AN ABSTRACT OF THE THESIS OF

Jean-Remy M. Makana for the degree of Master of Science in Forest Science presented on September 2, 1999. Title: Forest structure, Species Diversity and Spatial Patterns of Trees in Monodominant and Mixed Stands in the Ituri Forest, Democratic Republic of Congo.

Abstract approved: ______________________________

David E. Hibbs

Two rectangular 10-ha plots (200 x 500 m) were established in each of the two main forest types of the Ituri Forest, Democratic Republic of Congo (formerly Zaire). The description of stand structure and species diversity, the comparison of the two forest types, and the evaluation of the effects of canopy dominance on species richness were the main goals of the study. All shrubs and trees ≥ 1 cm dbh, and lianas ≥ 2 cm dbh were measured, tagged, mapped to the nearest half-meter, and identified. Stem density, basal area, species richness and spatial dispersion of species were determined. Statistical comparisons were performed using analysis of variance and the chi-square test. The density of trees ≥ 1 cm dbh was higher in mixed forest (8112 stems ha^{-1}) than in monodominant forest (6844 stems ha^{-1}). Density of stems ≥ 10 cm dbh was 438 ha^{-1}

and 358 ha^{-1} in mixed and monodominant stands, respectively. Monodominant stands, with 98 stems ≥ 30 cm dbh ha^{-1}, had more large trees than mixed stands (77 stems ha^{-1}). Basal area was 37.7 m^2 ha^{-1} and 32.6 m^2 ha^{-1} for trees ≥ 1 cm dbh and ≥ 10 cm dbh in monodominant forest, and 33.2 m^2 ha^{-1} and 26.2 m^2 ha^{-1} in mixed forest, respectively. Mean number of species per hectare was 178, 56, and 14 at 1 cm dbh, 10 cm dbh and 30 cm dbh, respectively, in monodominant forest; in the same order, mean species richness per hectare was 170, 68 and 27 in mixed forest. The density of *Gilbertiodendron dewevrei,* the dominant tree species of the monodominant stands, had a strong negative correlation with the species richness of trees ≥ 30 cm dbh. The vast majority of species exhibited significant clumping at all scales of analysis. No species had a significant regular dispersion pattern in the 10-ha plots. Small trees were more clumped than large trees and rare species were more clumped than more common species. Compared to many other tropical moist forests, the Ituri Forest was less diverse.

Forest Structure, Species Diversity and Spatial Patterns of Trees in Monodominant and Mixed Stands in The Ituri Forest, Democratic Republic of Congo

by

Jean-Remy M. Makana

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirement for the
degree of

Master of Science

Presented September 2, 1999
Commencement June 2000

ACKNOWLEDGEMENT

The establishment of the Ituri Forest Dynamics Plots (IFDP) was made possible by the collaboration of the Conservation and Parks Institution (ICCN) of the Democratic Republic of Congo. Through ICCN, the IFDP project received access to the Okapi Wildlife Reserve and to its research center, Centre de Formation et de Recherche en Conservation Forestière (CEFRECOF). Support for fieldwork came with a Smithsonian Institution Scholarly Studies grant to R. Condit and T. B. Hart and a continued backing of the Wildlife Conservation Society. My master's program was made possible by a scholarship from the Beinecke Memorial Scholarship Program and by financial support from Oregon State University (OSU).

I particularly thank Dr. David E. Hibbs for his advice and guidance during all the stages of my studies at OSU. Suzanne Lao, Hazel Hammond and Drs. Steven Acker and Richard Condit helped with the analysis of the data. Special thanks are due to the many collaborators who helped in the collection of the data, in particular, C. Ewango, I. Liengola, T. Hart, M. Bola, D. Batido, and to the field crew whose enthusiasm and readiness made this work possible. The expression of my gratitude would be incomplete if I do not mention the contribution of CEFRECOF's administrative crew whose organizational capability was essential for the realization of the Ituri Forest Plots project.

Many thanks to my friends, Robert Mwinyihali and Cyrille Adebu, who have been caring for my family while I am away from home. Above all, I am grateful to

Drs. John A. Hart and Terese B. Hart for their commitment to help in my quest to better my education; my studies at OSU will not have been possible without their support.

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DEDICATION

To the loving memory of my parents, Pierre Mekombo and Bernadette Nguzubay.

To Rosy M. Makana, my daughter who has accepted to endure the absence of her father for so long.

Jean-Remy Makana

FOREST STRUCTURE, SPECIES DIVERSITY AND SPATIAL PATTERNS OF TREES IN MONODOMINANT AND MIXED FOREST STANDS IN THE ITURI FOREST, DEMOCRATIC REPUBLIC OF CONGO

INTRODUCTION

Tropical forests play a number of roles of global significance. They host an important portion of the earth's biodiversity (IUCN 1992; Dalton et al. 1993), they constitute a large proportion of world's wood supply, and more recently they have been acknowledged as a potential sink of atmospheric carbon (Lugo and Brown 1993). Yet, even as tropical forests are being logged and converted to agricultural lands at an ever-increasing rate (Chapman and Chapman 1997), they still are very poorly understood.

Basic knowledge about tropical forest ecology is crucial to management and to the conservation of biodiversity. To answer the question of how tropical tree species diversity is maintained at a particular site, we first need to describe temporal patterns of species distribution. How are forests (density, diversity, species composition) changing through time? How much timber does the forest grow per unit of time? How different are species in demography and is this important for their coexistence in the community? The enumeration of trees in a reasonably large area and their monitoring over time can provide answers to these questions.

In the Congo basin, which contains more than half of Africa's rainforest (Dalton 1993), the canopy of mature forests on well-drained soils is often dominated by one or two tree species of the *Ceasalpiniaceae* family (Lebrun and Gilbert 1954). The most widespread of the single canopy-dominant forests in the region is the forest dominated by *Gilbertiodendron dewevrei* (De Wild.) Léonard (Hart 1985). In the Ituri Forest (northeastern Democratic Republic of Congo), which extends over approximately 70,000 km^2, there are two major forest types: the forest dominated by *G. dewevrei* and a mixed canopy forest (thereafter monodominant and mixed forests). The two forest types co-occur in the Epulu sector of the Ituri Forest (Figure 1.1). The borders between the two forest types are abrupt but do not correspond to topographic gradients (Hart 1985). The co-occurrence of monodominant and mixed forests at the same site and under similar environmental conditions offers a rare opportunity to explore the mechanisms producing and maintaining high species diversity in tropical forests.

Early studies of tropical forests were confined primarily to sampling trees within relatively small areas, 0.1 to a few hectares, and frequently only trees $\geq$ 10 cm dbh were measured (Gentry 1982). Recently, the Center for Tropical Forest Science (CTFS) of the Smithsonian Tropical Research Institute initiated the establishment of a network of large plots at several sites in the tropical forests of Central and Southern America, Asia, and Africa. A standard methodology is used at all sites – a complete census of all shrubs and trees down to 1 cm dbh (Condit 1995). After the first census, trees are re-measured every five years. The first African site is located in the Ituri Forest in the eastern part of the Democratic Republic of the Congo, formerly known as

Zaire (Makana et al. 1998). It is the basis of this study. Most of the studies on tropical forests have been carried out in Latin America or Asia, with very few in Africa. Data are needed from African forests in order to document similarities and differences among tropical forests of the world and to describe processes at work in these ecosystems.

The large plot study in the Ituri Forest will play an important role in increasing the knowledge of the tropical moist forest of the Congo. The detailed inventory of trees on a large area and their monitoring through time will provide information on plant species diversity, species abundance, growth and mortality rates and on changes in species composition. This knowledge can serve as a reference in forest management and sustainable extraction of forest resources. The primary forest of the Ituri region remains important to local populations as a source of game meat (the principal source of dietary protein in the area) and other forest products. It also has an international importance as the home of several rare mammals including the endemic Okapi (Hart and Murphy 1987). Along with similar studies in other tropical forests, the large plot in the Ituri Forest will contribute to the general understanding of tropical forest dynamics. Furthermore, the CTFS network is important to taxonomists who seek to identify rapidly the vast number of unknown plant species in these tropical forests.

Dominance by *G. dewevrei* has been reported to have profound consequences on the density and the diversity of both plants and of animals. Comparative studies of monodominant and mixed forests of the Ituri have shown that dominance by *G. dewevrei* is associated with a reduction in the diversity of tree species (Hart et al. 1989; Hart and Murphy 1987). Hart and Petrides (1987) found a significant negative relationship between canopy dominance by *G. dewevrei* and the density and the diversity of forest ungulates in the Epulu sector of the Ituri Forest. A better understanding of these communities is necessary for their management and their conservation. In the present study, I will describe the characteristics of two particular forest types, monodominant and mixed forests, in the Epulu sector of the Ituri Forest. The first chapter of the study will concern the description of stand structure and species diversity, and the second chapter will deal will the spatial patterns of trees within each 10-ha plot.

CHAPTER ONE

STAND STRUCTURE AND TREE SPECIES DIVERSITY OF A MONODOMINANT STAND AND OF A MIXED STAND IN THE ITURI FOREST

INTRODUCTION

The co-occurrence of mixed semi-evergreen forest and monodominant evergreen forest under similar environmental conditions such as occurs in the Epulu sector of the Ituri Forest has puzzled tropical ecologists for some time. It has been hypothesized that, in tropical regions, mixed forests are found on the most productive soils whereas single-species dominance depends on unfavorable soils characteristics (Richards 1996). Comparison of soil characteristics between mixed forest and monodominant forest in the Ituri has failed to support that hypothesis. Hart (1985) and Conway (1992) found no significant differences in soil texture and chemical composition under the two types. Although they observed that soils under mixed forest had more available nitrate and ammonium than in monodominant forest, Torti et al. (submitted) suggested that the lower nitrogen content in monodominant forest soils was a consequence rather than a cause of monodominance. The lower nitrogen content in monodominant forest soils, compared to that of mixed forest soils, could be the result of a nutrient depletion mechanism used by the dominant species as a mean to exclude the other species from utilizing that resource. Thus, several questions arise from these findings. How different are the two forest types? How do they persist together at one site under similar environmental conditions? What are the dynamics of the two? What is the disturbance history of these forest stands?

To address some of these questions, the Centre de Formation et de Recherche en Conservation Forestière (CEFRECOF) established two 10-ha plots in each of the two forest types. This protocol was motivated by the specific goal of comparing the two forest types. The dominant species (*Gilbertiodendron dewevrei* (De Wild.) Léonard) in the monodominant forest is a canopy species and occurs at a very high density, comprising up to 90 percent of trees above 30 cm dbh (diameter at breast height) in some stands (Hart et al. 1989; Gérard 1960). The strong canopy dominance by a single species would suggest that monodominant forests are less species-rich than mixed stands. Preliminary analysis, however, showed that the monodominant forest is as rich as the mixed forest, with rare species accounting for most of the diversity (Makana et al. 1998).

In this chapter, I propose to examine the stand structure (stem density, basal area, and size distribution) and species diversity of the two forest types in the areas encompassed by the plots. To what extent does dominance by a single species modify the overall forest structure and affect species diversity as compared to mixed-species stands? In various ecological studies, forests dominated by *Gilbertiodendron dewevrei* have been recognized as a distinct formation (Lebrun and Gilbert 1954; Devred 1958; White 1983). I will also investigate if any species are consistently positively or negatively associated with *Gilbertiodendron dewevrei.*

LITERATURE REVIEW

Structure of tropical forests

Studies of tropical forests in different regions have shown that characteristics such as stem density, basal area, and volume vary greatly among regions (Richards 1973, 1996). Richards (1996) reported that density of trees ≥ 10 cm dbh usually ranges from 300 to 700 trees ha^{-1} in tropical rainforests. He indicated that factors controlling tree density in rainforest include natural and anthropogenic disturbances, soil drainage, and other soil characteristics. Density of woody stems appears to be related to the amount and pattern of rainfall. In general, dry tropical forests have lower stem density and basal area than moist tropical forests. In a 50-ha plot of dry forest in India (1500 mm/year), Sukumar et al. (1992) reported only 520 stems ha^{-1} ≥ 1 cm dbh. Hubbell and Foster (1983) and Condit et al. (1992) reported 4844 stems ha^{-1} ≥ 1 cm in dbh in a 50-ha plot in a moist forest (2500 mm/year) with seasonal rainfall (four months of dry season) on Barro Colorado Island (BCI, Panama). A similar study at Pasoh Forest Reserve (Malaysia), a wet forest with aseasonal rainfall (2000 mm/year) had a much higher density, 6770 stems ha^{-1} (Manokaran and LaFrankie 1990).

The diameter distribution of trees in tropical forests is also variable. Some forests have large numbers of trees ≥ 30 cm dbh and others have few (Table 1.1). There is little correlation between the number of very large trees and the total number above some arbitrary lower diameter limit such as ≥ 10 cm dbh (Richards 1996). The diameter distribution of whole stands follows an exponential model fairly closely, but only for trees > 20 cm dbh (UNESCO 1978). Thus, if trees in a stand of rainforest are grouped in 10 cm intervals from 20 cm dbh upwards, the number of trees in each interval is generally about twice that in the next higher one (Richards 1996).

Table 1.1. Stem density (stems ha^{-1}) in different tropical forests[1].

Diameter class	Pasoh (Malaysia)	BCI (Panama)	Lenda (Congo)	Edoro (Congo)	Messa (Nigeria)	Okomu (Nigeria)	Ekobakoba (Gabon)
≥ 1 cm	6769	4880	6941	8070	-	-	-
≥ 10 cm	530	414	300	402	530	390	438
≥ 30 cm	75	83	90	68	38	47	124
≥ 100 cm	1.6	3.4	6	2	-	-	-

[1] Makana et al. 1998

Species diversity in tropical forests

Confusion surrounds the concept of species diversity (Magurran, 1988), largely because it consists of two components: variety (number of species) and relative abundance (number of individuals in each species). This has led to the existence of a large number of indices for summarizing species diversity. However, species richness (the number of species per unit area) remains the most commonly used measure of diversity in tropical forests. Species richness has been use to categorize forests as low- or high-diversity (Connell and Lowman, 1989). According to Johnston and Gillman (1995) low-diversity or species-poor forests may be defined as forests in which 50-80% of the canopy trees are represented by only one species. The authors hypothesized that several characteristics distinguish forests classified as low-diversity different from high-diversity forests:

1. For stems ≥ 10 cm dbh, species richness per ha in low-diversity forests is usually < 100 per ha;
2. Species and family dominance is high in low-diversity forests, with 6 species often accounting for more than 50% of stems and one species often accouting for more than 20% of the total number of trees;
3. The number of species with only one stem per ha is relatively low in low-diversity forests, i.e. less than 35% of all species. In high-diversity forests, between 40-60% of species have only a single tree in a hectare (Gentry 1988);
4. High dominance may occur in the understory level in low-diversity forests;

5. Species richness in low-diversity forests would appear to be mostly accounted by trees < 15 cm dbh.

Using trees ≥ 10 cm dbh, Johnston and Gillman (1995) found that the number of species in several plots in the neotropics was negatively correlated with the level of dominance. In four 1-ha plots at Kurupukari (Guyana), 25% of the stems were accounted for by 1-3 species and the average number of species per hectare was 63. The plot in which a single species represented at least 25% of stems had only 50 species whereas the plot in which 3 species accounted for 25% of stems had 67 species. Johnston and Gillman (1995) reported Gentry's findings in a study of 1 hectare of moist forest at Manaus (Brazil) where the 11 most abundant species accounted for 25% of stems and there were 165 species.

These observations were similar to data from three 50-ha plots in Asia and Central America. Kochummen et al. (1990) reported that the most common species at Pasoh Reserve (Malaysia) accounted for only 2.5% of stems and the average number of species ha^{-1} was 495 for trees ≥ 1 cm dbh. At Barro Colorado Island, the most abundant tree species represented 16.7% of the stems ≥ 1 cm dbh and there were 172 species ha^{-1} on average (Hubbell and Foster 1990). Sukumar et al. (1992) found an average of 26 species ha^{-1} in a dry forest at Mudumalay (India), with the most common species accounting for about 20% of individuals.

The amount and patterns of rainfall are other major environmental variables influencing the diversity of tropical plant communities. Species diversity of tropical forests decreases with increasing seasonality and increases with the total annual precipitation (Richard 1996). Thus, tropical deciduous and semideciduous forests are generally less rich in species than rain forests. It has been shown from a larger number of 0.1 ha plots that in lowland neotropical dry forests usually have about 50 plant species, moist forests have 100-150 and wet forests over 200 species (Gentry 1982).

Very few studies in tropical forests have included stems < 10 cm dbh. Available data show a great variability in stem density, basal area, and species richness among tropical forests. The mean number of stems per hectare drops rapidly with increasing diameter class. Although tropical forests are generally more diverse than temperate forests, tremendous differences exist among them. Some forests in Asia and South America are very diverse while others are less diverse. Factors that determine these differences in species diversity among tropical forests are still subject of debate but include rainfall, length of dry season, and soil characteristics.

OBJECTIVES

The overall objective of this chapter is to describe the stand structure and species diversity in one example of each of two tropical forest types in the Ituri Forest, and to evaluate the effects of canopy dominance on species diversity. Specific objectives are:

1) To compare stem density and basal area of the two forest types;
2) To compare species diversity indices of the two forests;
3) To describe patterns of species abundance in the two forest types;
4) To evaluate species accumulation patterns in each forest type by constructing species-area and species-individual curves in order;
5) To evaluate the effects of the dominance of the canopy by *Gilbertiodendron dewevrei* on species diversity and species accumulation patterns;
6) To compare the Ituri Forest to other evergreen tropical forests with respect to stem density and species richness.

Several hypotheses, related to these specific objectives, were tested. They were:

1. Monodominant and mixed forests have similar stem density and basal area. This hypothesis was tested by comparing mean stem density and mean basal area per hectare for the two forest types.

2. Monodominant forest is at least as rich in species as mixed forest. The alternative hypothesis is that monodominant forest is less rich than mixed forest. Mean number of species per hectare and values of Shannon's index and Simpson's index, calculated for individual hectares, were compared for these forests.

3. The asymptote of the species-area curve for the mixed forest is higher than that of monodominant forest. In other words, for similar areas monodominant forest has fewer species than mixed forest. This is tested by plotting the number of species against area.

4. Species-individual curves are similar for the two forest types. Mean number of species in a given area was plotted against mean number of stems for that area. The rationale for this hypothesis is that mixed forest is richer than monodominant forest only because it has more stems per unit area.

5. At the scale of a hectare, the Ituri Forest has fewer species than many Asian and Neotropical forests. African tropical forests have been reported to be less diverse than Asian and Neotropical forests (Richards 1973). Furthermore, the high representation of the most abundant species in both the Ituri monodominant and mixed stands would tend to reduce the local species richness.

STUDY SITE

The Ituri Forest is located in the northeastern part of the Congo Basin (Democratic Republic of Congo) and lies between the equator and 3° N and between 27° E and 30°E longitude (Hart et al. 1996). Elevation in the Ituri Forest ranges from 600 m above sea level in the west to about 1500 m where the forest borders savanna and transition montane forest in the east.

The vegetation in the Ituri Forest is mainly composed of two principal types of Guineo-Congolian rainforest: mixed moist semi-evergreen forest and single-dominant evergreen forest (Hart et al. 1996; White 1983). The height of the forest canopy, as determined by the dominant species, is 35 to 40 m, with scattered trees exceeding 45 m. There are also local areas of distinct vegetation such as swamp forest that occurs along streams in areas of poor drainage, and a xerophyllous vegetation occurring in isolated patches and restricted to dry hilltops in the northern part of the Ituri Forest between 28° and 29° E longitude (Makana et al. 1998). Both mixed semi-evergreen forest and single-dominant evergreen forest (hereafter mixed and monodominant forests) are dominated by members of *Caesalpiniodae.* The monodominant forest has a high representation of *Gilbertiodendron dewevrei,* which comprises up to 90% of the canopy trees in some stands (Gérard 1960; Hart 1985). *G. dewevrei* forms a homogeneous and continuous canopy at a height of 30 to 40 m, above which there may be occasional emergents (Richards 1996). Two species, *Cynometra alexandri* C.H. Wright and *Julbernardia seretii* (De Wild.) Troupin, comprise high proportions of the canopy trees in mixed forest and may account for 40% of the basal area of trees ≥ 30 cm dbh. The canopy of mixed forest is heterogeneous and broken by frequent emergent trees. Apart from the conspicuous absence of *G. dewevrei* in mixed forest, the two types share the same common tree species (Hart et al. 1989, Makana et al. 1998)

The Plots are located in the Epulu sector of the Ituri Forest (1°25’ N, 28°35’ E) (Figure 1.1). The sector lies along the transition between mixed semi-evergreen forest, which extends north and eastwards, and monodominant evergreen forest. Except for small areas of cleared agricultural fields in the vicinity of the village of Epulu, whose population is about 2000 people, closed canopy forest covers the entire Epulu sector. Epulu is more than 150 km south and west of the northeastern transition from the closed humid forest to the anthropogenic fire-maintained savanna (Makana et al., 1998). Elevation in the sector ranges from 700 to 850 m above sea level. The topography is gently undulating with occasional low hills containing exposed patches of shallow rocky soils.

Soils are derived from the underlying granitic Gondwanan shield rock (Hart 1985). Previous studies (Hart 1985; Conway 1992) showed that soils had a variable texture, ranging from loamy sand to sandy clay, but with uniformly low pH and low available phosphorus and nitrogen. These studies found no significant difference in soils between monodominant and mixed forests, but a more recent investigation revealed that mixed forest had significantly higher amount of available nitrate and ammonium than monodominant forest (Torti et al., submitted). Mean annual rainfall at Epulu is 1672 mm. Over a nine-year period (1987 - 1995), annual maximum precipitation was 2084 mm and the minimum was 1304 mm. Three months had mean precipitation below 100 mm, but January was the only month with mean precipitation under 50 mm. Mean daily average temperature was 25.5°C (Hart and Carrick 1996).

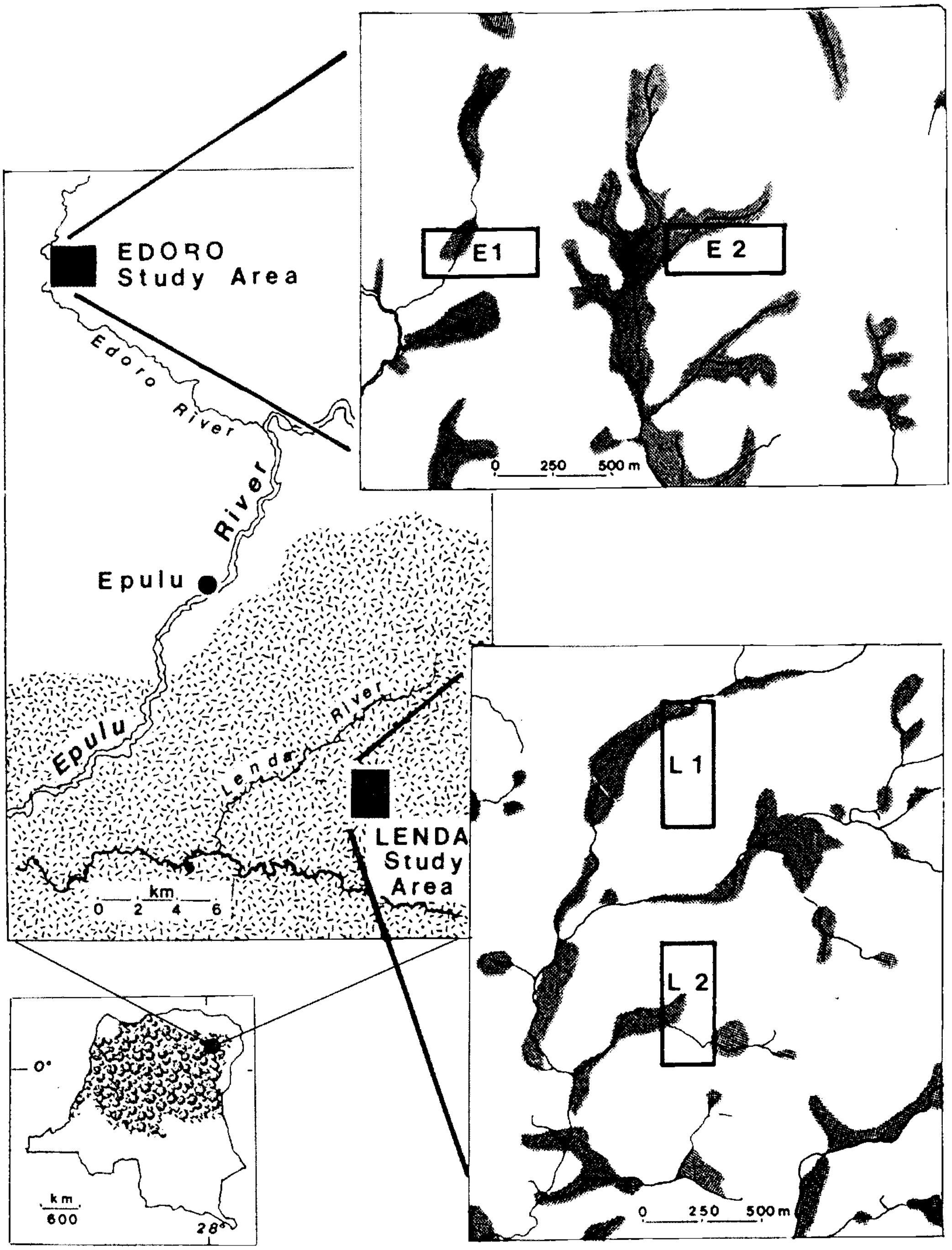


Figure 1. 1. The design of the Ituri Forest Dynamics Plots. Four plots, L1 and L2, and E1 and E2, are located on the Lenda and Edoro Study Areas at the transition between mixed semi-evergreen forest and monodominant evergreen forest mosaic (irregular hatching). Stipplings indicates swamp areas. The insert represents the Democratic Republic of Congo and the Congo basin rainforest block. The dot locates the Epulu sector of the Ituri Forest (from Makana et al. 1998).

METHODS

Research design

The study consisted of two rectangular, 10-ha plots at each of two sites, Lenda and Edoro (Figure 1.1). The two plots in the monodominant forest (Lenda 1 and 2) lie in a North-South line and were separated from each other by a 500m. The same pattern was used in the mixed forest, but the plots were oriented along a west-east line. Each 10-ha plot was 200m wide and 500m long, and was divided into quadrats and subquadrats. Each quadrat was 20m on a side, a length chosen because it was the longest distance that could be surveyed accurately through the dense forest cover. Subquadrats were 5 m on a side; a length chosen because it provided the largest area within which plants could be accurately mapped (Manokaran et al. 1990).

Plot surveying

The materials used for surveying the 10-ha plots included a transit instrument (TRACON S-25), a tripod, steel measuring tapes, surveying rods and wooden stakes. The starting point of the first plot in each forest type was arbitrarily chosen, and a post was placed at that point. Then the transit instrument was placed over that post. The instrument was plumbed to the center of the post and leveled. Then the scope was focused on geographical north using the instrument compass, and a second post was placed at a distance of 20 m. Once the second stake was put in place, the rotating azimuth ring was set at 0 degree against the second post. One post was then placed at each of the three remaining cardinal points (east, south and west) by rotating the ring and setting the scope at 90°, 180°, and 270°, respectively. The next step was to move the instrument and place it over one of the four posts surrounding the initial post, focusing the scope on the first post, and locking the rotating ring in place. In that way the scope was set in proper angular relationship with the existing grid. The new posts were placed as in the previous step. This procedure was repeated over and over until the whole plot was entirely surveyed (Figure 1.2). Newly positioned posts were regularly checked against previous posts to minimize the accumulation of errors.

A record of the survey was kept to determine the accuracy of the process, to locate possible sources of errors, and to construct topographic maps (Figure 1.2). Data were recorded into a waterproof field notebook. The following information was recorded:

a) Type of "shot", a "set shot" to set the scope, a "check shot" to verify the position of the post over which the instrument was placed against an existing post, or a "first shot" setting a new post;
b) Coordinates of the survey instrument;
c) Coordinates of the post to be surveyed;
d) The difference in elevation between the instrument location and the new post location;
e) The distance measured between the instrument and the point being surveyed.

A sketch of each new shot made and of obstacles that prevented the establishment of a new post or prevented the checking of an old post, was drawn as the work proceeded.

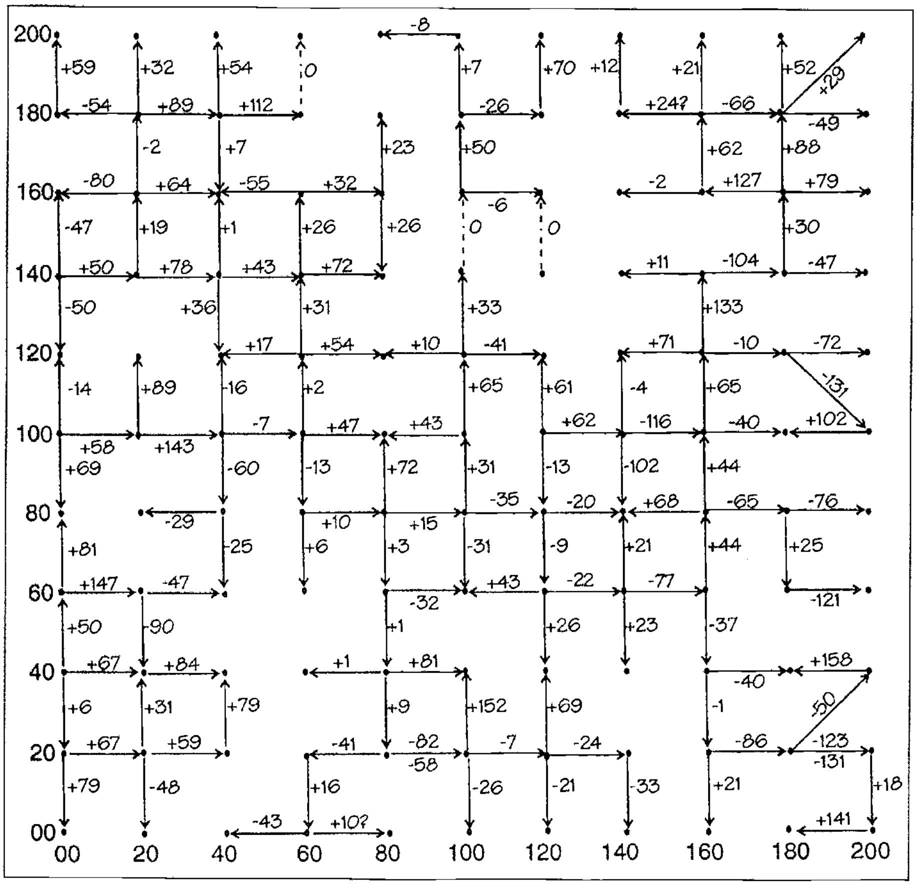


Figure 1.2. A sample map showing a portion of the Ituri Forest plots, indicating how the surveying was done. Vertical and horizontal distances between points (length of arrows) are 20 m, the diagonal distance is 28.28 m (the actual distance is corrected for slope, see text for details). Arrows indicate where the sightings were taken; elevation change (in centimeters) is shown next to the arrow. Dashed arrows indicate missing data (from Condit 1998).

Data collection

During botanical inventory and stem mapping, each 20 m x 20 m quadrat was temporarily subdivided into 16 5 m x 5 m subquadrats using wooden stakes, measuring tapes and nylon ropes. Botanical census and stem mapping started in February of 1994 and were completed in June of 1996. All free-standing stems ≥ 1cm in diameter at breast height (dbh) were measured for diameter at 1.3 m, mapped, tagged with pre-numbered six-digit aluminum tags, and identified to species whenever possible. Tags were attached to stems less than 5 cm dbh with termite-resistant braided nylon line, whereas they were attached to larger stems with aluminum nails. Lianas and stranglers were included in the census if they reached 2 cm dbh. For lianas and stranglers, as for free-standing stems, the point of measurement was marked with white, oil-based paint (Makana et al. 1998).

Mapping was done by hand within the 5 x 5 m subquadrats. Tree locations were recorded on a sheet of squared paper for each quadrat separately. For each quadrat the origin was located at the southwest corner of the quadrat for Lenda (monodominant forest) and at the northwest corner for Edoro (mixed forest).

In most cases the diameter of each tree was measured at 1.3 m above the ground. However, stems with irregular trunks were measured at the nearest lower point where the stem was cylindrical. Trees with buttresses rising near or beyond 1.3 m were measured at least 0.5 m above buttresses. Diameter at breast height was measured by calipers (stems < 4 cm) or by diameter tapes (stems ≥ 4 cm) and recorded to the nearest millimeter. Trees with multiple stems were counted as single individuals, but the diameter of each stem was measured and recorded separately.

The protocol for tree measurement and mapping was difficult to apply to lianas because some individuals run on the ground for a long distance before rising above 1.3 m. In practice, lianas were measured where their stems had a diameter ≥ 2 cm at 1.3 m height, but were mapped where they were rooted.

Species identification

Each census team included a field botanist whose primary objective was to identify tree species. Most familiar species were identified in the field. Botanical specimens were collected in cases where there was uncertainty. Pygmies (native people) collected samples from large canopy trees or from lianas that climb on those trees. Plant samples were pressed and dried. Dry specimens were compared to identified samples at the Center's herbarium in Epulu. This step permitted the identification of more species; unidentified samples were sent to taxonomic experts at different herbaria in Europe and the United States. The level of taxonomic identification of trees species in the Ituri Forest plots is presented on Table 1.2.

Table 1.2. Level of taxonomic identification of trees (≥ 1 cm dbh) and lianas (≥ 2 cm dbh) in in the Ituri Forest Dynamics Plots.

Groups	Identification to			Unidentified	Total
	Species	Genus only	Family only		
Trees	393*	9	8	1	411(61.2%)
Lianas	229	5	6	0	240 (35.7%)
Stranglers	21	0	0	0	21 (3.1%)
Total	643 (95.7%)	14 (2.1%)	14 (2.1%)	1 (0.1%)	672

* Includes one unnamed new species.

Data analysis

Dbh classes

Stem density and species richness were calculated for all trees using three lower dbh limits: 1 cm (all the stems included in the survey), 10 cm and 30 cm. These lower limits were chosen to match other studies in tropical forests (Condit 1995, Hubbell and Foster 1990, Manokaran et al. 1990). Different lower dbh limits were used for lianas; the lowest diameter limit was 2 cm dbh and liana density was also calculated for stems ≥ 5 cm and ≥ 10 cm dbh. These diameter limits yield overlapping classes such that individuals in ≥ 10 cm dbh are also included within the group ≥ 1 cm dbh. In addition, non-overlapping diameter classes were used to evaluate the distribution of size class within each forest type or for individual species and to evaluate the regeneration of the most common canopy species. Three diameter classes were used for regeneration analysis: < 10 cm, 10-29.9 cm and ≥ 30 cm dbh. Size distribution was calculated using the following classes: 1-9.9, 10-19.9, 20-29.9, 30-39.9, 40-49.9, 50-59.9, 60-69.9, 70-79.9, 80-89.9, 90-99.9, 100-109.9 and ≥ 110 cm dbh.

In this analysis, lianas and stranglers were always considered separately from free-standing shrubs and trees.

Density, relative abundance and dominance

Density is the number of individuals per hectare or the number of individuals/species/ha. Relative abundance of a species is the proportion of the total number of individuals represented by that species. Dominance is calculated by the proportion of basal area contributed by each species (Abdulhadi et al. 1998). The value of these two variables was calculated as follows:

Relative abundance = (number of stems of a species/total number of stems) x 100

Dominance = (basal area of a species/total basal area) x 100

Diversity indices

In addition to the number of species per unit area, two commonly used diversity indices were calculated: the Shannon-Wiener index and Simpson's index. The Shannon-Wiener index is computed as follows:

$$\Sigma_i -(f_i \ln f_i)$$

(Maguran 1988) where f_i is the relative abundance of species i.

Simpson's index is given by

$$\Sigma_i f_i^2.$$

(Kempton 1984). These indices were calculated for each individual square hectare in each plot. The resulting values were averaged to give mean value for each index for each plot.

Species-area and species-individual curves

To construct species-area curves, each plot was divided into non-overlapping square quadrats of varied sizes and the mean number of species in each quadrat size was calculated (Condit et al. 1996; 1998). Quadrats of the following dimensions were used: 5, 10, 20, 40, 80, 100, 160 and 200 m on a side. If the whole plot (200 x 500 m) did not divide evenly into the size of a quadrat, the northern edge and the eastern edge, in monodominant forest, or the western edge and southern edge, in mixed forest, were left out. The mean number of species for each quadrat size was then plotted against the quadrat area to produce species-area curves. The last point of each curve corresponds to the number of species in the whole 10-ha plot.

The same approach was used to generate species-individual curves, but instead of area, the number of species was plotted against the mean number of individuals in each quadrat size (Condit et al. 1996, 1998).

Statistical analysis

To compare the two forest types, values of stem density and species richness were averaged for the plots in each forest type. A chi-square test was used to examine differences in the distribution of trees in three non-overlapping size classes (< 10, 10-29.9 cm and ≥ 30 cm dbh) between monodminant and mixed stands. Analysis of variance was used to compare stem density and basal area between the two forest types for each of these size classes separately. Regression analysis was employed to evaluate the relationship between canopy dominance by *G. dewevrei* and species richness in the four plots. The number of species for three diameter limits (≥ 1 cm, ≥ 10 cm, and ≥ 30 cm) was regressed on the density of trees ≥ 30 cm dbh of *G. dewevrei*.

Variance-to-mean ratio (v/m) was used to describe patterns of spatial distribution of stem density and species richness. V/m values equal to 1 indicate randomness, those less than 1 suggest uniform distribution and values greater than 1 suggest clumping (aggregated patterns) (Brower and Zar 1984). Significance of departure from randomness was not tested in this exploratory analysis.

RESULTS

Description of Plots

Topography and vegetation

Both study areas were relatively level. Differences in elevation between the lowest and the highest points within the 10-ha plots were 24 m for Lenda1, 16 m for Lenda2, 14 m for Edoro1 and 21 m for Edoro2. The two plots located at the Lenda Study Area (LSA) were dominated by *Gilbertiodendron dewevrei* at the canopy level. One of these plots (Lenda1), however, included about two and a half hectares of mixed forest. The plots at Edoro Study Area (ESA) were constituted of mixed forest, with the exception of some monodominant patches at Edoro1. *Cynometra alexandri* and *Julbernardia seretii* (two members of the *Ceasalpiniodae* subfamily) were the most abundant canopy species at ESA. All plots at both study areas contained small areas of temporary or permanent swamp along streams.

Stem density and basal area

There was considerable variation in the number of trees among the four plots (Table 1.3). Edoro2, the only plot that did not have any patches of monodminant forest, had the highest stem density at the 1 cm and 10 cm dbh thresholds. Lenda2, which was entirely dominated by *G. dewevrei* at the canopy level (see density of *G. dewevrei* in Table 1. 4), had the lowest density of trees when all stems ≥ 1 cm dbh were considered. However, when only large trees (≥ 30 cm dbh) were considered, Lenda2 had the highest density; Lenda1 had the second highest density, while Edoro2 and Edoro1 ranked third and fourth respectively. It thus appears that the plots located at the ESA had higher density of small stems, whereas the plots at LSA had more large trees. The higher density of large trees in the Lenda plots resulted in higher basal area for these plots. Mean basal area calculated on a hectare basis was 37.06 m^2 ha^{-1} in Lenda1 and 38.86 m^2 ha^{-1} in Lenda2. Average basal area at Edoro1 and Edoro2 was 32.86 m^2 ha^{-1} and 34.07 m^2 ha^{-1}, respectively

Trees were not evenly distributed within each plot. Density of trees of all size-classes showed considerable variation in 400 m^2 quadrats. Mean density of trees ≥ 1 cm dbh in 400 m^2 quadrats was 284 stems in Lenda1 and 264 stems in Lenda2. Edoro1 averaged 305 stems while Edoro2 had a mean density of 343 stems per 400 m^2. Edoro1 had the largest variation: the densest quadrat, with 584 trees ≥ 1 cm dbh, was nearly five times as dense as the sparsest quadrat which had only 119 trees. The ratio of most dense to least dense 400 m^2 quadrat was 3.1 for Lenda1, 3.0 for Edoro2, and 2.6 for Lenda2 at the 1 cm dbh threshold.

Variance-to-mean ratio for stem density in 400 m^2 quadrats ranged from 7.74 to 17.63, suggesting a patchy distribution of stem density within each of the four plots. Although there was considerable variation in tree density, nearly all the frequencies fell within two standard deviations of the mean for each plot (Figure 1.3).

Table 1.3. Stem density and basal area (standard deviations in parentheses) in four 10-ha plots in the Ituri Forest.

Size class (cm)	Lenda1	Lenda2	Edoro1	Edoro2
		Stem density (trees ha^{-1})		
≥ 1	7098 (375)	6589 (620)	7628 (833)	8597 (1038)
≥10	343 (64)	372 (64)	425 (29)	451 (28)
≥ 30	90 (6)	106 (18)	76 (9)	78 (9)
Lianas (≥ 2 cm)	327 (183)	316 (114)	648 (127)	636 (158)
		Basal area (m^2 ha^{-1})		
≥ 1	37.02 (3.23)	37.96 (2.79)	32.71 (1.90)	33.70 (2.77)
≥10	31.94 (3.25)	33.21 (2.86)	26.08 (2.28)	26.31 (2.37)
≥ 30	26.42 (4.04)	27.44 (3.29)	19.26 (2.58)	19.37 (2.73)

Table 1. 4. Density and basal area of *Gilbertiodendron dewevrei* in four 10-ha plots in the Ituri Forest.

Dbh class	Lenda1	Lenda2	Edoro1	Edoro2
		Density (stems ha^{-1})		
≥ 1 cm	395 (5.6%)[1]	635 (9.6%)	89 (1.2%)	0
≥ 10 cm	138 (40.2%)	225 (60.5%)	16 (3.8%)	0
≥ 30 cm	53 (58.9%)	86 (81.1%)	6 (7.9%)	0
		Basal area (m^2 ha^{-1})		
≥ 1 cm	19.68 (53.2%)	27.48 (72.4%)	1.99 (5.9%)	0
≥ 10 cm	19.31 (60.5%)	26.87 (80.9%)	1.88 (7.2%)	0
≥ 30 cm	17.09 (64.7%)	23.37 (85.2%)	1.61 (8.4%)	0

[1] Percent of the total number of stems (or basal area) for the dbh limit.

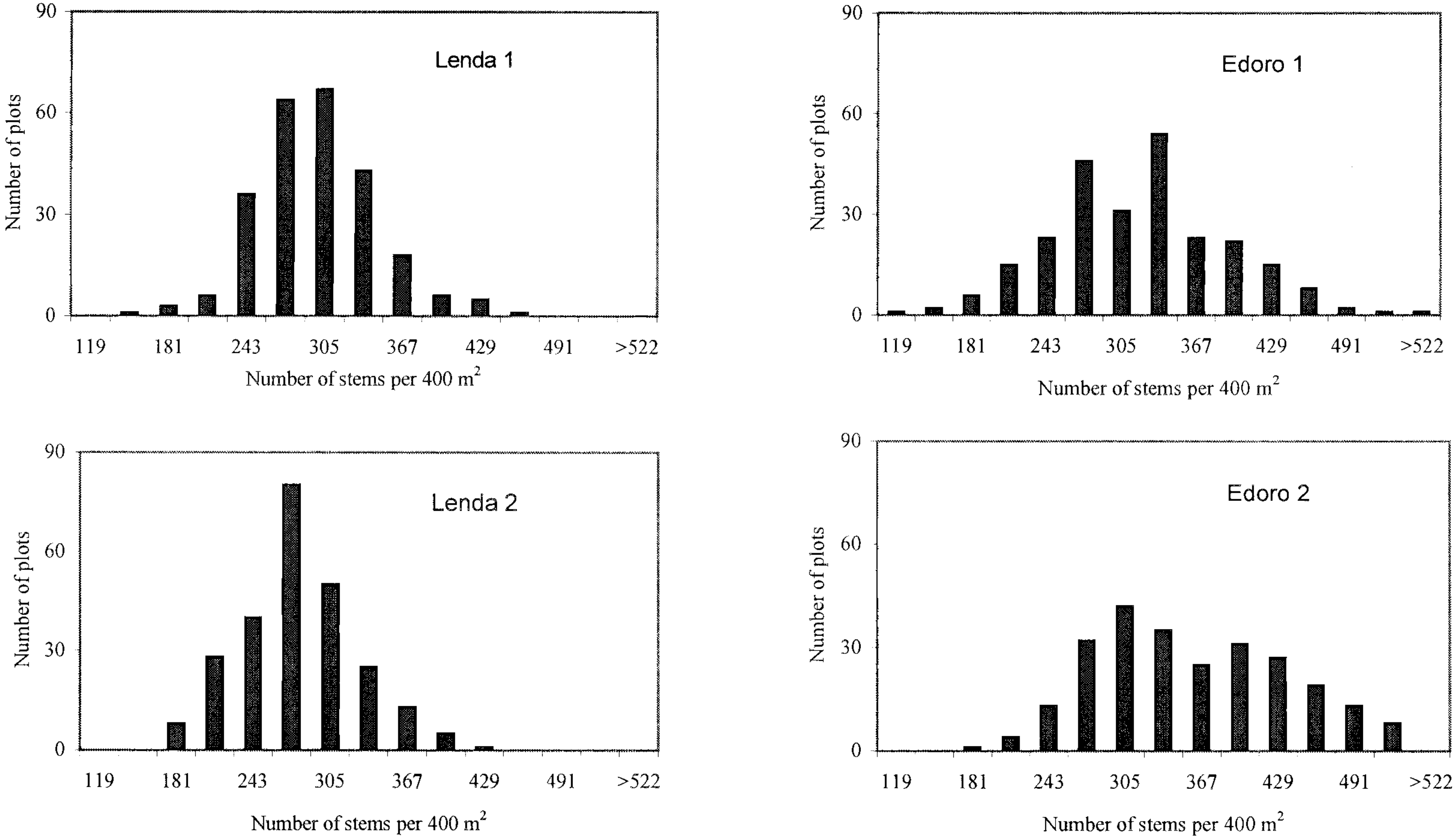


Figure 1.3. Distribution of the number of stems per 400 m^2 for the 10-ha plots in the Ituri Forest. All the graphs were brought at comparable scale by using the same interval widths. These interval widths were obtained by pooling the data from all the four plots and generating equal interval widths.

Lianas were abundant in the Ituri forest plots. Mean density of lianas ≥ 2 cm dbh was 327 stems ha^{-1} in Lenda1 and 316 stems ha^{-1} in Lenda2. The plots at Edoro had many more lianas than the Lenda plots. Edoro1 averaged 648 stems ha^{-1} and Edoro2 636 stems ha^{-1}. Although the Edoro plots had consistently more lianas than Lenda plots, the differences were less important for larger size classes (≥ 5 cm dbh and ≥ 10 cm dbh), (Table 1.5). Lianas were not randomly distributed within the plots, but showed very large variations in the local distribution of stem density. Variance to mean ratio on hectare basis ranged from 24.9 to 102.7, indicating aggregated patterns of liana density distribution. Lenda1 exhibited the largest variation in local density of lianas, having a 6.4-fold difference between the densest and the sparsest hectares.

Table 1.5. Density of liana (number of stems ha^{-1}) in four 10-ha research plots in the Ituri Forest, (standard deviations in parentheses).

Plot	≥ 2 cm dbh	≥ 5 cm dbh	≥ 10 cm dbh
Lenda1	327 (183)	43 (30)	4 (2)
Lenda2	316 (114)	62 (28)	6 (3)
Edoro1	648 (127)	72 (18)	6 (3)
Edoro2	636 (158)	78 (23)	7 (3)

Species richness

Total richness in the four plots was 411 species at the ≥ 1 cm dbh level, 288 species for trees ≥ 10 cm dbh, and 160 species at the 30 cm dbh threshold. Mean richness per hectare for all stems ≥ 1 cm dbh was 183 species in Lenda1 and 174 species in Lenda2; Edoro1 had an average of 173 species ha^{-1} while Edoro2 had an average richness of 166 species ha^{-1}. Richness of trees ≥ 10 cm dbh exhibited weak differences between the plots, with plots at LSA having slightly lower number of species per hectare than plots at ESA (Table 1.6). A similar but more pronounced pattern was observed when only trees above 30 cm dbh were considered. Both Edoro1 and Edoro2 were noticeably richer for trees ≥ 30 cm dbh than each of the plots at LSA.

Species richness in 400 m^2 quadrats showed less variation than did stem density. Despite the existence of large ranges between the poorest and the richest quadrats, especially for the plots at LSA, variances were quite small. Variance-to-mean ratio was less than one for Edoro1 (0.93) and Edoro2 (0.76), indicating a tendency toward uniform distribution patterns of species richness in 400 m^2 subplots. The largest variation was observed in Lenda1 where there were two peaks of species richness in 400 m^2 quadrats (Figure 1.4). Variance-to-mean ratio was 2.98 for Lenda1, suggesting a non-random distribution of species richness in 20 m x 20 m subplots. The ratio for Lenda2 was 1.33, indicating a fairly random distribution of species richness.

Table 1.6. Mean species richness ha^{-1} in monodominant (Lenda) and mixed (Edoro) stands in the Ituri Forest. (standard deviations in parentheses).

Plot	≥ 1 cm dbh	≥ 10 cm dbh	≥ 30 cm dbh
Lenda1	183 (22)	61 (28)	14 (9)
Lenda2	174 (12)	50 (17)	13 (6)
Edoro1	173 (14)	67 (7)	25 (4)
Edoro2	166 (8)	69 (8)	28 (6)

Monodominant and mixed stands in the Ituri Forest.

Stem density and basal area

Mean density and basal area for trees at the three different diameter limits (≥ 1 cm dbh, ≥ 10 cm dbh and ≥ 30 cm dbh) are presented in Table 1.7. For the two lower size limits, mixed forest had higher density of stems than monodominant forest whereas monodominant forest (98 trees ha^{-1}) had many more large trees (≥ 30 cm dbh) than mixed stands (77 trees ha^{-1}).

Both forest types exhibited great variation in the number of trees in individual hectares (Figure 1.5). Mixed forest had a greater variation than monodominant forest for trees ≥ 1 cm dbh. The number of trees in individual hectares ranged from 10280 to 6574 stems for mixed forest and from 7981 to 5781 stems for monodominant stands. But monodominant stands showed larger variation than mixed stands for both trees ≥ 10 cm dbh and ≥ 30 cm dbh (Figure 1.5). In monodominant forest, the density of trees in individual hectares ranged from 473 to 248 and from 141 to 78 stems for trees ≥ 10 cm dbh and ≥ 30 cm dbh, respectively. These densities ranged from 522 to 371 stems and from 96 to 61 stems in mixed forest.

Mean basal area in monodominant forest was 37.70 m^2 ha^{-1} for all trees ≥ 1 cm dbh. Basal area for individual hectares ranged from 32.06 to 44.19 m^2 ha^{-1} in this forest type. Mixed forest averaged 33.20 m^2 ha^{-1} of basal area, with individual hectare values ranging from 29.83 to 39.10 m^2 ha^{-1}. For all three diameter limits, monodominant stands had higher basal area than mixed forest (Table 1.7).

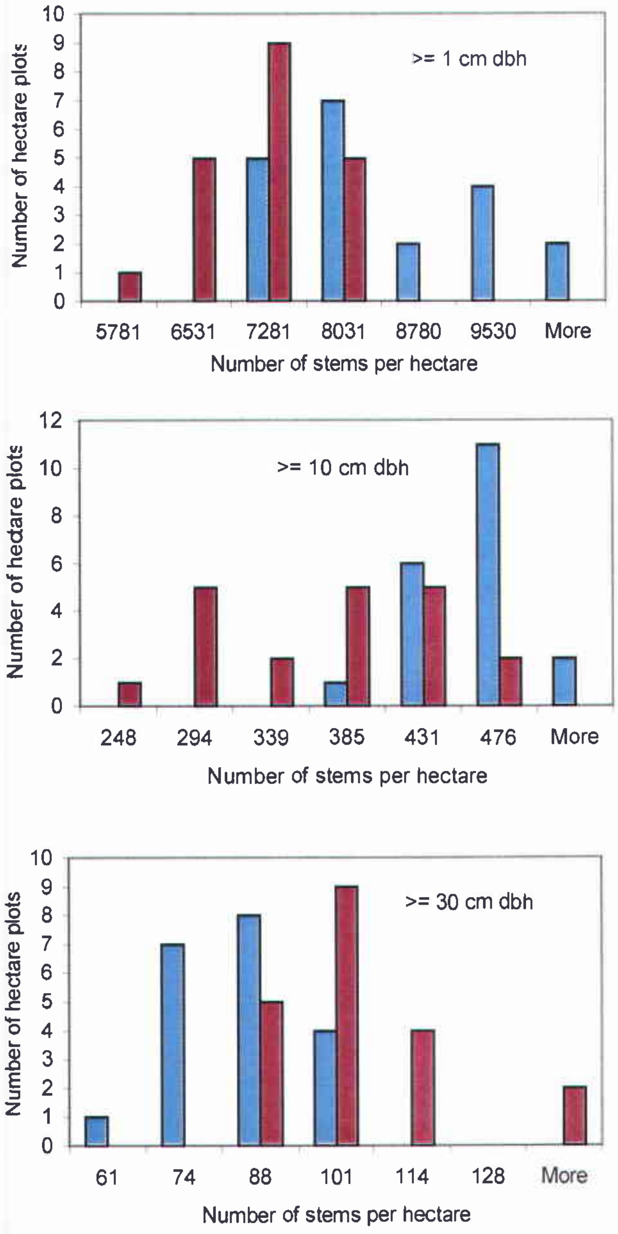


Figure 1.5. Distribution of stem density in square hectares (100 m x 100 m) in monodominant and mixed forests in the Ituri (n = 20 for each forest type). Mixed forest (dark bars); Monodominant stands (light bars). The numbers on x-axis are the upper boundaries of each density class.

Table 1.7. Stem density and basal area in monodominant and mixed stands in the Ituri Forest, (standard deviations in parentheses).

Size class (cm)	Mean density (stems ha^{-1})		Basal area (m^2 ha^{-1})	
	Mono	Mixed	Mono	Mixed
≥ 1	6844 (57)	8112 (1058)	37.70 (3.05)	33.20 (2.43)
≥ 10	358 (66)	438 (32)	32.57 (3.13)	26.20 (2.33)
≥ 30	98 (16)	77 (9)	26.93 (2.72)	19.31 (2.65)
Lianas	322 (153)	642 (143)	-	-

The density of lianas ≥ 2 cm dbh was nearly twice as high in mixed forest as in monodominant forest (Table 1.7). For larger size classes (≥ 5 cm dbh and ≥ 10 cm dbh), the differences were much smaller. In monodominant forest, for stems ≥ 5 cm dbh and ≥ 10 cm dbh, mean number of lianas was 52.5 stems ha^{-1} and 5 stems ha^{-1} respectively. Mixed forest averaged 75 stems ha^{-1} and 6.5 stems ha^{-1} for lianas ≥ 5 cm dbh and ≥ 10 cm dbh.

Comparison of monodominant and mixed forests

There was a significant difference in size distribution of free-standing stems between monodominant forest and mixed stands ($\chi^2 = 10.78$, d.f. = 2, $p = 0.005$). Mixed forest had more small stems (< 30 cm dbh) whereas monodominant forest had more large trees (≥ 30 cm dbh). An analysis of variance revealed that the difference in size distribution between the two forest types was mainly due to a significant difference in the density of medium-sized trees, 10-30 cm dbh (Table 1.8). The number of stems in that size class was much higher in mixed forest (361 stems ha^{-1}) than in monodominant forest (260 stems ha^{-1}). When the size of trees was taken into account and abundance expressed in terms of basal area, the two forest types showed significant differences for all three size classes. Mixed forest had higher basal area than monodominant stands for the size classes below 30 cm dbh, while monodominant forest exceeded mixed forest in the basal area of trees above 30 cm dbh (Table 1.8).

Table 1.8. Stem density and of basal area of monodominant forest and mixed forest of the Ituri region.

Dbh class (cm)	Plot size (ha)	Sample size[3]	Mono	Mixed	F-statistic[2]	p-value
			Mean number of stems ha^{-1}			
< 10	10	4	6486 ± 254[1]	7674 ± 472	4.79	0.16
10 - 30	10	4	260 ± 7	361 ± 13	50.19	**0.02**
≥ 30	10	4	98 ± 8	77 ± 2	5.74	0.14
Lianas	10	4	322 ± 6	643 ± 5	2053.15	**0.0005**
			Mean basal area (m^2 ha^{-1})			
< 10	10	4	5.13 ± 0.10	7.04 ± 0.21	24.40	**0.04**
10 - 30	10	4	5.72 ± 0.32	6.93 ± 0.18	80.45	**0.01**
≥ 30	10	4	27.11 ± 0.88	19.50 ± 0.60	218.10	**0.005**

[1] Standard errors of the means.

[2] The null hypothesis for the F-test is no difference in stem density or in basal area between monodominant forest and mixed forest.

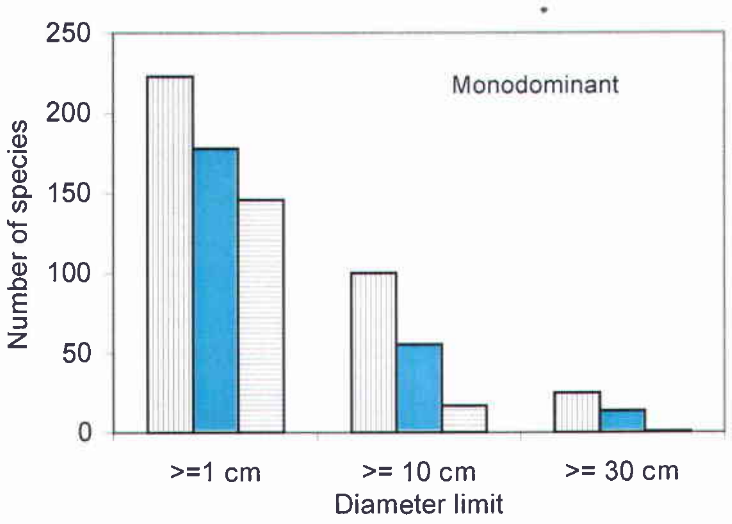
[3] There were two plots in each forest type.

Trees < 10 cm dbh accounted for 21% of the total basal area in mixed forest, but they represented only 13 % of the basal area in monodominant forest. Trees ≥ 30 cm dbh constituted 58 % and 72% of the total basal area in mixed and monodominant forests, respectively.

The density of lianas in each of these forest types was another important structural difference between monodominant forest and mixed forest. Analysis of variance revealed a significant difference in the density of lianas between monodominant and mixed stands ($F_{1,3} = 2053$, p-value < 0.001). Mixed forest had many more lianas than monodominant forest.

Species richness and diversity indices

Within the two 10-hectare plots of monodominant forest, a total of 344 species were recorded at 1 cm dbh limit for free-standing woody stems. Overall richness for the two 10-ha plots in mixed forest was 360 species. For all diameter limits, variations in the number of species in individual hectares were greater in monodominant forest than in mixed forest (Figure 1.6). Total richness for stems ≥ 10 cm dbh and ≥ 30 cm dbh was higher in mixed forest than in monodominant forest. However, the difference was statistically significant only for trees above 30 cm dbh (Table 1.8).



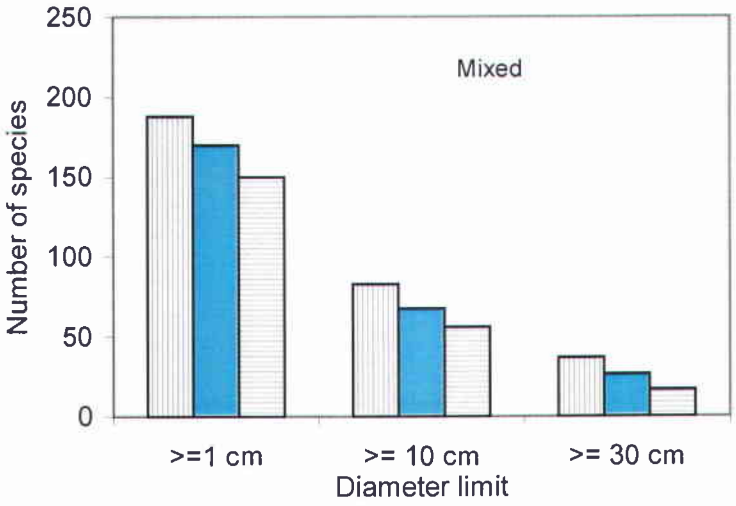


Figure 1.6. Spatial variation of species richness in monodominant and mixed stands in the Ituri Forest. For each size limit, the three bars represent the maximum number of species in one hectare (left), the mean (per ha) averaged over 20 individual hectares (middle) and the minimum number of species observed in one hectare (right). Monodominant forest has larger variations than mixed stands.

Shannon's and Simpson's diversity indices were significantly different between the two forest types only for the largest size limit (≥ 30 cm dbh), although there was also a suggestive but inconclusive evidence of a difference at the 10 cm dbh limit (Table 1.9). Shannon's and Simpson's diversity indices showed different relationships with size limit. In monodominant forest, Shannon's index decreased with increasing size limit while Simpson's index was the highest at 10 cm dbh threshold and the lowest at 30 cm dbh limit. In mixed forest, both indices had their highest values at 10 cm dbh limit. Shannon's index was the lowest at 30 cm dbh limit whereas Simpson's index had its smallest value at 1 cm dbh limit (Table 1.9).

The relationships between diversity indices and size limit reflect the considerable reduction of the number of species with increasing size class. These relationships are also related to the relative importance of the most abundant species at each diameter limit. The most abundant species at 1 cm dbh limit represented 45% of all the stems in monodominant forest; at the 10 cm dbh limit, the most common species accounted for 51% of the stems and the same species constituted 71% of trees above 30 cm dbh. Stem density showed the highest level of dominance at 1 cm dbh in mixed stands, with the most abundant species accounting for 42% of the stems. For trees ≥ 10 cm dbh and ≥ 30 cm dbh, the most common species represented 16% and 32% of the stems respectively. Shannon's index takes into account both the total number of species and the relative abundance of each species; it had its lowest value at 30 cm dbh in both forest types. Simpson's index, which is primarily influenced by the relative abundance of the most abundant species, was the smallest at 30 cm dbh in monodominant forest and at 1 cm dbh in mixed forest.

Table 1.9. Diversity indices for monodominant and mixed stands in the Ituri Forest and ANOVA for comparing diversity indices for the two forest types. Standard errors for the mean are given in parentheses.

Dbh class	Mono	Mixed	F-statistic[2]	p-value
	Richness (# of species/ha)			
≥ 1 cm	178 (4.4)	170 (2.7)	2.46	0.26
≥ 10 cm	56 (5.6)	68 (2.1)	5.83	0.14
≥ 30 cm	14 (1.8)	27 (1.3)	33.80	**0.03**
	Shannon's index[1]			
≥ 1 cm	1.150	1.198	0.24	0.67
≥ 10 cm	0.967	1.423	12.41	0.07
≥ 30 cm	0.482	1.110	38.60	**0.02**
	Simpson's index			
≥ 1 cm	4.966	5.808	0.48	0.61
≥ 10 cm	5.711	15.061	10.77	0.08
≥ 30 cm	2.573	7.688	22.18	**0.04**

[1] Shannon's and Simpson's diversity indices were calculated for square hectares (100 m x 100 m) in each plot, then values were averaged over all the 20 hectares within each forest type.

[2] The null hypothesis for the F-test is no difference in species diversity between monodominant and mixed forest based on Richness (number of species), and on Shannon's and Simpson's diversity indices.

Species-area and species-individual curves

The number of species increased rapidly with increasing area from 5 m x 5 m (0.0025 ha) quadrats to 200 m x 200 m (4 ha) subplots in both forest types at 1 cm dbh (Figure 1.7). The rate of increase decreased with area but did not plateau for the largest area, suggesting that more new species could be added if a larger area were surveyed.

Species-area curves of monodominant and mixed stands were quite similar at 1 cm dbh limit (Figure 1.7). At 10 cm dbh and 30 cm dbh limits, the number of species increased steadily with area up to 10 ha. The curves of the two forest types were also similar at 10 cm dbh, although the mixed forest curve was consistently higher than monodominant forest curve for areas less than or equal to 4 ha. Only for trees above 30 cm dbh were there consistent differences in the species-area curve. For the same area, mixed forest had many more species than monodominant forest. The curve for monodominant forest was nearly a straight line whereas that of mixed forest was concave downward, indicating that rate of accumulation of species decreased with increasing quadrat area. At the scale of 1 ha (100 m x 100 m), monodominant forest had only 51% of the richness in mixed forest, compared to 71% at the scale of 10 ha.

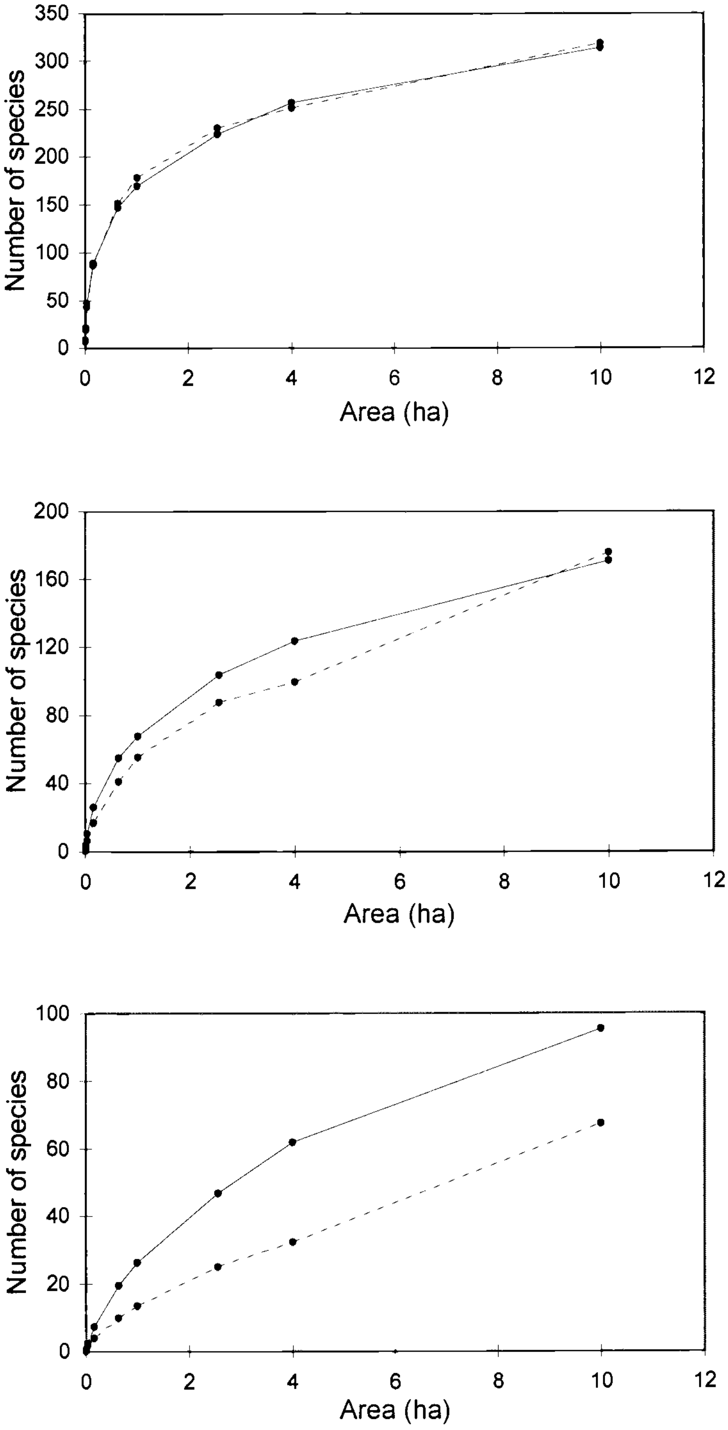


Figure 1.7. Species-area curves of monodominant stands (dotted lines) and of mixed stands (solid lines) in the Ituri Forest.

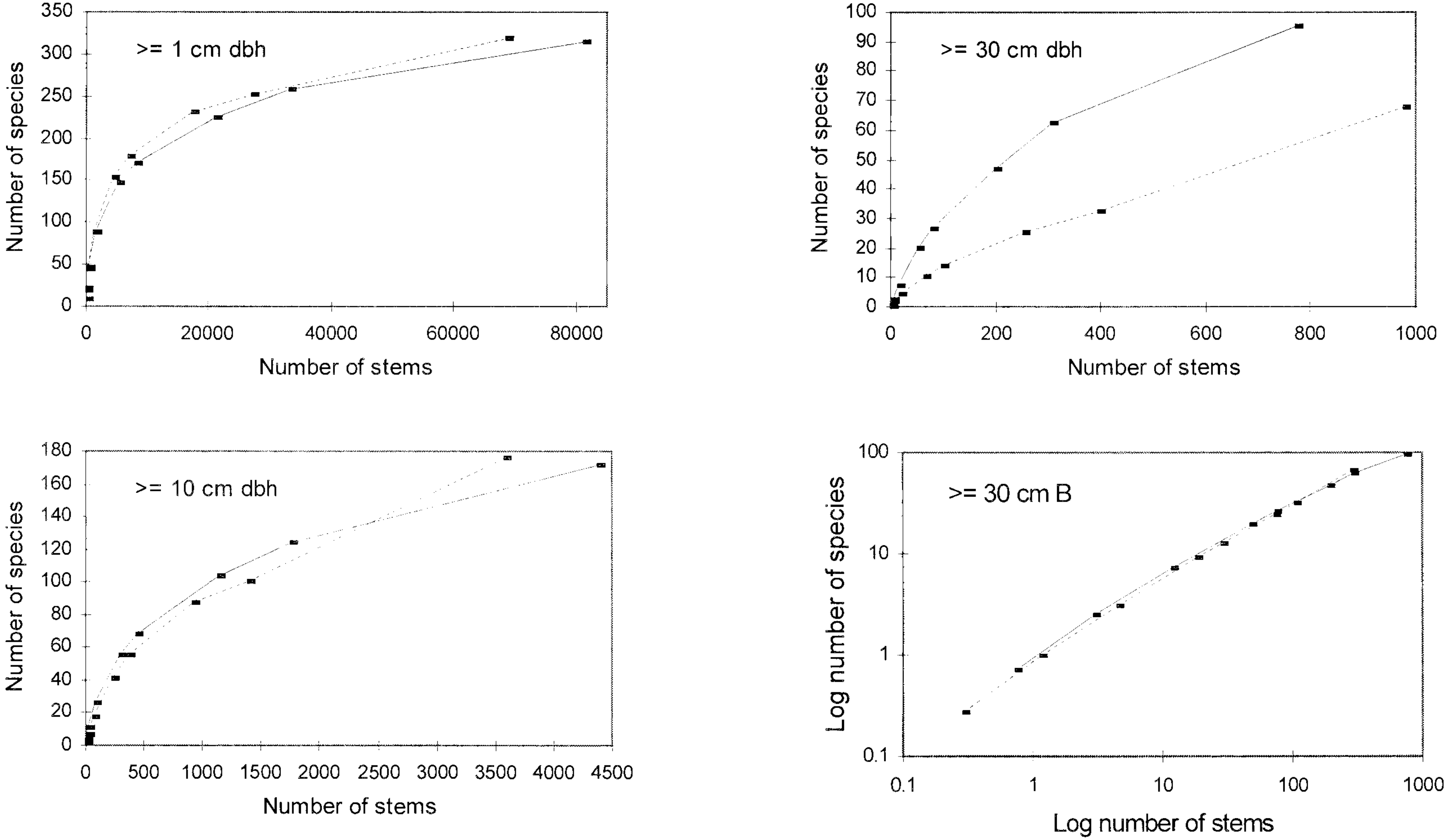


Figure 1.8. Species-individual curves for monodominant forest (dotted lines) and mixed forest (solid lines) in the Ituri. The graph on log scale is the species-individual curves for the two forest types when *G. dewevrei* is taken out.

Species-individual curves exhibited shapes similar to the species-area curves (Figure 1.8). At 1 cm dbh, the number of species quickly increased with stem counts up to about 1000 individuals. The two forest types had comparable shapes, although the curve for monodominant forest was slightly but consistently above the curve for mixed forest (Figure 1.8). For stems ≥ 10 cm dbh, the number of species for a given number of individuals increased more steadily in monodominant forest than in mixed forest with more species in the former at and above 2500 individuals. Species-individual curves for trees ≥ 30 cm dbh exhibited shapes quite similar to species-area curves: concave downward for mixed forest and a straight line for monodominant forest.

Species-individual curves were also constructed for species other than *G. dewevrei* in both forest types for trees above 30 cm dbh (Figure 1.8). There was a great reduction in the number of trees ≥ 30 cm dbh in monodominant forest when *G. dewevrei* was excluded from the count. The 10-ha plots in monodominant forest averaged only 287 trees each versus 745 trees in mixed forest. A log-log scale was thus used to bring the curves from the two forest types to a comparable scale. The results showed that for the same number of trees other than *G. dewevrei,* monodominant forest was almost as species-rich as mixed forest.

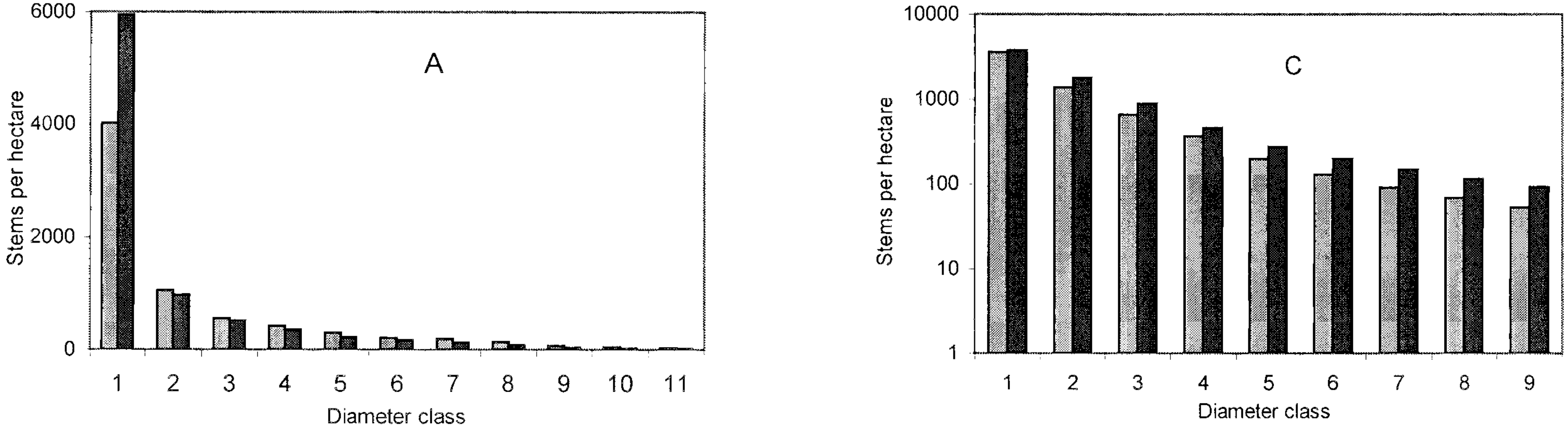
Size class distribution

Forest types

Mean number of trees per hectare for 10 cm diameter class intervals dropped rapidly in both monodominant and mixed forests (Figure 1.9a). Mean density of trees less than 10 cm dbh was 6495 stems ha^{-1} in monodominant forest and 7695 stems ha^{-1} in mixed stands, whereas the size class between 10 and 20 cm dbh averaged only 202 and 298 trees ha^{-1} in monodominant and mixed forest, respectively. There were very few trees with dbh greater than 100 cm. Monodominant forest averaged 4 trees ha^{-1} for that size class, and mixed forest had mean density of only 2.4 trees ha^{-1}. The largest tree in all the plots was 168.2 cm dbh.

The distribution of basal area across size classes showed two peaks (Figure 1.9b). The first peak corresponds to the smallest size class (< 10 cm dbh) in both forest types. The second peak occurred at the diameter class between 70 and 80 cm dbh for monodminant forest, while it occurred at diameter class between 40 and 50 cm dbh for mixed forest. Size classes below 20 cm had higher basal in mixed forest than in monodominant forest (Figure 1. 9b).

Mean density for stems < 10 cm dbh decreased through 1 cm diameter class intervals in a slightly concave fashion on a semi-log scale (Figure 1.9c). Mean density for trees < 2 cm dbh was 3554 stems ha^{-1} in monodominant forest and 3764 in mixed forest.



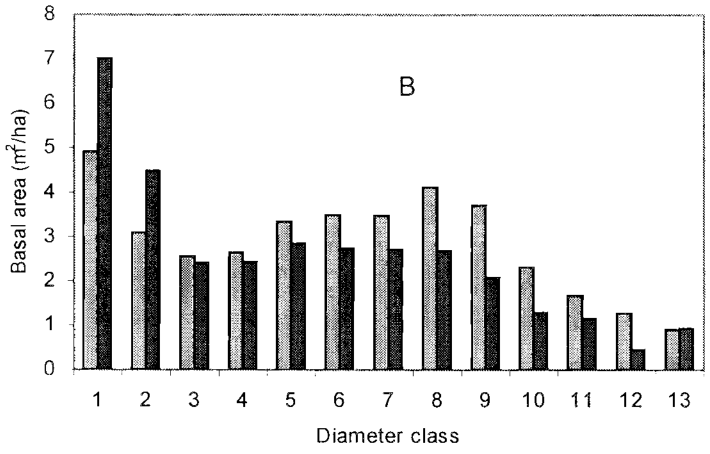


Figure 1.9. Distribution of stems and of basal area in 10 cm dbh intervals in monodominant (lighter bars) and mixed (darker bars) stands in the Ituri Forest. Stem density and basal area were calculated in square hectares (100 m x 100 m) in two 10-ha plots for each forest type. A, size class distribution for all stems ≥ 1 cm dbh; B, basal area distribution for all stems ≥ 1 cm dbh; C, size class distribution for stems < 10 cm dbh in 1 cm dbh intervals.

Mixed forest had consistently more stems than monodominant forest across all the 1 cm diameter class intervals for trees < 10 cm dbh (Figure 1.9c). The difference increased with increasing size class. For trees between 1 and 2 cm dbh, mixed forest was only 6% more dense than monodominant forest, while it was 74% more dense than monodominant forest for trees between 9 and 10 cm dbh.

Individual species

There were three basic types of the size class distributions for individual species. These types appear to result from attributes of the species such as shade tolerance.

1. Inverse J-shape distribution: the distribution of species in this group is similar to that exhibited by the forest as a whole. The typical examples are *G. dewevrei* in monodominant forest (Figure 1.10a) and *C. alexandri* in mixed forest (data not shown). Other species included in this group are *J. seretii, Cleistanthus michelsonii* among canopy species, and *Pancovia harmsiana, Lychnodiscus cerospermus* and *Dasilepis seretii* for subcanopy species. Each of these species is well represented in both forest types and seems to regenerate well in the shade.

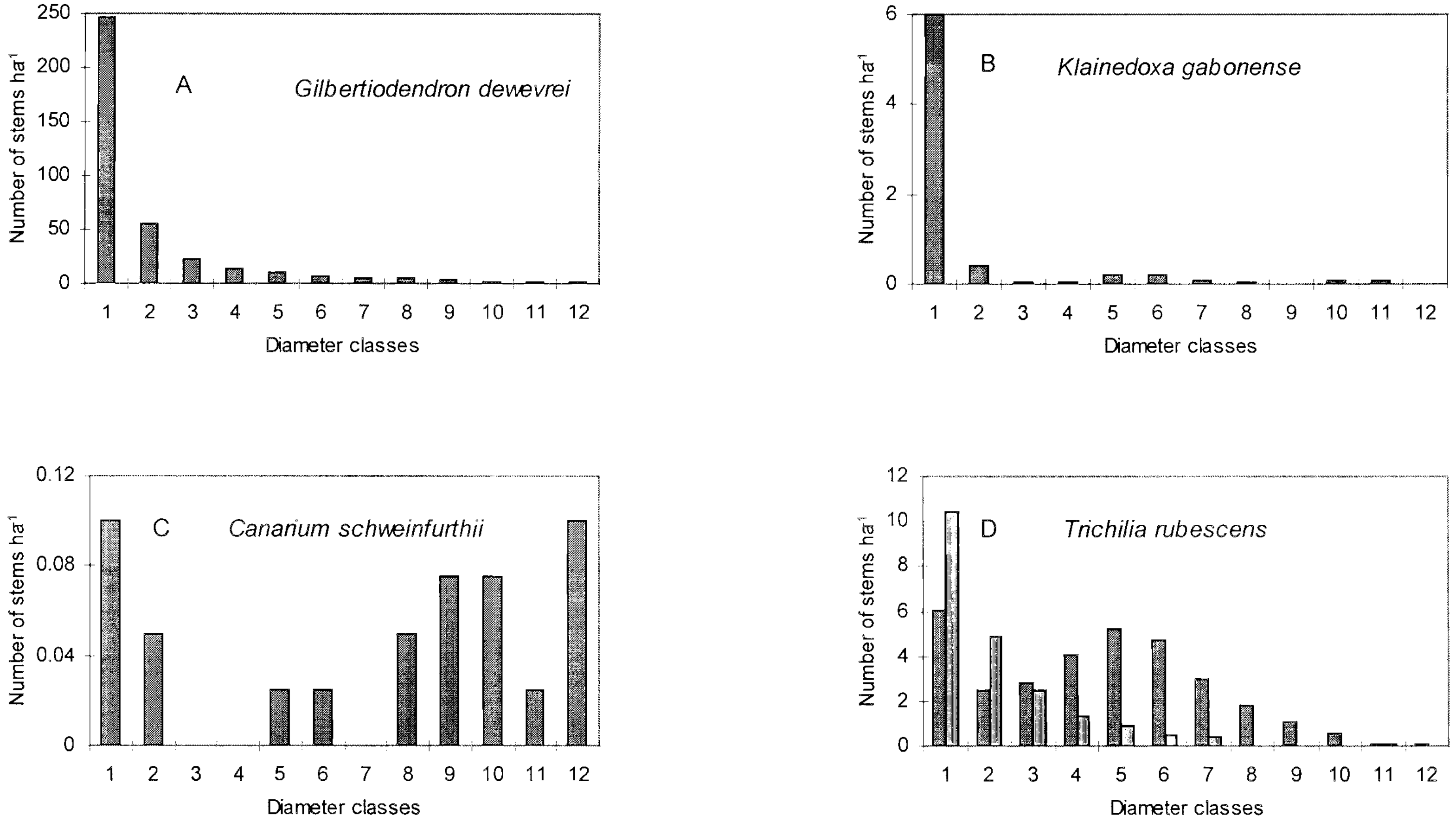


Figure 1.10. Size class distribution for individual species in monodominant and mixed stands in the Ituri forest. The graph for *Trichilia rubescens* represents the size class distributions of that species in monodominant forest (bars with vertical patterns) and in mixed forest (plain bars)

2. Irregular size class distribution: some species showed very irregular diameter distributions. Most of the species in this category were light demanding canopy species, and included *Canarium Schweinfurthii* (Figure 1.10c), *Fagara macrophylla* and *Alstonia bonei*. A swamp species, *Hallea stipulosa*, also exhibited an irregular diameter distribution. In general, these species had higher density of stems in mixed forest than in monodominant forest.

3. A third group of species showed completely different diameter distribution patterns in mixed forest and in monodominant forest. The typical examples were *Trichilia rubescens* (Figure 1.10d) and *Ochtocosmus africanus*. These species had a somewhat bell-shaped diameter distribution in mixed forest and a nearly inverse J-shape pattern in monodominant forest. Mean number of stems per hectare for these species was much higher in mixed forest than in monodominant forest stands.

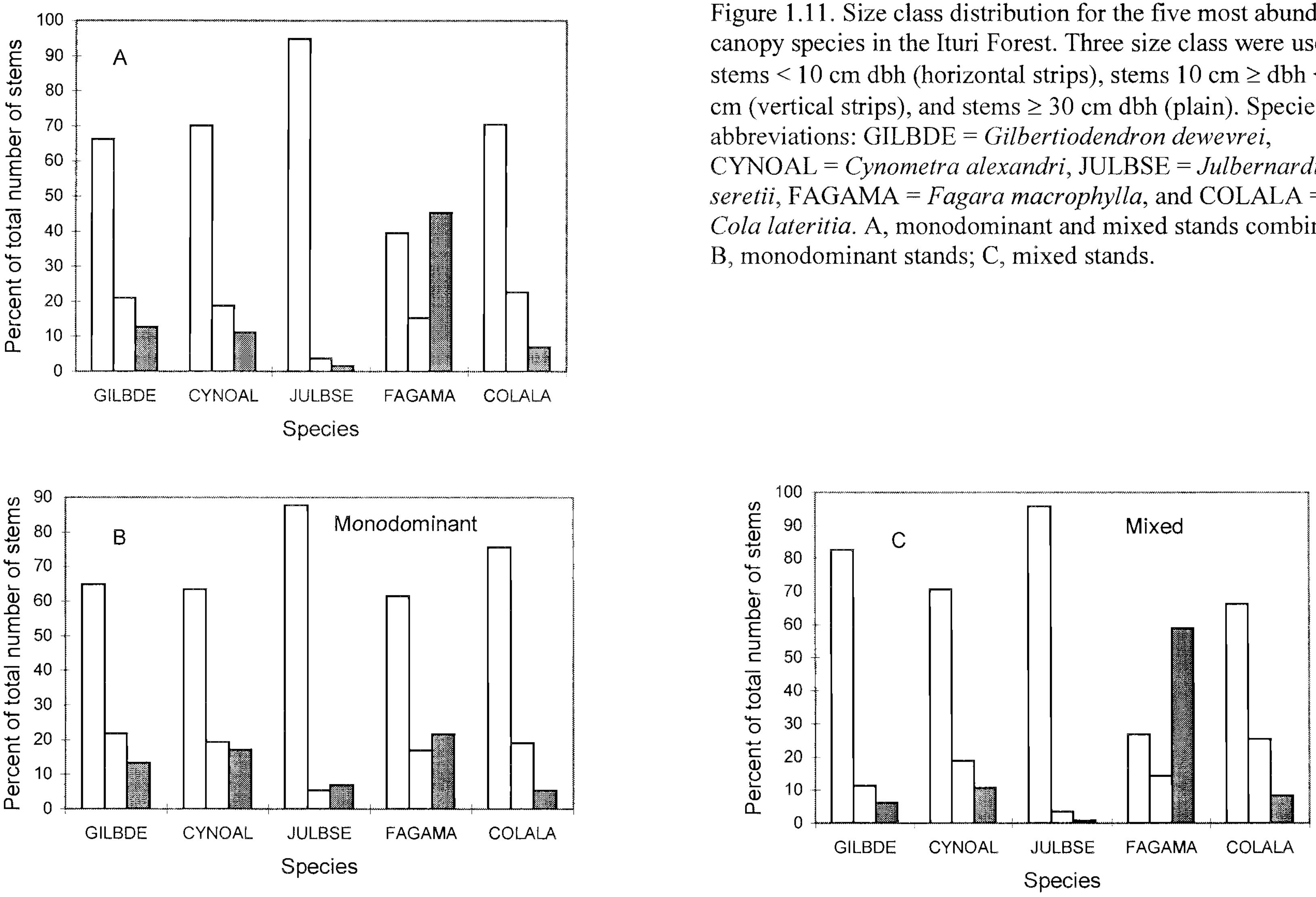


Figure 1.11. Size class distribution for the five most abundant canopy species in the Ituri Forest. Three size class were used: stems < 10 cm dbh (horizontal strips), stems 10 cm ≥ dbh < 30 cm (vertical strips), and stems ≥ 30 cm dbh (plain). Species abbreviations: GILBDE = *Gilbertiodendron dewevrei*, CYNOAL = *Cynometra alexandri*, JULBSE = *Julbernardia seretii*, FAGAMA = *Fagara macrophylla*, and COLALA = *Cola lateritia*. A, monodominant and mixed stands combined; B, monodominant stands; C, mixed stands.

Regeneration of canopy species

The most abundant canopy species in the Ituri forest were generally well represented in all size classes. Regeneration patterns were inferred from the analysis of size distribution for the five most abundant canopy species. For four of the species, the number of stems decreased with increasing size. These species (*G. dewevrei, C. alexandri, J. seretii* and *Cola lateritia*) are shade tolerant species that can regenerate under their own shade. For the fifth species, *Fagara macrophylla*, adults were the most numerous class, followed by small juveniles. The proportion of stems in the small juvenile class was higher for *J. seretii* than the other species. Small juveniles accounted for 95% of all the stems for *J. seretii*, 70% for *C. alexandri* and *C. lateritia*, 66% for *G. dewevrei*, and only 40% for *F. macrophylla.*

For two canopy species, patterns of diameter distribution were dependent on forest types. *F. macrophylla* exhibited significantly different patterns of size class distribution in the two forest types ($\chi^2 = 25.5$, d.f. = 2, p-value < 0.001). In monodominant forest, small juveniles of that species were more abundant than both large juveniles and adults combined. But in mixed forest, adults were more numerous than all juveniles (Figure 1.11). Size class distribution patterns were also significantly different in the two forest types for *J. seretii* ($\chi^2 = 509$, d.f. = 2, p-value < 0.0001). Small juveniles represented 88% of the stems and adults accounted for 7% of the stems in monodominant forest, whereas small juveniles made up 96% of the stems and adults represented only 1% of the stems in mixed forest.

Table 1.10. Abundance of the five most common tree species in monodominant and mixed stands of the Ituri Forest.

Monodominant forest			Mixed forest		
Species	Stems/ha	%	Species	Stems/ha	%
Scaphopetalum dewevrei	3069	44.84	*Scaphopetalum dewevrei*	3387	41.75
Gilbertiodendron dewevrei	515	7.52	*Julbernardia seretii*	792	9.76
Drypetes bipendensis	406	5.93	*Pancovia harmsiana*	600	7.4
Alchornea floribunda	379	5.54	*Alchornea floribunda*	300	3.7
Pancovia harmsiana	356	5.2	*Cynometra alexandri*	233	2.87
All other species	2119	30.96	All other species	2800	34.52
Total	6844	100	Total	8112	100

Relative abundance of species and dominance

More than half of all the stems ≥ 1 cm dbh were accounted for by only two species in both forest types (Table 1. 10 and Figure 1.12). A shrub species, *Scaphopetalum dewevrei,* was extremely abundant in both monodominant and mixed stands of the Ituri Forest; it represented roughly 45% of all the free-standing stems ≥ 1 cm dbh in monodominant forest and 42% in mixed forest. This species was almost strictly limited to the size class below 10 cm dbh and only rarely reached a dbh of 10 cm. The second most abundant species was *G. dewevrei* for monodominant forest (7.5% of stems ≥ 1 cm dbh) and *J. seretii* for mixed forest (9.8% of stems ≥ 1 cm dbh). Both species were dominant canopy species.

The eight most common species (2% of the total number of species) represented 75% of the stems and seventy-two species (19%) accounted for 95% of the stems in monodominant forest. In mixed stands, ten species (2.6%) and seventy species (18.5%) made up 75% and 95% of the stems, respectively.

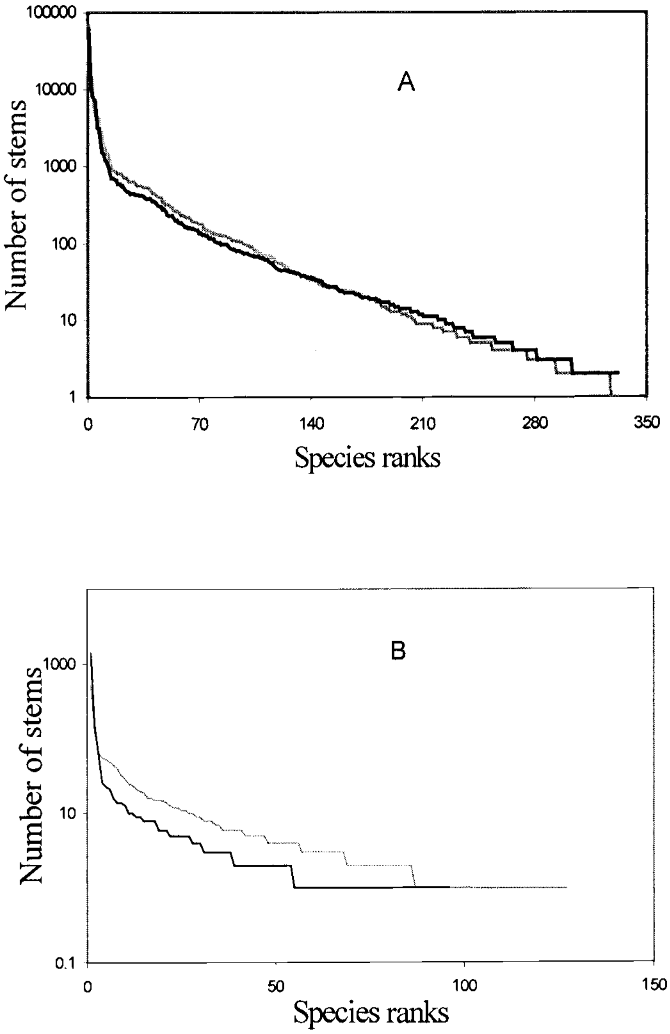


Figure 1.12. Dominance-diversity curves for monodominant and mixed stands in the Ituri Forest. Y-axis is the abundance of species in 20 hectares (two 10-ha plots) in each forest type. X-axis, the ranks of species according to their abundances (from the most abundant to the least abundant). A, all stems ≥ 1 cm dbh. B, stems ≥ 30 cm dbh. Lighter curve, mixed forest; darker curve, monodominant forest.

In monodominant forest, trees ≥ 30 cm dbh showed a higher level of dominance than in mixed forest. *G. dewevrei* represented 71% of stems in monodominant. The second and the third most common species, *J. seretii* and *C. alexandri*, constituted 8% and 3% of the stems respectively. Only three other species accounted for at least 1% of the stems ≥ 30 cm dbh. The six species (6% of total richness at 30 cm dbh limit) together represented 85% of the stems above 30 cm dbh in monodominant forest. The most abundant canopy species of mixed stands, *C. alexandri*, made up 32% of trees ≥ 30 cm dbh. The second most abundant species, which was the same as in monodominant forest, constituted 8% of the stems, and eighteen others species represented at least 1% of the stems each. Twenty species (16% of total richness for trees ≥ 30 cm dbh) accounted for 76% of trees at 30 cm dbh.

While a few species were very abundant, the majority of the species were rare (Figure 1.12). For all stems ≥ 1 cm dbh, more than fifty-three percent of all species had a mean density of less than one individual per hectare in both monodominant forest and mixed forest. The proportion of species represented by less than 1 individual per ha increased with size class. For stems 10 cm dbh and larger, this proportion was 81% for monodominant forest and 76% for mixed forest. Only 6.3% of the species in monodominant forest and 10.9% in mixed forest had a mean density of 1 individual per ha for trees ≥ 30 cm dbh.

Table 1.11. Species accounting for at least 1% of the basal area of trees ≥ 30 cm dbh and their density in monodominant and mixed stands in the Ituri Forest.

Monodominant forest			Mixed forest		
Species	Trees ≥ 30 cm dbh		Species	Trees ≥ 30 cm dbh	
	% Basal area	Stems/ha		% Basal area	Stems/ha
Gilbertiodendron dewevrei	74.5	69.1	*Cynometra alexandri*	31.9	25.0
Julbernardia seretii	7.3	8.0	*Julbernardia seretii*	10.7	6.3
Cynometra alexandri	2.9	3.0	*Fagara macrophylla*	6.3	3.3
Alstonia bonei	1.5	1.3	*Gilbertiodendron dewevrei*	4.2	2.8
Fagara macrophylla	1.0	0.7	*Erythrophleum suaveolens*	4.1	2.7
			Hallea stipulosa	3.4	2.5
			Uapacca guinensis	2.6	0.8
			Canarium schweinfurthii	2.5	0.6
			Alstonia boonei	2.5	2.0
			Cleistanthus michelsonii	2.1	1.6
			Cola lateritia	1.6	2.3
			Strombosiopsis tetrandra	1.3	1.3
			Klainedoxa gabonensis	1.2	0.8
			Anthonotha macrophylla	1.1	1.2
			Comiphyton gabonense	1.1	1.5
			Nauclea popegeni	1.0	1.1

Dominance was more concentrated in monodominant than in mixed forest. *G. dewevrei* accounted for 75% of total basal area of trees ≥ 30 cm dbh in monodominant forest, while only four other species constituted 1% of total basal (Table 1.11). In mixed forest, *C. alexandri* made up 32% of the basal area and fifteen other species had at least 1% of the total basal area. In mixed forest, some species such as *Canarium schweinfurthii, Uapacca guinensis* and *Klainedoxa gabonensis* were represented only by a few very large individuals (Table 1. 11).

Canopy dominance and species richness

Although there was no significant difference in the mean number of species per hectare between monodominant and mixed stands for stems ≥ 1 cm dbh, it appears that high canopy dominance by *G. dewevrei* is associated with a reduction of the number of species for larger size classes (Figure 1.13). When all trees ≥ 1 cm dbh were considered, a regression analysis showed no significant relationship between mean number of species per hectare and the density of large *G. dewevrei* ($r^2 = 0.30$, p-value = 0.45). For stems ≥ 10 cm and 30 cm dbh, the relationship between mean species richness and mean density of *G. dewevrei* ≥ 30 cm dbh was significantly negative (Figure 1.13).

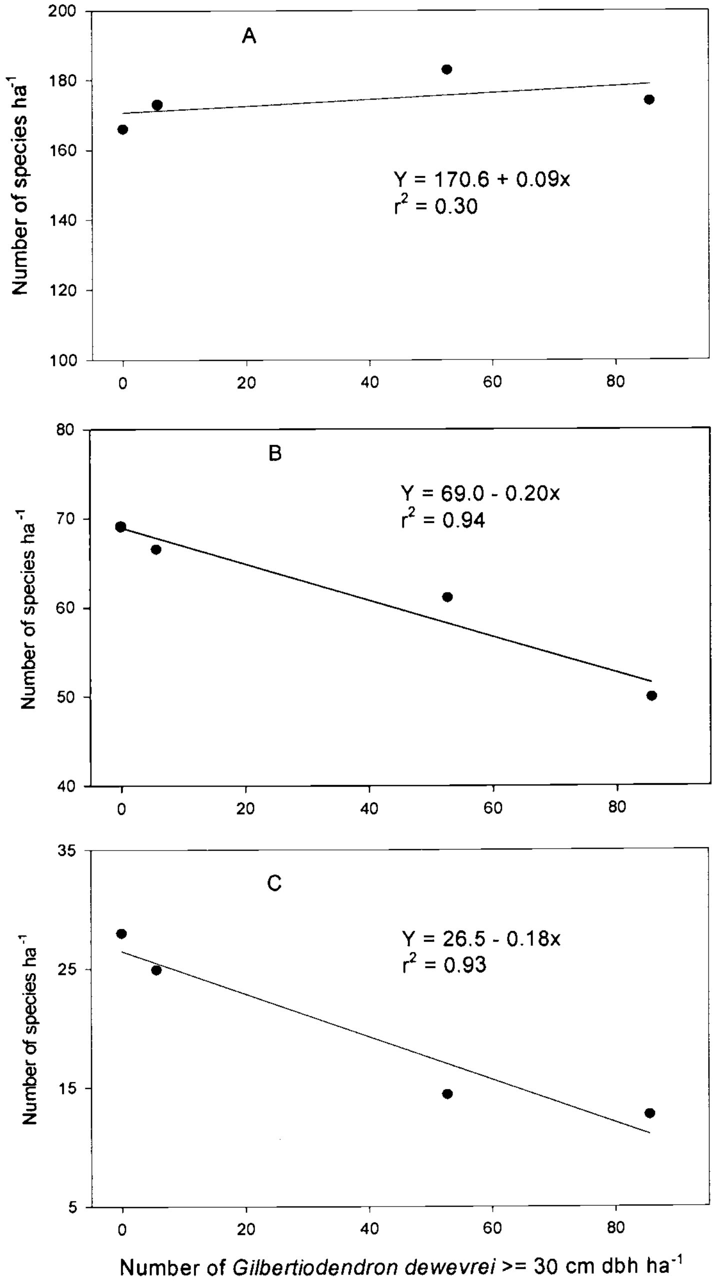


Figure 1.13. Regression of species richness of free standing stems on the density of *G. dewevrei*. A: richness for all trees ≥ 1 cm dbh (p-value = 0.45), B: richness for trees ≥ 10 cm dbh (p-value < 0.03), C: richness of trees ≥ 30 cm dbh (p-value < 0.04).

The densities of 50 common species were individually compared to the density of *G. dewevrei* ≥ 30 cm dbh for quadrats of 0.16 ha (40 m x 40 m) in the monodominant forest plots. Regression analysis was employed to evaluate the relationships between *Gilbertiodendron* dominance and each of these species. More than half (55%) of the species exhibited significant negative association with the density of large *G. dewevrei,* about a third (31%) of the species showed no evidence of a significant relationship with the dominant species and seven species (14%) were positively associated with *G. dewevrei.* Among the species that were positively associated with the dominant species, one species (*Diospyros hoyleana*) was completely absent from mixed forest; four species (*Manilkara bequaertii, Alchornea floribunda, Staudtia gabonensis* and *Chytranthus macrobotrys*) represented a higher proportion of total stem density in monodominant forest than in mixed forest. The remaining two species (*Strombosiopsis tetrandra* and *Scaphopetalum dewevrei*) had no significant difference in their representation within the two forest types.

DISCUSSION

Structure and richness of monodominant and mixed forests in the Ituri

Previous studies of the Ituri Forest using smaller plots found significant structural differences between the monodominant forest and mixed forest (Hart 1985; Hart et al. 1989). Overall, the mixed stands were noticeably more dense than monodominant stands. Mixed stands had about 19% more stems ≥ 1 cm dbh than monodominant stands. In 3-ha plots, Makana et al. (1998) observed that the closed and homogeneous canopy of monodominant forest created a more even shade in the understory whereas the canopy of mixed forest was usually broken. The understory of mixed forest was very dense. The present study, conducted on a much larger scale (20 hectares in each forest type), confirmed these earlier findings. Mixed forest had more stems of small sizes than monodominant forest and showed greater variation of density of stems ≥ 1 cm dbh. The closed and homogeneous canopy of monodominant forest was associated with a higher density of large trees. The higher abundance of large trees in monodominant forest resulted in higher basal area.

The density of lianas in each forest type provided another important structural difference between monodominant and mixed stands in the Ituri Forest. The mixed forest had nearly twice as many lianas ≥ 2 cm dbh. Lianas find especially favorable conditions for development in open places such as forest edges (roadsides and streamsides) and in disturbed environments such as tree fall gaps or gaps created by forest exploitation (Parren et al, submitted). Although the study site is free of major human disturbances, it has been shown that there were significantly more gaps in mixed forest than in monodominant forest (Hart et al. 1989). It was furthermore shown that tree crowns composing the canopy of mixed forest were often not contiguous, allowing more light in the understory (Makana et al. 1998). On the other hand, the monodominant forest canopy is homogeneous, formed by contiguous crowns of *G. dewevrei* trees. These observations might explain the higher density of lianas in mixed forest. However, as suggested earlier by Makana et al (1998), more detailed studies are required to determine the relationship between forest structure and liana density (e.g. light requirements for regeneration of the most abundant liana species).

For stems ≥ 1 cm dbh and ≥ 10 cm dbh, the data failed to reject the hypothesis that monodominant stands are as rich in species as mixed stands. For trees ≥ 30 cm dbh, however, the number of species per hectare, as well as the values of Shannon's and Simpson's diversity indices, were significantly different between the two forest types. Mixed stands had more species and higher values of diversity indices than monodominant stands for large trees.

Two factors greatly reduced the ability to detect significant differences in forest structure and species richness between monodominant and mixed stands. The first factor, the inclusion of transition zones in one of plot of each forest type, considerably increased variation within each forest type. The second factor, a small sample size of each forest, posed a serious limitation on the ability to detect statistical differences between monodominant forest and mixed forest. Since the main objective of the Ituri Forest project is to monitor the dynamics of individual species and changes in species composition over time, plots were made large enough to include large number of stems for many common species. The large size of the plots limited the number of replicates.

Ituri Forest and other tropical rain forests

Very few studies on tropical forests have included all trees ≥ 1cm dbh (Manokaran et al. 1990; Hubbell and Foster 1986; Condit et al. 1996). Most inventories of tropical forest communities have used relatively small plots, rarely more than one hectare (Gentry 1982). Thus, although other studies will be used for these comparisons, the most appropriate datasets are from the large plots (up to 50 ha) in the Center for Tropical Forest Science network, where all trees ≥ 1 cm dbh are measured (Condit 1995, 1998).

The Ituri mixed forest had high density of stems ≥ 1 cm dbh relative to many other tropical forests (Table 1.12). The higher stem density of the Ituri mixed forest was solely due to small trees (< 10 cm dbh). The density of trees ≥ 10 cm dbh in the both Ituri mixed and monodominant stands is below the median density for the sites included in the comparison. For trees ≥ 30 cm dbh, mixed forest is third lowest and below median, while monodominant forest is above median. Median basal area of trees ≥ 10 cm dbh was 31.7 m^2 ha^{-1}. Mixed forest, with 26.2 m^2 ha^{-1}, was lower than median whereas monodominant forest (32.6 m^2 ha^{-1}) was just slightly above median. The values of basal area for the sites used for comparison ranged from 23.8 to 56.9 m^2 ha^{-1} (Table 1.12).

Table 1.12. Comparison of tree density, basal area and species richness of the Ituri Forest with other tropical forests.

Site (Country) and Forest Type	Plot Size (ha)	Stem density (trees ha^{-1})			Basal area (m^2 ha^{-1})		Richness (# of species ha^{-1})			Source
		≥ 1 cm dbh	≥ 10 cm dbh	≥ 30 cm dbh	≥ 1 cm dbh	≥ 10 cm dbh	≥ 1 cm dbh	≥ 10 cm dbh	≥ 30 cm dbh	
Ituri, Monodominant Lowland moist forest	20	6844	358	98	37.5	32.6	178	56	14	(a)
Ituri, Mixed Lowland moist forest	20	8112	451	77	33.2	26.2	170	68	27	(a)
Pasoh (Malaysia), Lowland wet forest	50	6769	530	75	30.5	25.2	495	206	46	(b, c)
BCI (Panama), Lowland moist forest	50	4844	414	83	32.9	28.6	172	91	35	(c)
Lambir (Sarawak), Lowland moist forest	50	6696	630	118	43.4	37.6	613	242	66	(c)
Sinharaja (Sri Lanka), Lowland wet forest	25	8233	682	144	62.7	56.9	143	70	33	(c)
Luquillo (Puerto Rico), Tropical wet forest	15	-	808	129	-	36.4	-	43	26	(c)
Yasuni (Ecuador), Tropical wet forest	2	5708	654	80	31.9	26.4	644	240	51	(c)
Korup (Camerron), Lowland moist forest	1	7484	490	79	29.9	23.8	266	90	29	(c)
La Selva (Costa Rica), Lowland moist forest	12.4	-	446	-	-	27.8	-	96	-	(d)
Temburong (Brunei), Tropical moist forest	1	-	550	-	-	40.8	-	231	-	(f)

Table 1.12 (continued).

Site (Country) and Forest Type	Plot Size (ha)	Stem density (trees ha^{-1})			Basal area (m^2 ha^{-1})		Richness (# of species ha^{-1})			Source
		≥ 1 cm dbh	≥ 10 cm dbh	≥ 30 cm dbh	≥ 1 cm dbh	≥ 10 cm dbh	≥ 1 cm dbh	≥ 10 cm dbh	≥ 30 cm dbh	
Kade (Ghana), Tropical moist forest	2	-	552	-	-	30.8	-	89	-	(g)
Lambir (Sarawak), Tropical moist forest	2.4	-	693	-	-	51.2	-	149	-	(e)
Bako (Sarawak), Tropical moist forest	2.4	-	734	-	-	34.9	-	121	-	(e)
Volcán Barva (Costa R.) Lowland wet forest	3	-	477	-	-	26.1	-	118	-	(h)
Messa (Nigeria), Tropical moist forest	-	-	530	38	-	-	-	-	-	(i)
Ekobakoba (Gabon), Tropical moist forest	-	-	438	124	-	42.9	-	-	-	(i)
Median		6807	530	83	33.05	31.7	222	96	33	

[a] This study; [b] Manokaran and LaFrankie (1990); [c] S. Lao and R. Condit (personal communication); [d] Lieberman and Lieberman (1987); [e] Swaine et al. (1987); [f] Poulsen et al. (1996); [g] Swaine et al. (1987); [h] Heaney and Proctor (1990); [i] Makana et al. (1998).

Both monodominant and mixed stands of the Ituri Forest had consistently lower numbers of species than many other tropical forests, including African forests (Table 1.12). For stems ≥ 10 cm dbh, both monodominant and mixed stands of the Ituri Forest were noticeably species-poor relative to nearly all other tropical moist forests reported in this study. Only one site (Luquillo, Porto Rico) had fewer species per hectare than the Ituri Forest. The most diverse forests were located in Southeast Asia and in the Amazon. For trees ≥ 10 cm dbh, these forests had twice to four times as many species per hectare as the Ituri Forest. For trees ≥ 1 cm dbh, both monodominant and mixed forest along with Barro Colorado Island and Luquillo occupied the bottom half of the species richness. For trees ≥ 30 cm dbh, monodominant forest had the lowest number of species among all the forests, mixed forest ranked third lowest.

African forests were consistently less species rich than most other forests, confirming previous report on the relative species poor nature of African flora as compared to Asian and Neotropical forests (Richards 1973, 1996; Gentry 1982). The relative floristic paucity of African forests has been attributed to past geological and climatic conditions such as the warming during the Pleistocene (Richards 1973, 1996). According to Axelrod (cited by Richards 1996), the paucity of tropical Africa is due to the uplifting of its land surface in the Tertiary, which caused a dessication of the climate, especially during the Pleistocene. Another possible cause may be that, for topographical reasons, the refuges available for the African rain forest flora in the arid periods of the Pleistocene were fewer and smaller than those in other parts of the tropics.

Species accumulation in the Ituri Forest

Typically, accumulation of species in tropical forests is rapid at small scales, followed by a gradual slowing of accumulation as a plateau is approached (Kellman et al. 1994). Species-area curves of monodminant and mixed stands of the Ituri Forest showed a rapid increase at small scale but did not flatten out at the scale of 10-ha plots, suggesting that more new species would be added if the area were increased.

Species-area and species-individual curves in the two forest types were similar when all trees ≥ 1 cm dbh were considered (Figure 1.7&8). But the two forest types had distinctly different curves when only trees above 30 cm dbh were analyzed. For mixed forest, the curve was much higher than for monodominant forest. It seems therefore that the dominance of the canopy by *G. dewevrei* has no effect on the diversity of small trees, while it is associated with a significant reduction of the diversity of canopy species. This conforms to a general pattern of the effect of canopy dominance by a single species on species richness in tropical forests (Connell and Lowman 1989). The species-area and species-individual curves for trees ≥ 30 cm dbh are nearly linear, suggesting that a larger area will be required to include a substantial portion of the regional pool of such species.

Regeneration of canopy species and inferred dynamics

Major canopy species of the Ituri Forest are long-lived and grow very slowly under the canopy. Hart and Murphy (1987) and Hart (1995) note that seedlings of *G.*

dewevrei can persist for more than ten years on the forest floor with very slow growth rates. Thus, a long-term study may be needed to directly observe mortality, growth and replacement of tree species in the Ituri Forest.

Size-class distribution of common canopy species may provide useful insights on the changes in relative abundance of species and on the composition of the canopy over time. Static stand structure has been commonly used to infer stand dynamics in temperate forests (Johnson et al. 1994; Henry and Swan 1974; Foster et al. 1996) as well as in tropical forests (Newbery and Garthan 1996). Several early studies of African tropical forests suggested a lack of replacement of some canopy and emergent tree species (Aubréville 1938; Richards 1963). In a study of 1.4 ha plot in primary forest, Aubréville observed that seven out eight of "large-stemmed species lacked small individuals, whereas several species, which achieved larger sizes elsewhere, had many small trees in the plot". Such observations led to the "cyclic mosaic" concept in which regeneration of canopy species occurs away from established individuals in the canopy (Newbery and Garthan 1996; Swaine and Hall 1988).

The size-class distribution of major canopy species in monodominant and mixed forests in Ituri suggests that, without severe large-scale disturbance, both forest types are likely to continue to be dominated by their current dominant species. The three dominant canopy species of the Ituri monodminant and mixed forests (*G. dewevrei, C. alexandri* and *J. seretii*) are all well represented in the subcanopy layers. Patterns of size class distribution of these species suggests that *G. dewevrei* has a high recruitment rate in monodominant forest. *C. alexandri,* the most abundant canopy species in mixed forest stands, was also well represented at all size classes and had abundant juveniles. On the other hand, *J. seretii* appears to experience high mortality rates among size classes below 10 cm dbh, especially in mixed forest where trees < 10 cm dbh constituted 96% of its stems ≥ 1 cm dbh. It may also be that *J. seretii* has recently begun to recruit individuals.

Among the twelve most common canopy species in the surveyed areas, only one species (*Canarium schweinfurthii*) showed little evidence of regeneration. *C. schweinfurthii* was represented by 15 individuals in mixed forest plots, 11 of which were ≥ 70 cm dbh; only two trees were less than 10 cm dbh. *Alstonia bonei* had few small trees in mixed forest plots and few intermediate-sized trees in monodominant forest plots. Both *C. schweinfurthii* and *A. bonei* are gap colonizers; their size-class distributions suggest periodic regeneration in response to gap formation. The remaining ten species were well represented in all size-classes and had abundant regeneration in both forest types. Many species had higher proportion of large trees in mixed forest than in monodominant stands. The two most common canopy species of mixed forest (*C. alexandri and J. seretii*), however, had a slightly higher proportion of large trees in monodominant forest.

Thus, no evidence of the "cyclic mosaic" pattern of regeneration was observed at the scale of 10-ha plots. However, it is possible that the pattern occurs at finer spatial scales within the 10-ha plots. Newbery and Garthan (1996) observed that many common canopy tree species had bell-shaped size class distributions with few small trees in

0.64-ha plots at Korup and Douala-Edea (Cameroon). Newbery and Garthan (1996) speculated that such patterns of size-class distribution, when observed in non-pioneer species, might be indicative of recent climatic changes. Species showing these patterns were probably dominant in the past and are dying out due to long-term changes in environmental conditions.

There was little floristic evidence of recent major disturbance within the area covered by this study. Species indicative of large-scale disturbance were rare. *Musanga cecropioides*, a high light-demanding species that dominates roadsides and abandoned farm fields (Lebrun and Gilbert 1954), had 31 individuals in the four plots. Two other pioneer species (Makana, Pers. Obs.), *Ricinedendron heudelotii* and *Petersianthus macrocarpus*, were less abundant with only 23 and 2 individuals respectively. Gap specialists (T. Hart, Pers. Comm.) such as *Alstonia bonei, Fagara macrophylla, Macaranga monandra, M. spinosa* and *Albizia gummifera* were more abundant than the pioneer species. This suggests that tree-fall gaps play an important role in the dynamics of Ituri Forest. In an analysis of the floristic composition of the 50-ha plot in Barro Colorado Island (Panama), Hubbell and Foster (1990) suggested that pioneer species were maintained in the old-growth forest by continual immigration from a nearby secondary forest. The Ituri mixed forest plots, which had higher density of pioneer species than monodominant forest plots, are located more than 20 kilometers away from any secondary forests. Populations of pioneer species in these areas may be self-maintaining through a combination of factors such as frequent occurrence of tree-fall gaps, wind dispersal and a persistent seed bank.

Gilbertiodendron dominance in Ituri Forest.

The processes responsible for the complete canopy dominance of *G. dewevrei* have not yet been identified. Several mechanisms accounting for monodominance in tropical forests have been proposed. A single species might achieve complete dominance by reducing a limiting resource below the supply required by other species, thereby excluding all other species (Tilman 1990). Connell and Lowman (1989) suggested that the dominant species might be the most efficient in exploitative competition for resources such as light, water, and soil nutrients, or that the dominant species might be the most resistant of all local species to deleterious physical conditions. Torti et al. (submitted) found that *Gilbertiodendron* dominance in the Ituri Forest was associated with a strong reduction of light penetration in the understory and with a lower availability of ammonium (NH_4^+) and nitrate (NO_3^-). Their analysis further revealed that *G. dewevrei* had lower levels of nitrogen in leaf tissues compared to other species. It also has been found that *Gilbertiodendron* saplings had a higher survival rate than saplings of the second most abundant canopy species in the understory of monodominant forest (Hart 1995). Low levels of nutrients in leaf tissues, which suggests an adaptation to low nutrient availability, combined with a high tolerance of low levels of light availability during the saplings stage may provide a competitive advantage to *G. dewevrei* and thus enable it to become dominant.

In her review of monodominance in tropical forests, Hart (1990) observed: "as a single species assumes ever greater percentage of the basal area, other species lose representation in the canopy and rare [canopy] species become rarer." Within the 10-

ha plot that was entirely dominated by *G. dewevrei*, *G. dewevrei* represented 84% of the basal area and had a mean density of 86 stems ha^{-1} for trees ≥ 30 cm dbh. Only three other species had a mean density of at least one tree per hectare ≥30 cm dbh, one of which was a swamp specialist, a habitat that *G. dewevrei* cannot occupy. That most species in monodominant forest were not positively associated with *G. dewevrei* suggests that the species may displace the other species by a kind of "diffuse competition" (Hubbell and Foster 1986) affecting all the species similarly and mediated by a significant reduction of the amount of light that reaches the understory (Torti et al., submitted). Species-individual curves of canopy trees (≥ 30 cm dbh) in monodominant and mixed stands provided additional support for diffuse competition.

It is known that in highly diverse communities, where rare species have few or single individuals in plot samples, the number of species per plot is sensitive to reductions in density by random deletions of individuals (rarefaction, Cannon et al. 1998). In assessing the impact of logging on species richness, Cannon et al. (1998) predicted that species-individual curves of logged and unlogged stands would be similar if mortality due to logging were equivalent to rarefaction alone. This approach was used to evaluate the effects of *Gilbertiodendron* dominance on the diversity of canopy tree species in the Ituri plots. Individuals of *G. dewevrei* were taken out for the analysis to simulate the reduction in density. The resulting species-individual curves were similar for monodminant and mixed forest, suggesting that displacement by *G. dewevrei* is random with respect to species. Most of the canopy tree species present in mixed stands are also present, at very low density, in monodominant stands. It would only be necessary to sample proportionately larger area in monodominant forest to obtain similar numbers of non *G. dewevrei* individuals and thus similar species richness.

CHAPTER TWO

SPATIAL DISPERSION PATTERNS OF TREES IN TWO AFRICAN MOIST FORESTS

INTRODUCTION

Tropical forests are well known for their high diversity of tree species. In some highly diverse forests, one hectare may include over 200 species of trees ≥ 10 cm diameter at breast height (dbh) (Whitmore 1984; Kochummen et al. 1990). Several hypotheses have been proposed to explain why so many species can coexist in one site. The spacing hypothesis of Janzen (1970) and Connell (1971) is the most widely tested of these hypotheses (Hubbell 1979; Clark and Clark 1984; Lieberman and Lieberman 1994). According to this hypothesis, most species in any given forest will have low relative abundance and regular dispersion, resulting from distance- or density-dependent mortality caused by host-specific herbivores or parasites (Hubbell 1979).

Low relative abundance of species in tropical forests has been demonstrated by field studies. Kochummen et al. (1990) reported that the most abundant trees in a 50-ha plot in Pasoh Forest Reserve (Malaysia) accounted only for 2.5% of stems ≥ 1 cm dbh. In a similar study at Barro Colorado Island (Panama), the most abundant tree species represented 14% of stems ≥ 1 cm dbh (Hubbell and Foster 1990).

Regular distribution patterns, however, have seldom been supported by field investigations. Most studies indicate that individuals of many tropical tree species are spatially aggregated, that others are randomly distributed, and that very few species (if any) are regularly spaced (Hubbell 1979; Hubbell and Foster 1983, 1986; Forman and Hahn 1980; Lieberman and Lieberman 1994). Forman and Hahn (1980) argued that the Janzen-Connell spacing model is consistent with regular, random, or aggregated distributions, if the average intertree distances are large.

Species dispersion patterns may have important implications in the biology of tropical forest communities. Hubbell (1979) suggested that potential consequences of low-density and regular dispersion of adult trees in tropical species might include lower out-crossing success, reduction in deme size, and requirements for long-distance pollination. This may be significant for the management and conservation of tropical tree species diversity in fragmented forests. Forest reserves should thus be large enough to include minimum critical population sizes for most of the species of a regional pool of species.

In the present study, I will analyze dispersion patterns of trees in four 10-ha plots in monodominant and mixed stands in the Epulu sector of the Ituri Forest. Several domains will be considered including all trees independent of species, individual species populations and size classes. This analysis will permit a test of the Janzen-Connell spacing model in that particular site. If individuals of most species are spatially aggregated, small areas will contain relatively small proportions of the regional pool of species. Thus, spatial distribution of species may provide an indication on how representative the surveyed area is with respect to the species richness of the region.

BACKGROUND

Patterns of spatial distribution of species have been of great interest to tropical forest ecologists. Janzen (1970) and Connell (1971) hypothesized that the high diversity of tropical forests is maintained by species-specific predators that cause high mortality of seeds or seedlings close to parent trees, but that have less of an effect at greater distances. This predation pattern would result in a regular distribution with large distance between conspecific trees. Therefore, concentration of dominance in a few species would be averted and high diversity would be maintained (Hubbell 1979).

The data available on species distribution patterns indicate that individuals of many tropical tree species are spatially aggregated, others are randomly distributed and very few are regularly distributed. In a study of a Caribbean semi-evergreen forest, Forman and Hahn (1980) showed that roughly 75% of 28 species (trees ≥ 10 cm dbh) had aggregated distributions and that the average intertree distance was less than 10 m for most of the species. Aside from one species that was regularly distributed, all the remaining species were randomly distributed. Hubbell (1979) reported similar results for adult trees in a dry forest in Puerto Rico: 72% of species exhibited significant aggregated distributions, 28% of species were not different from random, and no species were regularly distributed. Lieberman and Lieberman (1994) observed the prevalence of random patterns in three plots (12.4 ha total) in a lowland wet forest at La Selva (Costa Rica); only the most abundant canopy tree species were regularly distributed. The prevalence of random and clumped (aggregated) patterns and the virtual absence of regular patterns in tropical tree species have been confirmed by other studies (Newbery et al. 1986; Hubbell and Foster 1983, 1986; Lang et al. 1971).

Most studies of intraspecific spatial patterns have employed small, unreplicated plots and are primarily limited to the most abundant species (Lieberman and Lieberman 1994). As is common for studies of tropical forests, the studies of spatial pattern seldom include trees below 10 cm dbh. Some exceptions are the study by Hubbell (1979) in which all woody plants ≥ 2 cm dbh were surveyed on a 12.4-ha plot, and the investigation by Lieberman and Lieberman (1994) in which dispersion patterns were measured and compared in three plots totaling 12.4 hectares. Hubbell's study showed that rare species were more clumped than more common species; microhabitat specialization was the proposed explanation. The comparative assessment of species distribution patterns (Lieberman and Lieberman 1994) revealed the idiosyncratic nature of intraspecific spatial distribution patterns. For many species, dispersion patterns varied from plot to plot, being aggregated in one plot and random in another plot.

Several hypotheses have been proposed to account for observed spatial patterns. According to Hubbell and Foster (1983), species exhibit random patterns in locations that are uniformly good (or bad) for successful establishment and maturation for the species. Thus, species with random patterns tend to have broad physiological adaptations. They suggested that aggregated patterns could be due either to competitive advantage on microhabitats, transient, patchy, disturbance, or dispersal limitations. Species that exhibit aggregated spatial patterns are either better competitors than randomly dispersed species on specific microhabitats or they are poorer competitors everywhere else. Clumping with no discernible relationship to topography would be accounted for by transient historical factors such as tree-fall gaps, recent spread from a few colonizing ancestors, and by poor seed dispersal. For Lieberman and Lieberman (1994), intraspecific competition, especially crown-to-crown competition for space, results in a regular spacing of competing individuals.

OBJECTIVES

The broad objectives of this study were to describe patterns of spatial dispersion of trees in a mixed stand and a monodominant stand in the Ituri Forest, and to evaluate the validity of the Janzen-Connell spacing model at these specific stands. Specific objectives were:

1) to identify patterns of spatial dispersion for individual species and for all trees irrespective of species;
2) to evaluate the effect of tree size on spatial distribution patterns; and
3) to assess the effect of population size on distribution patterns.

Hypotheses pertaining to the objectives of the study are:

1. Dominant (most abundant) canopy species are regularly distributed.

2. Juveniles of dominant canopy species have the same distribution patterns as conspecific adults.

3. Rare species and pioneer species have clumped dispersion patterns.

STUDY SITE

Four 10-ha, permanent plots were established in 1993 in the Epulu sector of the Okapi Wildlife Reserve (OWR) in the Ituri Forest (Figure 1.1). Sites were chosen to represent the two main forest types in the region: monodominant evergreen forest and mixed semi-evergreen forest. The monodominant forest is dominated by *Gilbertiodendron dewevrei* (De Wild.) Léonard at the canopy level, whereas *Cynometra alexandri* C.H. Wright and *Julbernardia seretii* (De Wild.) Troupin dominate the canopy of mixed stands (Hart et al. 1989). Elevation in the Epulu sector of the OWR ranges from 700 m to 850 m above sea level; the topography is gently rolling with occasional low hills. Mean annual rainfall is 1700 m and mean average daily temperature is 25.5°C (Makana et al. 1998). Further details on the climate, the vegetation, and the ecology of the Ituri Forest are provided elsewhere (Chapter 1; Hart 1985, 1995; Hart and Carrick 1996; Hart et al. 1989, 1996).

METHODS

Field methods

Two rectangular, 10-ha (200 m x 500 m) plots, separated by 500 m, were surveyed in each of the two main forest types of the Ituri Forest (see plot layouts in Chapter 1). Each plot was divided into 250 20 m x 20 m quadrats, delimited by painted wooden stakes. Botanical inventories were carried out between February 1994 and June 1996. All free-standing woody stems ≥ 1 cm dbh were measured, tagged, mapped to the nearest 0.5 m, and identified to species. During botanical inventories and tree mapping, each 20 m x 20 m quadrat was subdivided into 16 5 m x 5 m subquadrats. For further details on tree mapping, see Chapter 1 and Manokaran et al. (1990).

Data analysis

Most analyses of spatial pattern were made using Morisita's index of dispersion which is based on counts within quadrats. Morisita's index was calculated using a range of quadrat sizes in each 10-ha plot. In addition, two methods based on tree-to-tree distances were used: combined count-distance (Ripley's K) and nearest neighbor analysis.

Morisita's index (I_d) is based on the proportion of individuals in different quadrats of a given size. It is given by

$$I_d = q\,(\Sigma n\,(n-1)/(N\,(N-1))$$

(Brower and Zar 1984) where q is the number of quadrats, n the number of trees in each quadrat and N is the total number of trees in all quadrats. An I_d value of 1 indicates random distribution, with values less than 1 indicating regular spacing and values greated than 1 indicating clumping. Significance of departure from randomness is evaluated by computing the following test statistic:

$$I_d\,(N-1) + q-N.$$

The test statistic is compared to a chi-square with $q - 1$ degrees of freedom.

For all trees irrespective of species, Morisita's index of dispersion (I_d) was calculated using square quadrats 20, 40, 60, 80, 100, 120, 160, and 200 m on a side. For individual species, I_d was calculated for quadrats 20, 40 and 100 m on a side, and for quadrats 2, 5, 10, 25, and 50 m on a side for a few randomly selected species. Statistical comparisons between the two forest types for all trees ≥ 1 cm dbh were performed for quadrat sizes 20, 40 and 100 m. The 1 cm dbh limit was chosen for the comparison of mixed and monodominant forests because it includes more species than any other size class.

Spatial patterns were also measured for three non-overlapping size classes based on dbh (< 10 cm, 10 - 30 cm, and ≥ 30 cm) for the 27 most abundant canopy species using I_d.

The nearest neighbor method is based on a comparison of the observed mean distance to the nearest neighbor to the expected mean nearest neighbor distance under a completely spatial random pattern. The expected mean distance from a tree to its nearest neighbor for a random pattern is given by:

$$r^\wedge = 1/2\sqrt{\rho},$$

where $r^\wedge$ is the expected mean distance to nearest neighbor and ρ is the density of the trees (Moeur 1993). Tests of significance were not taken into account because I used this approach strictly to calculate observed, which was used to evaluate the relationship between population size and mean distance to the nearest neighbor.

While the nearest neighbor uses tree-to-nearest-tree distances, the combined count-distance (Ripley's K) approach takes into account the distances between all pairs of trees (Moeur 1993). The expected value of the index used for Ripley's K is given by

$$K\hat{}(t) = \pi t^2$$

where t is the distance class (the radius of a circular region around a randomly chosen tree). $K\hat{}(t)$ is usually replaced by $L\hat{}(t)$, which is a square root transformation that linearizes $K\hat{}(t)$, stabilizes its variance, and has expected value approximately zero under completely spatial random pattern:

$$L\hat{}(t) = \sqrt{(K\hat{}(t)/\pi)} - t.$$

Negative values indicate aggregated patterns and positives values indicate that trees are regularly distributed (Moeur 1993, Haase 1995). Departure from randomness was evaluated in a Monte Carlo simulation. In this case, nineteen simulations were performed to generate a 95% confidence interval (Haase 1995). Due to the limited availability of tree location data, distance-based methods were used only for trees ≥ 10 cm dbh from one half (100 m x 500 m) of Lenda1.

RESULTS

Spatial patterns of all trees

Trees were not randomly dispersed within the four 10-ha plots of the Ituri Forest. Significant clumping was observed at all scales, from 20 m x 20 m to 100 m x 100 m quadrats, for all four plots (Table 2.1). However, trees ≥ 30 cm dbh were randomly distributed in most cases. For all trees ≥ 1 cm dbh, for all species combined, Edoro plots (mixed forest) had significantly higher values of I_d than Lenda plots (monodominant forest) for 20 m x 20 m quadrats ($F = 31.1$, $p < 0.03$) and for 40 m x 40 m quadrats ($F = 64.8$, $p < 0.02$). There was no evidence of a significant difference in the values of I_d between plots in the two forest types at the scale of 100 m x 100 m quadrats ($F = 4.9$, $p > 0.15$).

Spatial patterns of trees were sensitive to scale. Morisita's index of dispersion (I_d) decreased steadily with increasing quadrat size from 20 m to 200 m for mixed forest plots. In monodominant forest, there was little change beyond 140 m (Figure 2.1a). Although there was no statistical difference in I_d between the plots in mixed forest and those in monodominant stands for quadrat size greater than 60 m, plots in mixed forest had consistently higher values of I_d than did monodominant forest plots, for all quadrat sizes less than or equal to 160 m (Figure 2.1a). In all cases, I_d showed very little change in its value for quadrat sizes beyond 120 m. For trees ≥ 30 cm dbh, I_d increase from quadrat of 20 m to quadrat of 40 m in all plots; but there was little change in the value of I_d for quadrat sizes beyond 40 m (Figure 2.1b).

Table 2.1. Morisita's index of dispersion and chi square values for test of departure from complete randomness for four 10-ha plots in the Ituri Forest.

Plot	Forest Type	Morisita's index of dispersion (I_d)				Chi square values[3]			
		ST1[2]	ST1-9	ST10-29	ST30	ST1	ST1-9	ST10-29	ST30
				100 m x 100 m quadrats					
Lenda1	Mono[1]	1.003	1.003	1.044	0.995	**221.9**	**211.9**	**117.0**	4.5
Lenda2	Mono	1.009	1.009	1.041	1.019	**602.0**	**569.0**	**116.6**	**29.9**
Edoro1	Mixed	1.012	1.013	1.005	1.000	**924.3**	**947.2**	**25.7**	9.0
Edoro2	Mixed	1.014	1.016	1.004	1.003	**1212.5**	**1314.9**	**23.3**	11.3
				40 m x 40 m quadrats					
Lenda1	Mono	1.013	1.015	1.055	0.974	**940.3**	**1028.4**	**186.2**	36.8
Lenda2	Mono	1.017	1.018	1.057	1.025	**1128.3**	**1127.3**	**203.7**	**84.2**
Edoro1	Mixed	1.034	1.036	1.020	1.005	**2558.6**	**2556.8**	**123.3**	62.6
Edoro2	Mixed	1.032	1.037	1.018	1.004	**2714.9**	**2974.7**	**121.0**	61.9
				20 m x 20 m quadrats					
Lenda1	Mono	1.024	1.026	1.051	0.914	**1952.4**	**2007.3**	**374.2**	172.2
Lenda2	Mono	1.028	1.030	1.057	1.025	**2094.0**	**2115.6**	**398.6**	275.2
Edoro1	Mixed	1.054	1.059	1.025	0.948	**4367.9**	**4507.1**	**332.7**	209.8
Edoro2	Mixed	1.047	1.053	1.025	0.954	**4289.4**	**4574.9**	**338.2**	213.8

[1] "Mono" stands for monodominant forest; "Mixed" stands for mixed forest.

[2] ST1, all stems ≥ 1 cm dbh; ST1-9, stems < 10 cm dbh; ST10-29, stems ≥ 10 cm dbh but < 30 cm dbh; ST30, stems ≥ 30 cm dbh.

[3] The critical value of chi-square for 100 m x 100 m quadrats is 16.9; this value is 78.0 and 286.8 for 40 m and 20 m quadrats respectively. Numbers in bold face indicate significant departure from random patterns (α-level is 0.05).

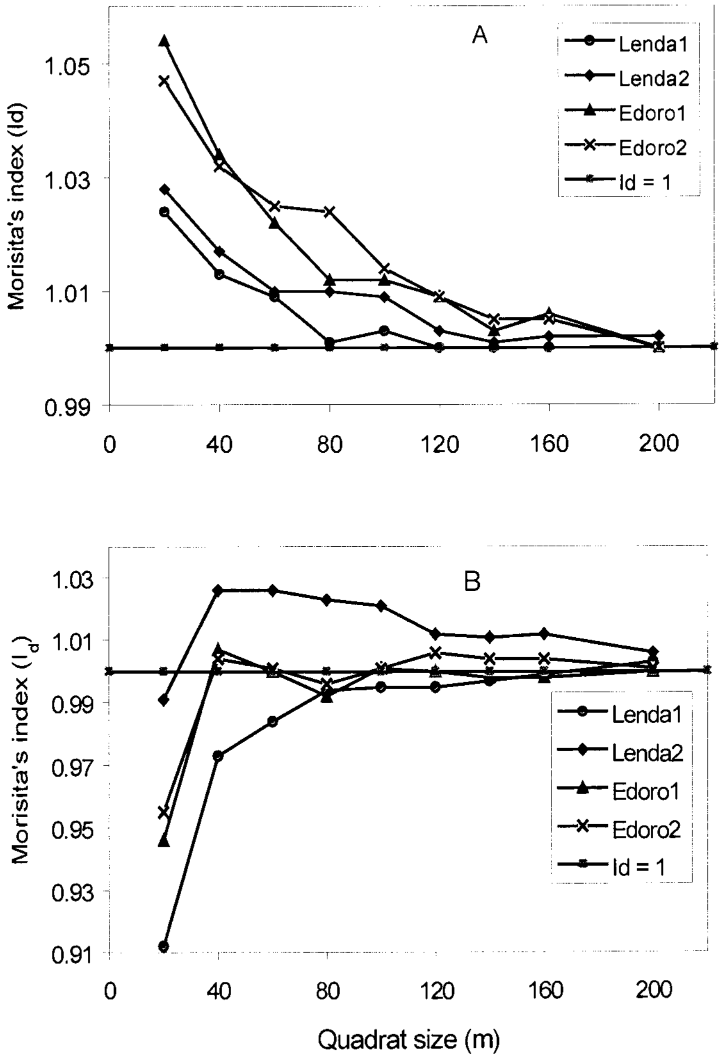


Figure 2.1. Relationships between Morisita's index of dispersion and quadrat size. Numbers on x-axis are lengths of the quadrat sides. Values of Morisita's index of dispersion are plotted on the y-axis. The horizontal line through $I_d = 1$ represents the expected value for complete random spatial dispersion. Circle = Lenda1; diamond = Lenda2; triangle = Edoro1; cross = Edoro2. A, all free-standing stems ≥ 1 cm dbh; B = trees ≥ 30 cm dbh.

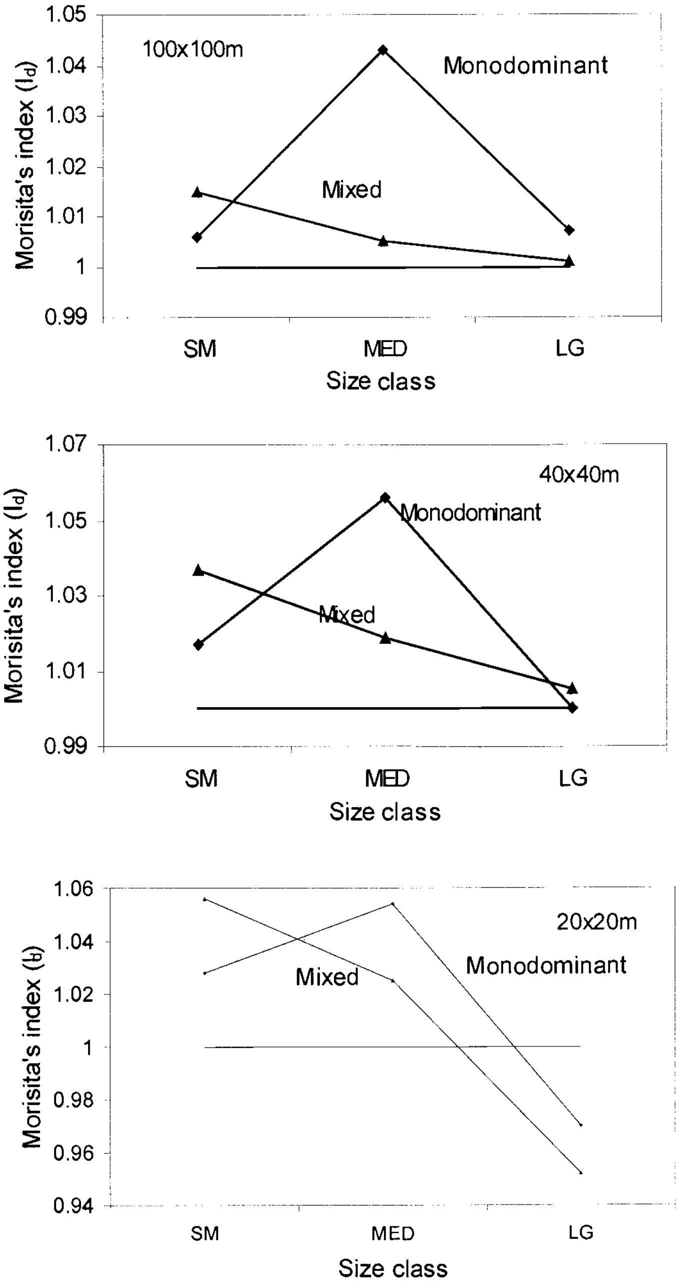


Figure 2.2. Relationships between Morisita's index of dispersion and tree size class. Three size classes were used for this analysis: SM, stems < 10 cm dbh; MED, stems ≥ 10 cm dbh and < 30 cm dbh; LG, trees ≥ 30 cm dbh. The horizontal line through Id = 1 indicates the expected value for randomly dispersed trees.

Distribution patterns of trees were dependent on size class. In mixed forest, small trees (< 10 cm dbh) had higher values of I_d than did larger trees, indicating that small trees are more clumped than large trees (Table 2.1). Plots in monodominant forest exhibited a different pattern; medium-sized trees had larger values of I_d than small trees (Figure 2.2). Trees in all size classes below 30 cm dbh exhibited significant clumping in all four plots. The level of clumping was higher in mixed forest than in monodominant forest for small trees (< 10 cm dbh) whereas monodominant forest showed higher levels of clumping than mixed stands for medium-sized trees (≥ 10 cm and < 30 cm dbh). Trees above 30 cm dbh were randomly dispersed in all plots but Lenda2 for quadrat sizes of 100 m and 40 m on a side; they showed random patterns in all plots for quadrat size of 20 m on a side. There was no instance of significant regular patterns in any plot.

Spatial dispersion patterns of all trees, regardless of species, were assessed for trees ≥ 10 cm dbh from one half (100 m x 500 m) of Lenda1 plot using the combined count-distance (Ripley's K) approach. Dispersion patterns were measured in each hectare (100 m x 100 m) separately. Trees were either randomly or regularly distributed, significant clumping was observed only at distance classes ≥ 10 m in hectare 1 (Table 2.2).

Table 2.2. Dispersion patterns of trees ≥ 10 cm dbh in five hectares (100m x 500 m) of Lenda1 plot (monodominant stands) in the Ituri Forest. Spatial dispersion patterns of trees were measured in individual hectares (100 m x 100 m) using Ripley's K. Distances of 1 to 30 m were examined.

Hectare	Stems ha^{-1}	Dispersion patterns		
		Trees ≥ 10 cm dbh	Trees < 15 cm dbh	Trees ≥ 30 cm dbh
1	426	Random	Clumped at distance classes ≥ 10 m	Regular at distance class 5 m
2	359	Regular at distance classes ≤ 10 m	Random	Regular
3	249	Regular	Random	Regular
4	260	Regular at small distance classes	Random	Regular at distance classes 5 to 17 m
5	411	Random	Random	Random

Regular patterns were common, especially for small distance classes. Large trees, ≥ 30 cm dbh, exhibited regular dispersion patterns in three hectares, and were randomly distributed in the remaining two hectares. In general large trees were regularly dispersed over a wider range at spatial scales than all trees ≥ 10 cm dbh (Figure 2.3). Trees < 15 cm dbh showed significant clumping in hectare 1 from distance class 10 m, but were randomly dispersed in all the other four hectares (Table 2.2). Increasing tree density was not associated with increased regularity at the hectare scale. The densest hectares showed few significant regular distribution patterns (Table 2.2, Figure 2. 3b).

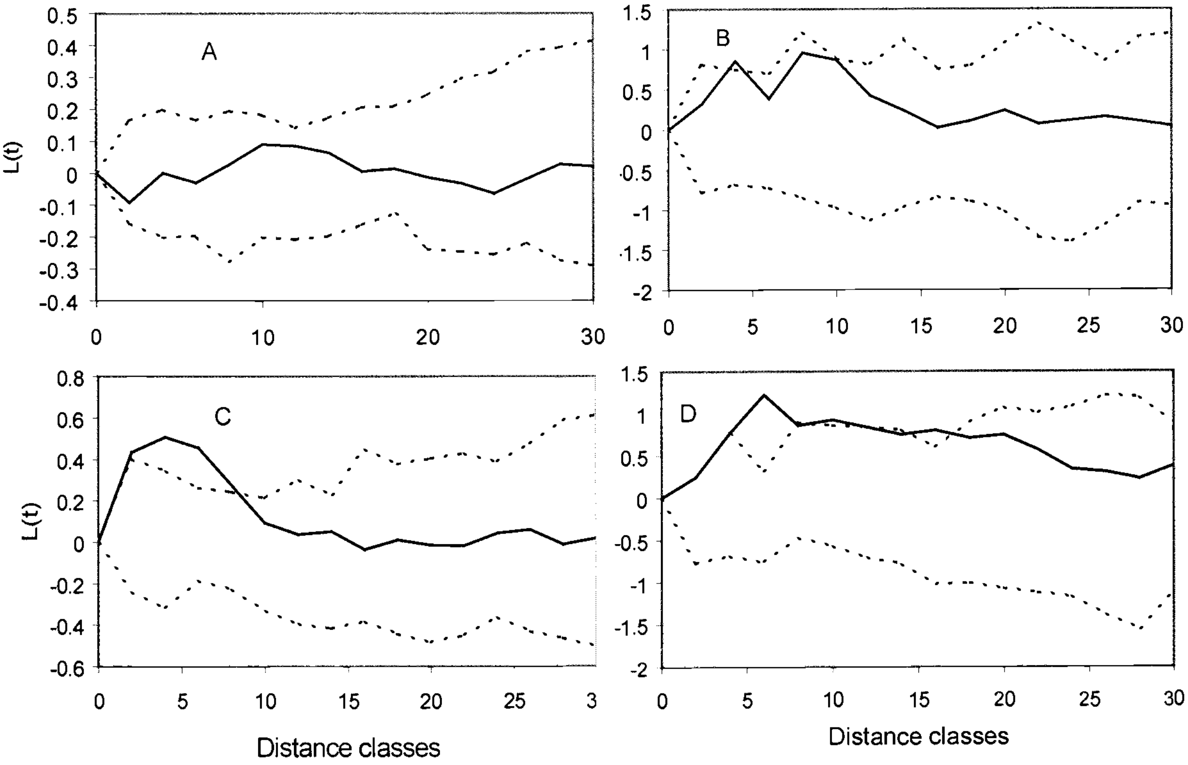


Figure 2.3. Dispersion patterns of all trees ≥ 10 cm dbh and ≥ 30 cm dbh in two hectares of Lendal 10-ha plot. Combined count-distance or Ripley' K was used for this analysis. L(t) = 0 indicates complete randomness; values > 0 indicate uniform dispersion patterns and those less than 0 (negative) suggest clumping. The dotted lines represent a 95% confidence interval for departures from random patterns. A, all trees ≥ 10 cm dbh in hectare 1; B, trees ≥ 30 cm dbh in hectare 1; C, all trees ≥ 10 cm dbh in hectare 4; D, trees ≥ 30 cm dbh in hectare 4.

Spatial patterns of individual species

Morisita's index of dispersion was computed for 345 populations of 139 different species. All individuals of a species in a 10-ha plot were considered as one population. At the 100 m scale, 89% of the populations were significantly clumped. Ninety-one percent of the populations were clumped at the 40 m scale and 93% were clumped at 20 m scale. No species had a significant regular distribution at any quadrat size. Non-significant values of I_d less than 1 were observed for some species, especially at the 20 m scale. The small values were generally associated with low population densities.

For some species, distribution patterns were idiosyncratic, changing from plot to plot. Of 37 species for which dispersion patterns could be measured in each of the four plots, 28 (76%) species showed significant clumping in all the plots, 6 (16%) species were clumped in three plots, 2 (5%) species were clumped in two plots, and 1 species exhibited significant clumping in only one plot.

For 14 randomly selected species, distribution patterns were evaluated at seven different quadrat sizes. For most species the change of I_d with quadrat size was similar to the pattern for all species combined (Figure 2.1), with I_d decreasing with increasing quadrat size (Figure 2.4). In most cases, I_d dropped rapidly from the smallest quadrat size to quadrat size 25 m, but there was little change in the value of I_d for quadrat size greater than 25 m. However, four species had the value of I_d equal to zero for the smallest quadrat sizes: *Pausinystalia macroceras, Monodora angolensis* and two other species not shown on Figure 2.4.

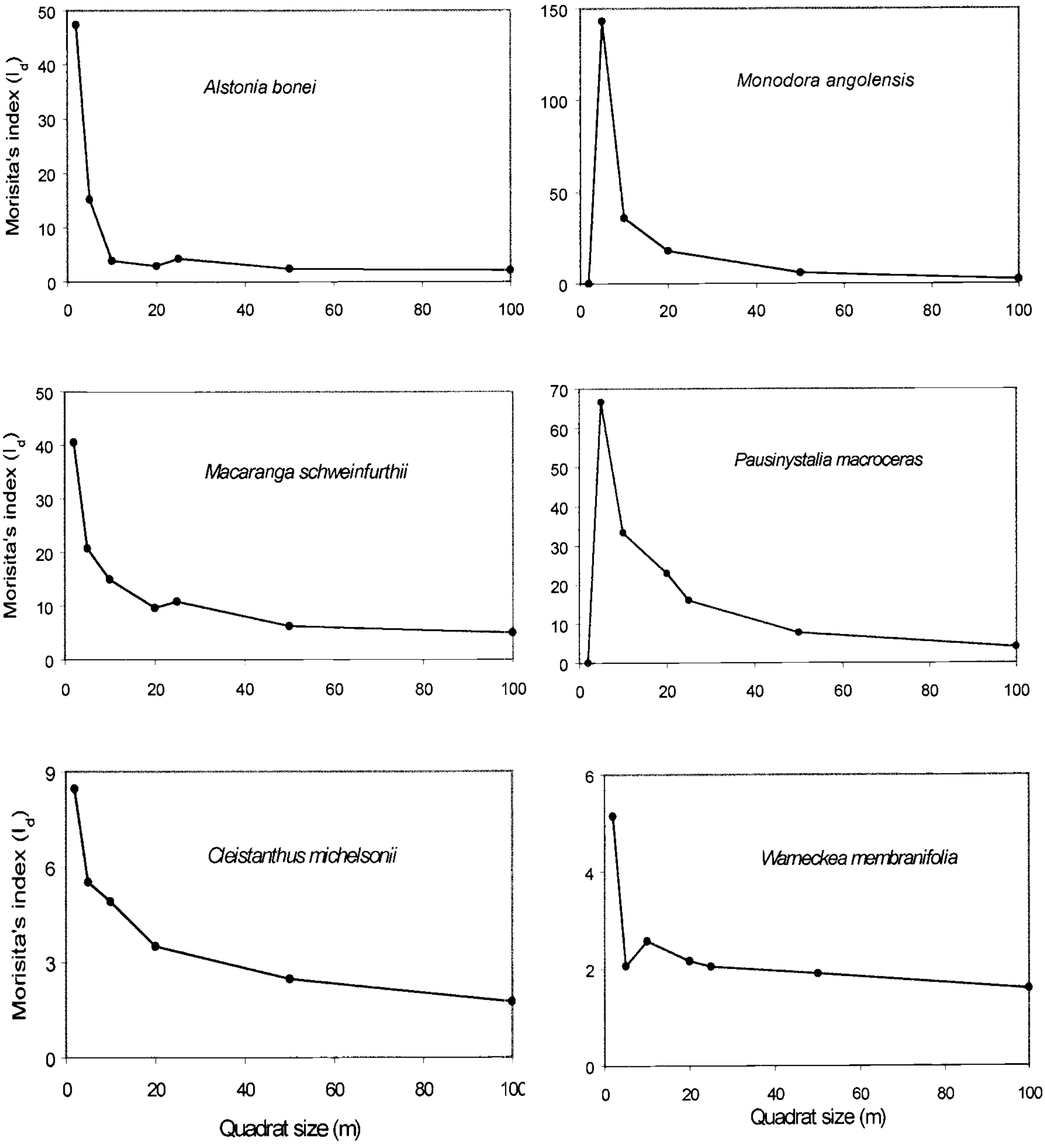


Figure 2.4. Morisita's index of dispersion (I_d) vs. quadrat size for six randomly selected species. All trees ≥ 1 cm dbh were included.

As for the analysis of all trees regardless of species, distribution patterns of individual species were dependent on size class. Small trees were more clumped than medium-sized trees and large trees at quadrats 100 m on a side (Table 2. 3). In Lenda1, for example, the proportion of species showing significant clumping dropped from 92% for small trees to 59% for medium-sized trees, and to 42% for trees ≥ 30 cm dbh. The proportions were 83%, 55%, and 24% for small, medium-sized and large trees respectively in Lenda2. The changes in the proportion of species exhibiting significant clumping with size class were less pronounced in mixed forest plots, especially for size classes above 10 cm. These proportions were 65%, 54% and 46% in Edoro1, and 73%, 25% and 29% in Edoro2 for small, medium-sized and large trees respectively.

Table 2. 3. Distribution patterns of the 27 most abundant canopy tree species in four 10-ha plots in the Ituri Forest. Morisita's index of dispersion was calculated for square quadrats 100 m on a side.

Species	Small stems				Medium-sized stems				Large stems			
	L1[1]	L2	E1	E2	L1	L2	E1	E2	L1	L2	E1	E2
Albizzia gummifera	C[2]	C	C	R	C	C	-	-	C	R	-	C
Alstonia bonei	C	R	R	-	R	-	R	R	C	R	R	C
Anonidium mannii	C	C	C	C	C	C	-	-	R	-	C	R
Bighia welwitchii	C	C	R	R	R	R	-	-	-	R	-	-
Canarium schweinfurthii	-	-	-	-	-	-	-	-	R	-	R	R
Celtis mildbraedii	C	C	C	C	R	-	R	R	R	R	R	R
Cleistanthus michelsonii	C	C	C	-	C	C	C	C	R	-	C	-
Cola lateritia	C	C	C	C	C	C	C	R	C	C	R	R
Comphyton gabonense	-	-	R	-	-	-	C	R	-	-	C	R
Cynometra alexandri	C	C	C	C	C	C	C	C	C	C	C	C
Dialium corbisieri	C	C	C	C	R	C	R	C	R	R	-	R
Dialium pentandrum	C	C	R	C	C	C	C	R	R	R	C	-
Erythrophleum suaveolens	C	R	R	R	C	-	R	R	C	C	R	R
Fagara macrophylla	C	C	R	C	R	R	C	R	C	-	C	C
Gambeya boukokoensis	C	C	C	C	C	C	R	R	-	-	R	R
Gilbertiodendron dewevrei	C	C	C	-	C	C	C	-	C	C	C	-
Irvigia excelsa	C	C	C	R	-	C	R	R	-	-	R	-
Irvingia robur	C	C	R	R	-	-	-	-	-	R	-	-
Julbernardia seretii	C	C	C	C	C	C	C	C	C	C	C	C
Klainedoxa gabonensis	C	R	C	C	C	-	R	-	R	R	R	R
Klainedoxa trilesii	R	R	R	R	C	R	-	-	R	R	C	-
Manilkara sp1	C	C	C	C	R	R	C	R	-	R	R	R
Manilkara sp2	C	C	-	-	R	R	-	-	-	-	-	-

Table 2.3 (Continued)

Species	Small stems				Medium-sized stems				Large stems			
	L1	L2	E1	E2	L1	L2	E1	E2	L1	L2	E1	E2
Ochcosmus africana	-	-	R	R	-	-	C	C	-	-	R	-
Strombosia pustulata	R	C	C	C	R	R	C	R	-	-	C	C
Strombosiopsis tetrandra	C	C	C	C	R	R	C	-	-	-	-	-
Uapaca guinensis	C	C	C	C	C	-	-	R	R	-	R	R

[1] L1 = Lenda1, L2 = Lenda2, E1 = Edoro1 and E2 = Edoro2.

[2] C, clumped patterns; R, random patterns. Spatial patterns were evaluated only for groups with at least 3 stems.

Species abundance

The relationships between population size and dispersion patterns were evaluated by a regression analysis. Morisita's index of dispersion was regressed on population size for 20 m quadrats. Both variables were log transformed because of large differences between the smallest and the largest values. Despite the large spread around the regression line, there was a significant negative relationship between Morisita's index of dispersion and population size (Figure 2.6). Almost in all cases, the most abundant populations had the smallest values of I_d (usually close to 1), indicating a less clumped pattern.

Mean distance to nearest neighbor was calculated for trees ≥ 10 cm dbh for the most common species in five hectares of Lenda1 plot. Expected mean distance to nearest neighbor, under completely spatial random patterns, decreased with population size. Observed mean distance to nearest conspecific neighbor, however, increased with increasing population size, indicating that individuals of rare species occurred closer to one another than did those from common species (Figure 2.7).

Microhabitat preference was associated with high levels of clumping. Species restricted to unusual microhabitats such as swamps, tree-fall gaps and steep slopes, exhibited extremely high values of I_d (Table 2. 4). Swamp specialists (*Hallea stipulosa, Drypetes sp., Macaranga schweinfurthii, Neoboutonia mellerii* and many other species), gap specialists (*Alstonia bonei*) and species restricted to steep slopes bordering swamps or stream beds (*Rinorea afzeli*) had some of the highest values of I_d.

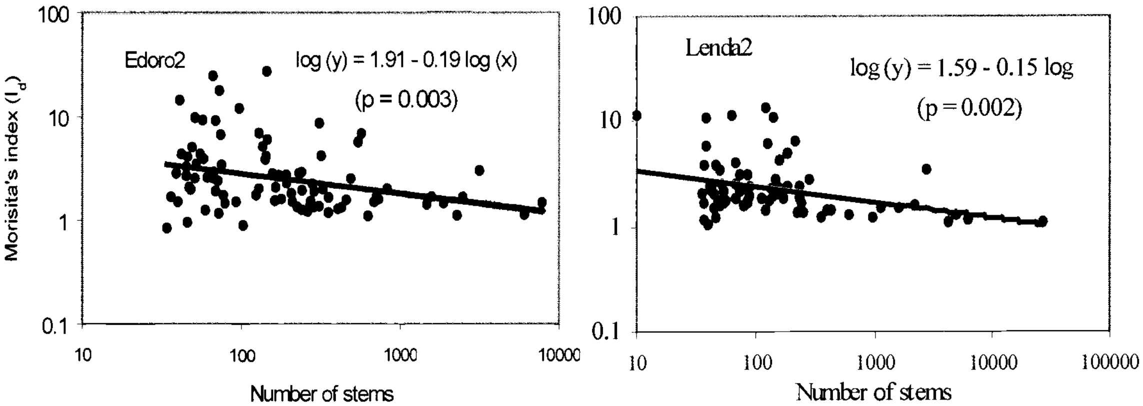


Figure 2.5. Log-log plot of Morisita's index of dispersion (I_d) on the number of stems in 10-ha

plots for common species in mixed (Edoro2) and monodominant (Lenda2) stands in the Ituri Forest.

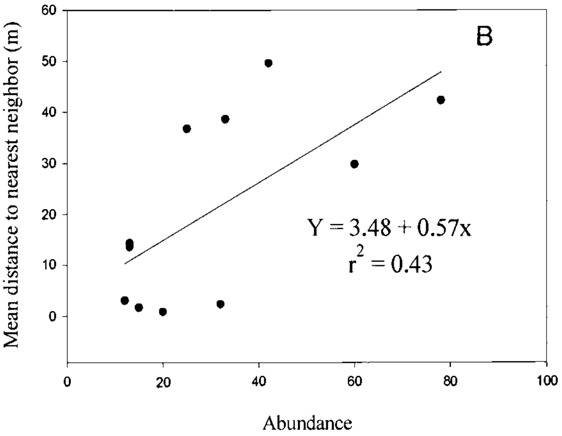


Figure 2. 6. Relationship between population size and mean distance to the nearest conspecific neighbor for ten trees species in one half (100 m x 500 m) of Lenda 1 plot (monodominant forest) in the Ituri Forest. Only trees ≥ 10 cm dbh were considered. A, expected mean distance; B, observed mean distance to the nearest neighbor.

Table 2. 4. Morisita's index of dispersion for species restricted to unusual microhabitats in four 10-ha plots in the Ituri Forest.

Species	Habitat	Morisita's index (I_d)[1]			
		Lenda1	Lenda2	Edoro1	Edoro2
Rinorea afzelii	Slope	19.6	11.0	61.4	24.9
Hallea stipulosa	Swamp	51.2	9.7	24.2	9.1
Drypetes sp.	Swamp	23.0	15.9	16.3	27.4
Neoboutonia melleri	Swamp	-	-	22.2	12.1
Macaranga schweinfurthii	Swamp	14.5	18.4	13.2	14.6
Nauclea popegeni	Swamp	21.8	18.4	7.7	4.9
Rothmania munsae	Swamp	13.4	10.6	12.8	8.7
Syzygium congolense	Swamp	35.0	4.3	2.9	6.9
Lasiodiscus mannii	Slope	-	-	9.0	-
Alstonia bonei	Gap	6.0	11.1	6.7	0.9
Barteria fistulosa	Gap	-	-	5.0	4.4
Median value of I_d[2]		2.5	2.1	2.1	2.0
Maximum value of I_d		51.2	18.4	61.4	27.4
Total number of species analyzed		86	78	98	96

[1] Morisita's index of dispersion was computed for square quadrats of size 20 m.

[2] Median and maximum values of I_d are for all the species analyzed in each plot.

DISCUSSION

The analysis of the Ituri Forest plot data did not support the Janzen-Connell spacing hypothesis. Most species were spatially clumped while others were randomly distributed. There were no significant regular patterns for any species in the 10-ha plots, although some species had non-significant values of I_d less than 1. These small values of I_d appeared to be associated with low population density and were frequent at small quadrat sizes, especially when the total number of individuals of a given species in a plot was much less than the number of quadrats used to compute the index.

The finding of many clumped patterns in this study conforms to results of other studies in tropical forests (Table 2. 5). Although differences in plot sizes, diameter limits and indices of spatial patterns complicate comparisons, it stands out that most species are either clumped or randomly distributed, and that very few species are regularly distributed.

Table 2.5. Summary of findings of studies of spatial dispersion patterns in tropical forests.

Site and Forest Type	Plot Size (ha)	Stem density (ha^{-1})	Trees Analyzed	Results	Source
Brazil Terra firma forest, Pará	3.5	432.4 ≥ 10 cm dbh	6 most abundant spp.	All random	(1)
Peninsular Malaysia Lowland dipterocarp forest, Jengka	20.6	134.4 ≥ 29 cm dbh	13 abundant spp.	6 random 7 clumped	(1)
			All trees	All random	
West Sarawak Mixed dipterocarp forest	2.9	376.5 ≥ 19 cm dbh	15 species	7 random 8 clumped	(1)
Panama Lowland moist forest, BCI	1.5	2712.8 ≥ 2.5 cm dbh	Size classes	> 20 cm dbh random < 20 cm dbh clumped	(2)
			All trees	Clumped	
Costa Rica Lowland dry forest, Guanacaste	13.4	1185.7 ≥ 2 cm dbh	All species	17 random 44 clumped	(3)
Ghana Lowland dry forest, Pinkwae	0.36	2671.4 ≥ 3 m height	14 most abundant species	6 random 8 clumped 1 regular	(1)

Table 2. 5 (Continued)

Site and Forest Type	Plot Size (ha)	Stem density (ha^{-1})	Trees analyzed	Results	Source
U.S. Virgin Islands Moist semievergreen forest	4.0	≥ 10 cm dbh	16 most abundant species	3 random 12 clumped 1 regular	(4)
Panama Lowland moist forest, BCI	5.0	171.2 ≥ 19 cm dbh	63 species	37 random 26 clumped	(5)
Sarawak Kerangas forest, Sabal F.R.	19.2	836.6 ≥ 9.7 cm dbh	64 most abundant species	34 random 30 clumped	(6)
Costa Rica Lowland wet forest, La Selva	12.4	446.0 ≥ 10 cm dbh	104 populations (65 spp.) with ≥ 10 individuals	85 random 13 clumped 5 regular	(1)
			Size classes	Large trees more hyperdispersed than small trees	
			Rare species	Random	
			Dominant species	Regular	
			All trees	Regular	

Sources: (1) Lieberman and Lieberman 1994; (2) Lang et al. 1971; (3) Hubbell 1979; (4) Forman and Hahn 1980; (5) Thorington et al. 1982; (6) Newbery et al. 1986

The increase of mean distance to nearest conspecific neighbor with increasing abundance is suggestive of species-specific predation. Johnston and Hahn (1980) argued that the Janzen-Connell model may be consistent with any dispersion patterns, provided intertree distances are large. They found, however, that for most species, intertree distances were less than 10 m, which may be less than the diameter of many umbrella-shaped crowns of canopy tree species in tropical forests (Richards 1996). Condit et al. (1992) and Hubbell et al. (1990) documented recruitment patterns consistent with Janzen-Connell model in many common species in the tropical forest of Barro Colorado Island (Panama). They suggested that these patterns were probably not strong enough to generate regular distribution because the patterns did not usually extend beyond 10 m away from the parent trees. Thus, one may argue from these observations that although host-specific predation does occur in nature, it has not been demonstrated to produce the patterns of species distribution posited by the Janzen-Connell model.

Clumping has been attributed to several factors such as inefficient seed dispersal (Poore 1968, Ashton 1969), vegetative reproduction by root suckers (Lieberman 1979), habitat heterogeneity and microhabitat preferences (Lieberman and Lieberman 1994; Forman and Hahn 1980; Hubbell 1979) and regeneration in tree fall gaps (Newbery et al. 1986). Habitat heterogeneity, coupled with microhabitat preferences, appeared to be the most obvious factor that accounted for clumping of many species in the Ituri Forest plots. Swamp specialists (*Hallea stipulosa, Macaranga schweinfurthii, Neoboutonia mellerii* and many other species), gap specialists (*Alstonia bonei*) and species restricted to steep slopes bordering swamps or stream beds (*Rinorea afzeli*) had the highest levels of clumping.

Peter (1983) argued that factors generating clumped dispersion patterns might vary with scale. According to Peter, "the nature of pattern generated by biological process can be affected by the physical scale on which the process is observed. At a sufficiently large scale most natural environments exhibit heterogeneity, which tend to produce aggregated patterns. At a smaller scale, environmental variation will be less pronounced and the major determinant of pattern may be the nature of interactions amongst events themselves." He then suggested that vegetative propagation of individual shoots, for instance, would tend to produce small-scale aggregation whereas competition for space will encourage regularity.

Morisita's index of dispersion decreased irregularly with increasing quadrat size for 14 randomly selected species, suggesting that clumping is more pronounced at small scale than at larger scales. Hubbell (1979) found similar results in a dry forest in Costa Rica. Hubbell speculated that such patterns were typical of populations having "point sources" of relatively high population density, surrounded by more diffuse clouds of individuals diminishing in density away from the centers. He argued that "small quadrats may contain the high-density centers, thereby producing large I_d values, whereas large quadrats tend to have lower I_d values because they average the density of the concentrated centers with the density of the more sparsely populated surroundings." The fact that similar patterns were observed in the analysis of all stems irrespective of species suggests that Hubbell's explanation may not be the major mechanism responsible for the phenomenon. Hubbell's explanation is species-specific and cannot apply for all species combined. It is also important to note that Morisita's index of dispersion is scale-sensitive and that the value of I_d itself may not tell much about the level of clumping. For a given value of I_d, the critical chi-square value for clumped patterns increases linearly with the number of quadrats (which is inversely proportional to the size of quadrats). For similar levels of clumping, small quadrats have higher values of I_d than do larger quadrats.

Size class

Within the Ituri Forest plots, spatial patterns of trees varied by size class. Small trees were more clumped than large trees, both within and across species. Lang et al. (1971) reported similar results for a lowland moist forest at Barro Colorado Island (Panama). Lang et al. observed that trees > 20 cm dbh were randomly dispersed whereas trees < 20 cm dbh had clumped distribution patterns. The decrease of the prevalence of clumping with increasing tree size may be interpreted as an evidence of Janzen-Connell spacing hypothesis (Clark and Clark 1984). The Janzen-Connell spacing model, however, does not apply to patterns of all trees independent of species because the postulated mechanism is host-specific. Lieberman and Lieberman (1994) argued that a more parsimonious explanation of decreased clumping with tree size is the progressive physical crowding of growing trees, more specifically crown-to-crown interactions among neighboring trees. Regular dispersion patterns will thus only occur in the densest populations. Results from this study are partly consistent with this proposition. The most abundant species had the smallest values of I_d (Figure 2.5), indicating less clumping.

Rare species

If trees are randomly or regularly distributed, as suggested by Janzen-Connell hypothesis, rare species would have greater intertree distances than common species. However, in the Ituri Forest plots, mean distance to nearest conspecific tree increased with increasing population size, indicating that were species are more clumped than common species. Greater clumping in rare species has been reported for a 13.4 ha plot in a dry forest in Costa Rica (Hubbell 1979). Hubbell argued that high level of clumping in rare species might suggest that rare species are at least locally successful when their microhabitat requirements are satisfied. This would be the case for species restricted to unusual microhabitats such as swamps, stream edge, or steep slopes within the plots. Forman and Hahn (1980) also proposed the importance of microhabitat specialization for uncommon tree species in tropical forests.

A well-known group of rare species within old-growth tropical forest stands is the gap colonizer species. Five gap specialists were analyzed in the present study; four of them (*Alstonia bonei, Albizia gummifera, Fagara macrophylla* and *Macaranga monandra*) showed significant clumping in all plots. The other species, *Canarium schweinfurthii*, was randomly distributed in the three plots where its pattern was tested (the fourth plot had too few individuals of this species to analyze its spatial pattern).

Canarium schweinfurthii was solely represented by a few large individuals, randomly scattered within each 10-ha plot. This species probably requires very large gaps and/or completely bare soil for its regeneration. It may also be that this species was common in earlier successional stages and that its current population represents the last survivors of the species in the area surveyed. The size distributions of most of the gap-specialists were either flat or skewed to the left, indicating a higher representation of large size classes.

The findings of this study are consistent with results obtained from several other investigations of tropical forests. Most species were either clumped or randomly dispersed, and very few species were regularly distributed. The occurrence of clumped patterns in the analysis of all trees irrespective of species suggests that species-specific mechanisms may not be the only factors controlling the spatial dispersion of trees in the Ituri Forest. Habitat heterogeneity, habitat specialization, poor seed dispersal, and regeneration in tree-fall gaps may account for the observed prevalence of clumped patterns. Competition for light and space apparently results in less clumping for large trees as compared to all size classes combined, both for individual species and for all trees. Rare species were more clumped than common species in both mixed and monodominant stands of the Ituri Forest.

CONCLUSIONS

The Ituri Forest plots permitted the first detailed, large-scale analysis of forest structure and composition and spatial patterns of trees in monodominant and mixed stands in the Epulu sector of the Ituri Forest. The comparison of forest structure in the two forest types corroborates results obtained from previous studies (Hart et al. 1989; Makana et al. 1998). Mixed forest has greater density of small stems, whereas large trees (≥ 30 cm dbh) are more abundant in monodominant stands. The higher density of large trees in monodominant forest resulted in higher basal area in this forest type. Lianas were much more abundant in mixed forest than in monodominant forest. A shrub, *Scaphopetalum dewevrei*, was the most abundant species in both forest types, accounting for at least 40% of the total number of stems ≥ 1 cm dbh in each forest type. Basal area was dominated by *Gilbertiodendron dewevrei* in monodominant forest and by *Cynometra alexandri* and *Julbernardia seretii* in mixed forest.

The assumption that mixed forest is richer in tree species than monodominant forest was not fully supported by the results of this study. Species richness was comparable in the two forest types at the 1 cm dbh limit, with monodominant forest having a slightly higher number of species than mixed forest at the one hectare scale. For canopy trees, though, mixed forest had significantly more species than monodominant forest. This trend was clearly shown by the significant negative relationship between the density of large *G. dewevrei* and the number of species per hectare for trees above 30 cm dbh. The paucity of canopy tree species in monodominant forest was mostly due to the high density of *G. dewevrei* in the canopy layer, which left little space for other tree species.

Compared to other tropical rainforests, monodominant forest showed both a low density trees ≥ 10 cm dbh and a high density of trees ≥ 30 cm dbh. The Ituri monodominant and mixed forests were clearly less rich in species than almost all the other forests reported here, especially at 10 cm dbh and above. The forests included in this study could be classified as "low-diversity" or "species-poor" forests by global standards for tropical rainforests.

The spatial patterns of all trees were either clumped or random; but Ripley's K found some significant regular patterns at the smallest scales for trees ≥ 10 cm dbh. Distribution patterns of individual species were mostly clumped, except for large trees which were more randomly distributed. Rare species were more clumped than more common species; they also had shorter intertree distances. Species generally restricted to unusual microhabitats such as tree-fall gaps, swamps and steep slopes had some of the highest level of clumping in the plots.

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