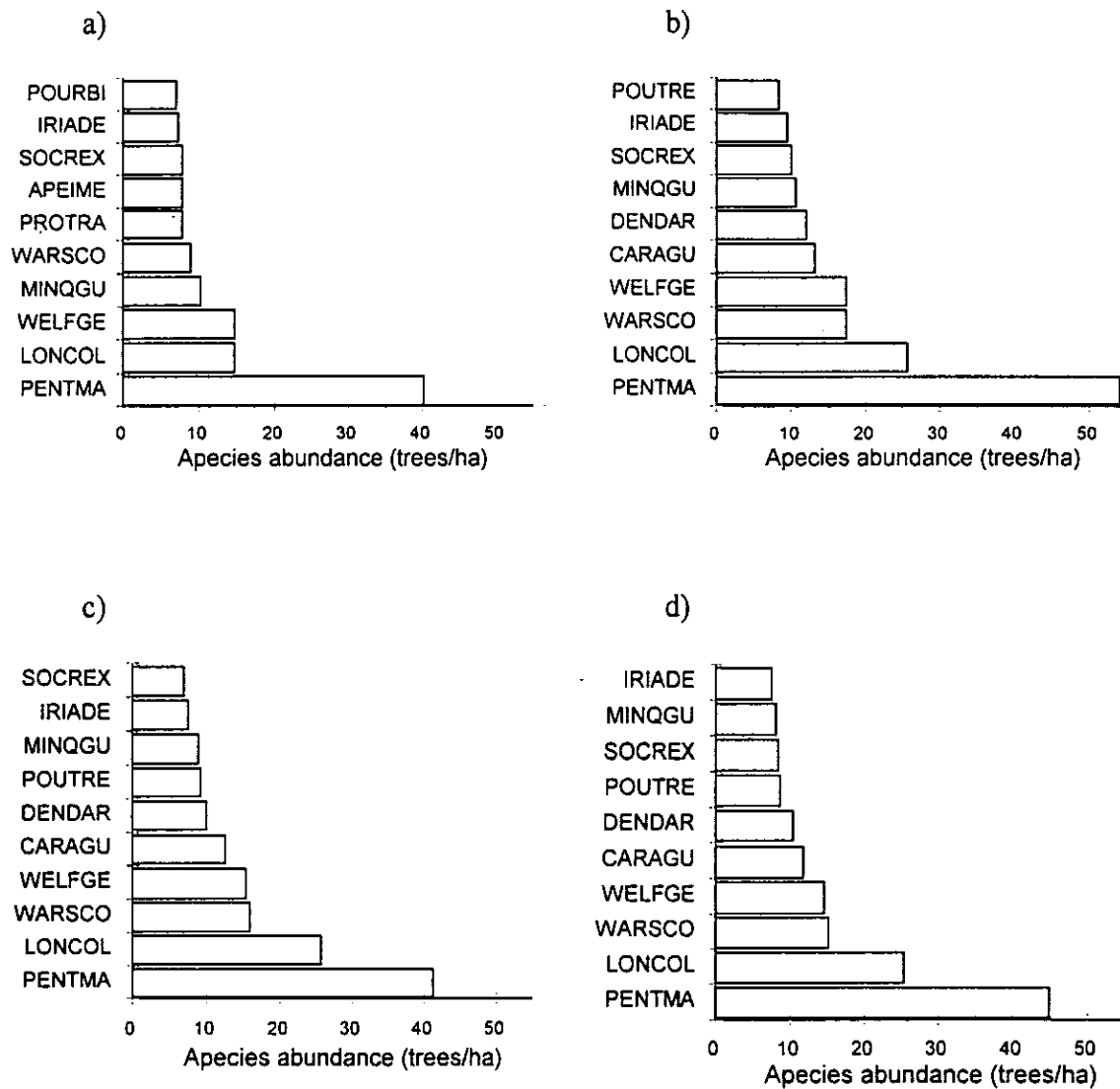


Figure 4.12 Non-disturbed scenario simulated species composition representing the 10 most abundant species at (a) the starting year, (b) at year 100, (c) at year 200, and (d) at year 400 simulated years respectively at Tirimbina starting from year 1996 using one-ha logged and silviculturally treated plot with 20 Monte Carlo simulations.

4.2.1.3 Species composition, richness and diversity

Some of the species-specific parameters, such as longevity, potential growth and maximum dbh (which affect directly or indirectly species abundance) were estimated at growth group level (adult size and growth rate – see Section 4.1.1). However, the probability of a species to be recruited is set at the individual species level by including the species abundance as a component of the whole probability together with species-group parameters. Simulation of species composition, richness and diversity are therefore functions of individual species by including species abundance, which is inversely proportional to species probability of extinction.

Simulated species composition is consistent with the expected pattern (Table 3.3). The most abundant species at the beginning of the simulation maintained their abundance rank through the simulation period (Figure 4.12). Seven of the ten most abundant species at year 400 were among the most abundant 10 species at the beginning of the simulation. Two of the five palms identified at Tirimbina, *Welfia georgii* and *Iriartea deltoidea*, were among the 10 most abundant species at the beginning of the simulation and maintained themselves within the most abundant species. In the four study sites described above (Section 0), the relative proportion of species varied just a little during the 10 years observation (Figure 3.3 c-f), and the abundant species at the beginning of the study maintained themselves until the end of the observation period. The model uses several parameters to control species composition and stability. Mortality and recruitment balance affect simulated species composition and, in general, if recruitment does not compensate mortality, the species abundance will decline and would likely disappear temporarily from the counts. Mortality and recruitment parameters have been discussed above.

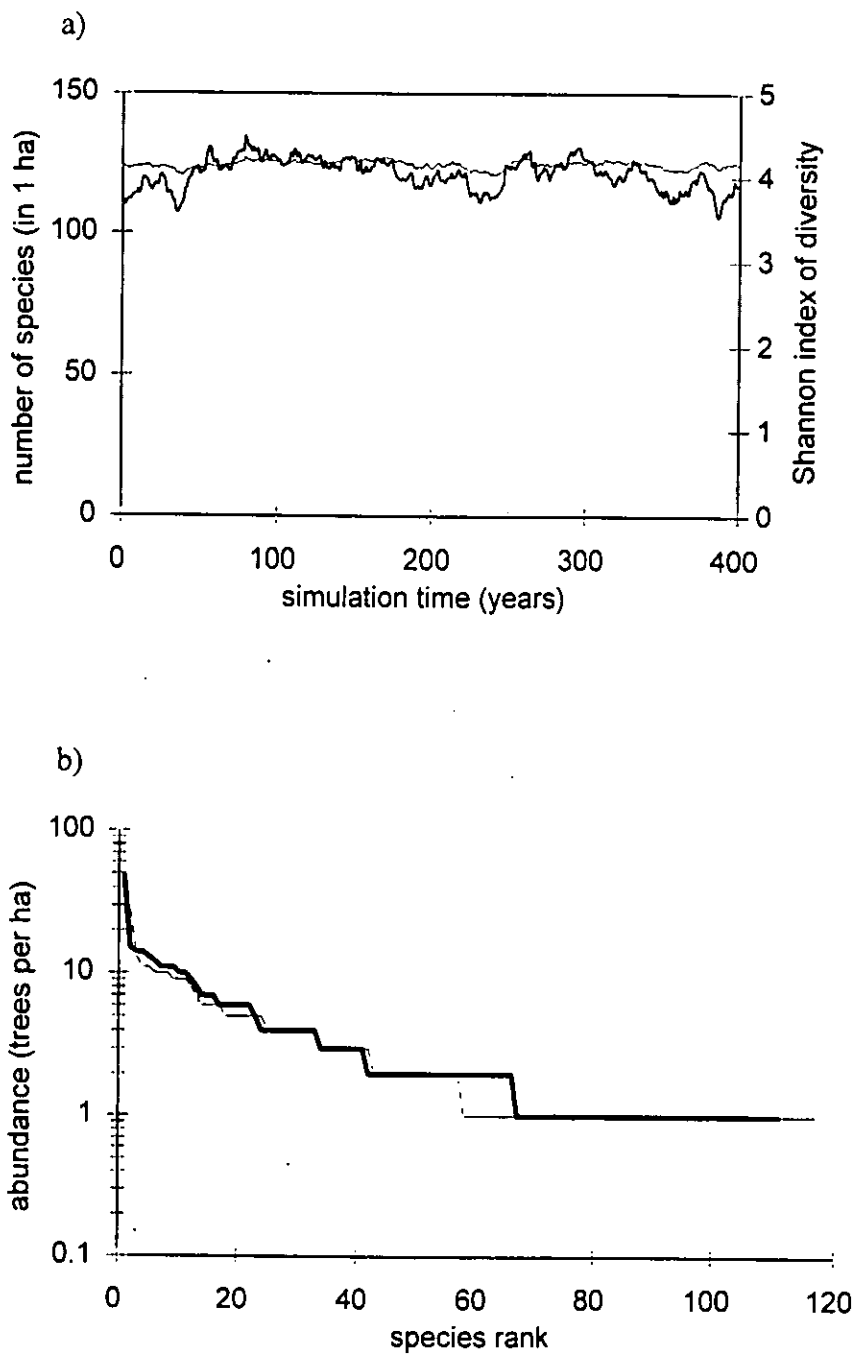


Figure 4.13 Non-disturbance scenario simulated species richness and diversity at Tirimbina starting from year 1996 using one-ha plots: (a) Total number of species (—) and Shannon diversity index (---); (b) Species rank abundance distribution at the beginning of the simulation (—) and at simulated year 400 (---).

Changes in species composition in the absence of drastic disturbance or climate change has been rarely reported in mature TRF. Since most species are rare, changes in composition could be due to temporary and local disappearance of the species from the considered measuring size classes. However, Swaine *et al.* (1987) suggest that although existing data is inadequate to characterise population dynamics in TRF, short period studies in different regions reveal that most species show little change in abundance over the period studied and few depart significantly. In the four *Pentaclethra* forests study sites described above, there were few changes in species composition and abundance. Most of the observed changes at these sites could be explained as effects of logging and silvicultural treatments. Finegan *et al.* (in prep.) for instance, explained the effect of liberation refinement on species abundance at Tirimbina, in which *Dystovomita paniculata* and *Pouteria campechiana*, both non-commercial species significantly reduced their abundance after silvicultural treatment.

Simulated species richness (Figure 4.13) did not differ from commonly observed values (Table 3.3). The Shannon diversity index started at 4.1 increased to 4.3 which was maintained over time. The rank species abundance distribution (Figure 4.13 c, d) showed the typical form of *Pentaclethra* forest with *Pentaclethra macroloba* particularly abundant, a few species following, and a large proportion of rare species with abundance less than 1.0 tree.ha⁻¹. Species richness is particularly maintained in the model by the parameter set as the probabilities of the species to establish given that a patch is actually in gap phase or not. The procedure to select species to be recruited provides a non-zero probability for all species on list to establish, even those with zero abundance at the beginning of the simulation. The probability of a pioneer species to establish in a gap and the probability of a species presently with zero abundance to establish were set arbitrarily but higher probability (but less than 1.0) for a pioneer to establish in a gap and a higher probability (but less than 1.0) for a species with no-zero abundance to establish (see Section 4.2.2 for evaluation of these parameters).

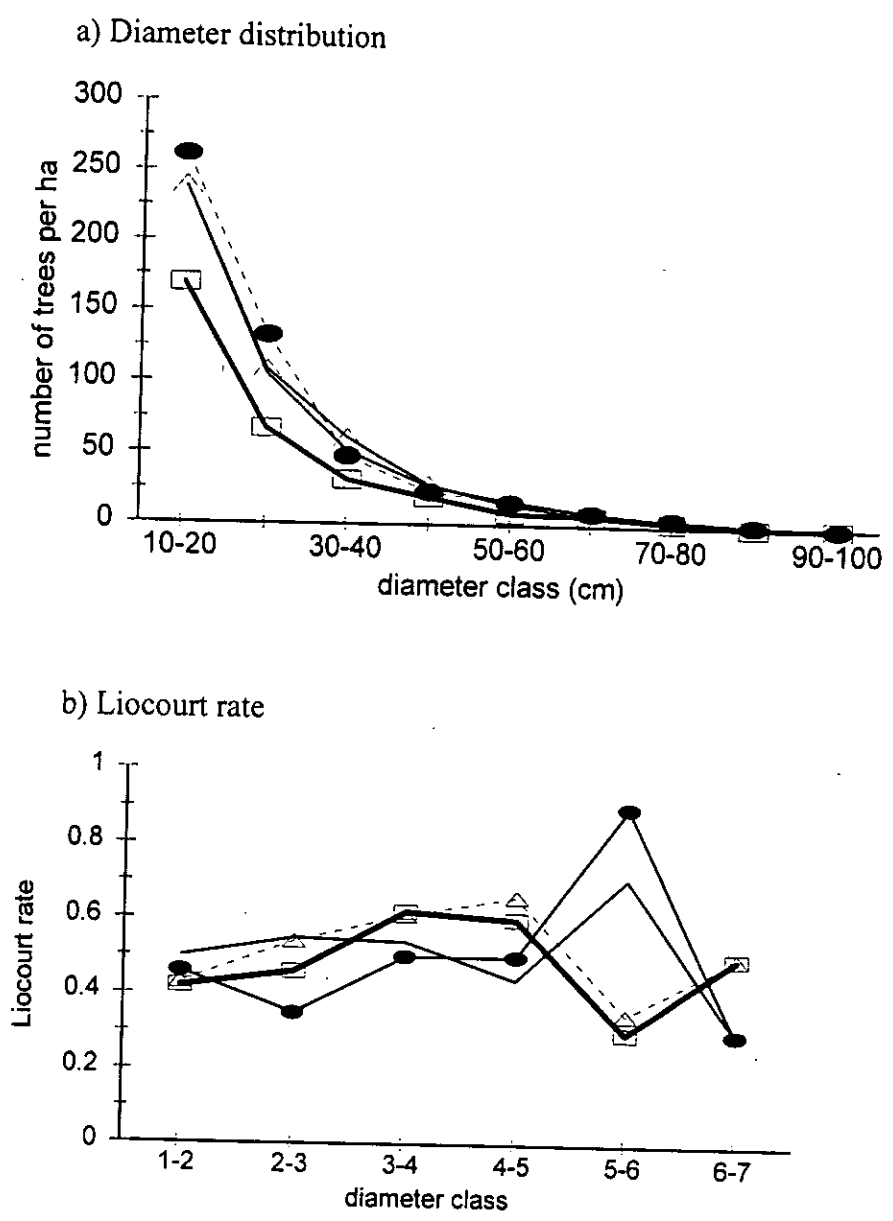


Figure 4.14. Non-disturbed scenario simulated diameter distribution at Tirimbina starting from year 1996 using one-ha logged and silviculturally treated plot. (a) Diameter distribution and (b) Liocourt rate at the (□) observed initial structure in 1996 and (●) simulated structure in year 100, (○) year 200, and (Δ) year 400.

The species to be recruited is drawn from the species pool of the simulated site whether they were present or not in the forest stand at the beginning of the simulation. This gives opportunity for those species not observed in a given year – the one used as the beginning year for simulation – to establish. The argument for recruiting species not observed at the beginning of the simulation has been discussed in Section 3.2.3. Simulated species could go locally extinct and reappear later. At Tirimbina, for instance, it was observed that from one year to another 3-10 species disappeared while 4-7 species re-entered the listing (UMBN, unpublished data). During the observation period 1990-1998, the balance was 18 species disappearing and 27 new species entering. The estimated probabilities for a species to establish, depending on the actual patch phase (gap or non-gap) and the probability for a not actually present species to be recruited also play an important role in the selection of the recruits species. In general, abundant species would have higher probability to establish than rare species. This property is used to maintain the simulated forest species richness and diversity.

4.2.1.4 Diameter distribution

The structure of the simulated forest is typical of that of an uneven aged natural forest with the reverse-J all over the simulation period (Figure 4.14 a). The Liocourt rates between 10-cm diameter classes vary slightly around 0.5, although the variation appears higher in larger diameter classes because of the small number of large trees (Figure 4.14 b). The Liocourt rate of the four *Pentaclethra* forest study areas reported in this study are lower in smaller diameter classes, meaning relatively large number of small trees. Vanclay (1994) found that this value could vary slightly around 0.5, the value considered “normal” for well regenerated undisturbed tropical rain forests. The simulated forest structure does not depart from the observed in tropical forests in general. The high number of small trees in these forests is inflated by the presence of palms, which comprise about 10% of the total number of stems ($dbh \geq 10\text{cm}$), and slow growing understory and intermediate species, which need several years before they can transit to higher diameter classes.

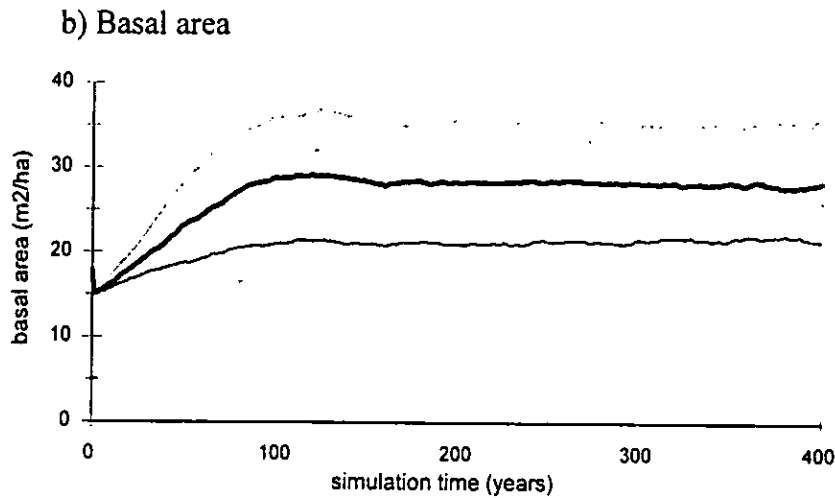
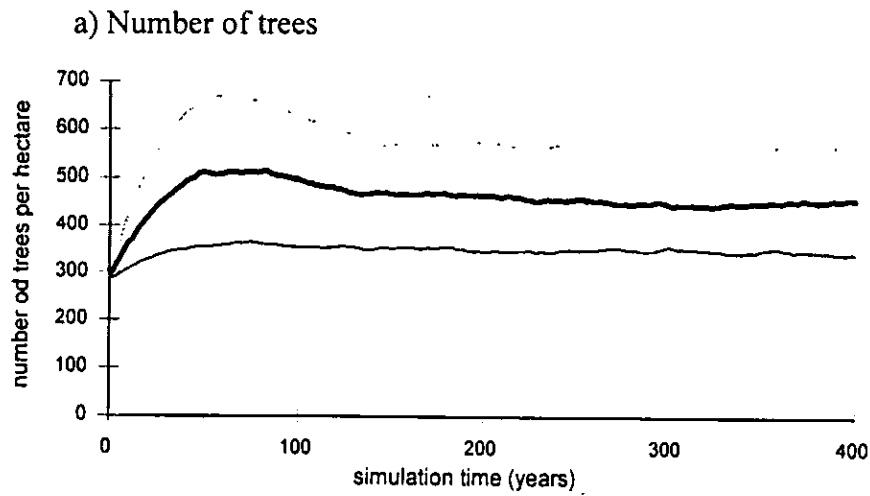


Figure 4.15 Sensitivity analysis of the number of recruits parameter (a) on simulated a-b) stand density. The dark intermediate line (—) represents the base line scenario ($a=1.35$) and the upper and the lower thin lines (---) $a+20%$ and (—) $a-20%$ respectively. All simulations were performed using 1-hectare plot with Monte Carlo 20 repetitions.

4.2.2 Evaluation of ecologically-based parameters

4.2.2.1 Recruitment parameters (a, b)

The change of $\pm 20\%$ to the recruitment parameter (a , the intercept) resulted in $\pm 25\%$ change in the level of steady state stand density, which is 570 and 350 stems.ha⁻¹ and basal area 35 and 20 m².ha⁻¹ respectively (Figure 4.15). The sensitivity of this parameter is $S_a=1.25$ considering stand basal area as the response variable. The species composition does not seem to change with this parameter. *Pentaclethra maculoba* and *Lonchocarpus oliganthus* maintain their dominant position in all the scenarios considered in this paragraph. Similar results are obtained by changing the slope parameter b by the same proportion.

The mechanism by which these parameters operate is by changing the level of average recruitment rate. The equilibrium average recruitment is the one that could stabilise the stand density at the desired level. Changes in 20% of one of the recruitment parameters, change the average recruitment rate by 25%, six and ten recruits per hectare per year respectively, compared to the eight recruits per hectare per year obtained with the base-line scenario parameters. The two recruitment parameters interact with the recruitment mortality parameters to stabilise the stand density and the structure.

4.2.2.2 Density independent mortality parameter (dim)

This parameter is set as the proportion of trees reaching maximum species longevity and the base-line value is 4%. A twenty-percent change in this parameter affects the overall and the annual simulated mortality rate by 16%. A 20% increase in dim results in 2.2% annual mortality rate, which is the higher extreme of the observed values in *Pentaclethra* forests and, in the model, it is higher than the recruitment rate, resulting in a forest stand steady

state lower than that observed. The opposite happens when this value is reduced by the same proportion, and the annual mortality rate reduces to 1.4%. Because this parameter is equal for all species groups, the simulated species composition is not affected. This parameter is used in the model to ensure that only a certain proportion will attain the maximum age by giving a constant mortality probability to all trees independent of size and growth rate. This value is set by providing the proportion of trees that would reach maximum age (Botkin 1993), the maximum period for a tree to grow from recruitment (10-cm dbh) to observed maximum species dbh (Lieberman and Lieberman 1985). This parameter justifies all mortality causes not justified by other causes considered in the model (see Section 3.2.4).

4.2.2.3 Gap formation and duration (G_{fd})

The base line scenario simulation produced an average of 0.30 gaps year⁻¹.ha⁻¹, with 1-2 patches not registering a single gap in 200 years while others register up to 7 gaps formed during the same period. Increasing mortality (of large trees), or increasing the proportion of damaged trees increases the rate of gap formation. These parameters should be estimated by using appropriate empirical data and the causes of increase in gap formation should be in accordance with observed trends.

In the model, when a gap is formed, it ceases to be a gap after a certain period. This affects the probability of species to be recruited according to the regeneration guild (pioneer or non-pioneer) they belong. In the base line scenario the duration of a gap after its formation (T_g) was established to two years based on the information on the literature (Denslow 1987), which gives 1.85% of the total number of trees to pioneer species. Increasing or decreasing this period by one-year changes the proportion of pioneer species by eight percent (to 2.0 and 1.6 % of the total simulated trees, respectively). The dominant species are not affected by these changes and the ten most abundant species maintain their position in all the cases. The mechanism by which this parameter works is by increasing or decreasing the number of simulated patches in gap phase during the simulation period.

Since one of the components of the probability of a species to establish is the regeneration guild, giving higher probability for pioneers to regenerate on gap-phase patches than in non-gap phase patches, the proportion of pioneers increases with the duration of the patch phase period.

4.2.2.4 Probability that a recruit will be a pioneer (P_{rg})

The base line scenario has this value at $P_{rg} = 0.9$ leaving the remaining probability of 0.1 for non-pioneers. These values interchange for non-gap patches in order to maintain the total probability of 1.0 for species guild (gap + non-gap) and gap phase (gap + non-gap) (see Section 4.1.4.1).

Reducing P_{rg} by 20% appears to give advantage to pioneer species, by the consequent providing higher probability for pioneers to establish in no-gap patches. A higher proportion of simulated pioneer species (3.8% of the total number of trees) is obtained and canopy pioneer species such as *Laetia procera* and *Apeiba membranacea* appear among the ten most abundant species with 10 and 7 trees ha^{-1} by the end of the simulation respectively. Increasing the value of this parameter to $P_{rg} = 0.99$ result in pioneer species becoming rare with only 0.6% of the total trees simulated being pioneers. This parameter interacts together with the gap formation rate and duration of the gaps after formation to affect the proportion of pioneer species in a long-term undisturbed forest.

Studies of species regeneration and establishment in tropical forests are unanimous that pioneer (light demanding) species are more likely to establish in gap areas than in non-gap areas (Hubel and Foster 1986 a, Swaine and Whitmore 1988, Whitmore 1989, Brokaw and Scheiner 1989, Schoop *et al.* 1989). For the sake of simplicity, we use the simplified concepts of 'gap' and 'pioneer' to make them operational in the model (see Section 4.1.4.1) by ignoring the differences in gap size, and other complexities of light environments, and the different degrees of species light requirement for regeneration and establishment. By doing this we have gap and non-gap areas and pioneer and non-pioneer species. However,

the probability of a pioneer to establish in a gap is higher, but less than 1.0, and the probability of a non-pioneer to establish in a non-gap area is also high but less than 1.0. (Schoop *et al.* 1989). This permits the establishment of non-pioneer species in gaps, as is realistic, and also allows for the occasional establishment of a pioneer in a high-light microsite not associated with a tree fall (Clark and Clark 1992).

4.2.2.5 Probability for a species not present at the beginning of the simulation to establish (P_{nb})

This parameter affects species richness, the total number of species that coexist within the simulated area. Changing the initial value of P_{nb} by 20%, the total number of species at the steady state changes by about 20% with higher richness for higher values of P_{nb} . The species diversity as indicated by the Shannon diversity index varies proportional to the value of P_{nb} . In both cases (increase or decrease the value of P_{nb} by 20%), the stand density and the structure are not affected. It should be noted that when the number of species not present at the beginning is higher, and P_{nb} is high there would be an increase in the number of new species not present at the beginning being recruited. The sensitivity of the parameter P_{nb} mentioned above was estimated with the simulation of one-ha plot with twenty Monte Carlo repetitions, and the average initial number of species was 96 out of 278 species in the species pool. However, in general, P_{nb} should be set to a non-zero value to maintain the species diversity as observed in the initial conditions, or species richness will decrease. In addition, turnover of rare species in permanent sample plots is observed in empirical studies and so should be considered realistic.

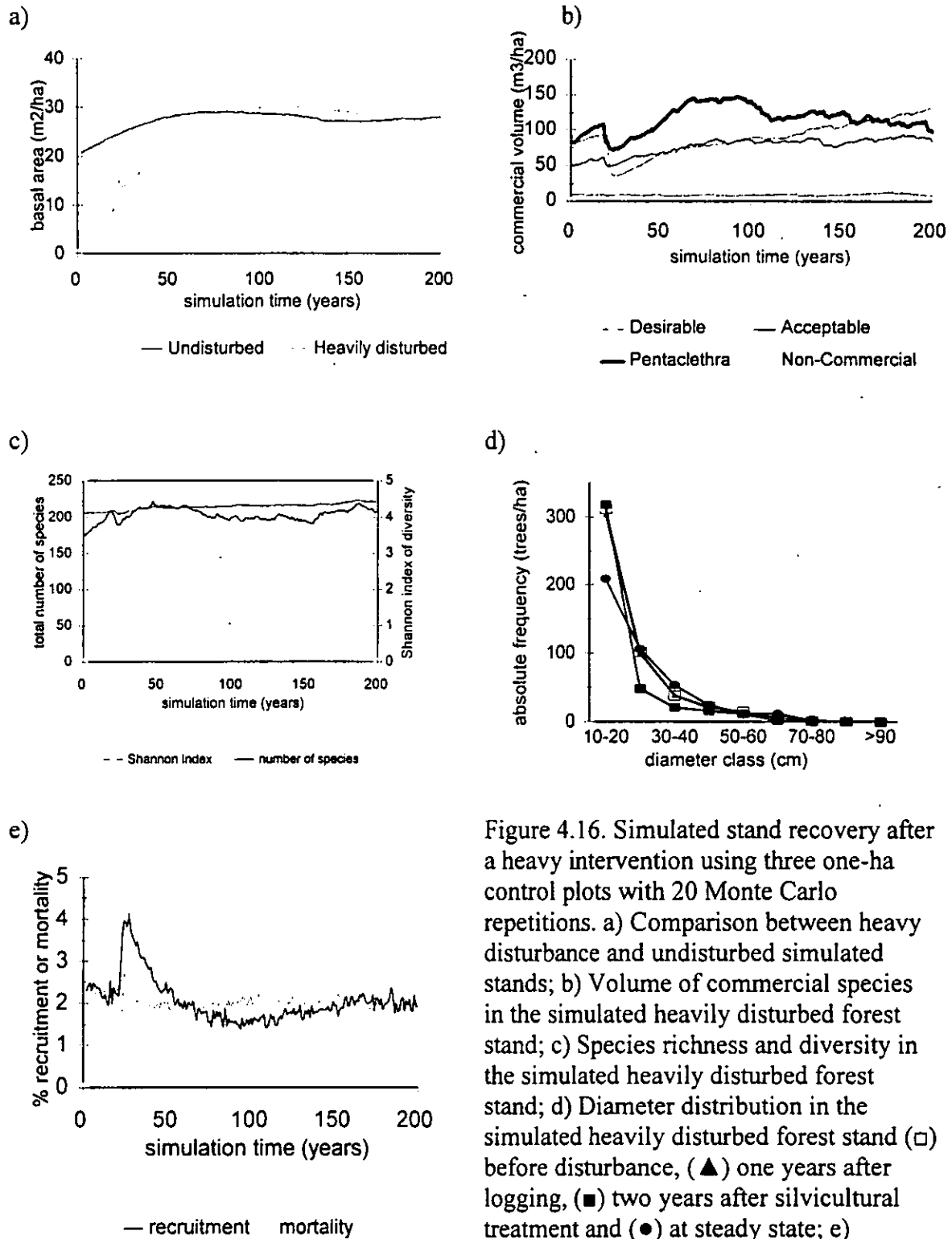


Figure 4.16. Simulated stand recovery after a heavy intervention using three one-ha control plots with 20 Monte Carlo repetitions. a) Comparison between heavy disturbance and undisturbed simulated stands; b) Volume of commercial species in the simulated heavily disturbed forest stand; c) Species richness and diversity in the simulated heavily disturbed forest stand; d) Diameter distribution in the simulated heavily disturbed forest stand (\square) before disturbance, (\blacktriangle) one years after logging, (\blacksquare) two years after silvicultural treatment and (\bullet) at steady state; e) Mortality and recruitment in the simulated heavily disturbed forest stand.

In a small area, of few hectares, not all tree species in the forest stand could be present within the considered minimum DBH limits. For most rare species this is true when the single (or just a few) individual present in the area dies. When this happens, the species is temporarily and locally extinct. However, it is very likely that the species is present in the seed bank and among the unrecruited saplings and could be recruited in the future (Swaine *et al.* 1987). If simulation starts at a given year, it should be unrealistic to consider only those species present at the initial simulation year. Species not present at the beginning of the simulation are given a non-zero probability to establish. We assume that this probability is lower than that of species present at the beginning of the simulation. A detailed discussion of species probability to establish is presented in Section 4.1.4.1.

4.2.3 Recovering capacity of the forest stand after intervention

In the heavy logging scenario, an average of 15 trees ha^{-1} (basal area $4.2 \text{ m}^2 \cdot \text{ha}^{-1}$ and volume $53.6 \text{ m}^3 \cdot \text{ha}^{-1}$) were logged and $8.3 \text{ tree} \cdot \text{ha}^{-1}$ ($0.23 \text{ m}^2 \cdot \text{ha}^{-1}$ and $1.88 \text{ m}^3 \cdot \text{ha}^{-1}$) were killed by falling logged trees. This represented a reduction of 18% of the initial basal area ($24.0 \text{ m}^2 \cdot \text{ha}^{-1}$) just before logging. The treatment intervention affected $113.3 \text{ trees} \cdot \text{ha}^{-1}$ ($7.9 \text{ m}^2 \cdot \text{ha}^{-1}$, $86.8 \text{ m}^3 \cdot \text{ha}^{-1}$) of which 73% were of non-commercial species. Of the treated trees, 89.6% died within the first two years after treatment and the remaining died in the period of five years after treatment.

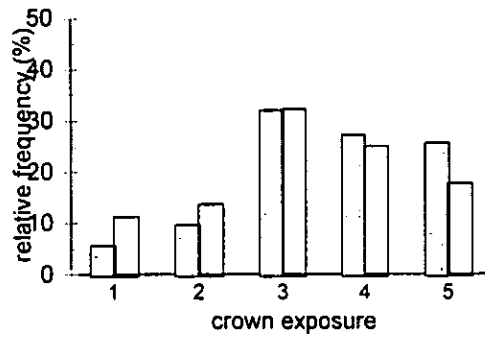
The simulated forest stand recovered its initial stand density about 25 years after disturbance and attained the steady state after 40 years after disturbance. The steady state reached with the heavy disturbance scenario did not differ from that obtained with the undisturbed scenario either in stand density (Figure 4.16 a) or in species richness and diversity (Figure 4.16 c).

In general, selective logging of commercial species such as simulated in this study, does not change the pattern of diameter distribution (Figure 4.16 d). Among the species of commercial value (58 species) at Tirimbina, most of them have low abundance, but

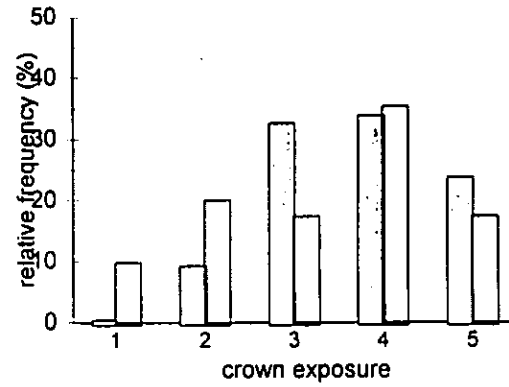
Pentaclethra maculosa, comprised 66% of the presently harvestable number of trees. Previous logging operations (between 1960-1989) were selective and of light intensity (Finegan and Camacho 1999). *Pentaclethra* abundance as commercial species could be because it just entered the timber market in the last few decades, and it was not harvested in the previous logging operations. The silvicultural treatment of refinement changed the forest structure by reducing the number of trees mainly in the 20-50 cm range. The diameter distribution at the steady state was similar to that of the initial conditions but with less small size trees (diameter class 10-20 cm). This is mainly due to the reduction over time of the number of recruits associated with increase in stand density. Logging and silvicultural treatment increase recruitment in the years subsequent to the intervention, which decreases with time until steady state was attained. Within this period, the balance recruitment-mortality was positive and became negative before equilibrium (Figure 4.16 e). The simulation indicates that forest recovery after heavy disturbance is likely to be rapid if it is largely controlled by density-dependent patterns of recruitment and mortality. However, the model does not take into account the possibility that mortality increases after canopy opening due to increased wind turbulence and other factors (Finegan and Camacho 1999).

The aim of the silvicultural treatment is to increase the growth space for the potential crop trees, which is expressed in the model, by reduction in stand density and light competition index. The reduction in stand density had direct consequence in stimulating recruitment as discussed above. The light competition index expressed by the standard distance of the tree total height to the patch mean height, which was converted to Dawkins crown exposure index (see Section 4.1.3.1 for details) increased for potential crop trees after treatment (Figure 4.17 a-c). Crown exposure is one of the parameters used in the model to estimate diameter increment. By improving crown exposure conditions, the diameter increment increases in the proportion of the effect of crown exposure as parameter of the growth function (Figure 4.17 d). Because crown form is also an important predictor of diameter increment, the increase in diameter increment may not necessarily be as high as it has been observed in the field.

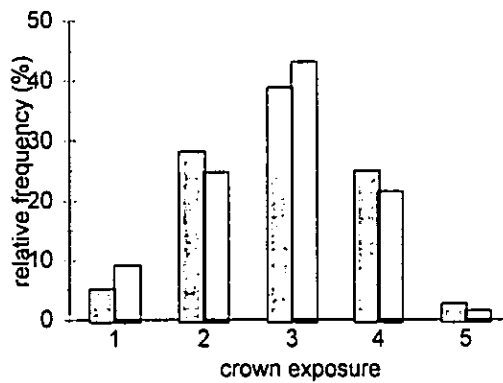
a) Commercially acceptable species



b) Commercially desirable species



c) *Pentaclethra macroloba*



d) Median diameter increment

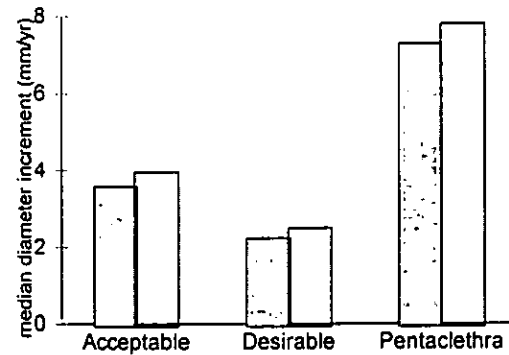


Figure 4.17. Simulated change in crown exposure (a-c) of potential crop trees (■) before and (□) two years after silvicultural treatment. The median diameter increments (d) after treatment were estimated in the four-five years after silvicultural treatment. The relative frequency is the percentage of the total number of trees within each commercial group.

Crown form is the most statistically significant growth parameter used in the model but it is not improved by the silvicultural treatment. Finegan *et al.* (in press) found that potential crop trees at Tirimbina doubled their median diameter increment after liberation treatment was applied. In the simulated silvicultural treatment presented above, the diameter increment increased but not at the same proportion observed in the field.

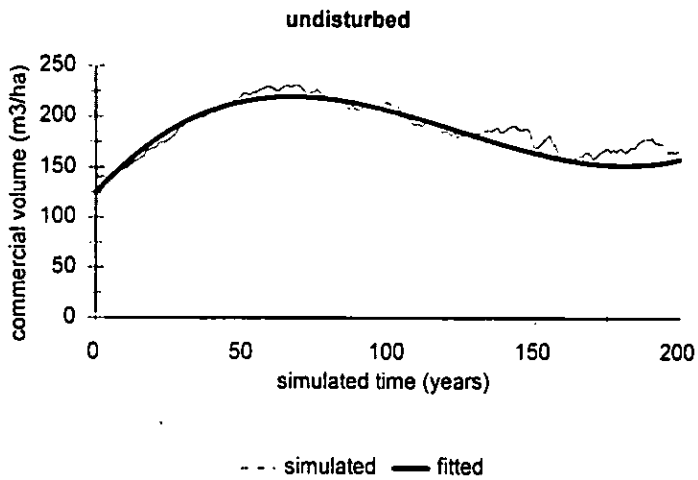
There are several aspects that could be concurring for the failure to represent the effect of silvicultural treatment, among them the parameters used for diameter growth estimation and the structure of the patch model. Within the model, diameter increment is function of tree initial dbh, crown form and exposure and species characteristics, which include maximum dbh, maximum diameter increment and maximum height. While dbh, crown form, and species specific parameters are factors of high significance in diameter increment, crown exposure is affected by the tree neighbourhood (see section 4.1.3.1). The patch model concept of neighbourhood, although it represents part of the tree condition, may not be adequate to accurately describe the individual tree "true" neighbourhood. Results of the effect of silvicultural treatment based on field observation differ with simulated ones mainly because only a small set of parameters among the "true" factors is used in the model and that the individual tree neighbourhood could not be adequately described using the neighbourhood concept of the gap models. However, qualitative response of diameter increment is obtained as expected – the median of diameter increment of potential crop trees increases.

4.3 Applications of the model

4.3.1 Estimating cutting cycles

The third degree polynomial functions fitted well for the simulated period ($R^2=0.92$ for undisturbed scenario and $R^2=0.88$ for after treatment of the logging scenario and treated scenario - Figure 4.18) with all estimated parameters highly significant ($P<0.0001$). The commercial volume increment was higher after treatment and tended to decrease with time after treatment increases until steady state, where volume oscillates around zero increment.

a)



b)

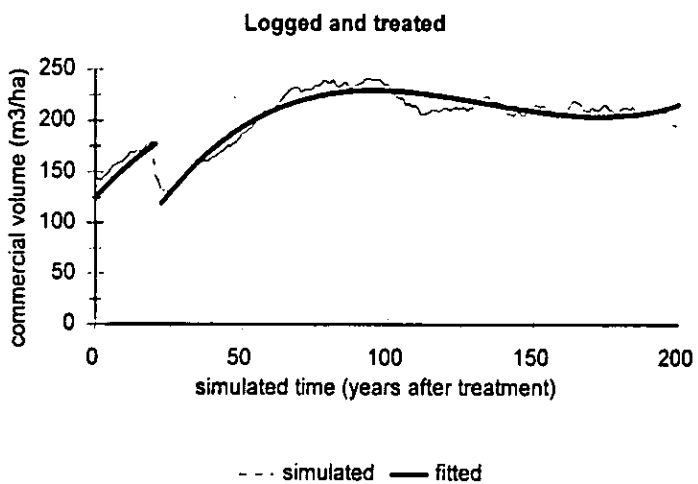


Figure 4.18 Volume of commercial species fitted to third degree polynomial function on simulated values; a) undisturbed forest: $125.175+3.240X-0.03337X^2+0.00009X^3$ ($R^2=0.92$, $P<0.0001$, $n=200$), X is the simulation year; and b) after heavy logging and silvicultural treatment: $119.46+3.62X-0.03685X^2+0.00011X^3$ ($R^2=0.88$, $P<0.0001$, $n=178$), X is the number of years after treatment. The simulations were executed with 20 Monte Carlo repetitions with 3 one-ha control plots.

The maximum volume increment (β_1) was $3.24 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ for undisturbed scenario and $3.62 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ for after treatment scenario.

The undisturbed scenario suggested a logging operation in 15-25 years (upper and lower curves respectively) after the beginning of the simulation. This period, theoretically, corresponds to the necessary for the next logging in the simulated control plots of Tirimbina. In the logging scenario, the planned logging volume ($20 \text{ m}^3 \cdot \text{ha}^{-1}$) could be accumulated at year 20-30 after silvicultural treatment. If the two values above could be used together, it could be suggested that the simulated plots could be logged at year 15-25 (from 1996), yielding up to $30 \text{ m}^3 \cdot \text{ha}^{-1}$, and apply a post logging silvicultural treatment which could re-stock the forest for a similar logging in 20-30 years.

The increment in commercial volume depends on the abundance of commercial species in the site and comparisons among sites should be done with care. At Tirimbina for instance, in all nine plots in 1996, commercial species comprised about 35% of the total number of stems and 60% of the total basal area. The cutting cycle, as consequence of volume increment, will be affected by commercial species abundance. De Graaf (1996) found commercial volume increments (in a 12-years period) between $0.2\text{-}4.5 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ and up to $10 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for all species in experiments with different treatment intensity in Suriname. Silva *et al.* (1995), working in the Brazilian Amazon forest, found $5.2 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ volume increment of all species and $0.8 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ with an old (1979) commercial species list and $1.8 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ with the amended commercial species list in a 11-years period.

The cutting cycles presented above should be interpreted with care and bear in mind that these result from the mean estimations of volume of a stochastic simulation. The 95% estimation error for the mean of volume of commercial species at year 25-30 is about 5 m^3 and should be considered in the evaluation of the cutting cycles. The median of the simulated diameter increment after silvicultural treatment does not increase as observed in the field (see Section 4.2.1) which could result in overestimating the period of the next cut.

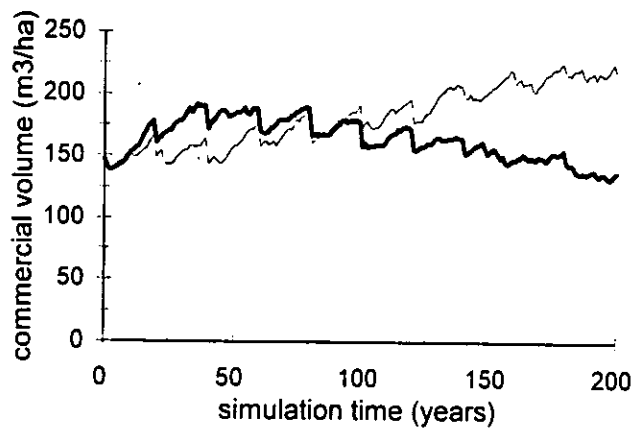


Figure 4.19 Simulated volume of commercial species in simulated successive logging interventions with the (—) traditional log-and-leave and (---) logging with silvicultural treatments.

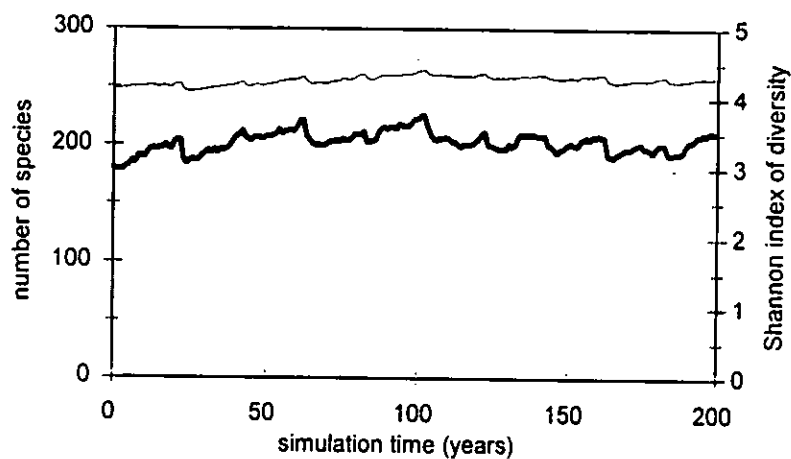


Figure 4.20 Simulated species richness and diversity in the logged and treated forest stand. The number of species is the total simulated in three one-ha control plots. (—) Number of species; (---) Shannon index of diversity.

4.3.2 Ecological implications of successive logging and silvicultural treatments

Selective logging, in conditions such as the simulated forest, does not produce significant changes in forest structure, but could cause changes in species composition. Successive removal of species of commercial value could give advantage for non-commercial species to colonise the forest stand if no treatment is applied. The role of silvicultural treatments, among others, is to reduce that advantage of non-commercial species resulting after a logging operation. For a sustainable forest timber production, silvicultural treatments may be necessary to increase the commercial value of the forest stand and reduce the effect of competing non-commercial species on post-logged stand.

An average of $20 \text{ m}^3 \cdot \text{ha}^{-1}$, most of which is *Pentaclethra maculosa*, was harvested each 20 years and in general, the volume of commercial species increase over time. The increase in the amount of commercial species volume suggesting that the sustainable yield in silviculturally treated stands could be higher than that of non treated stands in which commercial species volume decreases continually (Figure 4.19). It should be noted that in the initial years of silvicultural treatments the treated stands have a lower stocking commercial volume because of the decrease associated with silvicultural treatments. Trees of commercial species with poor stems are removed in silvicultural treatments to free resources for potential crop trees. However, the successive silvicultural treatments create conditions for an overall increase of commercial species volume. In the traditional log-and-leave technique, non-commercial species increase abundance with time, while silvicultural treatments reduce non-commercial species abundance in favour of commercially timber species. In the simulated plots (Table 4.6) when no silvicultural treatments were applied non-commercial species were more abundant (69.7%) compared to the silviculturally treated scenario (64.4%).

Table 4.6 Simulated species abundance in successively logged stands over 200 years. Ab – species abundance (trees/ha) and percentage of the total number of trees. Timber merchantability: (A) commercially acceptable species and (D) commercially desirable species.

a) Log and treat			b) Log and leave		
Species	Ab	%		Ab	%
<i>Pentaclethra macroloba</i> (A)	61.0	12.8	<i>Pentaclethra macroloba</i> (A)	50.0	10.6
<i>Ferdinandusa panamensis</i>	32.7	6.8	<i>Ferdinandusa panamensis</i>	31.3	6.6
<i>Welfia georgii</i>	19.0	4.0	<i>Welfia georgii</i>	16.0	3.4
<i>Dendropanax arboreus</i> (A)	17.0	3.6	<i>Macrolobium costaricense</i>	15.0	3.2
<i>Laetia procera</i> (A)	12.7	2.6	<i>Dendropanax arboreus</i> (A)	14.0	3.0
<i>Euterpe precatoria</i>	12.0	2.5	<i>Ardisia fimbrillifera</i>	13.7	2.9
<i>Warsewiczia coccinea</i>	12.0	2.5	<i>Socratea exorrhiza</i>	11.0	2.3
<i>Ardisia fimbrillifera</i>	11.3	2.4	<i>Euterpe precatoria</i>	11.0	2.3
<i>Iriartea deltoidea</i>	10.7	2.2	<i>Dystovomita paniculata</i>	9.7	2.0
<i>Macrolobium costaricense</i>	10.3	2.2	<i>Warsewiczia coccinea</i>	9.3	2.0
<i>Tetragastris panamensis</i> (A)	9.7	2.0	<i>Iriartea deltoidea</i>	9.3	2.0
<i>Socratea exorrhiza</i> (A)	9.0	1.9	<i>Marila laxiflora</i>	9.0	1.9
<i>Tapirira guianensis</i> (A)	8.3	1.7	<i>Tetragastris panamensis</i> (A)	9.0	1.9
<i>Protium ravenii</i>	8.0	1.7	<i>Brosimum lactescens</i>	7.7	1.6
<i>Dystovomita paniculata</i>	8.0	1.7	<i>Protium schippii</i>	7.3	1.6
<i>Miquartia guianensis</i> (D)	7.3	1.5	<i>Pouteria campechiana</i>	7.0	1.5
<i>Carapa guianensis</i> (D)	7.3	1.5	<i>Protium ravenii</i>	7.0	1.5
<i>Casearia arborea</i>	7.0	1.5	<i>Laetia procera</i> (A)	6.7	1.4
<i>Marila laxiflora</i>	6.7	1.4	<i>Tapirira guianensis</i> (A)	6.3	1.3
<i>Pouteria campechiana</i>	6.0	1.3	<i>Miquartia guianensis</i> (D)	6.3	1.3
<i>Protium pittieri</i>	5.3	1.1	<i>Naucleopsis naga</i>	5.3	1.1
Most abundant commercial	123.3	25.8	Most abundant commercial	92.3	19.5
Most abundant non-commercial	158.0	33.0	Most abundant non-commercial	169.7	35.9
Total commercial	170.3	35.6	Total commercial	143.0	30.3
Total non-commercial	308.0	64.4	Total non-commercial	329.7	69.7
Total	478.3	100.0	Total	472.7	100.0

With the simulation conditions set above, logging and silvicultural treatments alter forest stand species composition, richness and diversity in the short term only. The long-term trend species richness did not change. Species lost during silvicultural treatments were recovered few years after intervention (Figure 4.20). Low abundance species, represented by few individuals, were the most likely to get lost during silvicultural treatments, however, since the model assumes that any species considered in the species-pool could be represented in the seed bank or as non-established saplings, its loss is only temporary. At Tirimbina, observed silviculturally treated plots, for instance, there were no differences of species richness between control (logging only) and silviculturally treated plots seven years after the treatment (Finegan *et al.* in prep.).

Species richness decrease after logging or silvicultural treatment has been observed in tropical rain forests (Cannon *et al.* 1998, Webb and Peralta 1998). Although selective logging removes few large trees, the associated logging damage kills an additional number of small trees, which could reduce abundance of some species. However, species richness has been observed to recover to those of unlogged forest level in relatively short time (e.g. 8 years – Cannon *et al.* 1998). Species richness recovery is believed to be associated with habitat differentiation (Cannon *et al.* 1998) originated by canopy opening and soil disturbance. Webb and Peralta (1998) observed a higher number of recruits and species in selectively logged forest compared to undisturbed forest. These observations suggest that the species richness is stimulated after intervention by opening gaps and creating conditions for several species to establish. The mechanism of the simulated species richness loss and recovery after intervention obtained in this study is similar to the observed and in general, the model supports that species richness in silviculturally managed forest could be maintained over time. The decrease observed just after intervention is unavoidable but could be minimised by using low impact logging practices. The reduction in stand density and create conditions for higher number of recruits and the gaps opened create conditions for light demanding species to establish, thus increasing the possibilities to recover in relatively short time the species richness.

General discussion

The model presented in this chapter is one of the possible approaches to simulate tropical forest dynamics. Its structure and procedures have been defined mainly by data availability and certain assumptions were considered for this version. It should be bore in mind that the objective of this model is to "broaden and deepen the knowledge of the growth, commercial yield and natural regeneration" as specified by one of the CATIE research lines (Campos *et al.* 1997, CATIE 1995). Most of the data and information available in *Pentaclethra* forests, including ecological and silvicultural aspects have, been summarised in a single model. The model is based on general ecological principles and should guide research and further data collection. In this chapter we presented the statistical evaluation of the growth and allometric functions and in Chapter four there is an evaluation of ecological and silvicultural aspects of the model.

The findings of this chapter suggest that theoretical growth functions could fit somehow the tropical rain forest data. Clark and Clark (1999) argued that species could not be classified by a single criteria as fast or slow growing, and that growth functions that tend to zero when tree dbh tends to species maximum dbh are not adequate for tropical rain forests. However, we do not agree with their point. The results in this chapter and the information on *Pentaclethra* forests (which is the same as the study area as the authors above) suggest that rather than the growth function, or criteria to classify species according to their growth rate, it is data which is inadequate. For instance, the concept of maximum diameter used in the growth functions should be refined for tropical forests where large trees are scarce and almost all trees die before reaching maximum size. The comparisons performed in this chapter between growth projections based on observed growth and simulated growth using theoretical functions shows no discrepancy in the outcomes. Single criteria species classification, apart from being desirable, does not have any inconsistency with the observed data. Finegan and Camacho (1999) used growth speed as one of the criteria to classify species together with adult position. The same criterion was used in this study and

parameters such as species potential growth were derived by single criteria of growth speed and we believe the results of the growth simulation obtained are satisfactory.

Based on the results of this chapter, it is suggested that data collection be concentrated on species-specific information. This same suggestion have been provided by Bugmann *et al.* (1995) for gap-models in general, but ought to be re-emphasised here because of its great importance specially in the tropics where several species coexist on the same stand. Regeneration strategies, growth rates and effects of microenvironmental conditions at tree level should be well investigated to enhance a better understanding of individual tree growth in particular and the stand dynamics in particular. Including spatial information (tree position) in growth characteristic estimation is expected to increase the predicting ability and the accuracy of the individual tree growth rate. It is desirable that in the future, other modelling approaches be developed so that a selection could be done among different views of forest dynamics.

The model presented in this study includes gap dynamics, species light requirement for regeneration, and species mortality patterns as the main driving forces for species composition and forest stand structure. Several parameters among empirically estimated (based on long-term field observations and statistically and mathematically estimated), and ecologically based are used simultaneously to simulate individual trees, which interact to reproduce population and community characteristics. The model takes advantage of previous work in the study site, particularly species identification and species aggregation strategies, which is difficult to find in TRF (Finegan and Camacho 1999), to enable the model to simulate species diversity and represent most of the variability of growth patterns characteristic of tropical lowland rain forests. The model allows testing hypothesis about several ecological aspects related to forest stand dynamics. We have explored some of them in Chapter 4.2, but actually the model offers much more options to evaluate different levels of disturbance and concepts on forest stand dynamics, which are not commonly available in traditional TRF growth models (see for example Vanclay 1989,1994, Alder 1995, Alder and Silva 2000).

The model has certain limitations, as it could not represent all the complexity of tropical forest stands. The rarity of many species in these forests (Clark and Clark 1999, Finegan *et al.* 1999) prevents a realistic characterisation of these species. Species and individual tree interactions such as intra- and inter-specific competition are not fully understood, at the same time that technical limitations impose real difficulties. It is not easy to represent ecological knowledge in quantitative terms. In fact some of the ecological concepts still need a better definition in terms of current language (see for example Whitmore 1989, Brokaw and Scheiner 1989, Lieberman *et al.* 1989, Meer *et al.* 1994 for discussion on gap versus non-gap and pioneer versus non-pioneer). The model uses the simplified ecological concepts to reduce the model complexity at the same time that the essential is maintained.

The results of the four hundred years simulation of a silviculturally managed forest without further intervention presented in Section 4.2.1 are in accordance with current level of understanding of tropical forest ecology and the understanding of *Pentaclethra* forests. The steady state conditions could be reached by a careful combination of recruitment and mortality parameters. Site specific information should be used to calibrate the observed recruitment and mortality rates, as well as the stand density of a mature undisturbed forest. Since the model is a simplified version of the reality, these results should not be viewed as they used to be in the real forest. The causes, and the factors included in the model are simplifications of the field conditions and complex factors were aggregated in few parameters to keep the model simple (Grimm, 1999). For instance, density-independent mortality rate is represented by two parameters (species longevity and the proportion of trees reaching maximum longevity). This mortality rate includes all mortality reasons not explicit in the model such as wind throw, uprooting, pathogens, among others. The idea here is to use a single set of parameters to represent mortality independent of stand density, tree size, and growth rate. Other mortality factors are explicit in the model and include competition, senescence, logging, liberation, or tree fall damage.

Aggregating factors, such as with density independent mortality as well as aggregating species, such as with species growth groups, reduces the realism of the model since within each aggregation the variability of the simulated output reduces as consequence of using average conditions within groups. However, it was assumed that by doing this it could be possible to capture the essential for the objectives defined for the model. The alternative procedure of no aggregating species would result impractical given the rarity of TRF tree species. Plot-less census method, such as that used by Clark and Clark (1999) is practical only if few species are to be modelled, but modelling forest management units would require that all or most of the species be modelled and stand information be presented in terms of species composition and structure.

The combination of functions and parameters selected provide an ecologically consistent and robust model, which can represent long-term conditions similar to those of tropical rain forests. The growth functions could not represent accurately the individual tree growth but stand and species group statistics. This failure is, among others, an intrinsic limitation of distance-independent model structure (see below). The long-term stand conditions are not affected by the growth functions but mortality and recruitment parameters. Most of the ecological parameters evaluated in Chapter 4.2 are moderately sensitive ($1.06 \leq S_p \leq 1.25$) and could be used to calibrate the model to site specific conditions such as mortality and recruitment rates, stand density, and species composition at the simulated steady state.

The model outputs suggest that it could adequately represent long-term forest dynamics by maintaining a dynamic equilibrium, mortality and recruitment rates, median diameter increments of the stand density and species composition similar to those of real forests. Species diversity and richness are maintained over the simulation period if no major disturbances are simulated. Rare species may go locally and temporarily extinct and species not present at the beginning of the simulation (but present in the species pool) would establish as it happens in tropical rain forests (see Swaine *et al.* 1987 and Finegan *et al.* in prep.).

The model simulates average conditions of species compositions since patch specific characteristics such as soils and topography were not considered for species recruitment. Delgado and Finegan (1999) found particular tendencies of species preferring top hills or bottom valleys at Tirimbina. This information is not included in this version of the model, but we believe it could be included, as spatial information becomes included in the model. Peng (2000) recognised that individual-tree distance-independent models are limited in their ability to provide accurate individual tree development information. However, introducing spatial information for individual tree growth estimation would increase model complexity and uncertainty since all trees, specially recruits would need to be carefully placed within the forest stand. Lack of data (few experiments include tree coordinates mensuration, although these data do exist for La Tirimbina) and the difficulty to represent large stands are among the major inconveniences of distance dependent models (Peng 2000). While simulation resources (computer memory and time) could be overcome by using powerful machines, model complexity and uncertainty would reduce our ability to interpret the results since a simple decision of placing a recruit in a certain position would be loaded by subjectivity and uncertainty and data on spatial distribution of tree species will be required.

The simulated forest stand is resilient and it could recover even in heavy disturbances. It recovered from a simulated heavy disturbance, which reduced about 50% of the initial basal area down to $12 \text{ m}^2 \cdot \text{ha}^{-1}$. Heavier disturbances, including clear cut, were experimented and the simulated forest stand recovers within reasonable time and stabilises at a steady state similar to that of undisturbed forest after a couple of smooth oscillations (Unpublished data). Because the model structure was designed for selective logging and moderate silvicultural treatments in non-secondary forests, the results obtained after a clear cut may be unrealistic. However, the current parameters could be adjusted for the transition secondary forest developing after clear cut.

Gap models have been intensively used in temperate zones and presently there is a large variety of gap models which have been enhanced to perform specific tasks (Peng 2000)

among evaluation of forest sustainability and the effects of harvesting regimes, analysis of wildlife habitats and biodiversity, evaluation of the potential effects of climate change on tree species composition, and ecosystem structure and function. Because of their flexibility, gap models could also be used to simulate a variety of conditions in tropical rain forests. This study has demonstrated this ability and emphasises the need for deeper research in simulation of TRF in order to enhance the current understanding of these ecosystems.

5 Conclusions and recommendations

In general, the contribution of this study is to provide a research and management tool that could be used not only to evaluate forest management practices but also to stimulate research and data collection. The model, as is in this version, is a first approach of modelling *Pentaclethra* forest using a combination of empirical functions with ecological concepts at the individual tree level, allowing evaluation of silvicultural management options. One of the aims that stimulated the development of this model was to “broaden and deepen knowledge of the growth, commercial yield and natural regeneration” of tropical lowland rain forests of Central America. The stage at which this model has taken should be considered as an initial stage on integration of ecological and silvicultural knowledge into a single working tool that could be used to test new hypothesis on forest dynamics. Several aspects were learned with this model at the same time that gaps of knowledge were evidenced. For instance, it was learnt the possibility to use the information available so far, to predict stand development in terms of stand density, structure, species composition, commercial yield, regeneration, and the effects of silvicultural interventions, among others. However, gaps in knowledge and data availability were also highlighted, such as the lack of knowledge in among tree and tree-site interactions – which may have limited the ability to accurately predict individual tree growth. These and other aspects discussed in this study, suggest the need to feedback the research process by stimulating new data collection and new research objectives, which should be incorporated into the model. It is strongly recommend that other model initiatives be considered, since no single model could respond to all the questions that ought to be asked in forestry and only by means of modelling could be answered quickly and cost-effectively. If the model presented in this study could be enhanced with an economic analysis component, and enforced the ecological aspects, by incorporating the nutrient cycling and climate change effects, it could represent another advance in the ability to evaluate not only forest production aspects, but also environmental consequences of forest interventions. Activities like tree spatial information, and among tree interactions (competition indices) are among the priority data and research need. Most of these recommendations, have been however, identified by other

studies but become more evident in this study by limiting the model ability to predict some of desired aspects, such as the individual tree diameter increment.

The Gavilan model presents some innovative approaches to evaluate tropical rain forest species richness, composition and diversity by incorporating individual species properties as well as group-specific characteristics, such as growth rates and regeneration guild, to predict the dynamics of forest stand species composition. Botanical species identification was crucial for the success of this model to evaluate change in species composition. Note that several models in tropical rain forests rely on common species identification or to groups of species (commercial or ecological). The simplified versions of species characterization, such as the differentiation among pioneer versus non-pioneers, were used instead of the continuum of regeneration guilds in order to make the model simple. On the other hand, because several species are represented by few individuals, characterization of these species is generally difficult due to lack of representative samples. The model could include more species-specific information as soon as these become available. Species characterization is one of the research needs in tropical rain forests in general and in *Pentaclethra* forests in particular and should be considered to improve the model performance.

The model is driven by density-dependent processes, leading to a steady state in stand density (number of trees, basal area, volume, and species composition). This characteristic is particularly favoured while no climate change are considered in the model and within the assumption that the mature undisturbed *Pentaclethra* forests known today are close to the steady state, which is intrinsic in this model. Whether presently known *Pentaclethra* forests are in steady or represent an earlier successional stage is not well documented. However, the fact that large extensions of this forest type along Central America exhibit comparable characteristics and few changes have been observed in the study areas without disturbance may be used as an argument in favour that these forests are close to the steady state. Because the model was initially build with data from a primary forest with low intensity logging and silvicultural treatment it is not secure that it could properly simulate highly disturbed or secondary forests. Further studies should emphasize in the usage of the

model in secondary forests as well as highly disturbed forests and analyse the reaction of the model in these conditions.

There are several factors that affect growth of tropical trees which were not considered in the growth functions considered in this study. Factors such as soil properties, genetic properties, and the forest fauna were not incorporated in the model, while among-tree competition is not well understood and it was represented in a simple way that could not represent fully the process being simulated. Some of the factors indicated above are not easy to understand in complex and diverse tropical rain forests and it is not envisaged that in the next few years this will change significantly unless research objectives explicitly become oriented for this purpose. Several forest tree competition indices were developed during the decades of eighties but most of them were specific for monospecific plantations adapted for diverse tropical rain forests. Differences in competition ability among species and among individual trees should be considered to better represent the real competition status of forest trees. In the Gavilan model, an effort was spent to improve the competition status among species of different growth groups by considering the competition-induced mortality within growth groups. This improvement did not increase the ability of the model to represent individual tree growth as such but the species composition, richness and diversity. When this differentiation was not made, slow growing species presented higher mortality rates and in some cases disappeared from the stand and species diversity in the stand was low that observed in the field.

Silvicultural interventions (logging and treatment) could be better represented with an individual tree model than with aggregated models. In individual tree models, each tree could be selected for liberation treatment or for logging, which is the current practice in selective polycyclic silvicultural systems in the tropics. Gavilan can represent realistic silvicultural interventions as it allows selection of potential crop trees as well as trees that could be eliminated in a silvicultural treatment. The criteria and indicators for sustainability of tropical rain forests of Costa Rica have been included in the design of silvicultural interventions. Protection of rare species, maintenance of minimum canopy cover, protection of slopy areas, among others are some of the measures considered in Gavilan.

6. Bibliography

- Aguirre RR. 1999. Mortalidad de arboles en dos tipos de bosque tropical humedo sometidos a manejo forestal en la vertiente Atlantica de Centroamerica. M.Sc. Thesis, CATIE, Turrialba, Costa Rica. 81p + annexes.
- Alder D. 1995. Growth modelling for mixed tropical forests. Tropical Forestry Paper Nr 30. Oxford Forestry Institute, G.B. 231p.
- Alder D. 1997. SIRENA: Modelo de simulación para el manejo del bosque tropical en la Zona Norte de Costa Rica. Manual de usuario y notas técnicas. Consultancy Report. 32 p.
- Alder D and Silva JNM. 2000. An empirical cohort model for management of Terra Firme forests in the Brazilian Amazon. *For. Ecol. Manag.* 130:141-157.
- Alder D and Synnott TJ. 1992. Permant sample plots techniques for mixed tropical forests. Oxford Forestry Institute, Department of Plant Sciences, University of Oxford. Tropical Forestry Paper 25, 124p.
- Amateis RL. 1994. An approach to developing process-oriented growth and yield models. *For. Ecol. and Manag.* 69:7-20.
- Baur G. 1964. The ecological basis of rain forest management. Sidney, Australia. FAO, 499p.
- Bertalanffy L von. 1968. General system theory. Foundations, developments, applications. George Braziller, New York. 295p.
- Bormann FH and Berlyn G (Ed.) 1981. Age and growth rate of tropical trees: New directions for research. Proceedings of the workshop and growth rate determination for tropical trees. Harvard Forest, Petersham, Massachusetts, 1-3 April 1980. Yale University Bulletin No 94.
- Bossel H and Krieger H. 1994. Simulation of multispecies tropical forest dynamics using a vertical and horizontally structured model. *For. Ecol. and Manag.* 69:123-144.
- Botkin DB. 1993. Forest dynamics: an ecological model. Oxford University Press. Oxford, U.K. 309p.
- Botkin DB, Janak JF, and Wallis JR. 1972. Some ecological consequences of a computer forest growth. *Journal of Ecology* 60:840-872.
- Brandani A, Hartshorn GS, and Orians GH. 1988. Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. *J. Trop. Ecol.* 4:99-119.

- Brokaw NVL and Scheiner SM. 1989. Species composition in gaps and structure of a tropical forest. *Ecology* 70:538-541.
- Bugmann HKM, Xiaodong Y, Sykes MT, Martin P, Lindner M, Desanker PV, and Cumming SG. 1995. A comparison of forest gap models: model structure and behaviour. *Climatic Change* 34:289-313.
- Cabrelli D. 1992. Efectos de la radiación solar bajo dosel sobre el crecimiento de la regeneración de especies heliófitas durables en el bosque húmedo tropical y su respuesta a la intervención silvicultural. M.Sc. Thesis CATIE, Turrialba, Costa Rica 132 p.
- Camacho M. in prep. Estructura y dinámica del rodal en un bosque húmedo no intervenido del nordeste de Costa Rica. (draft of June 1999).
- Campos JJ, Finegan B, Kent J, Louman B and Marmillod D. 1997. Research Line 5: development of technologies for the sustainable management of natural forests and their biodiversity (second draft, March 1997). CATIE, Turrialba, CR. 22p.
- Cannon HC, Peart DR and Leighton M. 1998. Tree species diversity in commercially logged Bornean rain forest. *Science* 281:1366-1368.
- Canonizado JA. 1978. Simulation of selective forest management regimes. *The Malayan Forester* 41:128-142.
- Castillo A. 1997. Analisis de la composición y estructura horizontal de un bosque aprovechado selectivamente en la zona de Rio San Juan, Nicaragua. M.Sc. Thesis. CATIE, Turrialba, Costa Rica. 83p.
- CATIE (Centro Agronómico Tropical de Investigación y Enseñanza). 1995. Proyecto CATIE/COSUDE, Silvicultura de Bosques Naturales, PROSIBONA. Plan operativo octava fase 1996-98. CATIE, Turrialba, CR.42p.
- Clark DA and Clark DB. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs* 62(3):315-344.
- Clark DA and Clark DB. 1987. Análisis de la regeneración de árboles del dosel en bosque muy húmedo tropical: aspectos teóricos y prácticos. *Rev. Biol. Trop.* 35(1):41-54.
- Clark DA and Clark DB. 1999. Assessing the growth of tropical rain forest trees: issues for forest modeling and management. *Ecological Applications* 9:981-997.
- CNCF (Comisión Nacional de Certificación Forestal, CR). 1999. Estándares y procedimientos para el manejo sostenible y la certificación forestal en Costa Rica. 54p.

- David CA. 1997. Managing the invisible: ecosystem management and macronutrient cycling. IN: Boyce M and Haney A (Eds.) Ecosystem management, applications for forest and wildlife resources. Yale University Press, New Haven. Pp. 94-129.
- Dawkins HC. 1958. The management of the natural tropical high forest with special reference to Uganda. Imperial Forestry Institute, University of Oxford, U.K. 155p.
- Deaton ML and Winebrake JI. 1999. Dynamic modelling of environmental systems. Springer, New York. 194p.
- Delgado LD. 1995. Efectos de la riqueza, composición y diversidad florística producidos por el manejo silvícola en bosque húmedo tropical de tierras bajas de Costa Rica. M.Sc. Thesis CATIE, Turrialba, CR. 97p.
- Delgado LD and Finegan B. 1999. Biodiversidad vegetal en bosques manejados. Revista Forestal Centroamericana 25:14-20.
- Denslow JS. 1987. Tropical rain forests gaps and tree species diversity. Ann. Rev. Ecol. Syst. 18:431-51.
- Desanker P. and Prentice IC. 1994. MIOMBO – a vegetation dynamics model for the miombo woodlands of Zambezi Africa. For. Ecol. and Manag. 69:87-95.
- Díaz J. 1995. Caracterización de la iluminación de micrositios de regeneración de 14 especies arbóreas en un bosque húmedo intervenido en Costa Rica, y el efecto de la intervención sobre la abundancia de la regeneración natural. M.Sc. Thesis CATIE, Turrialba, Costa Rica. 91p.
- Dinerstein E, Olson DM, Graham DJ, Webster AL, Primm SA, Bookbinder MP, and Ledec G. 1995. A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. World Bank/ World Wildlife Fund, Washington DC.
- Doyle TW. 1981. The role of disturbance in the gap dynamics of a montane rain forest: an application of a tropical forest succession model. IN: DC West, HH Shugart, and DB Botkin (Editors) Forest Succession: concepts and applications. 99:56-73. Springer Verlag, New York.
- FAO 1997. Environmentally sound forest harvesting: testing the application of the FAO Model Code in the Amazon in Brazil. Forest Harvesting Study-Case 8. Rome, Italy. 78 p.
- Favrichon V. 1998. Modeling the dynamics and species composition of a tropical mixed-species uneven-aged natural forest: effects of alternative cutting regimes. For. Sci. 44(1):113-124.
- Finegan B and Camacho M. 1999. Stand dynamics in a logged and silviculturally treated Costa Rican rain forest, 1988-1996. For. Ecol. and Manag. 121:177-189.

- Finegan B, Camacho M, and Zamora N. 1999. Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. For. Ecol. and Manag. 121:159-176.
- Finegan B, Delgado D, and Camacho M. (in prep.) The evaluation of ecological sustainability in neotropical rain forests managed for timber production, with emphasis on plant biodiversity: a discussion, and the implications of a case study.
- Finegan B and Sabogal C. 1988. El desarrollo de sistemas de producción sostenible en bosques tropicales húmedos de bajura: un estudio de caso en Costa Rica. El Chasqui 18:16-24.
- Gardner RH and Mankin JB. 1981. Analysis of biomass allocation in forest ecosystems of the IBP. IN: Reichle DE (ed.) Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, UK. 451-498.
- Gourlet-Fleury S, Bar-Hen A, and Fauvet N. 1999. The silvicultural experimental plots of Paracou in French Guiana: example of use and limits of the available data for developing individual growth model. IN: Kleinn C and Kohl M. Long-term observations and research in forestry. IUFRO International Symposium, CATIE, Turrialba, February 1999. 127-142 pp.
- Graaf NR. De 1986. A silvicultural system for natural regeneration of tropical rain forest in Suriname. Agricultural University, Wageningen. The Netherlands. 250p.
- Grimm V. 1999. Ten years of individual-based modeling in ecology: what have we learned and what could we learn in the future? Ecological Modeling 115:129-148.
- Guariguata MR and Duduy JM. 1997. Forest regeneration in abandoned logging roads in lowland Costa Rica. Biotropica 29(1):15-28.
- Guariguata MR and Pinard MA. 1998. Ecological knowledge of regeneration from seed in neotropical forest trees: implications for natural forest management. For. Ecol. and Manage. 112:87-99.
- Haefner JW. 1996. Modelling biological systems, principles and applications. Chapman and Hall, NY. 473p.
- Hawkes C. 2000. Woody plant mortality algorithms: descriptions, problems and progress. Ecological Modelling 126:225-248.
- Herrera B. 1996. Evaluación del efecto del sitio en la productividad de las poblaciones de dos especies dominantes en un bosque tropical de la tercera fase de la sucesión secundaria en Costa Rica. M.Sc. Thesis, CATIE, Turrialba, C.R. 152p.
- Herrera B, Campos JJ, Finegan B and Alvarado A. 1999. Factors affecting site productivity of a Costa Rican secondary rain forest in relation to *Vochysia*

- ferruginea*, a commercially valuable canopy tree species. For. Ecol. Manage. 118:73-81.
- Hilborn R and Mangel M. 1997. The ecological detective: confronting models with data. Monographs in Population Biology. Princetown University Press, New Jersey. 315 p.
- Holdridge L. 1982. Ecología basada en zonas de vida. San José, Costa Rica, IICA 216p.
- Hubell SP and Foster RB. 1986a. Canopy gaps and the dynamics of a Neotropical forest. IN: MJ Crawley (Ed.) Plant ecology. Blackwell Scientific publications, Oxford.
- Hubell SP and Foster RB. 1986b. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. IN: ME Soulé (Ed.) Conservation biology: the science of scarcity and diversity. Chapter 10, pp. 205-231.
- Hutchinson ID. 1987. Aspectos relevantes sobre inventarios forestales. Notas de Clase del I Curso Intensivo Internacional de Silvicultura y Manejo de Bosques Naturales Tropicales. CATIE, Turrialba, Costa Rica.
- Inglis CJ, Sutton G, and Lawson GJ. 1997. Research and monitoring for sustainable forest management in North-West Guyana 27-35 pp. IN: Research on environmentally sound forest practices to sustain tropical forests. Proceedings of the FAO/IUFRO Satellite Meeting held in conjunction with the IUFRO XX World Congress, Tampere, Finlandia 4-5 August 1995. FAO, Rome, Italy.
- IUCN (The World Conservation Union) 1997. Red list of threatened plants. IUCN.
- Jeffers JNR. 1982. Modelling: outline studies in ecology. Chapman and Hall, London. 80p.
- Jonkers WBJ. 1987. Vegetation structure, logging damage, and silviculture in a tropical rain forest in Suriname. Agricultural University, Wageningen, The Netherlands 172.
- Jorgensen SE. 1997. Integration of ecosystem theories: a pattern (Second revised edition). Kluwer Academic Publishers, Dordrecht. 338 p.
- Kaufmann M and Troendle C. 1981. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. For. Sci. 27(3):477-482.
- Koop H and Sterck FJ. 1994. Light penetration through structurally complex forest canopies. For. Ecol. and Manag. 69:111-122.
- Kopelman R. 1990. Damage caused by selective logging in a Neotropical rain forest. MSc thesis, Agricultural University, Wageningen, The Netherlands. 59 p.

- Lamprecht H. 1990. *Silviculture in the tropics*. Eschborn, Germany. 335p.
- Landsberg JJ. 1986. *Physiological ecology of forest production*. Academic Press, London, U.K. 198p.
- Levins R. 1966. The strategy of model building in population biology. *American Scientist* 54:421-431.
- Levins R. 1993. A response to Orzack and Sober: formal analysis and the fluidity of science. *The Quarterly Review of Biology* 68(4):547-555.
- Lieberman D and Lieberman M. 1985. Simulation of growth curves from periodic increment data. *Ecology* 66(2):632-635.
- Lieberman D and Lieberman M. 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). *Journal of Tropical Ecology* 3:347-358.
- Lieberman D, Lieberman M, Peralta R and Hartshorn GS. 1985a. Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *J. Ecol.* 73:915-924.
- Lieberman M, Lieberman D and Peralta R. 1989. Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70(3):550-552.
- Lieberman M, Lieberman D, Hartshorn G and Peralta R. 1985b. Small-scale altitudinal variation in lowland wet tropical forest vegetation. *J. of Ecology* 73:505-516.
- Lieberman M, Lieberman D, Peralta R and Hartshorn G. 1995. Canopy closure and the distribution of forest tree species at La Selva, Costa Rica. *Journal of Tropical Ecology* 11:161-178.
- Lieberman M, Lieberman D, Peralta R, and Hartshorn G. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *J. Ecol* 84:137-152.
- Liu J and Ashton P. 1995. Individual based simulation models for forest succession and management. *For. Ecol. and Manag.* 73:157-175.
- Mankin JB, O'Neill RV, Shugart HH, and Rust BW. *s.d.* The importance of validation in ecosystem analysis. Chapter 7. Pp 63-70.
- Manta MN. 1988. Análisis silvicultural de dos tipos de bosque húmedo de bajura en la vertiente Atlántica de Costa Rica. M.Sc. Thesis CATE, Turrialba, CR. 150p.
- Martini AMZ, Rosa NA and Uhl C. 1994. An attempt to predict which Amazonian tree species may be threatened by logging activities. *Environmental Conservation* 21(2):152-162.

- Mata R. 1997. Estudio detallado de suelos: Area de demostracion e investigacion La Tirimbina, Sarapiquí, Heredia, Costa Rica. Universidade de Costa Rica, Centro de Investigaciones Agronómicas. San Jose, Costa Rica. 52p.
- McDade L, Bawa KS, Hespeneide HA and Hartshorn GS (Eds.). 1994. La Selva: ecology and natural history of a neotropical rain forest. The University of Chicago Press. 486 p.
- Meer PJ van der, Bongers F, Chatrou L and Riéra B. 1994. Defining canopy gaps in a tropical rain forest: effects on gap size and turnover time. *Acta Ecologica* 15(6):701-714.
- Mejia AC. 1994. Analisis del efecto inicial de un tratamiento de liberacion sobre la regeneracion establecida en un bosque humedo tropical aprovechado en rio San Juan, Nicaragua. M.Sc. Thesis. CATIE, Turrialba, Costa Rica. 67p.
- Mervart J. 1972. Growth and mortality rates in the natural high forest of Western Nigeria. *Nigeria Forestry Information Bulletin* 22. Ibadan, Nigeria. 52p.
- MINAE (Ministero del Ambiente y Energía, CR). 1997. Decreto Nr. 25700-MINAE. *La Gaceta* 11:9-10
- MIRENEM (Ministerio de Recursos Naturales, Energía y Minas, CR). 1994. Manual de procedimientos para el manejo y aprovechamiento forestal en Costa Rica. MIRENEM, San José, Costa Rica.
- Montès N, Gauquelin T, Badri W, Bertaudière V and Zaoui EL. 2000. A non-destructive method for estimating above-ground forest biomass in threatened woodlands. *For. Ecol. and Manage.* 130:37-46.
- Moore AD. 1989. On the maximum growth equation used in forest gap simulation models. *Ecol. Modelling* 45:63-67.
- Morataya R. 1996. Desarrollo de modelos de predicción para peso de follaje y volumen de albura: aplicación de la teoria del modelo vascular (TMV) e implicaciones en el manejo, en *Tectona grandis* L. y *Gmelina arborea* Roxb., Hojanca, Guanacaste, Costa Rica. M.Sc. Thesis, CATIE, Turrialba. 118p.
- Nelder JA and Mead R. 1965. A simplex method for function maximization. *Computer Journal* 7:308-13.
- Neter J, Kutner MH, Nachtsheim CJ, and Wasserman W. 1996. Applied linear statistical models (Fourth Edition). Irwin, Chicago. 1408p.
- Nygren P, Rebottaro S and Chavería R. 1993. Application of the pipe model theory to non-destructive estimation of the leaf biomass and leaf area of pruned agroforestry trees. *Agroforestry System* 23(1):63-77.

- O'Hara K and Valappil N. 1995. Sapwood-leaf area prediction equations for multistaged ponderosa pine stands in Western Montana and Central Oregon. *Can. J. For. Res.* 25(9):1553-1557.
- Odum EP. 1971. *Fundamentals of Ecology*, 3rd Edition W.B. Saunders, Philadelphia. PA.
- Ong R and Kleine M. 1995. DIPSIM: a Dipterocarp forest growth simulation model for Sabah. FRC Research Paper Nr 2. Forestry Department, Sabah, Malaysia. 94p.
- Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK and Ribbens E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* 66(1):1-43.
- Parton WJ, McKeown R, Kirchner V and Ojima D. 1992. Users guide for the CENTURY model. Colorado State University.
- Peng C. 2000. Growth and yield models for uneven-aged stands: past, present and future. *For. Ecol. and Manage.* 132:259-279.
- Peralta R, Hartshorn GS, Lieberman D and Lieberman M. 1987. Resena de estudios a largo plazo sobre composicion floristica y dinamica del bosque tropical en La Selva, Costa Rica. *Revista de Biologia Tropical* 35(1):23-40.
- Pertunen J, Sievanen R, and Nikinmaa E. (1998) LIGNUM: a model combining the structure and the functioning of trees. *Ecological Modelling* 108:189-198.
- Philip MS. 1983. *Measuring trees and forests*. Aberdeen University Press, Aberdeen. 338p.
- Prabhu R, Colfer CJP, Venkateswarlu P, Tan LC, Soekmadi R, and Wollenberg E. 1996. Testing criteria and indicators for the sustainable management of forests: Phase 1. Final Report. CIFOR, Jakarta, Indonesia, 75p + annexes.
- Press WH, Flannery BP, Teukolsky SA, and Vetterling WT. 1989. *Numerical recipes in Pascal: the art of scientific computing*. Cambridge University Press, U.K. 759 p.
- Quiros D and Finegan B. 1994. Manejo sustentable de un bosque natural tropical en Costa Rica: definición de un plan de manejo y resultados de su aplicación. Colección Silvicultura y Manejo de Bosques Naturales, CATIE, Turrialba, Costa Rica. 25p.
- Quiros D and Finegan B. 1996. Manejo de un bosque muy húmedo premontano: Area de demostración e investigación La Tirimbina. IN: CATIE – Silvicultura y manejo de bosques naturales tropicales: curso intensivo. Volume 2. Estudios de caso. CATIE, Turrialba pp13-24.
- Ramirez H and Torres A. 1998. Parametrización de un modelo de simulación de base individual como herramienta para el manejo de un bosque tropical Venezolano.

- IN: (Editors) Simposio Internacional "Posibilidades de manejo forestal sostenible en América Tropical". Bolivia, Santa Cruz. pp224-233.
- Reichle DE (Editor) 1981. Dynamic properties of forest ecosystems. IBP 23, Cambridge University Press, Cambridge.
- Rich P. 1986. Mechanical architecture of arborescent rain forest palms. *Principles* 30(3):117-131.
- Ricklefs RE. 2000. Rarity and diversity in Amazonian forest trees. *Trends in Ecology and Evolution* 15(3):83-84.
- Rogers R and Hinckley T. 1979. Foliar weight and area related to current sapwood area in oak. *For. Sci.* 25(2):298-303.
- Ryan M. 1989. Sapwood volume for three subalpine conifers: predictive equations and ecological implications. *Can. J. For. Res.* 19(11):1397-1401.
- Saenz G, Finegan B and Guariguata M. 1999. Crecimiento y mortalidad en juveniles de siete especies arboreas en un bosque muy humedo tropical intervenido de Costa Rica. *Revista de Biología Tropical* 47(1-2):45-57.
- SAS Institute Inc. 1989. SAS/STAT User's guide, Version 6 (Fourth Edition, Vol 1,2). Cary, NC. SAS Institute Inc., 1686p.
- Schneider SH. 1992. The climatic response to greenhouse gases. *Advances in Ecological Research* 22:1-32.
- Sokal RR and Rohlf FJ. 1995. *Biometry*. Third edition. WH Freeman and Company, NY. 887p.
- Schupp EW, Howe HF, Auspurger CK and Levey DJ. 1989. Arrival and survival in tropical treefall gaps. *Ecology* 70:562-564.
- Sheil D. 1995. A critique of permanent sample methods and analysis with examples from Budongo Forest, Uganda. *For. Ecol. and Manage.* 77:11-34.
- Sheil D and May RM. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *J. Ecology* 84:83-90.
- Shifley SR and Brand GJ. 1984. Chapman-Richard growth function constrained for maximum tree size. *For. Sci.* 30(4):1066-1070.
- Shugart HH. 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York. 278p.
- Shugart HH. 1998. *Terrestrial ecosystems in changing environments*. Cambridge Studies in Ecology. Cambridge University Press. U.K. 537p.

- Shugart HH and Noble IR. 1981. A computer model of succession and fire response to the high altitude Eucalyptus forest of the Brindabella Range, Australian Capital Territory. *Australian Journal of Ecology* 6:149-164.
- Silva JNM, Carvalho JOP, Lopes CA, Almeida BF, Costa DHM, Oliveira LC, Vanclay JK, and Skovsgaard JP. Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging. *For. Ecol. and Manage.* 71:267-274.
- Sit V and Poulin-Costello M. 1994. Catalog of curves for curve fitting. Biometrics information, Handbook No. 4. Ministry of Forests, BC, Canada, 110p.
- Sitoe AA, Finegan B, and Camacho M. 1999. Modeling Pentaclethra forest - an important Central American lowland rain forest type - for timber production. IN: Kleinn C and Kohl M (Eds.) Long-term observations and research in forestry. Proceedings of the IUFRO S4.11 International Symposium held at CATIE, Turrialba, Costa Rica, February 23-27, 1999. Pp 143-149.
- Sitoe AA. 1992. Crecimiento diamétrico de especies maderables en un bosque humedo tropical bajo diferentes intensidades de intervención. M.Sc. Thesis, CATIE, Turrialba, Costa Rica. 119p.
- Smith TM, Shugart HH, Bonan GB and Smith JB. 1992. Modelling the potential response of vegetation to Global Climate Change. *Advances in Ecological Research* 22:93-116.
- Smith W. 1994. An empirical evaluation of a three-dimensional crown model for predicting volume growth. *For. Ecol. and Manag.* 69:199-209.
- Snell K and Brown J. 1978. Comparison of tree biomass estimators-dbh and sapwood area. *For. Sci.* 24(4):455-457.
- Soares MT, Skovsgaard JP and Vanclay JK. 1995. Evaluating a growth model for forest management using continuous forest inventory data. *For. Ecol. and Manage.* 71:251-265.
- Swaine MD and Whitmore TC. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81-86.
- Swaine MD, Lieberman D and Putz FE. 1987. The dynamics of tree populations in tropical forest: a review. *J. Trop. Ecol.* 3:357-366.
- Swaine MD. 1989. Population dynamics of tree species in tropical forests. IN: Tropical forests: Botanical dynamics, speciation and diversity. Holm-Nielsen LB, Nielsen IC and Balslev H (Eds.). 101-110.
- Synnott TJ. 1979. A manual of permanent sample plots procedures for tropical rain forests, C.F.I. Oxford, Great Britain. Tropical Forestry Paper 14, 67p.

- Torres A, Ramirez H, and Baldoce R. 1998. Predicción de la respuesta de un bosque tropical Venezolano a diferentes estrategias de manejo. IN: (Editors) Simposio Internacional "Posibilidades de manejo forestal sostenible en América Tropical". Santa Cruz, Bolivia, pp. 234-240.
- Uchmanski J and Grimm V. 1996. Individual-based modeling in ecology: what makes the difference? *Trends in Ecology and Evolution* 11:437-441.
- Urban 1993. A User's guide to ZELIG version 2. Department of Forest Sciences. Colorado State University. Fort Collins, Colorado.
- Valentine HT. 1999. Estimation of the net primary productivity of even-aged stands with a carbon-allocation model. *Ecological Modelling* 122:139-149.
- Vanclay JK. 1989a. A growth model for North Queensland rainforests. *For. Ecol. and Manag.* 27:245-271.
- Vanclay JK. 1989b. Modelling selection harvesting in tropical rain forests. *J. Trop. For. Sci.* 1(3):280-294.
- Vanclay JK. 1991a. Aggregating tree species to develop diameter increment equations for tropical rainforests. *For. Ecol. and Manag.* 42:143-168.
- Vanclay JK. 1991b. Data requirements for developing growth models for tropical moist forests. *Comm. For. Rev.* 70:248-271.
- Vanclay JK. 1992. Modelling regeneration and recruitment in a tropical rain forest. *Can. J. For. Res.* 22:1235-1248.
- Vanclay JK. 1994. Modelling forest growth and yield: applications to mixed tropical forests. CAB International, U.K. 312 p.
- Vanclay JK. 1995. Growth models for tropical forests: a synthesis of models and methods. *Forest Science* 41:7-42.
- Vanclay JK and Skovsgaard JP. 1997. Evaluating forest growth models. *Ecological Modelling* 98:1-12.
- Vitousek PM and Denslow JS. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rain forest. *Journal of Ecology* 74:1167-1178.
- Webb EL. 1999. Growth ecology of *Carapa nicaraguensis* Aublet. (Meliaceae): Implications for natural forest management. *Biotropica* 31:102-110.
- Webb EL and Peralta R. 1998. Tree community diversity of old swamp forests in Northern Costa Rica, and changes associated with controlled selective logging. *Biodiversity and Conservation.* 7:565-582.

Weiner J. 1990. Asymmetric competition in plant populations. *Trends in Ecology and Evolution* 11(5):360-364.

Whitmore TC. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70(3):536-538.

Whitmore TC. 1990. An introduction to tropical rain forests. Clarendon Press. Oxford. U.K. 226p.

Annex 1. List of tree species at Tirimbina with selected growth parameters. Additional parameters could be found in respective growth group in Tables 3.2, 3.4 and 3.4.

Nr	Code	Adult	Guild	Comm.	Group	g	MaxAge	MaxD	MaxH	Scientific Name
1	DESCON	Uncias	Non-Pio	Non-com	25	29	130	716	247	Desconocido
2	ABARAD	Subcan	Non-Pio	Non-com	12	53	248	1058	1036	Abarema
3	ABARMA	Canopy	Pioneer	Non-com	17	29	256	1156	589	Abarema
4	ALCHLA	Interm	Pioneer	Non-com	6	24	392	764	471	Alchornea
5	ALCOFL	Subcan	Pioneer	Non-com	13	118	96	636	276	Alchorneopsis
6	AMPEMA	Subcan	Non-Pio	Non-com	13	118	96	636	276	Ampelocera
7	ANAXCR	Interm	Non-Pio	Non-com	6	24	392	764	471	Anaxagorea
8	ANDIIN	Subcan	Non-Pio	Desira	11	26	384	837	578	Andira
9	ANNOAM	Canopy	Non-Pio	Non-com	18	44	216	1320	660	Annona
10	ANNOMO	Interm	Non-Pio	Non-com	6	24	392	764	471	Annona
11	ANNOSP	Interm	Non-Pio	Non-com	6	24	392	764	471	Annona
12	APEIME	Canopy	Pioneer	Non-com	18	44	216	1320	660	Apeiba
13	ARDIFI	Interm	Non-Pio	Non-com	6	24	392	764	471	Ardisia
14	ARDISP	Unders	Non-Pio	Non-com	1	28	208	450	313	Ardisia
15	ASPISP	Canopy	Non-Pio	Desira	16	42	425	1155	327	Aspidosperma
16	ASTRGO	Interm	Non-Pio	Non-com	26	0	200	-1	327	Astrocaryum
17	BALIEL	Canopy	Pioneer	Non-com	19	87	80	1282	727	Balizia
18	BEILCO	Subcan	Non-Pio	Non-com	14	92	40	988	553	Beilschmiedia
19	BEILPE	Subcan	Non-Pio	Non-com	13	118	96	636	276	Beilschmiedia
20	BOROPA	Interm	Non-Pio	Non-com	6	24	392	764	471	Borojoa
21	BOROSP	Unders	Non-Pio	Non-com	1	28	208	450	313	Borojoa
22	BROSGU	Interm	Non-Pio	Non-com	6	24	392	764	471	Brosimum
23	BROSLA	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Brosimum
24	BYRSCI	Subcan	Pioneer	Non-com	13	118	96	636	276	Byrsonima
25	CALOBR	Canopy	Non-Pio	Desira	16	42	425	1155	327	Calophyllum
26	CAPPEI	Unders	Non-Pio	Non-com	1	28	208	450	313	Capparis
27	CARAGU	Canopy	Non-Pio	Desira	16	42	425	1155	327	Carapa
28	CASEAR	Interm	Non-Pio	Non-com	8	96	152	820	287	Casearia
29	CASECO	Interm	Non-Pio	Non-com	6	24	392	764	471	Casearia
30	CASECR	Interm	Non-Pio	Non-com	8	96	152	820	287	Casearia
31	CASESP	Interm	Non-Pio	Non-com	8	96	152	820	287	Casearia
32	CASPGU	Interm	Non-Pio	Non-com	6	24	392	764	471	Cassipourea
33	CECRIN	Interm	Pioneer	Non-com	8	96	152	820	287	Cecropia
34	CECROB	Interm	Pioneer	Non-com	8	96	152	820	287	Cecropia
35	CECRSP	Interm	Pioneer	Non-com	8	96	152	820	287	Cecropia
36	CEDROD	Canopy	Pioneer	Desira	18	44	216	1320	660	Cedrela
37	CEIBPE	Canopy	Pioneer	Accept	16	42	425	1155	327	Ceiba
38	CELTSC	Interm	Non-Pio	Non-com	7	30	120	728	384	Celtis
39	CESPPA	Canopy	Non-Pio	Accept	17	29	256	1156	589	Cespedesia
40	CHIMPA	Subcan	Non-Pio	Accept	13	118	96	636	276	Chimarrhis
41	CHRCGL	Interm	Non-Pio	Non-com	6	24	392	764	471	Chrysochlamys
42	CHRCSP	Interm	Non-Pio	Non-com	7	30	120	728	384	Chrysochlamys
43	CHRYCO	Subcan	Non-Pio	Non-com	11	26	384	837	578	Chrysophyllum
44	CHRYVE	Interm	Non-Pio	Non-com	6	24	392	764	471	Chrysophyllum
45	CINNCH	Interm	Non-Pio	Non-com	7	30	120	728	384	Cinnamomum
46	CLETME	Interm	Non-Pio	Non-com	6	24	392	764	471	Clethra
47	COCCOU	Canopy	Non-Pio	Accept	16	42	425	1155	327	Coccoloba
48	COJOVA	Interm	Non-Pio	Non-com	6	24	392	764	471	Cojoba
49	COLUSP	Unders	Non-Pio	Non-com	1	28	208	450	313	Colubrina
50	CONCPL	Subcan	Pioneer	Non-com	12	53	248	1058	1036	Conceveiba
51	CONOSU	Interm	Non-Pio	Non-com	6	24	392	764	471	Conostegia
52	CORDBI	Interm	Pioneer	Accept	9	256	72	661	312	Cordia
53	CORDDW	Interm	Non-Pio	Non-com	6	24	392	764	471	Cordia
54	CORDLU	Interm	Non-Pio	Non-com	6	24	392	764	471	Cordia
55	CORDSP	Interm	Non-Pio	Non-com	6	24	392	764	471	Cordia
56	COUEPO	Subcan	Non-Pio	Non-com	12	53	248	1058	1036	Couepia
57	COUSHO	Unders	Non-Pio	Non-com	1	28	208	450	313	Coussarea
58	CROTSC	Unders	Non-Pio	Non-com	2	46	80	274	127	Croton
59	CROTSM	Interm	Pioneer	Non-com	10	541	32	677	309	Croton
60	CUPAGL	Interm	Non-Pio	Non-com	6	24	392	764	471	Cupania
61	CUPARU	Interm	Non-Pio	Non-com	6	24	392	764	471	Cupania
62	CYATMI	Unders	Pioneer	Non-com	26	0	200	-1	471	Cyathea
63	DENDAR	Interm	Non-Pio	Accept	6	24	392	764	471	Dendropanax
64	DICHDO	Interm	Non-Pio	Non-com	6	24	392	764	471	Dichapetalum
65	DRYPST	Interm	Non-Pio	Non-com	6	24	392	764	471	Drypetes
66	DUSSO1	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Dussia
67	DUSSMA	Canopy	Non-Pio	Accept	16	42	425	1155	327	Dussia
68	DYSTPA	Interm	Non-Pio	Non-com	6	24	392	764	471	Dystovomita
69	ELA EGL	Subcan	Non-Pio	Non-com	11	26	384	837	578	Elaeoluma
70	ERYTHA	Interm	Non-Pio	Non-com	6	24	392	764	471	Erythroxyllum
71	EUGE01	Unders	Non-Pio	Non-com	1	28	208	450	313	Eugenia
72	EUGE02	Unders	Non-Pio	Non-com	1	28	208	450	313	Eugenia
73	EUGEAC	Interm	Non-Pio	Non-com	6	24	392	764	471	Eugenia
74	EUGEGL	Interm	Non-Pio	Non-com	7	30	120	728	384	Eugenia
75	EUGEME	Unders	Non-Pio	Non-com	1	28	208	450	313	Eugenia

Nr	Code	Adult	Guild	Comm	Group	g	MaxAge	MaxD	MaxH	Scientific Name
76	EUGEOC	Unders	Non-Pio	Non-com	1	28	208	450	313	Eugenia octopleura
77	EUGESA	Unders	Non-Pio	Non-com	1	28	208	450	313	Eugenia sarapiquensis
78	EUGESP	Unders	Non-Pio	Non-com	1	28	208	450	313	Eugenia sp.
79	EUGEVA	Unders	Non-Pio	Non-com	1	28	208	450	313	Eugenia valerii
80	EUTEPR	Interm	Non-Pio	Non-com	26	0	200	-1	313	Euterpe precatorea
81	FARAOC	Unders	Non-Pio	Non-com	1	28	208	450	313	Faramea occidentalis
82	FERDPA	Interm	Non-Pio	Non-com	22	37	168	358	307	Ferdinandusa panamensis
83	FICUTO	Interm	Pioneer	Non-com	7	30	120	728	384	Ficus tonduzii
84	GARCIN	Interm	Non-Pio	Non-com	6	24	392	764	471	Garcinia intermedia
85	GAROMA	Interm	Non-Pio	Non-com	6	24	392	764	471	Garcinia madruno
86	GLOEDI	Interm	Non-Pio	Non-com	7	30	120	728	384	Gloeospermum diversipetalum
87	GOETME	Canopy	Pioneer	Accept	6	24	392	764	471	Goethalsia meiantha
88	GRAFGA	Interm	Non-Pio	Non-com	20	126	50	355	239	Graffenrieda galeottii
89	GRIAFE	Interm	Non-Pio	Non-com	6	24	392	764	471	Grias fendleri
90	GUARBU	Interm	Non-Pio	Non-com	6	24	392	764	471	Guarea bullata
91	GUARGL	Interm	Non-Pio	Accept	6	24	392	764	471	Guarea glabra
92	GUARGU	Interm	Non-Pio	Non-com	6	24	392	764	471	Guarea guidonia
93	GUARUK	Interm	Non-Pio	Accept	7	30	120	728	384	Guarea kunthiana
94	GUARMA	Interm	Non-Pio	Non-com	6	24	392	764	471	Guarea macrophylla
95	GUARPY	Interm	Non-Pio	Non-com	6	24	392	764	471	Guarea pyriiformis
96	GUARRH	Interm	Non-Pio	Non-com	6	24	392	764	471	Guarea rhopalocarpa
97	GUARSP	Interm	Non-Pio	Non-com	7	30	120	728	384	Guarea sp.
98	GUARTA	Unders	Non-Pio	Accept	1	28	208	450	313	Guarea talamancana
99	GUATAE	Interm	Non-Pio	Non-com	6	24	392	764	471	Guatteria aeruginosa
100	GUATDI	Interm	Non-Pio	Non-com	7	30	120	728	384	Guatteria diospyroides
101	GUATRE	Interm	Non-Pio	Non-com	8	96	152	820	287	Guatteria recurvisepala
102	HAMPAP	Interm	Pioneer	Non-com	9	256	72	661	312	Hampea appendiculata
103	HASSFL	Interm	Pioneer	Non-com	6	24	392	764	471	Hasseltia floribunda
104	HEDYSC	Unders	Non-Pio	Non-com	2	46	80	274	127	Hedyosmum scaberrimum
105	HEISCO	Unders	Non-Pio	Non-com	1	28	208	450	313	Heisteria concinna
106	HENRTU	Interm	Non-Pio	Non-com	6	24	392	764	471	Henriettea tuberculosa
107	HERNDI	Subcan	Pioneer	Non-com	14	92	40	988	553	Hernandia didymantha
108	HIPPAL	Unders	Non-Pio	Non-com	1	28	208	450	313	Hippotis albiflora
109	HIRTLE	Interm	Non-Pio	Non-com	6	24	392	764	471	Hirtella lensii
110	HIRTTR	Subcan	Non-Pio	Non-com	12	53	248	1058	1036	Hirtella triandra
111	HUMIDI	Canopy	Non-Pio	Accept	18	44	216	1320	660	Humiriastrum diguense
112	HYERAL	Canopy	Pioneer	Desira	19	87	80	1282	727	Hyeronima alchorneoides
113	HYEROB	Interm	Pioneer	Accept	6	24	392	764	471	Hyeronima oblonga
114	ILEXSK	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Ilex skutchii
115	INGAAC	Interm	Pioneer	Non-com	6	24	392	764	471	Inga acuminata
116	INGAAE	Canopy	Pioneer	Non-com	19	87	80	1282	727	Inga allenii
117	INGAAL	Canopy	Pioneer	Non-com	19	87	80	1282	727	Inga aiba
118	INGAAR	Interm	Pioneer	Non-com	8	96	152	820	287	Inga acrocephala
119	INGACO	Interm	Pioneer	Non-com	7	30	120	728	384	Inga cocleensis
120	INGADE	Interm	Pioneer	Non-com	7	30	120	728	384	Inga densiflora
121	INGAED	Interm	Pioneer	Non-com	6	24	392	764	471	Inga edulis
122	INGALE	Canopy	Pioneer	Non-com	18	44	216	1320	660	Inga leiocalycina
123	INGAMO	Interm	Pioneer	Non-com	7	30	120	728	384	Inga mortoniana
124	INGAPE	Subcan	Pioneer	Non-com	13	118	96	636	276	Inga pezizifera
125	INGAPU	Subcan	Pioneer	Non-com	13	118	96	636	276	Inga punctata
126	INGASE	Interm	Pioneer	Non-com	7	30	120	728	384	Inga sertulifera
127	INGASM	Interm	Pioneer	Non-com	9	256	72	661	312	Inga samanensis
128	INGASP	Interm	Pioneer	Non-com	8	96	152	820	287	Inga spectabilis
129	INGATH	Interm	Pioneer	Non-com	8	96	152	820	287	Inga thibaudiana
130	INGAUM	Interm	Pioneer	Non-com	8	96	152	820	287	Inga umbellifera
131	IRIADE	Subcan	Non-Pio	Non-com	26	0	200	-1	287	Iriartea deltoidea
132	JACACO	Interm	Pioneer	Accept	9	256	72	661	312	Jacaranda copaia
133	LACIAG	Interm	Non-Pio	Non-com	7	30	120	728	384	Lacistema aggregatum
134	LACMPA	Canopy	Non-Pio	Non-com	18	44	216	1320	660	Lacmellea panamensis
135	LACUPA	Interm	Non-Pio	Non-com	7	30	120	728	384	Lacunaria panamensis
136	LAETPR	Canopy	Pioneer	Accept	17	29	256	1156	589	Laetia procera
137	LECYAM	Canopy	Non-Pio	Desira	18	44	216	1320	660	Lecythis ampla
138	LICASA	Interm	Non-Pio	Non-com	6	24	392	764	471	Licaria sarapiquensis
139	LONCOL	Interm	Non-Pio	Accept	6	24	392	764	471	Lonchocarpus oliganthus
140	LONCSP	Interm	Non-Pio	Accept	6	24	392	764	471	Lonchocarpus sp. 01
141	LOZAPI	Interm	Non-Pio	Non-com	7	30	120	728	384	Lozania pittieri
142	MACRCO	Interm	Non-Pio	Non-com	6	24	392	764	471	Macrolobium costaricense
143	MAQUCO	Interm	Non-Pio	Non-com	7	30	120	728	384	Maquira costaricana
144	MARAPA	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Maranthes panamensis
145	MARILA	Interm	Non-Pio	Non-com	6	24	392	764	471	Marila laxiflora
146	MATAOP	Canopy	Non-Pio	Non-com	17	29	256	1156	589	Matayba oppositifolia
147	MELIGL	Interm	Non-Pio	Non-com	6	24	392	764	471	Meliosma glabrata
148	MELISP	Interm	Non-Pio	Non-com	6	24	392	764	471	Meliosma sp. 01
149	MICO05	Interm	Non-Pio	Non-com	7	30	120	728	384	Miconia sp. 05
150	MICOAF	Interm	Non-Pio	Non-com	6	24	392	764	471	Miconia affinis
151	MICOCH	Interm	Non-Pio	Non-com	7	30	120	728	384	Miconia chrysophylla
152	MICOMI	Interm	Non-Pio	Non-com	7	30	120	728	384	Miconia minutiflora
153	MICOMU	Interm	Non-Pio	Non-com	8	96	152	820	287	Miconia multispicata
154	MICOPU	Interm	Non-Pio	Non-com	7	30	120	728	384	Miconia punctata
155	MICOSI	Unders	Non-Pio	Non-com	2	46	80	274	127	Miconia simplex

Nr	Code	Adult	Guild	Comm	Group	g	MaxAge	MaxD	MaxH	Scientific Name	
156	MICOSP	Interm	Non-Pio	Non-com	7	30	120	728	384	Miconia	sp.
157	MICOST	Interm	Non-Pio	Non-com	6	24	392	764	471	Miconia	stevensiana
158	MINQGU	Canopy	Non-Pio	Desira	23	33	160	827	522	Minquartia	guianensis
159	MOLLCO	Unders	Non-Pio	Non-com	1	28	208	450	313	Mollinedia	costaricensis
160	MOLLPI	Unders	Non-Pio	Non-com	1	28	208	450	313	Mollinedia	pinchotiana
161	MOURGL	Subcan	Non-Pio	Non-com	11	26	384	837	578	Mouriri	gleasoniana
162	MYRCLE	Interm	Non-Pio	Non-com	7	30	120	728	384	Myrcia	leptoclada
163	MYRCSP	Interm	Non-Pio	Non-com	7	30	120	728	384	Myrcia	splendens
164	NAUCNA	Interm	Non-Pio	Non-com	6	24	392	764	471	Naucleopsis	naga
165	NECTCI	Subcan	Non-Pio	Non-com	12	53	248	1058	1036	Nectandra	cissiflora
166	NECTGA	Subcan	Non-Pio	Non-com	11	26	384	837	578	Nectandra	glabrescens
167	NECTME	Subcan	Non-Pio	Non-com	13	118	96	636	276	Nectandra	membranacea
168	NECTPU	Subcan	Non-Pio	Non-com	12	53	248	1058	1036	Nectandra	purpurea
169	NECTSA	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Nectandra	salicina
170	NECTSF	Canopy	Non-Pio	Non-com	17	29	256	1156	589	Nectandra	salicifolia
171	NEEAEL	Unders	Non-Pio	Non-com	1	28	208	450	313	Neea	elegans
172	NEEASP	Unders	Non-Pio	Non-com	1	28	208	450	313	Neea	sp.
173	OCHRPY	Interm	Pioneer	Non-com	9	256	72	661	312	Ochroma	pyramidale
174	OCOTAT	Interm	Non-Pio	Non-com	6	24	392	764	471	Ocotea	attirrensis
175	OCOTCE	Interm	Non-Pio	Non-com	6	24	392	764	471	Ocotea	cernua
176	OCOTFL	Subcan	Non-Pio	Non-com	11	26	384	837	578	Ocotea	floribunda
177	OCOTIN	Interm	Non-Pio	Non-com	7	30	120	728	384	Ocotea	insularis
178	OCOTIR	Subcan	Non-Pio	Non-com	12	53	248	1058	1036	Ocotea	ira
179	OCOTLA	Interm	Non-Pio	Non-com	6	24	392	764	471	Ocotea	laetevirens
180	OCOTLE	Subcan	Non-Pio	Non-com	13	118	96	636	276	Ocotea	leucoxylon
181	OCOTMA	Subcan	Non-Pio	Non-com	13	118	96	636	276	Ocotea	macropoda
182	OCOTMO	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Ocotea	mollifolia
183	OCOTNI	Interm	Non-Pio	Non-com	6	24	392	764	471	Ocotea	nicaraguensis
184	OCOTSP	Interm	Non-Pio	Non-com	12	53	248	1058	1036	Ocotea	sp. 01
185	ORMOCO	Subcan	Non-Pio	Non-com	12	53	248	1058	1036	Ormosia	coccinea
186	ORMOVE	Subcan	Non-Pio	Non-com	12	53	248	1058	1036	Ormosia	velutina
187	OSSARO	Unders	Non-Pio	Non-com	1	28	208	450	313	Ossaea	robusta
188	OTOBNO	Canopy	Non-Pio	Accept	18	44	216	1320	660	Otoba	novogranatensis
189	PACHAQ	Subcan	Non-Pio	Accept	11	26	384	837	578	Pachira	aquatica
190	PARAFU	Unders	Non-Pio	Non-com	1	28	208	450	313	Parathesis	fusca
191	PARAPA	Interm	Non-Pio	Non-com	6	24	392	764	471	Parathesis	pallida
192	PARASP	Unders	Non-Pio	Non-com	1	28	208	450	313	Parathesis	sp.
193	PENTMA	Canopy	Non-Pio	Pentac	21	52	208	1220	581	Pentaclethra	macroloba
194	PERAAR	Unders	Non-Pio	Non-com	1	28	208	450	313	Pera	arborea
195	PERSSP	Unders	Non-Pio	Non-com	1	28	208	450	313	Persea	sp. 01
196	PESCAR	Interm	Non-Pio	Non-com	7	30	120	728	384	Peschiera	arborea
197	PHYLSK	Interm	Non-Pio	Non-com	6	24	392	764	471	Phyllanthus	skutchii
198	PLEULI	Interm	Non-Pio	Non-com	7	30	120	728	384	Pleuranthodendron	lindenii
199	POSOLA	Interm	Non-Pio	Non-com	6	24	392	764	471	Posoqueria	latifolia
200	POSOPA	Interm	Non-Pio	Non-com	6	24	392	764	471	Posoqueria	panamensis
201	POURBI	Interm	Non-Pio	Non-com	8	96	152	820	287	Pourouma	bicolor
202	POURMI	Subcan	Non-Pio	Non-com	13	118	96	636	276	Pourouma	minor
203	POUTCA	Subcan	Non-Pio	Non-com	11	26	384	837	578	Pouteria	calistophylla
204	POUTCM	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Pouteria	campechiana
205	POUTCO	Subcan	Non-Pio	Non-com	11	26	384	837	578	Pouteria	congestifolia
206	POUTDU	Subcan	Non-Pio	Non-com	12	53	248	1058	1036	Pouteria	durlandii
207	POUTRE	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Pouteria	reticulata
208	POUTSP	Subcan	Non-Pio	Non-com	11	26	384	837	578	Pouteria	sp.
209	POUTSU	Interm	Non-Pio	Non-com	11	26	384	837	578	Pouteria	subrotata
210	POUTTO	Subcan	Non-Pio	Non-com	11	26	384	837	578	Pouteria	torta
211	POUTVI	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Pouteria	viridis
212	PROTCO	Interm	Non-Pio	Non-com	7	30	120	728	384	Protium	costaricense
213	PROTPA	Interm	Non-Pio	Non-com	7	30	120	728	384	Protium	panamense
214	PROTPI	Subcan	Non-Pio	Non-com	11	26	384	837	578	Protium	pittieri
215	PROTRA	Interm	Non-Pio	Non-com	24	38	96	506	336	Protium	ravenii
216	PROTSC	Interm	Non-Pio	Non-com	6	24	392	764	471	Protium	schippii
217	PROTSP	Interm	Non-Pio	Non-com	7	30	120	728	384	Protium	sp.
218	PSEUSP	Subcan	Non-Pio	Non-com	11	26	384	837	578	Pseudolmedia	spuria
219	PSYCLU	Unders	Non-Pio	Non-com	1	28	208	450	313	Psychotria	luxurians
220	PSYCPA	Unders	Non-Pio	Non-com	1	28	208	450	313	Psychotria	panamensis
221	PSYCSP	Unders	Non-Pio	Non-com	1	28	208	450	313	Psychotria	sp.
222	PTERRO	Subcan	Pioneer	Accept	12	53	248	1058	1036	Pterocarpus	rohrii
223	QUALPA	Canopy	Non-Pio	Accept	18	44	216	1320	660	Qualea	paraensis
224	QUARBR	Interm	Non-Pio	Non-com	6	24	392	764	471	Quararibea	bracteolosa
225	QUIISC	Interm	Non-Pio	Non-com	6	24	392	764	471	Quina	schippii
226	RAUVAF	Interm	Non-Pio	Non-com	7	30	120	728	384	Rauvolfia	aphlebia
227	RICHOB	Interm	Non-Pio	Non-com	7	30	120	728	384	Richeria	obovata
228	RINODA	Unders	Non-Pio	Non-com	1	28	208	450	313	Rinorea	dasyadena
229	ROLLPI	Subcan	Pioneer	Accept	13	118	96	636	276	Rollinia	pittieri
230	SACOTR	Canopy	Non-Pio	Accept	17	29	256	1156	589	Sacoglottis	trichogyna
231	SAPIGL	Interm	Non-Pio	Non-com	6	24	392	764	471	Sapium	glandulosum
232	SAPISP	Interm	Pioneer	Non-com	6	24	392	764	471	Sapium	sp.
233	SAPRVI	Interm	Non-Pio	Non-com	7	30	120	728	384	Sapranthus	viridiflorus
234	SCLECO	Subcan	Non-Pio	Protec	12	53	248	1058	1036	Sclerolobium	costaricense
235	SIMAAM	Canopy	Pioneer	Accept	19	87	80	1282	727	Simarouba	amara

Nr	Code	Adult	Guild	Comm	Group	g	MaxAge	MaxD	MaxR	Scientific Name
236	SIPAGU	Interm	Non-Pio	Non-com	6	24	392	764	471	Siparuna guianensis
237	SLOAME	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Sloanea medusula
238	SLOASP	Interm	Non-Pio	Non-com	7	30	120	728	384	Sloanea sp.
239	SOCREX	Subcan	Non-Pio	Non-com	26	0	200	-1	384	Socratea exorrhiza
240	SPACCO	Canopy	Non-Pio	Accept	17	29	256	1156	589	Spachea correae
241	SPONRA	Interm	Pioneer	Non-com	8	96	152	820	287	Spondias radlkoferi
242	STERRE	Canopy	Pioneer	Accept	17	29	256	1156	589	Sterculia recordiana
243	STRYMI	Canopy	Pioneer	Accept	19	87	80	1282	727	Stryphnodendron microstachyum
244	SWARCU	Canopy	Non-Pio	Non-com	16	42	425	1155	327	Swartzia cubensis
245	SWARSI	Unders	Non-Pio	Non-com	1	28	208	450	313	Swartzia simplex
246	SYMLOI	Interm	Non-Pio	Non-com	6	24	392	764	471	Symplocos sp. 01
247	SYMPGL	Interm	Non-Pio	Non-com	7	30	120	728	384	Symphonia globulifera
248	SYMPSP	Subcan	Non-Pio	Non-com	12	53	248	1058	1036	Symphonia sp.
249	TABERO	Canopy	Non-Pio	Desira	17	29	256	1156	589	Tabebuia rosea
250	TABRAM	Unders	Non-Pio	Non-com	1	28	208	450	313	Tabernaemontana amygdalifolia
251	TALAGL	Interm	Non-Pio	Non-com	6	24	392	764	471	Talauma gloriensis
252	TALINE	Unders	Non-Pio	Non-com	1	28	208	450	313	Talisia nervosa
253	TAPIGU	Canopy	Non-Pio	Accept	18	44	216	1320	660	Tapirira guianensis
254	TERMMAM	Canopy	Non-Pio	Accept	17	29	256	1156	589	Terminalia amazonia
255	TERMBU	Canopy	Non-Pio	Accept	18	44	216	1320	660	Terminalia bucidoides
256	TERMOB	Canopy	Pioneer	Accept	18	44	216	1320	660	Terminalia oblonga
257	TETRAP	Canopy	Non-Pio	Accept	16	42	425	1155	327	Tetragastris panamensis
258	THEOAN	Interm	Non-Pio	Non-com	6	24	392	764	471	Theobroma angustifolium
259	THEOSI	Interm	Non-Pio	Non-com	6	24	392	764	471	Theobroma simiarum
260	TREMMI	Interm	Pioneer	Non-com	8	96	152	820	287	Trema micrantha
261	TRIOGA	Interm	Non-Pio	Non-com	8	96	152	820	287	Trichospermum galeottii
262	TROPIN	Interm	Non-Pio	Non-com	6	24	392	764	471	Trophis involucrata
263	UNONPI	Interm	Non-Pio	Non-com	6	24	392	764	471	Unonopsis pittieri
264	VANTBA	Subcan	Non-Pio	Accept	11	26	384	837	578	Vantanea barbourii
265	VIROKO	Canopy	Non-Pio	Accept	18	44	216	1320	660	Virola koschnyi
266	VIROMU	Subcan	Non-Pio	Non-com	13	118	96	636	276	Virola multiflora
267	VIROSE	Canopy	Non-Pio	Accept	13	118	96	636	276	Virola sebifera
268	VIROSP	Subcan	Non-Pio	Non-com	17	29	256	1156	589	Virola sp.
269	VISMMA	Interm	Pioneer	Non-com	7	30	120	728	394	Vismia macrophylla
270	VITECO	Canopy	Pioneer	Desira	17	29	256	1156	589	Vitex cooperi
271	VOCHF	Canopy	Pioneer	Accept	19	87	80	1282	727	Vochysia ferruginea
272	VOUAAN	Subcan	Non-Pio	Non-com	13	118	96	636	276	Vouarana anomala
273	WARSCO	Interm	Non-Pio	Non-com	6	24	392	764	471	Warszewiczia coccinea
274	WELFGE	Interm	Non-Pio	Non-com	26	0	200	-1	471	Welfia georgii
275	XYLOBO	Interm	Non-Pio	Non-com	6	24	392	764	471	Xylopia bocatorena
276	XYLOSE	Subcan	Pioneer	Non-com	13	118	96	636	276	Xylopia sericophylla
277	ZANTEK	Interm	Pioneer	Accept	8	96	152	820	287	Zanthoxylum ekmanii
278	ZYGIGI	Interm	Non-Pio	Non-com	6	24	392	764	471	Zygia gigantifoliola