This is to certify that the

dissertation entitled

The Ecology of a Single-Species-Dominant Forest
and of a Mixed Forest in Zaire, Africa

presented by

Terese Butler Hart

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Botany and Plant Pathology

Peter G. Murphy
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Date November 14, 1985

THE ECOLOGY OF A SINGLE-SPECIES-DOMINANT FOREST AND OF A MIXED FOREST IN ZAIRE, AFRICA

By

Terese Bulter Hart

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Botany and Plant Pathology

ABSTRACT

THE ECOLOGY OF A SINGLE-SPECIES-DOMINANT FOREST AND OF A MIXED FOREST IN ZAIRE, AFRICA.

By

Terese Butler Hart

Low species diversity and pronounced dominance have been considered atypical for tropical humid forests. In the Ituri Forest of Zaire, however, a principal forest type is dominated by a single species. In mbau forest, *Gilbertiodendron dewevrei* accounts for approximately 90% of the canopy-level trees. A second forest type, the more species-rich mixed forest, is found at similar altitudes and on similar topography as mbau forest. The co-occurrence of these two communities suggests that some factor other than climate determines the diversity difference between the two forest types.

Four general hypotheses to account for the differences in diversity were tested. Each hypothesis offered contrasting predictions for the two forest types and was tested as follows:

1. Monodominance is symptomatic of early secondary growth. Forest maturity was inferred from the representation of shade-tolerant species in the canopy and understory.

2. Low tree species diversity is found on very poor soils. Soils types were compared for differences in texture and chemical composition.

3. Frequent and/or large natural disturbances interfere with

the ability of any single species to attain dominance. Treefall size and frequency was determined.

4. Heavy seed predation under parent trees prevents dominance by any single species. Seeds of canopy trees were monitored for survival both near and distant from adult conspecifics.

The results failed to show that any of the proposed hypotheses account in a major way for the maintenance of the two patterns of diversity and dominance in the Ituri Forest. Both forest types have the structure and composition of mature communities and the mbau forest is not restricted to soils too poor for mixed forest. As predicted, there were more frequent treefalls in mixed forest than mbau forest; however, there was great variance in size and frequency of gaps in both forest types. Finally, the dominance of *G. dewevrei* cannot be attributed to a larger proportion of its seeds escaping predators. It is suggested that natural disturbance of a larger scale and more ancient than measured by this study may been a determinant of present forest distributions.

This dissertation is dedicated to the
memory of CHUKIZA, son of ANJIANI, nephew
of KENGE, who enthusiastically shared
his knowledge of the forest
and to the memory of PH. GERARD whose
enjoyment of mbau forest is alive
in his writing.

AKNOWLEDGMENTS

The research project in the Ituri Forest of Zaire was made financially possible by a grant from the United States Man and the Biosphere Program (federal grant number 4789-6). The project was facilitated by the cooperation of the Institut Zairois pour la Conservation de la Nature (IZCN). Financial support during the period of data analysis and redaction was provided by the African Studies Center and the Department of Botany and Plant Pathology at Michigan State University.

Dr. Peter Murphy's confidence and support were the catalyst for the research proposal and essential to its realization. John A. Hart has shared in, and contributed substantially to, all phases of this project. His field assistance, stimulating discussions, and companionship provided direction and the ability to persevere, as needed.

Work in the forest would have been many times more difficult without the enthusiastic assistance of the Mbuti Pygmies of the Epulu area, notably, Chukiza, Kenge, Atoka, Mayalimingi, Avion, and Amanjau. Dr. H. Breyne, curator of the national herbarium in Kinshasa, deserves a special thanks for his logistical support and the identifications of plant specimens. Many additional identifications were provided by L. Liben of the National Botanical gardens in Meise, Belgium.

The dissertation has been greatly improved by the editorial comments and constructive criticism of Dr. Peter Murphy and my committee members, Dr. John Beaman, Dr. George Petrides, and Dr. Jean Stout.

The questions and observations of colleagues have been incorporated into the conception, realization, and analysis of this study. In particular I wish to thank Dr. N. Brokaw, Dr. J. Connell, Dr. D. Hibbs, Dr. D. Livingstone, the ecology group at Kellogg Biological Station, especially, M. Leibold, Dr. T. Miller, and Dr. A. Winn, and my fellow students in the laboratory, especially, V. Dunevitz and Dr. G. Donnelly.

In completing this study, as has been the case for all my projects, large and small, I feel deep gratitude toward my family. The encouragment of my parents and parents-in-law has been a constant source of strength. I owe a very special thanks to my husband, John, for his unfaltering good humour and his lavish praise, and, also, to our daughters, Sarah and Rebekah, who never doubted and always provided welcome distraction.

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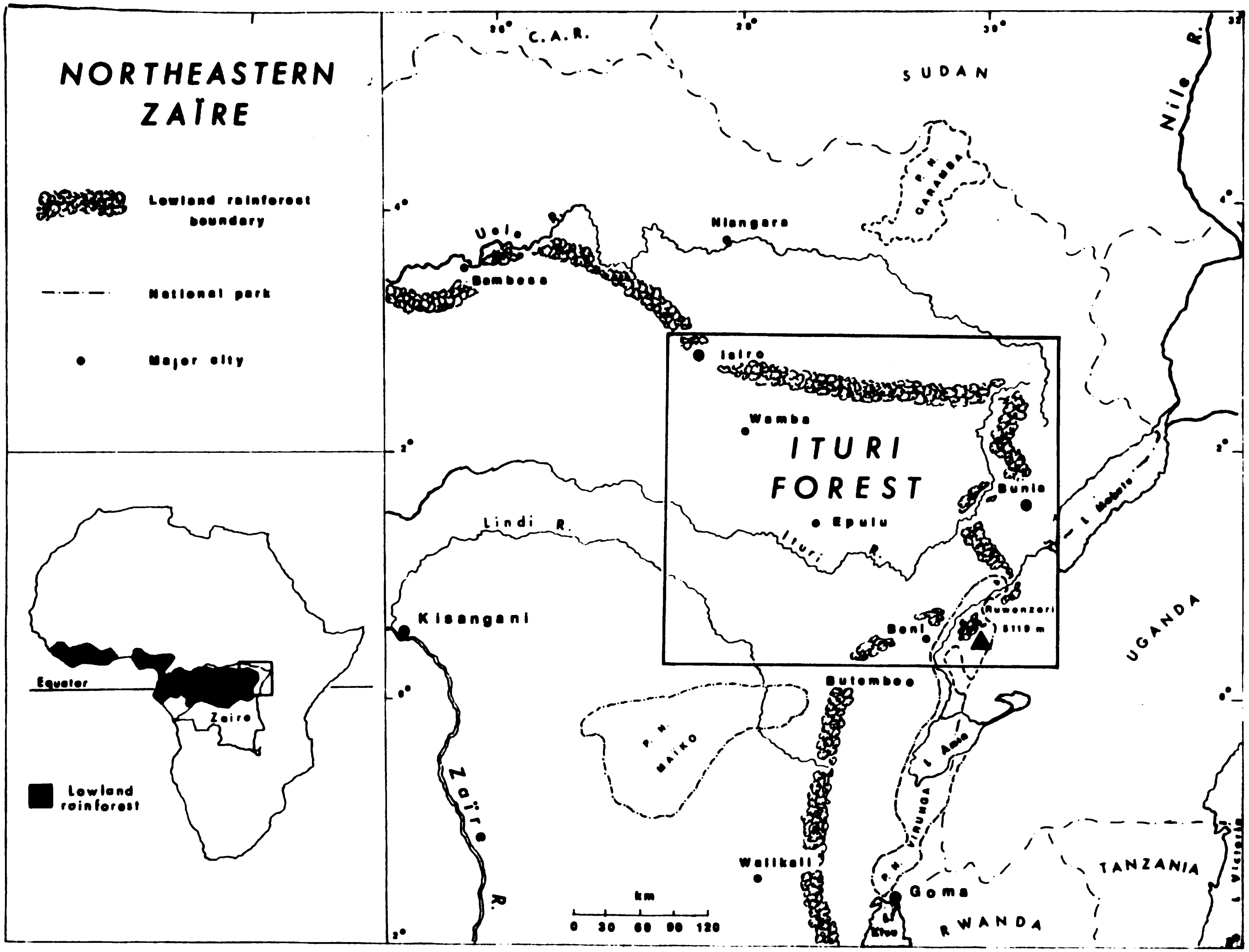
INTRODUCTION

High tree species diversity is one of the outstanding characteristics of many tropical forests (Richards 1952, Walter 1973, Whitmore 1984). Tropical forests "with an extremely large number of trees of one predominating species are rare" (Letouzey, 1978).

An exception to the general pattern occurs in the Ituri Forest of northeastern Zaire (Figure 1). There are two major forest types in the Ituri watershed, each of which covers thousands of contiguous square kilometers. One of these types, the mbau forest, is dominated by a single species of tree which commonly comprises 90% or more of canopy level individuals. The canopy of the mixed forest type, on the other hand, is closer to that expected in the tropics. Rarely does a single species or even a combination of two species account for more than 50% of the crowns present.

These two forest types co-occur in the southern and western two thirds of the Ituri Forest, whose total area is approximately 70,000 km^2. The borders between the two types are floristically abrupt but do not correspond to topographic gradients. Furthermore, as a result of their widespread co-occurence, both forest types share a similar climatic regime. It is thus possible to contrast a species-rich tropical forest with a relatively species-poor, single-species-dominant tropical forest under similar environmental conditions, allowing a comparative approach in exploring causes of

Figure 1. The Ituri Forest, Zaire.


NORTHEASTERN ZAÏRE
Lowland rainforest boundary
National park
Major city
Equator
Zaïre
Lowland rainforest
26°
28°
30°
32°
4°
2°
0°
2°
C.A.R.
SUDAN
Nile R.
P. N. GARAMBA
Uele R.
Niangara
Bambesa
Isiro
Wamba
ITURI FOREST
Epulu
Ituri R.
Bunia
L Mobutu
Lindi R.
Kisangani
Ruwenzori 5119 m
Beni
Butembo
UGANDA
P. N. MAIKO
L Amin
P. N. VIRUNGA
Zaïre R.
Walikali
Goma
L Kivu
RWANDA
TANZANIA
L Victoria
km
0 30 60 90 120

species richness in tropical forests.

The principle behind this comparative approach is that different biotic and/or abiotic factors, having a strong influence on species distributions and abundances, led to the diversity differences of the two forest types and continue to maintain these differences. It should, therefore, be possible to detect mechanisms perpetuating differences in species richness by comparing the two forests. Relevant hypotheses tested in this manner include the following:

In chapter one:

1. The species-poor mbau forest developed due to specific soil conditions different from those which support relatively species-rich forests.
2. The mbau forest, dominated by a single species, is part of a successional sequence leading toward a more species-rich community.

In chapter two:

3. The greater species diversity of the mixed forest is maintained by a natural disturbance regime different from that characteristic of mbau forest (more treefalls, larger gaps, etc.).
4. One forest type is more resilient to damage than the other and is more likely to become established after major disturbance.

In chapter three:

5. Tree species in the mixed forest may be able to co-exist as a

result of specialization to relatively narrowly defined "regeneration niches". The single dominant in mbau forest can produce seed and become established under a broader array of conditions.

6. No single species is able to dominate in mixed forest because of relatively high seed and seedling mortality, particularly in the vicinity of parent trees. Conversely, in the mbau forest, the dominant tree is relatively free of seed predators.

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CHAPTER I

THE MBAU FOREST IN ZAIRE:
EDAPHIC AND SUCCESSIONAL GRADIENTS IN RELATION TO
SINGLE-SPECIES DOMINANCE IN AN AFRICAN TROPICAL FOREST

INTRODUCTION

The latitudinal gradient in species diversity is regarded as "the most important geographical pattern" regarding the number of species in communities (Ricklefs 1973). Leigh (1982), Whitmore (1984), and Gentry (1982) have recently reviewed this trend as it applies to the number of tree species in a given area of tropical forest. They confirm the generalization of earlier authors (Richards 1952) that tropical forests are considerably more diverse than temperate forests.

The generalization is applied only to mature or "climax"[1] tropical forests. There are references in the literature to tropical secondary forests which are relatively species poor (1-10 woody species, Budowski 1970) or locally dominated by single species (Richards 1952 and Whitmore 1984). The presumed course of tropical succession, therefore, is towards increased numbers of tree species and decreased dominance by any single tree species (Budowski 1970).

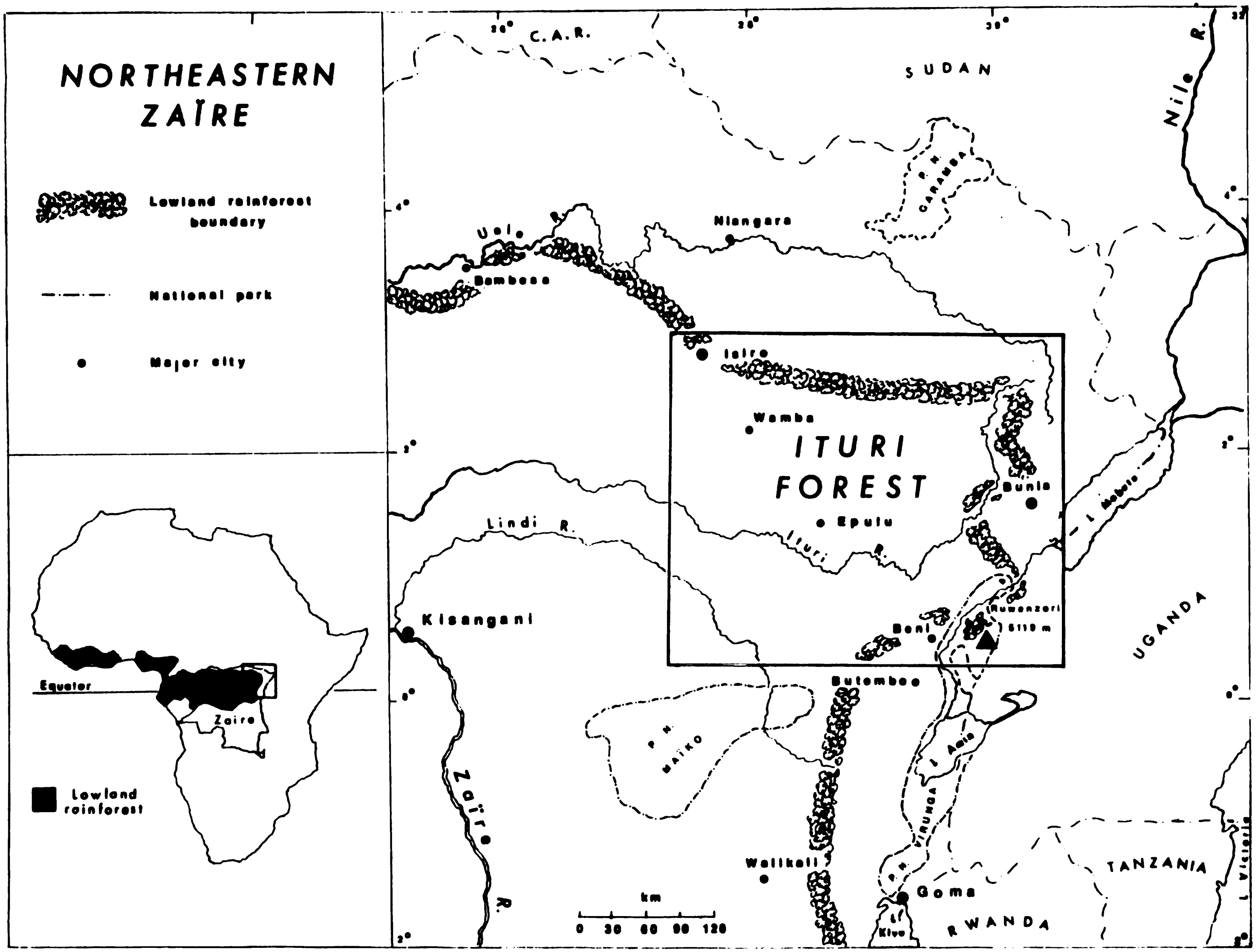
Janzen (1974) pointed out that, contrary to expectation, stable tropical forest communities do exist that are species poor (1974). He attributed this floristic poverty to limiting edaphic conditions as exemplified by the Heath Forest growing on bleached sands or podsols of Bako National Forest, Sarawak. Richards (1941) had earlier commented on the similarity between the forests on podsols in southeast Asia and forests on similar soils in British Guiana (now Guyana) in South America. He inferred that forests on relatively unfavorable soils show a tendency toward single species dominance (Richards 1952). A single caesalpiniaceous species, *Eperua falcata*, dominates Wallaba Forest on white sands in Guyana (Davis and Richards 1934). Ashton (1971) suggested that the Heath Forest in Sarawak demonstrated a general relationship between soil conditions and tree species diversity in tropical forests: "the ideal soil conditions for the development of a high tropical rain forest rich in tree species is therefore where the soil is deep, rich in nutrients, well drained but with constantly available water. The opposite of these three conditions is the worst, and leads to poverty in size and number of species..." According to Brunig (1973) the limiting site conditions lead to a reduction of the available niche-hyperspace resulting in low species diversity and dominance by only a few species.

Less easily categorized are the species-poor tropical forests which were considered the "climatic climax"[2] by botanists and ecologists working in a particular area. Notable are the tropical forests dominated by single species. There have been a number of detailed studies of such forests where the field workers failed to comment on any correlation between single species dominance and a given soil type and yet the community was considered mature (Beard 1946, Eggeling 1947, Germain and Evrard 1956, Gerard 1960, Lee 1967). Particularly in the earlier literature, reference to such tropical forests was not uncommon (Zon 1915, Laan 1927, Koopman and Verhoff 1938). Two recent studies reported single species dominated forests occurring on soils similar to those of adjacent mixed forests (Rankin 1978, Swaine and Hall 1981).

In this paper I examine a forest dominated by the single species *Gilbertiodendron dewevrei* (Caesalpiniaceae). The study site was in the Ituri Forest of northeastern Zaire (Figure 1). The forest type studied, called mbau forest after the local name for the dominant species, is well represented in much of the Zaire (Congo) basin. It is considered by some as representative of the climatic climax for equatorial Africa on well-drained soils (Lebrun and Gilbert 1954, Gerard 1960, Jongen et al.. 1960). Other authors suggest that this forest type is actually "edaphically determinined" (Richards 1952, Janzen 1981).

The field study reported here compares mbau forest, dominated by *G. dewevrei*, with adjacent mixed forest. The compositions of the two forests, their edaphic status, and successional states are compared. In addition to field data, literature concerning mbau forest was consulted in order to construct a larger scale view of variation relative to soils. Other tropical single-dominant forest studies were also reviewed in order to determine the generality of this study's

Figure 1. The Ituri Forest, Zaire.


NORTHEASTERN ZAÏRE
Lowland rainforest boundary
National park
Major city
Equator
Zaïre
Lowland rainforest
26°
28°
30°
32°
4°
2°
0°
2°
C.A.R.
SUDAN
Nile R.
P. N. Garamba
Uele R.
Niangara
Bambesa
Isiro
Wamba
ITURI FOREST
Epulu
Ituri R.
Bunia
L. Mobutu
Lindi R.
Kisangani
Beni
Ruwenzori
5119 m
UGANDA
Butembo
P. N. Maiko
L. Amin
P. N. Virunga
Zaïre R.
Walikali
Goma
L. Kivu
RWANDA
TANZANIA
L. Victoria
km
0 30 60 90 120

findings and its relevance to other tropical areas.

BACKGROUND

Variation of tropical forest composition with soil factors and successional stages.

Tropical biologists do not agree as to how much of the observed variation in tropical forest composition is caused by variation in substrate. There is also no consensus as to the types of substrate changes most likely to result in changes in community composition.

Kruckeberg (1969), citing examples from temperate North America, asserts that "within areas of broad climatic similarity...geological variability provides the major source of regional biotic diversity". Goldberg (1985) working in Mexico demonstrated that species from one forest type were excluded from an adjacent forest type by soil characteristics originating from different parent materials. On the other hand, researchers with wide experience in the tropics have doubted any direct relationship between parent material and forest composition. Lemée (1961) gave an example from Ivory Coast of a forest type growing, without detectable difference, on soils derived from different parent materials. Likewise Wong and Whitmore (Pasoh, Malaya, 1970), Hall and Swaine (Ghana 1981) and Leigh (Barro Colorado Island, Panama, 1982) all reported that different geological substrates do not give rise to forests of significantly different composition.

Hall and Swaine (1981) suggested that this lack of correlation may be due to extensive weathering of the tropical substrates, the parent rock having been buried under great depths of weathered material. Likewise, Kruckeberg (1969) commented that the influence of the parent material was most obvious where the processes of soil formation were impeded. It is, therefore, not unexpected that in southeast Asia tropical forests growing on rapidly eroding limestone are frequently characterized by the presence of endemic species and unusual species distributions (Whitmore 1984).

Observers have pointed out the unique vegetation growing on highly leached white sand soils in both the neo- and paleotropics as evidence for the impact of soil nutrient availability (Richards 1961, Ashton 1971). But when less extreme soils are looked at the relationship becomes ambiguous. Ashton (1977) and Brunig (1983) suggest that the greatest forest diversity is found on soils with intermediate levels of available nutrients.

Much of the work attempting to correlate soil variables with vegetation variables has been carried out in Southeast Asia. Multivariate analyses have, in some cases, shown that tree species associations were correlated with complex soil factors including nutrient status (Austin et al. 1972, Ashton 1976, Baillie and Ashton 1983, Newberry and Proctor 1984). The results of such analyses have not been consistent. A study in Sarawak (Newberry and Proctor 1984) found significant associations between vegetation "classes" and soil mineral parameters in Heath Forest and Alluvial Forest but not in

Dipterocarp Forest or forest over limestone. Tree species that appeared to have narrow and different edaphic ranges in Borneo occur together in a single forest type in Malaya (Austin, et al. 1972). In some cases plots known to have distinctly different soils failed to show differences in vegetation (Austin, et al. 1972). As summarized by Whitmore (1984) studies relating soil chemistry to tropical forest composition have, so far, provided only "cryptic results" and "enigmatic correlations".

Among the first published, and most cited, examples of change in tropical forest composition along an edaphic gradient is the study by Davis and Richards (1933, 1934) at Moraballi Creek in British Guiana. Five forest types were distinguished within close proximity. In three of these, the dominant species made up more than 60% of all large trees (> 41 cm diameter). From their observations they generalized that the series of forest types was determined by changes in physical characteristics of the soil, perhaps in combination with changes in soil depth. They assumed soil chemistry to be similar along the soil gradient as the parent material and soil pH did not change.

Forest composition changes have been linked to changes in soil texture because of the influence of soil texture on soil moisture-holding capacity. Lemée (1961) mentions two floristically distinct forest types in Ivory Coast that occur on soils with different water retention capabilities. He also states that near their climatic distribution limit species may become restricted to moister soils. Hall and Swaine (1981) report that drier forest types occur on shallow soils and that species diversity increases with wetter conditions.

According to a 1977 Unesco/UNEP/FAO report: "The role of hydromorphology and texture (as a factor of water retention) needs to be underlined as regards the distribution of humid tropical forests" (p 261).

In summary there are three substrate factors that have been cited as being important determinants of forest type. These are: differences in geology or soil parent material, differences in the nutrient status of the soil, and differences in soil texture or water-holding capacity. The importance of these three factors as regards changes in tree species composition varies from site to site. In general it appears that the influence of parent material is most pronounced where soils are young; the chemical composition of soils has the greatest impact where the contrast in available nutrients is large with extreme nutrient deficiency in one forest type; finally, the water-holding capacity of the soil is most influential where local precipitation is marginal relative to the moisture requirements of the species in question.

Vegetation discontinuities, that might be attributed to soil discontinuities, have at times been found to represent different seral stages on the same substrate. Some tropical forest areas have large scale natural disturbances such as earthquakes (Garwood et al., 1979) and wind storms (Wyatt-Smith 1954, Whitmore 1974) that are common enough to result in large areas of successional forests. These younger forests may have abrupt boundaries and, as in the case of the storm forest in Kelantan (Wyatt-Smith 1954), may be dominated by a single c

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tree species.

Without historical records, it is difficult to identify areas of past disturbance. Confusion between late secondary forest and primary forest is likely (Davis and Richards 1934, Budowski 1970). A survey of the abundance of tree species whose juveniles are shade-tolerant and of the size-class distribution of those species has been used to compare the successional status of different forest types (Whitmore 1974). As a forest matures it is likely to be increasingly dominated by shade-tolerant species which eventually become more important than light-demanding species in the canopy (Horn 1971). The maturity of a forest can be assessed by surveying the abundance and size class distribution of shade-tolerant species. A forest in which the canopy species are well represented in several levels of the understory is likely to have a relatively stable species composition.

Single-species dominant forests in tropical Africa and other tropical areas.

Upland single-dominant forests cover large areas of tropical central Africa. They have frequently been considered the climatic climax by plant ecologists and botanists (Eggeling 1947, Lebrun and Gilbert 1954, Germain and Evrard 1956, Devred 1958, Gérard 1960). The dominant species are usually of the Caesalpiniaceae with different species important in different areas, including : *Gilbertiodendron dewevrei* (De Wild.) Léonard, *Brachystegia laurentii* (De Wild.) Louis, *Cynometra alexandri* C.H.Wright, *Julbernardia seretii* (De

Wild.) Troupin, *Michelsonia microphylla* (Troupin) Hauman. Forests dominated by one or another of these species reach their greatest extent in Zaire although *C. alexandri* forests are found in Uganda (Eggeling 1947, Hamilton 1981) and *G. dewevrei* dominated forests occur in Central African Republic, Cameroon, and Gabon (Letouzey 1970).

In the Congo basin, single-dominant forests are often evergreen communities occuring on well-drained soils. Such forests were classified as "les forêts ombrophiles equatoriales" (closed equatorial forests) and given the rank of order, Gilbertiodendretalia Dewevrei, by Lebrun and Gilbert (1954). They believed this order to correspond to the association, Tarrietia-Mapanietum, also apparently characterized by single dominance, described by Mangenot (1950) for the Ivory Coast in West Africa. In central Africa, the order is best represented in a large arc surrounding the Congo basin to the north and east. The Ituri Forest occurs in this area. Lebrun and Gilbert (1954) surmised that the poor representation of this forest type in the low-lying interior of the Congo basin was probably due to the abundance of marshy and flooded substrates.

Single-dominant evergreen forests on well-drained soils occur in the American tropics (Beard 1946, Richards 1952), tropical Australia (Joseph Connell, personal communication), and Southeast Asia (Zon 1915, Laan 1927, Koopman and Verhoff 1938, Whitmore 1984). In many of the mentioned forests the dominant accounts for more than 80% of the canopy-size trees.

Single-dominant forests are sometimes confined to relatively small areas within a sea of mixed tropical forest, as, for instance, *Talbotiella gentii* Hutch. & Greenway (Caesalpiniaceae) forest in Ghana (Swaine and Hall 1981), *Brachystegia laurentii* forest in Zaire (Germain and Evrard 1956) and *Lecomptedoxa klaineana* (Pierre) Dubard (Sapotaceae) forest in Cameroon (Duncan Thomas, personal communication). They are also found covering thousands of hectares, as with *Mora excelsa* Benth. forest in Malaya (Lee 1967, Whitmore *Dryobalanops aromatica* Gaertn. forest in Malaya (Lee 1967, Whitmore 1984), and *Gilbertiodendron dewevrei* forest in Zaire (Gérard 1960).

Gilbertiodendron dewevrei dominates extensive areas of upland forest at the center of its range; however, it is also found as smaller patches or galleries along watercourses in areas where the principal forest type is mixed (Louis 1947, Gérard 1960, Pecrot and Leonard 1960, Jamagne 1965). It has been suggested that small islands of the monodominant forest might be restricted to moister areas beyond the "real" climatic limit of the forest type (Gérard 1960).

OBJECTIVES

The objective of this study was to investigate the possibility that monodominance by *Gilbertiodendron dewevrei* in mbau forest depends on successional stage or soil conditions. It was assumed that if either factor was critical, it would be significantly different between mbau forest and the adjacent mixed forest in which *G.*

dewevrei is essentially absent. The hypotheses tested were:

1. The mbau forest is a younger successional forest than mixed forest. This is tested by determining the relative importance of shade-tolerant species in different size classes.

2. Soil conditions in mbau forest, including soil texture and chemical composition, are different from in mixed forest. This is tested by comparing these soil parameters in both forest types.

As suggested in the background section, the transition between the two forest types in the study area may represent a climatic limit for either *G. dewevrei* or important species of the mixed forest. If this is the case it may be reflected in the species composition of the forest islands located beyond the main transition area. The climatically-stressed species were expected to have a lower representation and to exhibit poorer regeneration in the forest islands than in the main forest blocks. Alternatively the soil texture of outlying "islands" may compensate for the climatic stress in the surrounding forest resulting in range-extended moisture-limited species on soils with good water-holding capacity. The hypotheses tested were:

3. The representation of *G. dewevrei* in canopy and/or juvenile size classes is lower in small isolated islands of mbau forest than in large unbroken blocks of mbau forest. This is tested by comparing the density of the species in randomly-located plots both in mbau forest islands and in areas where mbau forest is well established over two or more contiguous square kilometers.

4. The soil texture is significantly different in small islands of

one forest type from the soil texture of the surrounding forest type. This is tested by comparison of the percent sand composition of these soils.

It was beyond the scope of this study to make field visits to mbau forests in other parts of the range of *G. dewevrei*. The components of forest composition and structure which suggest the community is successional or mature in the Ituri region may not be consistent for mbau forest in other parts of its range. Likewise, interpretation of an association between certain edaphic factors and mbau forest distribution in the study area would be improved by information concerning mbau forest soils in other areas.

Comparison of forest composition and structure between the mbau forest in the study area and another mbau forest is made possible by the detailed study of mbau forest made by Gérard (1960) in the Uele region, 400-500 km northwest of the Ituri research site. Gérard carried out a floristic inventory of mbau forest modelled on the Braun-Blanquet phytosociological method but with an important modification. He collected quantitative data on species' presence by circumference class. This permited a comparison of the relative importance of dominant species in different size classes for the Uele and Ituri forests.

There are also published reports which provide evidence of the various edaphic conditions which have supported mbau forest. In the 1950s and the 1960s several installments of a larger project to map the soils and vegetation of the then Belgian Congo were published (Frankart 1960, Jamagne 1965, Jongen, et al. 1960, Pecrot and Leonard 1960, Wambeke and Evrard 1954). This project was not finished. The areas mapped did not include the center of *Gilbertiodendron dewevrei*'s range but peripheral areas to the northwest and south were included. These studies along with our own observations and those of Gérard (1960) and Louis (1947) allowed an assessment of the range of soils, over a large area, on which mbau forest occurs.

STUDY SITE

The field study was conducted between January 1981 and June 1983 in the central part of the Ituri Forest. Most field work occurred within a 15 km radius of the town of Epulu (1°25'N, 28°35'E) at a transition zone between mbau forest, dominated by the single species, *Gilbertiodendron dewevrei*, and mixed forest (Figure 2). The Ituri Forest is bordered to the north and northeast by savanna (Figure 1). The closest savanna/forest transition is 150 km from Epulu. To the east and southeast the Ituri Forest is bordered by mountain forest. To the south and west there is continuous forest.

The soils in the central Ituri Forest developed from granites, gneisses, and "very metamorphosed rock" of Precambrian age (Cahen and Lepersonne 1948). Along with mbau and mixed forest there are areas of periodically flooded forest along river courses and drier hilltop forests. The two latter communities showed distinct structural and compositional characteristics and were not included in this study.

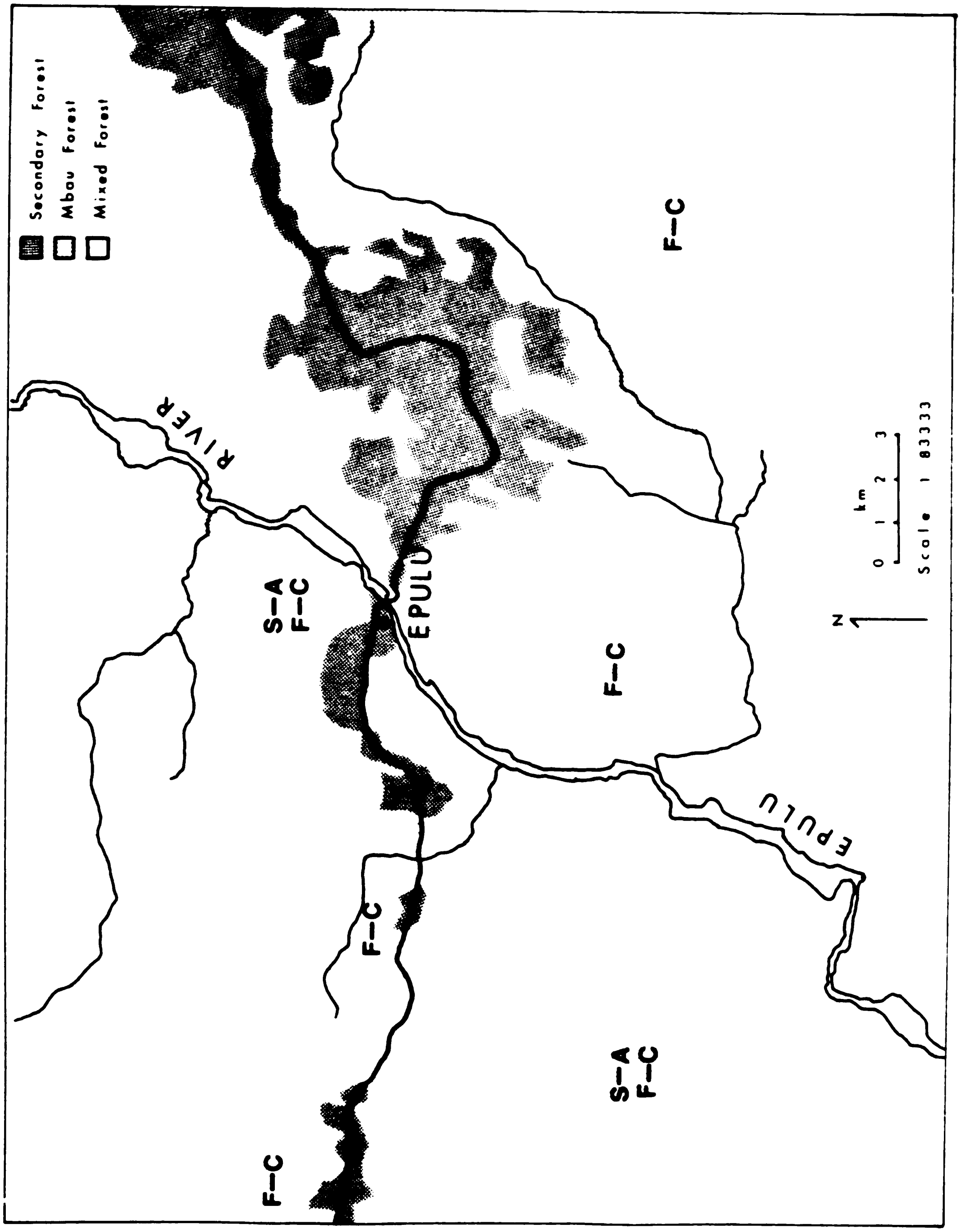
The transition from mbau forest to mixed forest is abrupt and

Figure 2. The central Ituri Forest study site, with locations of forest types and research areas.

Plot locations:

S-A ... Species-area relationships

F-C ... Forest composition


▨ Secondary Forest
☐ Mbau Forest
☐ Mixed Forest
F—C
S—A
F—C
RIVER
EPULU
F—C
EPULU
F—C
S—A
F—C
F—C
N
0 1 2 3
km
Scale 1 83333

occurs without any altitudinal or other apparent change in topography. Edaphic differences related to topography were avoided by sampling only mbau and mixed forest from well-drained upland sites. The two forest types have extensive common borders; therefore, the same pool of tree species is available for colonization of both communities along the transition zone.

There has been no long-term collection of meteorological data in the Ituri Forest. Bultot (1971) has the most complete compendium of climatic data for Zaire. He estimates annual rainfall to be between 1700 and 1800 mm for the Ituri Forest based on 30 years of records at surrounding stations. He further projects that once in forty years an annual maximum of between 2200 and 2400 mm and an annual minimum of between 1400 and 1600 mm of rainfall will occur. According to Bultot, three months, December, January, and February, are likely to receive less than 100 mm of rain per month. This corresponds to observations made at Epulu during this study. Of the three "dry seasons" in 1981-1983, two had monthly rainfalls of less than 100 mm for January and February.

The climatic records most pertinent to this study were collected, starting in the 1930s, at Kisangani and Yangambi, 460 and 520 km west, respectively, from the Epulu study site. Forests similar to those at Epulu occur in the vicinity of Yangambi and Kisangani. There are areas of forest dominated by the same species which are dominant at Epulu, notably *B. laurentii* and *G. dewevrei*. The elevation at Yangambi is 470 m whereas the Epulu study site is at 750 m. The change in elevation is gradual but is likely associated with lower mean annual temperatures at Epulu. Latitudes are similar (0°49'N at Yangambi and 1°25'N at Epulu) and the mean annual precipitation is similar, 1700 - 1800 mm rainfall. The annual mean temperature at Yangambi is 24.5°C (for years 1932-1938) with no monthly means greater than 25.2°C (Bernard 1945). The mean annual biotemperature is, therefore, equal to the mean annual recorded temperature (see Holdridge et al. 1971).

Using these data it is possible to classify Yangambi according to the Holdridge Life Zone system (Holdridge et al. 1971) as Subtropical Moist Forest, warm transition. Epulu is also in the same Life Zone although possibly not the warm transition.

This classification, however, seems inappropriate on two counts. First, the subtropical category is misleading as both sites are less than 2° from the equator and both span the equator. The second has to do with the physiognomy and phenology of the forests themselves. Subtropical moist forests as described by Holdridge et al. (1971: 703-711) are shorter, more deciduous and drier than the central African forests. As described by Holdridge et al., in this Life Zone trees larger than 25 cm dbh (diameter at 1.5 m from the ground) are uncommon, lianas are rare and no distinct species-dominants are present. None of these characteristics fit the forests encircling the Congo basin. A possible reason for the striking difference in forests which are purportedly of the same Life Zone is the difference in seasonality. The Subtropical Moist Forests described by Holdridge et al. (1971) had longer, more accentuated dry seasons.

The fact that the Holdridge Life Zone system is not easily used for classification of central African vegetation does not mean that the distribution of dominant species is independent of climatic factors. Nor does it follow that the physiognomy of the forest is not correlated with climatic factors. Gérard (1960) has suggested that the northern limit of forests dominated by *G. dewevrei* corresponds roughly with the northern limit of the Am climatic region as defined by Koppen and mapped by Bultot (1950). However, this has not been verified throughout the range of this forest type.

White (1983) classifies the vegetation of Africa into relatively broad categories. The scheme was developed uniquely for African vegetation. The Ituri Forest and most of the forest in the Guineo-Congolian region are classified as "rain forest". The forests in this group are generally greater than 30 m in height, are primarily evergreen, and contain abundant lianas. Within this broad classification the Ituri Forest would likely fall into two of White's subgroups: the mbau forest belonging to "single dominant moist evergreen and semi-evergreen rain forest" and mixed forest belonging to "mixed moist semi-evergreen rain forest". All the dominants in the Ituri Forest are evergreen but the canopy contains scattered deciduous elements as well.

White's classification, which is based on physiognomy, has no pretension of being finely tuned to climatic variation. He does, however, make the general observation that African rain forests are dry relative to the so-called rain forests in other tropical regions.

METHODS

Species-area curves were generated for both mixed forest and mbau forest from one series of nested plots in each forest type (located in Figure 2 as S-A). The smallest plot was a square of 10m on a side; this was included in a plot of 20 m on a side which was included in a plot of 40 m on a side and so on. The dimensions of each plot were twice those of the previous plot with the largest plots being a square of 160 m on a side (= 2.56 ha). Only stems greater than 2.5 cm dbh were counted, with all new species on any plot being added to the cumulative total to make the next point on the species-area curve.

Recognizing the possibility for local and regional differences in forest diversity and structure, forest composition data were collected from six different sites, three in mixed and three in mbau forest (located on Figure 2 as F-C). There were eight plots surveyed per site totaling 24 square plots, of 625 m^2 per plot, in each forest type. All trees > 10 cm dbh and all lianes > 2.5 cm diameter were identified to species or common name. At each site four of the eight 25 m x 25 m plots were divided into smaller nested plots. In 15 m x 15 m plots all saplings > 2.5 cm dbh and $\leq$ 10 cm dbh were identified. In 5 m x 5 m plots stems > 0.5 m in height but $\leq$ 2.5 cm dbh were identified. Finally, seedlings $\leq$ 0.5 m in height were sampled in 2.5 m x 2.5 m plots. The diameter at breast height (1.5 m) or above buttresses was measured for all individuals > 10 cm dbh. These larger individuals were also permanently marked with aluminum tags.

Field identifications were made by local field workers using Kibila, the vernacular, common names. We worked with a group of men from several local bands of semi-nomadic hunter-gatherers. Although the composition of the field crew fluctuated over the 30-month study period all workers assisted in both mbau and mixed forest. Two elder men who were consistently part of the work crew made identifications separately.

Our main aim was to differentiate between biological species. Along with vernacular names, bark, slash, and leaf characteristics were used. Whenever an identification was suspect (possibly the same or different from previous identifications) we sent a climber to collect leaves to be used for later comparisons

In conjunction with the forest composition work, 464 fertile collections of botanical specimens, primarily trees, were made. These were identified with the help of H. Breyne at the national herbarium in Kinshasa, Zaire, L. Liben at the Jardin Botanique at Meise, Belgium, and Terry Pennington at Kew, Surrey, England. Additional identifications were made by A.J.M. Leuwenberg (Apocynaceae) and F. White (Ebenaceae). Sterile specimens were compared to our duplicates of the fertile material of the same common name. We have confidence in the integrity of biological species identified at each site. There is a greater possibility that the same species might have been given more than one name or that different species might have been given the same name at different sites. All calculations, therefore, were made on a site by site basis. Full collections of the fertile specimens are at the national herbarium in Kinshasa, Zaire, and at the Jardin Botanique National at Meise, Belgium.

Two to four soil samples at a 20 cm depth were taken at each of the six sites (F-C, fig. 2) for a total of 22 samples. This depth was chosen to be below the immediate influence of leachates from the litter yet within the root zone of established seedlings. An additional 11 soil samples were taken at 150 cm depth. Textural analysis of the soils was made using a soil hydrometer method (Brower and Zar 1977). Soil was mixed 1:1 with water for pH readings. Chemical analyses were made following the recommendations of the North Dakota Agricultural Experiment Station Bulletin #499 (Dahnke 1980). Phosphorus was extracted with hydrochloric acid in ammonium fluoride and the concentration determined with a colorimeter. Exchangeable cations were extracted with ammonium acetate and their concentration determined with the atomic absorption spectrophotometer at the Michigan State University soil laboratory.

A soil sample was taken from the center of each of three small islands of mbau forest (consisting of approximately 10-20 mature *G. dewevrei*). Two samples were also taken from the surrounding mixed forest on opposite sides of each mbau island. The soils from five islands of mixed forest isolated within mbau forest were similarly sampled. The islands of mixed forest were less than 1000 m^2 in size, and were areas conspicuously lacking *G. dewevrei* (generally dominated by *B. laurentii*). A textural analysis (hydrometer method) was made of these soils.

The floristic composition of four islands of mbau forest, surrounded by mixed forest, was sampled. These islands are too small to appear on Figure 2. They varied in size from approximately 0.1 ha to 1.0 ha. All stems > 2.5 cm dbh were identified to species or common name in two 15 m x 15 m plots in each island. Diameter measurements were taken on all trees > 10 cm dbh. *G. dewevrei* seedlings were recorded in a 5 m x 5 m plot included in each larger plot. Seedlings were noted as being in one of two size classes: $\leq$ 0.5 m in height or stems > 0.5 m in height but $\leq$ 2.5 cm dbh.

Structural and floristic differences among the study sites were examined by Student's *t* test or by analysis of variance (nested design, and single classification with pre-planned comparisons). Differences in the soil characteristics were examined separately by Student's *t* test but, due to the inflated error rates that result if *t*-test procedures are applied to more than one outcome measure (Harris 1975), Hotelling's T^2 test is used to test the overall null hypothesis that soils in the two forests do not differ in their means for any of the measured parameters.

RESULTS

Forest Description

The striking visual difference between single-dominant mbau forest and the mixed forest results from their contrasting structures (Table 1). Both are tall forests with most canopy crowns attaining between 30 and 40 meters in height. At this height, the mbau forest crown is homogeneous, formed of the contiguous crowns of *G.*

dewevrei trees. Crowns of this species are deep and narrow. The crown frequently accounts for more than half of a tree's total height with a diameter of no more than 10 or 15 meters (G{rard 1960, pers. obs.)

The mixed forest canopy, on the other hand, is more heterogeneous with frequent emergents of 50 or more meters in height. Canopy level crowns are often not contiguous. The openess this creates in the upper level of the forest is accentuated by the fact that the most abundant species have broad crowns with the leaves often concentrated towards the ends of branches (Germain and Evrard 1956). Crown diameter of *B. laurentii*, one of the most frequent canopy species, averages 20 to 30 meters (pers. obs.).

The understories of both forest types are open, allowing easy foot passage and good visibility for 10 meters or more. In mixed forest a subcanopy layer between 10 and 25 meters in height becomes dense in irregular patches. Although isolated individuals of all heights are present in mbau forest, an identifiable middle layer above 10 meters is absent.

Standard diversity indices from mixed forest are significantly higher than those from mbau forest (Table 1). The difference was significant for both Simpson's and Shannon's diversity indices, both of which take into account not only the number of species but also the proportion of the total which occurs in each species.

Three dominance indices were calculated; all show significantly greater dominance by a single species in mbau forest than mixed forest (Table 1). In mbau forest *G. dewevrei* accounted for

Table 1. **Structure and composition of mixed forest and mbau forest in the Ituri Forest of Zaire.**

		mbau forest	mixed forest	
canopy at 35-40 meters		closed canopy contiguous crowns crowns deep and narrow	broken canopy frequent emergents crowns shallow and wide	
subcanopy		open middle layer absent	open middle layer, 10-25 m	
diversity[a]				
Ds	$\bar{x}$	0.37	0.89	P<.01[b]
	SD	(0.10)	(0.05)	
H'	$\bar{x}$	0.45	1.35	P<.001
	SD	(0.12)	(0.11)	
dominance[c]				
% stems	$\bar{x}$	79.13	28.37	P<.01
	SD	(6.5)	(11.6)	
Simpson 1	$\bar{x}$	0.63	0.11	P<.01
	SD	(0.10)	(0.05)	
IR	$\bar{x}$	0.68	0.22	P<.001
	SD	(0.06)	(0.06)	

[a] The mean of three site values for each forest type; each site value was calculated for eight combined 625 m plots at each site. Calculated only for stems >10 cm dbh.

Ds : Simpson diversity index : $\frac{\sum ni(ni-1)}{N(N-1)}$ where ni is the number of individuals of species i and N is the total number of individuals.

H' : Shannon diversity index : $-\sum(ni/N)\log(ni/N)$

[b] Analysis by Student's *t* test; arcsine transformation of percentages used for calculations.

[c] The mean of three sites, as with the diversity indices.

% stems : percentage of all stems > 10 cm dbh accounted for by the most abundant species (G. dewevrei in mbau forest; B. laurentii in mixed forest).

Simpson 1 : Simpson's dominance index $\frac{\sum ni(ni-1)}{N(N-1)}$

IR : Importance Ratio $\frac{RD + Rf + RC}{3}$ where RD, Rf, and RC are the density, frequency, and coverage of the most abundant species in each forest type relative to the density, frequency and coverage of all other species present.

79% of all stems >10 cm dbh. *B. laurentii*, the most common canopy species in mixed forest, accounted for only 28% of all stems >10 cm dbh. Simpson's dominance index, which incorporates densities of all species present, was significantly higher for mbau forest than for mixed forest. The importance ratio, also significantly greater for *G. dewevrei* in mbau forest than *B. laurentii* in mixed forest, included in each case, the relative frequency, density, and coverage (measured as basal area) of the dominant species in its forest type.

Species-area relationships were compared after censusing 2.56 ha plots in each forest type. The mixed forest area contained 143 woody species > 2.5 cm diameter, 111 of which were trees. The remainder were lianas. The mbau forest area contained a total of 95 species > 2.5 cm diameter of which 74 were trees (Appendix A). These values represent 33.6% fewer total species and 33.3% fewer tree species, respectively, than in mixed forest. The species-area curve (Figure 3) showed greater leveling off for mbau forest, on the largest plots, than was shown for mixed forest. There was only a 7.9% increase in cumulative number of species between the 1.28 ha and 2.56 ha plots for mbau forest whereas, for the same increase in sample area, there was a 16.3% increase in cumulative number of species for mixed forest (Appendix A).

A statistical comparison of species richness for different size classes was made from the replicated plots. There were consistently more tree species in mixed forest plots than in mbau forest plots for all size classes sampled (Table 2). Even the largest size class (stems > 50 cm dbh), where mixed forest averaged fewer trees

Figure 3. Species-area curves generated for stems >2.5 cm dbh in mixed and mbau forest types of the Ituri Forest, Zaire.

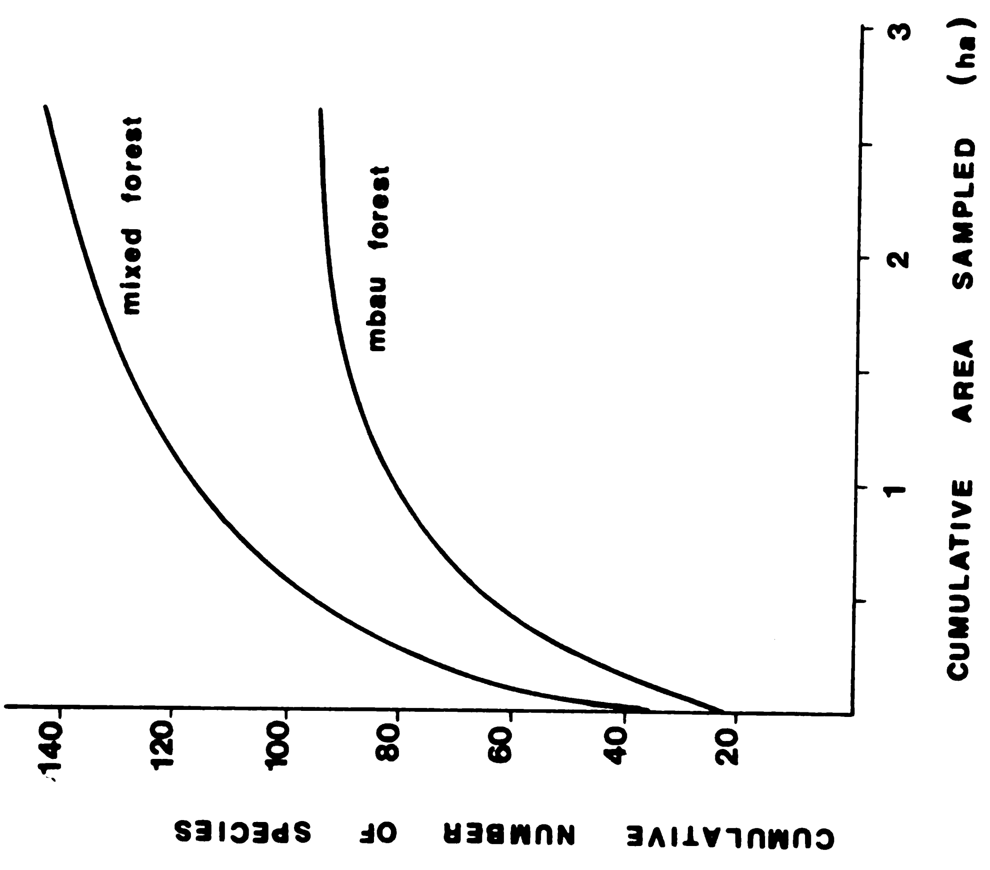

CUMULATIVE NUMBER OF SPECIES
140
120
100
80
60
40
20
mixed forest
mbau forest
1
2
3
CUMULATIVE AREA SAMPLED (ha)

TABLE 2. Species richness and stem density for different size classes in mixed and mbau forests types of the Ituri Forest, Zaire.

size class[a]	plot size(m^2)	plot number per forest	Average number of species per plot: mbau forest	Average number of species per plot: mixed forest	P[b]	Average number of stems per hectare: mbau forest	Average number of stems per hectare: mixed forest	P[b]
seedlings	25	12	--	--		28,000	21,833	NS
saplings	225	12	12.5	19.4	P<.01	1,911	2,700	P<.001
poles	625	24	3.5	12.3	P<.001	191	344	P<.001
trees	625	24	1.5	3.8	P<.01	77	96	NS
large trees	625	24	1.2	1.8	P<.05	55	37	P<.05

[a] Size classes: seedlings, >0.5 m height ≤2.5 cm dbh; saplings, >2.5 cm dbh ≤10 cm dbh; poles, >10 cm dbh ≤25 cm dbh; trees, >25 cm dbh ≤50 cm dbh; large trees, >50 cm dbh.

[b] Analysis by 1-way ANOVA with preplanned comparisons.

for a given area, contained more tree species in that area (Table 2). An average of 18 species (SD=3.6) per 0.5 ha sampled occurred in mbau forest whereas, there were 65 species (SD=11.8) for the same area sampled in mixed forest for all trees > 10 cm dbh.

Mixed forest had significantly fewer large trees per hectare but its sapling (>2.5 cm dbh ≤10 cm dbh) and pole (>10 cm dbh ≤25 cm dbh) size classes were significantly denser than in mbau forest (Table 2). This difference in size class distribution may correspond to the contrasts in forest structure especially the more broken upper canopy and denser middle story observed in mixed forest.

Despite different distributions across the size classes, mean basal area for the two forests was not significantly different ($P > .05$) for trees > 10 cm dbh. Mbau forest basal area is 34.0 m^2 per ha and mixed forest basal area is 30.4 m^2 per ha.

Major Species

In mbau forest a significantly greater proportion of the basal area was accounted for by a single species than in mixed forest. *Gilbertiodendron dewevrei* accounted for 88% of the mbau forest basal area whereas the species accounting for the greatest basal area in mixed forest, *Brachystegia laurentii*, only made up 32% of the total basal area ($P < .001$, Student's t test). Calculated over all three sites, *G. dewevrei* had a mean basal area of 29.9 m^2 per ha; this was almost three times the basal area of *B. laurentii* in mixed forest, 10.1 m^2 per ha.

Despite the difference in dominance between the two forest types, the species composition of subdominants was remarkably similar. After *Brachystegia laurentii*, the species with the greatest basal area in mixed forest were *Cynometra alexandri* with a mean basal area of 4.99 m^2 per ha, *Cleistanthus michelsonii* with 3.27 m^2 per ha, and *Klainedoxa gabonensis* with 0.9 m^2 per ha (Table 3). These three species were also present in mbau forest. Along with *B. laurentii* and *Uapaca guineensis* (Don) Muell. Arg. (Euphorbiaceae) they made the most significant addition to basal area after *G. dewevrei*. Their contribution, however, was much less in mbau forest than in mixed forest (Table 3) and their occurrence more erratic. *C. alexandri*, for instance, is absent from all eight plots of two of the mbau forest sites. This pattern is exemplified by *U. guineensis* (not in Table 3) whose basal area contribution averaged over all three sites was 0.54 m^2 per ha; however, most of this was due to a single large tree of over 100 cm dbh occurring in a single plot.

The dominant species in mbau forest and the most important species in mixed forest are taxonomically related. *Gilbertiodendron dewevrei* and *Brachystegia laurentii* belong to the same tribe, Amherstieae, of the Caesalpiniaceae. The Congo basin is also the center of distribution for both these species although *G. dewevrei* is known from throughout the central Guineen Region including Gabon, Cameroun, and northern Angola. The second most important species in mixed forest, *Cynometra alexandri*, (Table 3) is also a member of the Caesalpiniaceae; however, it belongs to the tribe Cynometreae. *C. alexandri* extends farther east than the two former species, into

TABLE 3. Basal area of species accounting for >0.5% of basal area in mbau forest and/or mixed forest.[a]

site[b]	*Brachystegia laurentii*	*Cleistanthus michelsonii*	*Cynometra alexandri*	*Klainedoxa gabonensis*	*Gilbertiodendron dewevrei*
MBAU FOREST					
Abeto	0.91	0.23	0.00	0.29	26.57
Sambo	0.66	0.19	0.00	0.42	29.41
Mangb.	0.00	0.00	0.42	1.20	33.62
$\bar{x}$	0.52	0.14	0.14	0.64	29.87
(SD)[c]	(0.47)	(0.12)	(0.24)	(0.49)	(3.55)
MIXED FOREST					
Kapit.	9.75	4.03	3.85	0.55	0.00
Apanz.	8.20	3.99	3.80	0.55	0.00
Epulu	12.38	1.80	7.32	1.59	0.00
$\bar{x}$	10.11	3.27	4.99	0.90	0.00
(SD)	(2.11)	(1.28)	(2.02)	(0.60)	0.00

[a] Basal area is presented as the sum for each species, over the eight 625 m^2 plots at a given sampling site, reported as m^2 per hectare.

[b] site abreviations: Mangb. = Mangbara, Kapit. = Kapituri, Apanz. = Apanzoki.

[c] SD = standard deviation.

the westernmost pockets of forest in Uganda. The next two most important species belong to different families; *Cleistanthus michelsonii* is of the Euphorbiaceae and *Klainedoxa gabonensis* is of the Irvingeaceae (Simaroubaceae).

Distribution of Shade-tolerant Species

All the canopy species with large basal area in either forest type were present in the shadey understory as well (Table 4). *Gilbertiodendron dewevrei* and *Brachystegia laurentii* had the greatest representation of shade-suppressed regeneration in the subcanopy; however, the subdominant species were found in smaller size classes under undisturbed canopy as well (Table 4). The typical pattern for shade-tolerant species, of decreasing density from small to large diameter classes, was shown for *C. michelsonii* (mixed forest and mbau forest), *C. alexandri* (mixed forest), *B. laurentii* (mixed forest), and *G. dewevrei* (mbau forest).

Some species occurred as large emergents in both forest types but were unrepresented in the understory. This group included more species than the shade-tolerant group but the individual species were considerably rarer. On the plots sampled, this group of species was represented by some of the largest individuals, including in mixed forest : *Irvingia gabonensis* (Lecomte ex O'Rorke) Baille (Irvingiaceae), *Irvingia robur* Mildbr. (Irvingiaceae), *Irvingia grandifolia* (Engl.) Engl. (Irvingiaceae), *Klainedoxa gabonensis* Pierre (Irvingiaceae), *Alstonia boonei* De Wild. (Apocynaceae), *Celtis adolphi-friderici* Engl. (Ulmaceae), *Pterocarpus soyauxii*

TABLE 4. Size class distribution of dominant and sub-dominant canopy species in the understories of mbau and mixed forests.

size class[a]	Mean number of individuals per hectare				
	C.michelsonii	*C.alexandri*	*K.gabonensis*	*B.laurentii*	*G.dewevrei*
MBAU FOREST					
saplings	7.4	0.0	0.0	18.5	307.0
poles	2.7	0.0	0.0	2.0	138.0
trees	1.3	1.3	0.7	3.3	62.0
large trees	0.0	0.0	2.0	0.0	66.0
MIXED FOREST					
saplings	55.6	18.5	7.4	178.0	0.0
poles	25.3	15.3	0.0	86.0	0.0
trees	10.0	8.0	0.0	39.0	0.0
large trees	4.7	11.0	2.7	11.0	0.0

[a] Size classes: seedlings, >0.5 m height ≤2.5 cm dbh; saplings, >2.5 cm dbh ≤10 cm dbh; poles, >10 cm dbh ≤25 cm dbh; trees, >25 cm dbh ≤50 cm dbh; large trees, >50 cm dbh.

(Papilionaceae), *Parinari congensis* (Rosaceae), *Piptadeniastrum afrcanun* (Hook.f.) Brenan (Mimosaceae). In mbau forest, on the plots sampled, fewer such species occurred, probably because of the rarity of all species other than *G. dewevrei*. Large emergents in the mbau forest plots included *Irvingia gabonensis*, *Tessmannia africana* Harms (Caesalpiniaceae) and *Uapaca guineensis* (Euphorbiaceae). These species, represented by large individuals, are apparently shade intolerant as juveniles and may indicate areas of past treefall disturbance in each forest type.

Soils

The soils under both mixed and mbau forest ranged in color from reddish brown through ocher to yellowish brown. Soils were generally deep, uniform in texture, and lacking distinct horizons from approximately 3 cm to 150 cm depth. Such uniformity is characteristic of tropical oxisols (Sanchez 1976). In only one of the 12 soil pits dug to take 1.5 m soil samples was there hard substrate. This was at 135 cm in one of the mbau forest pits. Red clay soils are uncommon in the central Ituri Forest; however, during the course of the study both forest types were seen growing on such soils.

There was no significant difference between mixed forest and mbau forest for most soil factors tested (Table 5). Although there was a significant difference in soil pH between the two forest types at 20 cm depth, both forests occurred on very acidic soils (mean pH of 3.9 and 4.2 for mixed and mbau respectively). Furthermore at 150 cm depth the difference in pH was no longer significant suggesting that the

TABLE 5. Soil properties in mixed forest and mbau forest types of the Ituri Forest, Zaire.

a. Mean values of the soil parameters analysed. Comparison was by student's *t* test, null hypothesis: no difference between forest types. nd = not detectable.

	mbau forest	mixed forest	P
20 cm depth	n = 12	n = 10	
pH	4.17	3.96	$P<.05$
% sand	71.7	64.4	NS
K ppm	88.0	77.0	NS
Ca ppm	130.0	150.0	NS
Mg ppm	nd	nd	
P ppm	nd	nd	
150 cm depth	n = 7	n = 4	
pH	4.24	4.00	NS
% sand	68.4	54.7	NS
K ppm	45.0	107.0	$P<.01$
Ca ppm	152.0	119.0	NS
Mg ppm	nd	nd	
P ppm	nd	nd	

b. Hotelling's T^2 test for all parameters analysed on 20 cm depth soil samples. The null hypothesis: there is no significant difference between the soils of mixed forest and the soils of mbau forest.

Hotellings *T* Square	6.7871	
F value	1.4423	
Degrees of freedom	4,17	
P value	< 0.2631	NS

slightly higher pH in mbau forest resulted from some difference in leachates from the distinctive and relatively thick leaf litter of mbau forest.

Phosphorus deficiency is common in acid soils (Andrew 1978); however, the failure to measure any available phosphate may have been a result of the extraction technique used. Bray-1 extracts calcium- and aluminum-bonded phosphates but not iron-bonded phosphates (Sanchez 1976). The proportion of total exchangeable phosphorus accounted for by iron phosphates increases with weathering as well as acidity (Sanchez 1976); therefore, the failure to detect available phosphorus using the Bray-1 procedure is indirect evidence of extensive weathering of the soils under both forest types.

The difference in potassium content of soils at 150 cm depth is unexplained (Table 5). There were only four sampling points for mixed forest at this depth and all of them were within a few kilometers of one another.

There were no significant differences in soil texture between the two forest types (Table 5). Mbau forest soils ranged from loamy sand to sandy clay with the majority of samples being either sandy loam or sandy clay loam. Mixed forest soils ranged from sandy clay loam to sandy clay with most being the former.

The difference between mean values of all measured soil variables for the two forest types at a 20 cm depth was tested simultaneously with Hotellings T^2 (Table 5b). It was concluded that the variation between the soils did not constitute a significant difference.

Forest Islands

The comparison between soil texture from isolated islands of one forest type and soil texture from the surrounding forest failed to reveal any significant differences (Appendix B). This was true for both mbau forest islands in mixed forest and mixed forest islands in mbau forest.

The floristic composition of mbau forest islands was not intermediate between mbau forest and mixed forest. The composition resembled that of the major blocks of unbroken mbau forest in the area. This similarity was apparent in the pattern of dominance for different size classes. Relative frequency (RF), relative density (RD) and relative coverage (RC) of large individuals of *G. dewevrei* in mbau islands consistently resembled the values for *G. dewevrei* in mbau forest more than the values of *B. laurentii* in mixed forest (Table 6a). Consequently the Importance Ratio, IR = (RF+RD+RC) - 3, for *G. dewevrei* in small islands of mbau forest paralleled the IR of *G. dewevrei* in large areas of unbroken mbau forest, for the size classes measured, more closely than the IR of the mixed forest dominant (Figure 4). The data were not available to calculate these values for smaller size classes;however, the absolute density and frequency of smaller stems of the dominant in mbau islands also followed the pattern of *G. dewevrei* in mbau forest more closely than the pattern of *B. laurentii* in mixed forest (Table 6b).

Correspondence was particularly close between the values for mbau forest and mbau islands in the largest size classes (>25 cm dbh,

Table 6. Average importance values of G. dewevrei in 4 mbau forest islands, compared to the importance of G. dewevrei in a large block of unbroken mbau forest and the importance of the principal dominant (*B. laurentii*) in a large block of unbroken mixed forest.[a]

a. Large size classes (> 10 cm dbh).[b]

	Size classes in cm dbh											
	>10 ≤25				>25 ≤50				>50			
	Rf	Rd	Rc	IR[a]	Rf	Rd	Rc	IR	Rf	Rd	Rc	IR
G.dewevrei in mbau islands	0.22	0.53	0.38	0.38	0.60	0.78	0.77	0.72	1.00	1.00	1.00	1.00
G.dewevrei in mbau forest	0.29	0.72	0.75	0.59	0.65	0.87	0.86	0.79	0.82	0.93	0.94	0.90
B.laurentii in mixed forest	0.08	0.25	0.29	0.21	0.21	0.41	0.40	0.34	0.25	0.31	0.27	0.28

b. Small size classes (< 10 cm dbh).[b]

	Size classes					
	<0.5 m height		>0.5 m height ≤2.5 cm dbh		>2.5 cm dbh ≤10 cm dbh	
	density	frequency	density	freq.	density	freq.
G.dewevrei in mbau islands	3,900	0.87	10,200	1.00	360	1.00
G.dewevrei in mbau forest	8,000	1.00	11,500	1.00	307	1.00
B.laurentii in mixed forest	15,467	0.83	1,467	0.75	178	0.92

[a] IR (importance ratio) = (Rf + Rd + Rc) ÷ 3 where:
Rf (relative frequency) = the frequency of the given species as a proportion of the sum of frequencies of all species; relative frequency.
Rd (relative density) = the density of individuals of the given species as a proportion of the summed density of all species.
Rc (relative coverage) = the basal area for the given species as a proportion of the total basal area for all species.

[b] Plot size: the two plots in each island of mbau were combined for calculations resulting in a plot size of 450 m in each of the islands for larger size classes. Size classes in mature forest as described in the text.

Figure 4. Importance ratios of the dominant species for different size classes in islands of mbau forests, large areas of mbau forest and mixed forest. (For derivation of importance ratios, see Table 6).

KEY:

✱—✱	*Gilbertiodendron dewevrei* in mbau forest islands.
□—□	*G. dewevrei* in large areas of mbau forest.
○—○	*Brachystegia laurentii* in large areas of mixed forest.

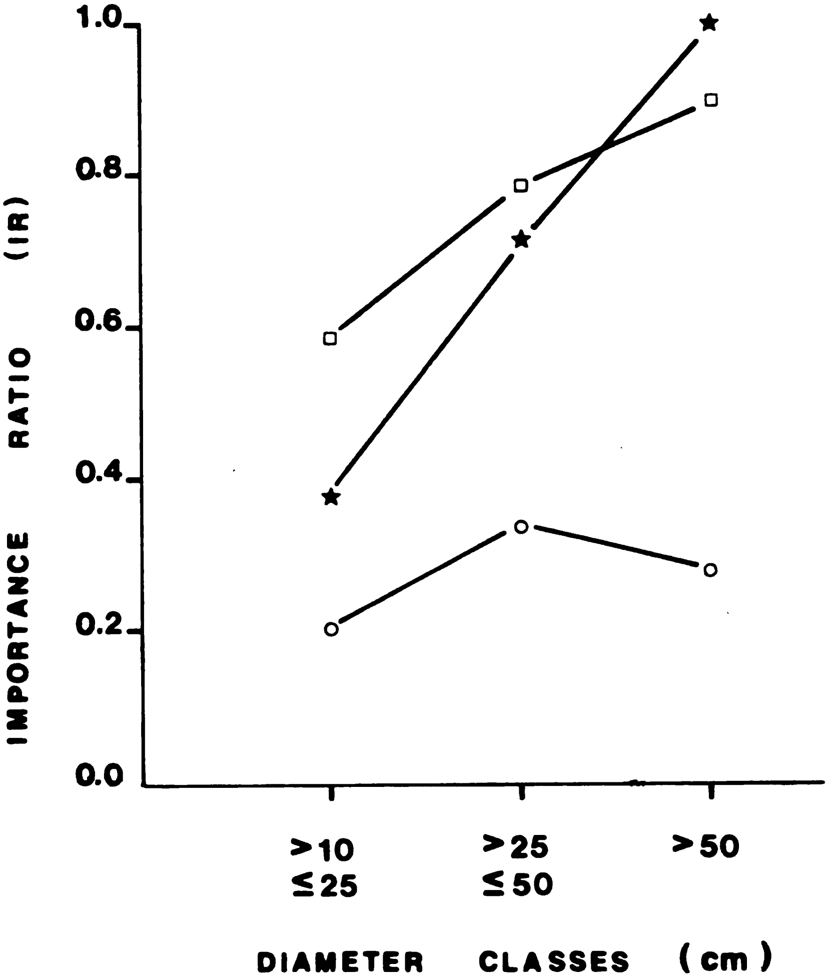

1.0
0.8
0.6
0.4
0.2
0.0
IMPORTANCE RATIO (IR)
>10
≤25
>25
≤50
>50
DIAMETER CLASSES (cm)

Table 6a) as well as in the large seedling and sapling size classes (>0.5 m height ≤10 cm dbh, Table 6b). The small seedling size class showed the greatest discrepancy between mbau forest and mbau island plots (Table 6b). The density of small seedlings of *G. dewevrei*, although variable, was frequently less in mbau islands than in unbroken mbau forest. The discrepancy was transitory across size classes; in the large seedling and sapling size classes, densities of *G. dewevrei* were similar in mbau islands and mbau forest. The reason for the relatively sparse layer of young seedlings in mbau islands was not determined although increased seed predation may be important (see chapter 3). In any case, advanced regeneration of *G. dewevrei* was abundant in mbau forest islands and, in general, regeneration of the dominant appeared to follow the same pattern in islands of mbau forest as in large blocks of mbau forest. In both cases the greatest density occurred in the size class between 0.5 m in height and 2.5 cm dbh. This is contrasts with *B. laurentii* in -ixed forest, which had a steadily decreasing density with increasing size classes (Table 6b).

DISCUSSION

The mbau forest in the Ituri study area.

The pronounced dominance by *G. dewevrei* and low species richness characterized mbau forest relative to mixed forest. Wherever

G. dewevrei occurred in the study area, it was overwhelmingly the canopy dominant. The species was never found as scattered individuals in mixed forest but only in apparently self-regenerating stands.

Despite the clear differentiation of the two communities they had similar basal areas. There did not appear to be any species restricted to one or the other forest type except *G. dewevrei*, which is restricted to mbau forest. Furthermore, the most abundant canopy trees in mixed forest are also the most frequent subdominants in mbau forest.

Neither forest type appeared to be successional. All the important canopy elements occurred in subcanopy size classes, indicating that the forests were self-replacing without major disturbance.

Neither mbau nor mixed forest was associated with a particular substrate in the Ituri area. Texture, color, depth and chemical composition of the soils were comparable.

Isolated stands of *G. dewevrei* occurring in mixed forest showed no evidence of being moisture-stressed outliers at the climatic limit of the species. The soil texture in forest islands was not different from the surrounding forest. The floristic composition of the islands was also similar to that of unbroken mbau forest as regards the degree of dominance of *G. dewevrei* in all size classes.

In summary, the distribution of the single-dominant mbau forest on the study site was not defined by soil factors. Neither the mbau forest nor the adjacent mixed forest appeared to be successional. At least at the scale of the central Ituri transition zone, it is necessary to look for other biotic or historical factors to account for the differences between the two forest types.

Mbau forests in other parts of G. dewevrei's range.

Wherever forests containing *G. dewevrei* have been described, the composition suggests that these are mature self-replacing communities. Vegetation surveys in the north and northeastern evergreen forests of Zaire have noted the dominance of *G. dewevrei* in all size classes whenever the species was encountered (Louis 1947, Jongen et al 1960; points C and E respectively in Figure 5). A recent report (Gauthier et al. 1977) described *G. dewevrei* forests in the central basin of the Zaire River in the Equateur Region. This is outside the area of principal representation of this forest type as delineated by Lebrun and Gilbert (1954). Nevertheless, wherever *G. dewevrei* occurred it was well represented in all size classes and usually dominant. Letouzey (1970) has reported "pure" stands of *G. dewevrei* in Central African Republic, Cameroun, and Gabon, sometimes covering dozens of hectares.

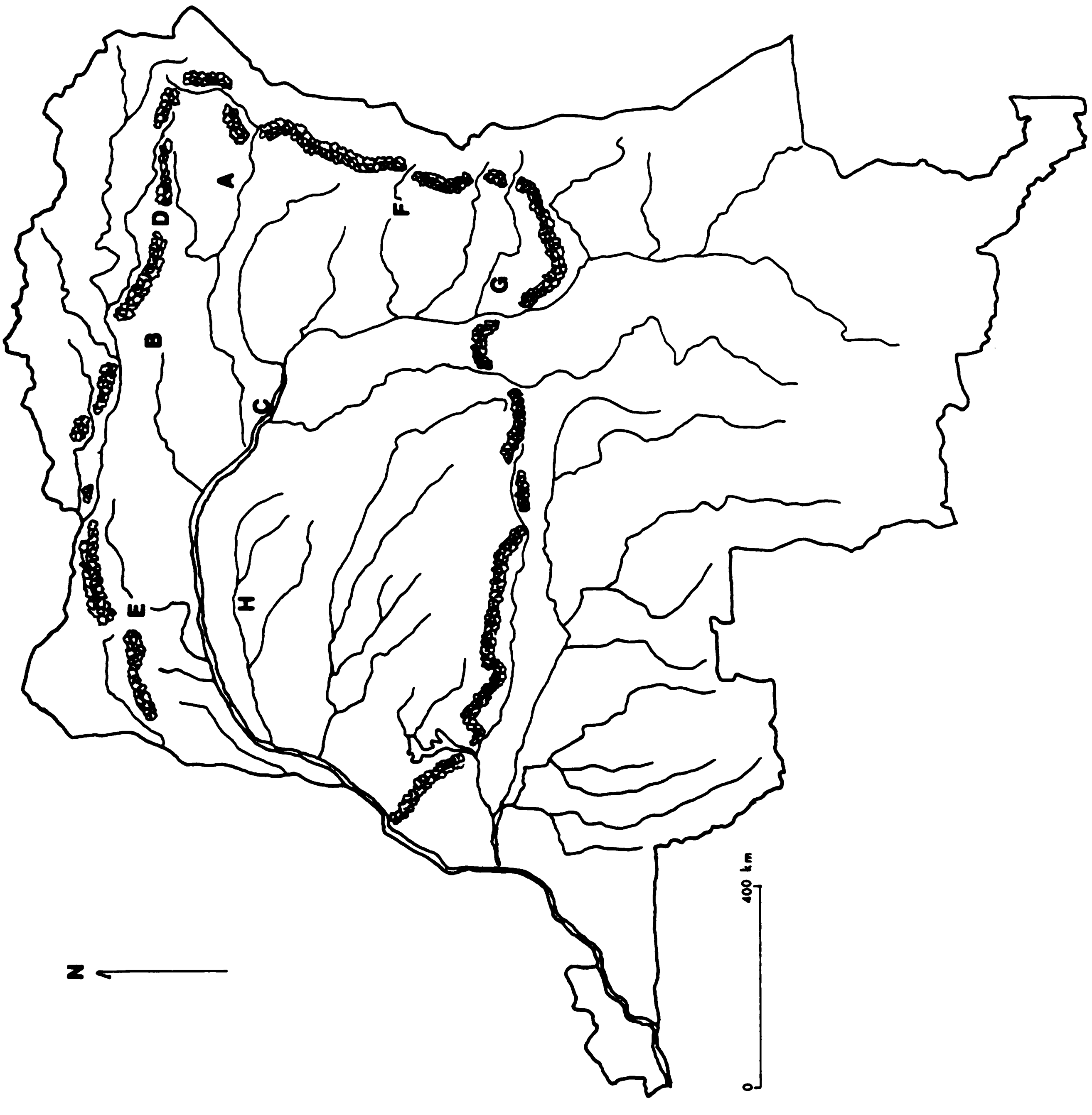
The most detailed study of an mbau forest outside of the Ituri region was made by Gérard (1960) in the Uele region (B on Figure 5). The canopy in nine of Gérard's 12 plots (each 2500 m^2) contained *G. dewevrei*. These are the plots used for comparison with the Ituri Forest, the other three plots were dominated by *Julbernardia seretii*.

The Uele plots that contained *G. dewevrei* were as clearly

Figure 5. Reported occurrences of mbau forest within the evergreen forest block of Zaire.

KEY:

▨ boundary of evergreen forest
A = Central Ituri (Epulu) study area
B = West Uele (Gérard 1960)
C = Yangambi (Louis 1947, Wambeke & Evrard 1954)
D = East Uele (Frankart 1960)
E = Ubangi (Jongen et al. 1960)
F = Kivu plateau (Pecrot & Leonard 1960)
G = Maniema (Jamagne 1965)
H = Equateur (Gauthier et al. 1977)


A
B
C
D
E
F
G
H
N
0
400 km

dominated by that species as were the mbau forest plots in the Ituri region even though they were more than 400 km to the southeast (Table 7). The largest two circumference classes had 87% and 90%, respectively, of all stems accounted for by *G. dewevrei* (Table 7). In the Ituri region the percent *G. dewevrei* in these size classes was 92% and 89%. The smallest circumference class, 10-50 cm, showed the greatest discrepancy with only 19% of stems in the Ituri being *G.dewevrei* whereas, in Uele, 34% were *G. dewevrei*. The smallest circumference class was the only class for which it was not possible to match the Ituri and the Uele size classes due to different data collection methods between the two sites. The inclusion of smaller individuals in the Ituri samples (down to 7.8 cm circumference) may have contributed to the seemingly greater dominance of *G. dewevrei* among saplings of the Uele forest.

Gérard did not present the information necessary for calculation of basal area; however, basal area was estimated from his data using the mid-point of each circumference class. If a mid-point of 80 cm dbh is used for the largest size class then the basal area of *G. dewevrei* in the Uele mbau forest is approximately 31 m^2 per hectare. This is similar to the 30 m^2 basal area of *G. dewevrei* for the same size classes in the Ituri mbau forest. There is evidence that 80 cm dbh is a reasonable mean for the largest size class from other data Gérard presents from a nearby (Batite) mbau forest (1960).

The structural similarity between the two forests is apparent from Gérard's evocative descriptions. He states that the mbau

TABLE 7. Comparative densities of *Gilbertiodendron dewevrei* in the mbau forests of the Uele and Ituri regions for different girth classes.

G. dewevrei stems	Size class (cm of circumference)							
	>200		100 - 200		50 - 100		10-50	
	Ituri	Uele	Ituri	Uele	Ituri	Uele	Ituri	Uele
stems per hectare ($\bar{x}$)	24	36	73	42	76	80	383	340
% of all stems	92	87	89	90	85	80	19	34

forest distinguishes itself from other "monophytique" or single-dominant forests by the extremely closed nature of its canopy. The canopy is almost exclusively *G. dewevrei* crowns that touch on all sides. There appear to be only two strata, with the space between shrub and canopy layers lightly filled by pole-size *G. dewevrei*. He further mentions that the herbaceous layer seems to be absent, "so much is the eye, from the first instant, struck by the single color and extent of the thick layer of large dead leaves" (Gérard 1960, p. 63, T. Hart translation). These "leaves" were the fallen leaflets of *G. dewevrei*. His descriptions are equally applicable to the Ituri mbau forest.

Floristic differences are among the most provocative between the two forests. *Julbernardia seretii* and *Staudtia stipitata* Warb. (Myristicaceae) were common subdominants in the Uele canopy and absent in the Ituri canopy. *Cleistanthus michelsonii* and *Brachystegia laurentii* occurred regularly in the Ituri mbau forest canopy but were absent from the Uele canopy. The distributions of these four evergreen species are restricted and unique to each species. The most widespread canopy level or emergent trees appear to be the rare deciduous ones; these latter species were similar at both Uele and the Ituri.

In summary, the dominance by *G. dewevrei* and its occurrence in all size classes appears to be consistent wherever the species occurs. There is not, however, a consistent group of tree species associated with *G. dewevrei*. The subdominant species vary and are shared with the mixed forest types in any given area. Tree species are not excluded from mbau forest. The common species of adjacent mixed forest occur in mbau fores, however, at low density.

Outside of the central Ituri Forest, mbau forest occurs on soils derived from a diversity of parent materials. In the central and northern range of *G. dewevrei* dominated forest (Ituri, Uele, and Ubangi), the soils are derived from Precambrian eruptive and metamorphic rocks. At its northern limits, mbau forest occurs on soils formed from decomposing lateritic shield dating from the end of the Tertiary (Ubangi and Uele). In the western part of the mbau forest distribution (Yangambi), the parent material is aeolian sand deposits of Pleistocene age whereas at the southern limit of its range (Kivu, Maniema),*G. dewevrei* occurs on soils from sedimentary rocks of Carboniferous and Permian age (Cahen and Lepersonne 1948, Heinzelin 1952, Wambeke and Evrard 1954, Gérard 1960, Jongen et al 1960, FAO/Unesco 1976).

The soils supporting *G. dewevrei*-dominated forest are at least as variable as the parent materials. In Uele, mbau forest is found on red clay soils and yellow gravelly soils with a sandy-clay matrix (Frankart 1960). On the Kivu plateau, mbau forest occurs on soils ranging from heavy yellow clay to yellow sandy alluvial soils (Pecrot and Leonard 1960). In Ubangi, *G. dewevrei*-dominated forest is found on red sandy clay soil as well as soils containing numerous chips of dismantling lateritic shield (Jongen et al. 1960). At Yangambi, mbau forest is found on white sands and yellow, ocher to brown sandy soils with variable clay content up to 30-40% (Louis 1947, Wambeke and Evrard 1954). Locations of these studies are given in Figure 5.

Gérard's study of mbau forest in the Uele region (1960) demonstrated the diversity of soils on which this forest type can be found even in a relatively restricted area. The plots surveyed were from several topographic positions. Plots taken at the bottom of slopes had deep sandy soils which were white to ocher. On the slopes the plots were on clay soils, red in color, and apparently underlain by a broken and weathering hard lateritic layer. Gérard did, however, report that depth of soil was an important local determinant of forest type. On shallow soils mbau forest was replaced by forest dominated by *Julbernardia seretii*.

In all the cartographic studies cited above, where both vegetation type and soil type were mapped, the borders of *G. dewevrei*-dominated forest failed to follow the outlines of soil types. This is in spite of the fact that in all of the mapped areas, blocks of mbau forest coexisted with blocks of more diverse mixed forest.

In summary, on the scale of the full range of *G. dewevrei* in Zaire there is no evidence that the single dominant mbau forest is restricted to poor soils or soils of any particular texture or parent material. In local areas mbau forest is sometimes restricted to galleries along rivers (Gérard 1960, Pecrot and Leonard 1960, Jamagne 1965). This may indicate that *G. dewevrei* is moisture limited on the higher ground. Alternatively, it may be the pattern left after cutting and cultivation of the upland forests. Although in the Ituri

Forest both of the principal forest types have the structure and composition of mature forests, in more accessible parts of the forest with longer histories of settlement by agriculturalists, secondary forest is likely much more widespread. A mosaic of mbau forest and secondary forest may exist.

A comparison of other single-dominant tropical forests with the mbau forest of central Africa.

There are a number of intriguing similarities between the single-dominant mbau forest and other single-dominant tropical forests. Excluding young secondary forests and communities of flooded or swampy substrates, there still remain reports of numerous such forests in the literature (Table 8).

The climatic information available indicates that evergreen forests dominated by a single species occur under a variety of rainfall regimes in the tropics (Table 8), including perhumid and seasonal areas. The information is not sufficient to preclude, however, that particular conditions may be more favorable to such forests than others.

The published descriptions do not support the view that these forests are distinct associations with characteristic species not found in other forest types. As was the case for mbau forest, the species which co-occur with the canopy dominant are usually also found in more diverse mixed forests (Table 8). Beard (1946), for instance, found that in Trinidad the species associated with *Mora excelsa* changed

Table 8. Summary of published information on single species dominant moist tropical forests.

Location	Dominant Species	rainfall cm/yr	Source	Size of Stands	Dominance	Substrate Specificity	Associated Species	Dispersal	Shade Tolerance
Malaya	*Shorea curtisii* (Dipterocarpaceae)	>200	Whitmore 1984 Burgess 1969, 1970	groves on hills	excludes other dominants	hill crests	similar to lowland Dipterocarp forest	poor dispersal	persistent seedlings
Malaya, Sumatra	*Dryobalanops aromatica* (Dipterocarpaceae)	>250	Whitmore 1984 Lee 1967	several thousand km^2	60-90 % timber volume	wide range of soils and topography	similar to adjacent Dipterocarp forest	?	very shade tolerant
Borneo, Sumatra	*Eusideroxylon zwageri* (Lauraceae)	>200	Koopman & Verhoef 1938	several thousand km^2	pure stands	wide range of soils	?	large, heavy seeds	shade tolerant
Trinidad	*Mora excelsa* (Caesalpiniaceae)	>200	Beard 1946	largest stand >21,000 ha	85-95 % canopy	wide range of soils variable topography	similar to adjacent mixed forest	falls beneath parent	shade tolerant
West Africa	*Talbotiella gentii* (Caesalpiniaceae)	about 100	Swaine & Hall 1981	1-2 ha	pure stands	varaible soils: parent material & pH	few associated canopy species	?	shade tolerant

Table 8. (continued)

Location	Dominant Species	rainfall cm/yr	Source	Size of Stands	Dominance	Substrate Specificity	Associated Species	Dispersal	Shade Tolerance
East Africa	*Cynometra alexandri* (Caesalpiniaceae)	about 180	Eggeling 1947	>11,000 ha	>75 % canopy	variable soil type	shared with mixed forest	poor dispersal	shade tolerant as sapling and larger
Central Africa	*Brachystegia laurentii* (Caesalpiniaceae)	about 180	Germain & Evrard 1956	2-15 ha	>90 % canopy	probably variable soil type	shared with mixed forest	poor dispersal	shade tolerant
Central Africa	*Gilbertiodendron dewevrei* (Caesalpiniaceae)	about 180	Gerard 1960 Louis 1947	10000-10,000 ha	>90 % canopy	wide range of soils variable topography	shared with adjacent mixed forest	very poor dispersal	shade tolerant
Central Africa	*Julbernardia seretii* (Caesalpiniaceae)	about 180	Gerard 1960	?	>90 % canopy	shallow soils	shared with adjacent mixed forest	?	shade tolerant

with location but were always the same as in the adjacent mixed forest.

From the available information, it is evident that single-dominant forests are not restricted to poor substrates. Edaphic factors may limit the distribution of some of these forests (Table 8), for instance those dominated by *S. curtisii* and *J. seretii*. Others span a diversity of edaphic conditions, for instance, forests dominated by *E. zwageri*, *M. excelsa*, *T. gentii*, and *C. alexandri*, as well as *G. dewevrei*. It is also worth noting that, in the case of *D. aromatica*-dominated or kapur forests, the single-dominant forest was assumed to be restricted to soils derived from sedimentary rocks (Whitmore 1984). A detailed field study found, however, that kapur forests "cut across edaphic boundaries in the same way as other Dipterocarp forests not containing kapur" (Lee 1967). The view of monodominant tropical forests as "anomalous" and "edaphic climaxes" is so entrenched in the lore of tropical ecology that such forests are assumed to be environmentally determined even when evidence to support this is lacking.

In all cases the dominant species was reported to be shade-tolerant (Table 8). The understory of these single-species-dominant forests contained abundant regeneration of the dominant. This is strong evidence for the maturity of these forests, all of which were considered self-replacing by the authors of their respective studies.

It is tempting to suggest that all these tropical single-dominant forests of well-drained upland sites constitute a cohesive forest type. This would suggest that similar mechanisms led to the relative poverty in species and strong dominance by a single species in all cases. The studies needed to substantiate this have not yet been done; neverthless, two characteristics shared by most, if not all, of the dominant species in these single dominant forests indicate that similar mechanisms may be involved in the maintenance of single species dominance. All species for which information was found had large poorly dispersed seeds which produced an abundance of shade tolerant juveniles (Table 8). Dispersal was generally ballistic expulsion of heavy propagules. There may or may not be other traits, shared by the forest dominants, affecting their competitive ability or stress tolerance.

A number of the studies reported that the boundaries of the single-dominant forest were not stable and that they appeared to be steadily encroaching on adjacent mixed forest (Beard 1946, Eggeling 1947, Louis 1947). In some areas, the current boundaries of the single-dominant forest may only reflect a slow rate of dispersal of the dominant species after ancient large-scale disturbance or climatic change.

In summary, there are mature "climax" tropical forests which are species poor and dominated by single tree species. Such communities do not exist solely because the dominant tree is the only available species that can tolerate severe edaphic conditions. Single-dominant forests and more diverse forests occur on the same substrates. Many of these monodominant forests span a variety of soil types and topographic positions.

The results of this study do not demonstrate that soil characteristics are unrelated to the floristic composition of mature tropical forests. They do, however, demonstrate that in the case of the single-dominant mbau forest, the mechanisms leading to monodominance by *G. dewevrei* are not closely linked to edaphic factors. As suggested in the literature, this may be the case for other tropical single-dominant forests as well.

FOOTNOTES

[1] The term "climax" is here given the meaning ascribed to it by H. S. Horn (1974), the stage when "changes in the specific composition of the community become undetectably slow or cease altogether".

[2] The term "climatic climax" is used to refer to the expected mature community in a given climatic zone wherever conditions (soils, topography, etc.) are not severely limiting.

APPENDIX A. Number of species > 2.5 cm dbh as a function of area in mixed and mbau forest.

area m^2	trees and lianes	number of species added	% increase	trees only	number of species added	% increase
MBAU FOREST						
100	14	--	--	8	--	--
200	16	2	14.3	10	2	25.0
400	26	10	62.5	20	10	100.0
800	34	8	30.8	28	8	40.0
1600	44	10	29.4	37	9	32.1
3200	56	12	27.3	47	10	27.0
6400	67	11	19.6	56	9	19.1
12800	88	21	31.3	70	14	25.0
25600	95	7	7.9	74	4	5.7
mean % increase			27.9			34.2
(SD)			(16.4)			(28.4)
MIXED FOREST						
100	19	--	--	15	--	--
200	26	7	36.8	20	5	33.3
400	37	11	42.3	30	10	50.0
800	54	17	45.9	42	8	26.7
1600	68	14	25.9	52	10	23.8
3200	85	17	25.0	66	14	26.9
6400	107	22	25.9	83	17	25.8
12800	123	16	14.9	95	12	14.5
25600	143	20	16.3	111	16	16.8
mean % increase			29.1			27.2
(SD)			(11.4)			(11.0)

APPENDIX B. Soil texture, measured as percent sand, of soils from forest islands and of soils from the surrounding forest type.[a]

a. Soils from islands of mbau forest and surrounding mixed forest.

	mbau forest islands	adjacent mixed forest	P[b]
	46.72	46.20	
		54.03	
	56.79	47.98	
		54.33	
	42.71	41.55	
		43.85	
mean	48.74	47.99	NS
(SD)[c]	(7.25)	(9.05)	

b. Soils from islands of mixed forest and surrounding mbau forest.

	mixed forest islands	adjacent mbau forest	P[b]
	54.57	50.13	
		49.40	
	48.68	65.65	
		54.09	
	53.07	55.33	
		57.10	
	57.67	63.79	
		52.80	
	58.24	52.54	
		66.37	
mean	54.45	56.72	NS
(SD)[c]	(3.87)	(6.33)	

---

[a] Composition reported as the arcsine transformation of percent sand.

[b] Student's *t* test was used to examine the null hypothesis that there is no significant difference in composition between soils inside and outside the island. NS = P>.05.

[c] SD = standard deviation.

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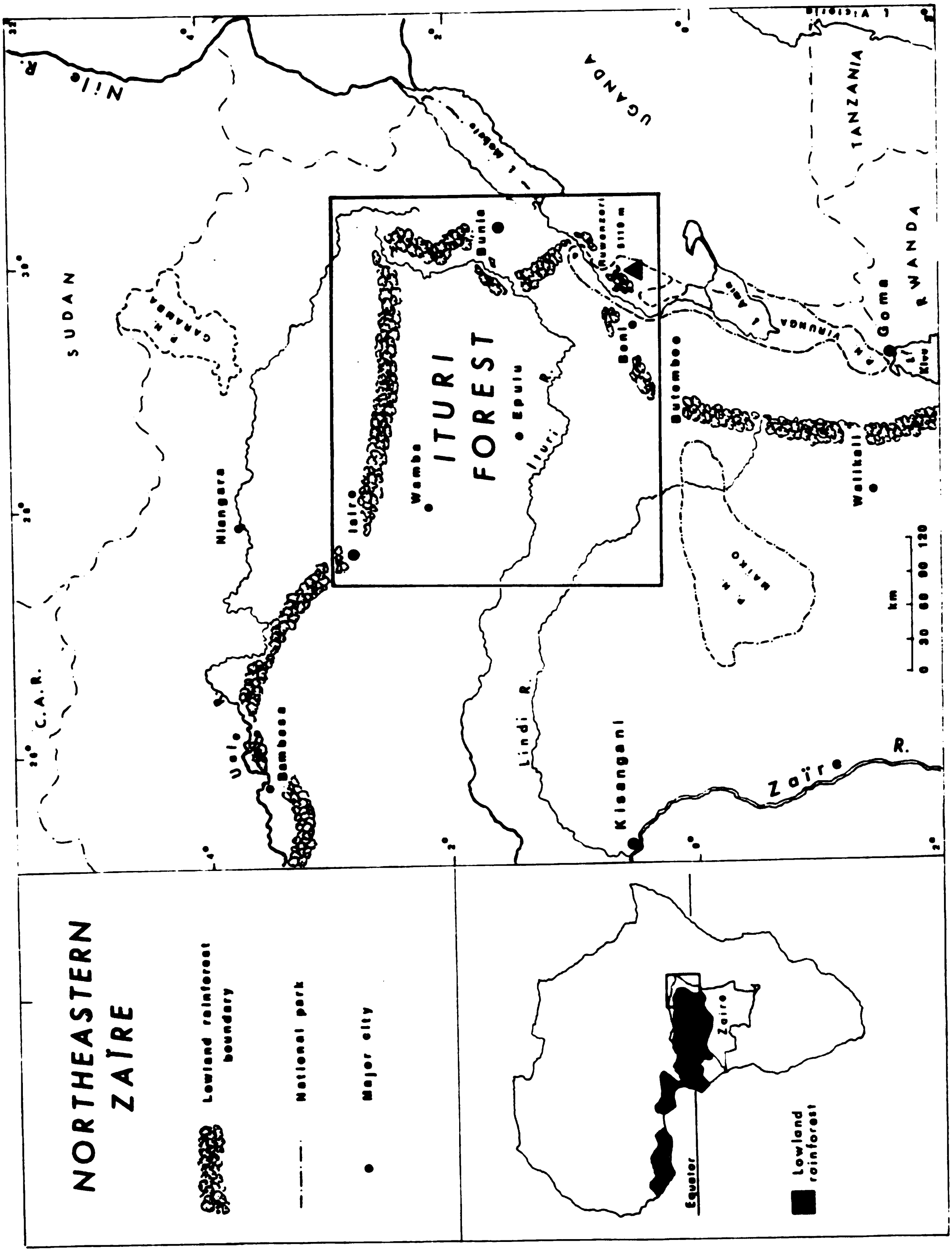
CHAPTER II

A COMPARATIVE STUDY OF THE IMPACT OF NATURAL DISTURBANCE ON FOREST COMPOSITION IN NORTHEASTERN ZAIRE.

INTRODUCTION

It has recently been suggested that the composition of tropical forests is strongly influenced by the pattern of natural disturbance sustained by these forests (Connell 1978, Hartshorn 1978, Oldeman 1978, Whitmore 1978, 1982, Denslow 1980, Florence 1981, Leigh 1982, Orians 1982, Pickett 1983). The rain forests[1] of northeastern Zaire provide a case by which this relationship can be examined. There are two forest types in the Ituri Forest (Figure 1), both of which are apparently mature[2], but each having different dominant tree species and different species diversities. The mbau forest is dominated by a single species, *Gilbertiodendron dewevrei*, (Caesalpiniaceae) which makes up 80% or more of the stems reaching canopy level. As a result, mbau forest is less diverse than the mixed forest. *Brachystegia laurentii* (Caesalpiniaceae), *Cynometra alexandri* (Caesalpiniaceae), and *Cleistanthus michelsonii* (Euphorbiaceae), are dominant in the latter forest type, but no species

Figure 1. The Ituri Forest, Zaire.


NORTHEASTERN ZAÏRE
Lowland rainforest boundary
National park
Major city
Lowland rainforest
Equator
Zaïre
ITURI FOREST
Epulu
Ituri R.
Wamba
Isiro
Bunia
Beni
Butembo
Walikali
Goma
L. Kivu
L. Mobutu
L. Amin
Ruwenzori 5110 m
Virunga N.P.
Garamba N.P.
Maiko N.P.
SUDAN
C.A.R.
UGANDA
TANZANIA
RWANDA
Nile R.
Uele R.
Bambesa
Niangara
Lindi R.
Kisangani
Zaïre R.
km
0 30 60 90 120
24°
26°
28°
30°
4°
2°
0°

accounts for more than 30% of total tree density (>10 cm dbh).

Both forest types cover thousands of square kilometres over a wide range of soils and are without intervening topographic discontinuities. Over most of their range, soil differences do not appear to have been important in determining forest type as both forests occur on soils derived from the same parent material and with similar chemical and textural qualities (see chapter 1; also, for forest dominated by *G. dewevrei*, see Louis 1947, Gérard 1960, and Jongen et al 1960; for forest dominated by *B. laurentii* see Germain and Evrard, 1956).

In this paper I investigate the relationship between natural disturbance and the two forests' floristic composition by comparing natural disturbance regimes and the process of regrowth after treefall. The resilience of the forest communities, and of the dominant species in particular, are assessed by comparing secondary forests with the primary forests.

BACKGROUND AND LITERATURE REVIEW

Disturbance can affect community composition in a number of ways. As defined by Grime (1979: 39) and used here, disturbance "consists of the mechanisms which limit the plant biomass by causing its partial or total destruction". Disturbance may interfere with species interactions such that species already present in the environment can continue to coexist, or it may create open patches, allowing disturbance-adapted species to invade. These possibilities are briefly described below.

Periodic destruction of biomass may interfere with the assertion of dominance by one or a few species. In the absence of disturbance, in some communities resource monopoly by a single species is likely to result either from that species' superior competitive ability or from its greater resistence to stress and predation (Paine 1984, referring to marine sessile organisms). Both Connell (1978) and Hubbell (1980) have hypothesized that the non-equilibrium conditions resulting from repeated disturbance promote species coexistence in tropical forests by preventing dominance by single species of trees.

Treefall disturbances in tropical forests have been interpreted as providing a resource dimension along which tree species have specialized. Denslow (1980) and Pickett (1983) suggested that tree species are capable of reaching maturity within only a limited range of gap sizes. These species are categorized as small and large gap specialists. It has also been suggested that different species may be specialized to exploit particular microsites within a gap (Orians 1982). Thus, mechanisms maintaining tree species diversity in tropical forests are envisioned as analagous to those hypothesized for animal species such that "diversity of species is proportional to the diversity of resources" (MacArthur, 1972, page 177). In the case of tropical forests the resources include establishment sites in treefall gaps.

Apart from its influence on species richness, the disturbance regime will determine the relative proportions of shade tolerant and shade intolerant species in the forest. With increasing size and frequency of treefalls, species adapted to germinate and grow under the environmental conditions provided by gaps will be favored (Hartshorn 1978, 1980; Whitmore 1974, 1982).

Typical character syndromes have been suggested for gap species (Whitmore 1978, Hartshorn 1980) and field data have shown that certain tree species which are regular components of mature tropical forest benefit from gaps. Stores of quiescent seeds which germinate after exposure to light have been found in the soils of numerous humid tropical forests (Guevara and Gomez-Pompa, 1972, Cheke et al. 1979, Hall and Swaine 1981, Putz 1983, Uhl and Clark 1983). The survival of all nine species of wind-dispersed tree seedlings tested by Augspurger (1984) in Panama was greatly enhanced by transplantation of the seedlings into light gaps. In a five year study, Brokaw (1985, Barro Colorado Island) found that "pioneer" species grew poorly or not at all in small gaps and the fastest growing "pioneers" were in large gaps. The same conclusion, i.e. that certain tree species important in the forest canopy are unable to persist under the shade of the canopy, has been reached by studying the distribution of seedlings and saplings at a given point in time (Hubbell 1979, Veblen et al. 1979). Juveniles of some species are found only in gaps.

Most disturbance studies in tropical forests have focused on the effects of disturbances which can be witnessed and measured in human lifetimes (some exceptions to this include extrapolations made from studies of major windstorm damage (Wyatt-Smith 1954, Webb 1958, Whitmore 1974). This is not the case in temperate latitudes where the impact of past glaciations (Davis 1976) and prehistoric fires (Walker

1982) on present forest composition has been studied with the help of pollen profiles. Comparable data are not available for such studies in tropical ecosystems, but buried charcoal horizons indicate that a number of presumably primary humid tropical forests have burned during the Holocene (Sanford et al. 1985 in Venezuela, and Hart, this study, in Zaire). Studies of modern lightning damage suggest the same for some areas of forest in Sarawak (Anderson 1964).

Apparent differences in forest composition seen today are possibly a reflection of large-scale disturbances several centuries or even millenia past. This interpretation seems tenable given the slow growth and poor dispersal of many of the dominant trees in mature tropical rain forest and the growing evidence for climatic shifts in tropical regions during the Holocene (Flenley 1979, Livingstone 1980a, 1980b, Lewin 1984, Talbot et al. 1984, Leyden 1985).

From the above discussion several hypotheses can be developed regarding the two forest types in the Ituri region of Zaire:

Hypotheses concerning species diversity

1. The mixed forest has had more frequent and larger disturbances than the mbau forest.

   Rationale: The single species dominance of the mbau forest may represent a resource monopoly established in the absence of significant disturbance.

2. The mixed forest has more varied treefall gaps than mbau forest, providing a greater diversity of microsites for seedling establishment.

   Rationale: If tree species have specialized relative to different within-gap establishment sites, then the more diverse forest may provide a greater variety of such sites.

Hypotheses concerning species composition

3. Gap species account for a greater proportion of the tree species in mixed forest than in mbau forest.

   Rationale: The greater diversity of mixed forest may result from the abundance of gap-dependent species.

4. One of the two forest types is composed of species more resilient to major disturbance.

   Rationale: The pattern of forest type distribution may be a reflection of major past disturbance. The spread of the original forest into the destroyed area may be very slow.

Not all of the above hypotheses are easily tested, nor do they cover all of the possible relationships between species diversity and disturbance in these forests. Nevertheless, they provide a framework in which to investigate the possibility that differences in species dominance and species diversity between mixed and mbau forest are due to differences in disturbance regime.

METHODS

Gap size, frequency, and distribution were measured in both forest types. A survey was made of four 2.5 ha plots (50 m x 500 m) at each of three sites in both forest types such that a total of 30 ha was surveyed for both mixed forest and mbau forest (G-D in Figure 2). A map was made of all recent treefall gaps showing size, shape, and

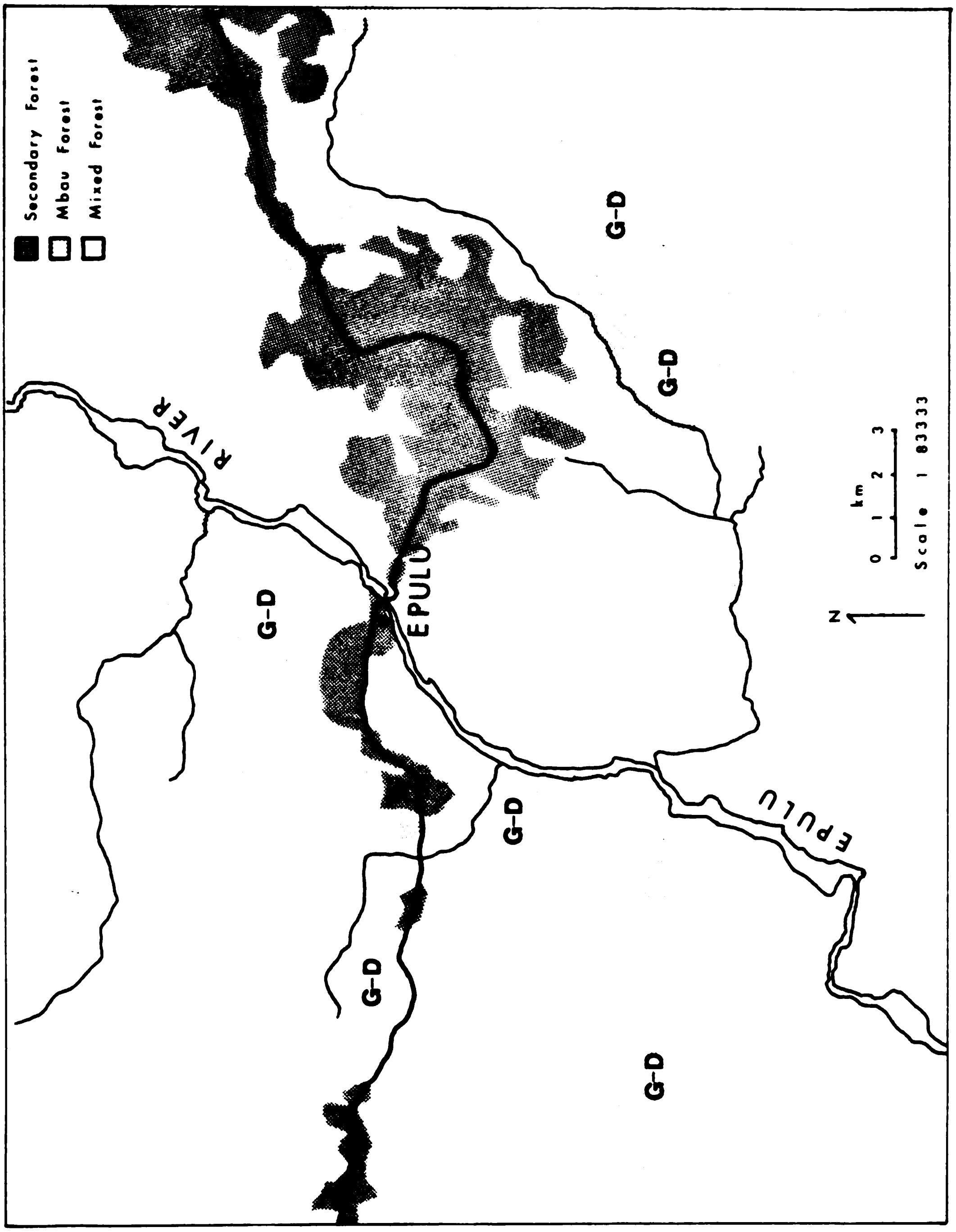
Figure 2. The central Ituri Forest study site, with locations of forest types and research areas.

Plot locations:

G-D ... Gap dynamics

S ..... 15 year-old secondary forest

40 year-old secondary forest was 20 km west of Epulu.


Secondary Forest
Mbau Forest
Mixed Forest
EPULU RIVER
EPULU
G-D
G-D
G-D
G-D
G-D
G-D
N
km
0 1 2 3
Scale 1 83333

orientation. A treefall gap was considered recent enough to include if the height of the new growth was less than 3 m and the fallen tree trunk was intact. If there were signs of advanced decay, such as moist and crumbly wood, other evidence for the recent nature of the gap was sought (small pioneer seedlings, freshly broken understory species...). Only treefall disturbances large enough to have caused canopy gaps were censused.

Two area measurements were made of each gap. The ground-level disturbance was determined by judging the approximate shape of the gap and then taking the measurements necessary to calculate the area. In this case the edge of the gap was defined by the stems of unaffected vegetation. The second area determined was the canopy gap or the actual area of open sky exposed by the treefall. In this case the edge of the gap was defined by the bordering crowns of adjacent standing trees. The necessary measurements were made by sighting upward or, where the ground gap was smaller than the canopy opening, by estimation.

Old treefall disturbances and mature light-dependent trees were enumerated on each plot. The disturbances were identified as rotted logs on the forest floor with canopy gaps above. The trees were species known to germinate and grow in large treefall gaps. The frequency of old gaps and mature pioneer species served as estimations of past treefall disturbance. Analysis was by 1-way ANOVA with preplanned comparisons (Sokal and Rohlf, 1969, pages 226-235).

The process of regrowth in treefall gaps was studied in relatively recent gaps within a six kilometer radius of the base camp at Epulu. A total of 41 gaps, in which the new growth did not exceed 3 m in height were surveyed. Gaps were included as they were encountered except that small branchfalls were usually passed up in favor of larger treefall openings. Rather than follow paths, a given direction was chosen and then traversed with forest guides. Additionally, two sample surveys were made in a 70-100 ha blowdown in mixed forest.

Gap age was approximated by comparing the size of the largest pioneer tree seedling in these gaps with the size of the largest pioneer seedling of the same species growing on a favorable site in a gap of known age. It was estimated that all but six of the treefall gaps were less than one year in age when first visited.

The gaps were measured by the same method used on the 2.5 ha plots. Mature trees adjacent to the gap were identified. The entire gap was systematically searched and all newly-germinated seedlings were identified. An individual seedling was determined to have germinated since gap formation by a combination of characteristics: 1. condition of the leaves (not coriaceous, without epiphylls); 2. number of leaf scars (few); 3. lack of woodiness in stem; and 4. absence of the species as a seedling under the closed canopy of the mature forest. The last characteristic was not absolute as shade tolerant species could germinate in gaps as well. The largest of the newly germinated seedlings were measured and tagged. Samples of light-released seedlings or saplings of the dominant forest species were also measured and tagged. In the later gaps surveyed (13), released sapling and pole-size stems were enumerated throughout the gap, recorded and identified.

Percent canopy cover was measured with a concave spherical densiometer; readings were taken at 5 m intervals along the major axis of each gap. Readings were taken while standing on fallen trunks or branches at about 3 m height, and thus above the dense regrowth and fallen debris. Notes were taken on litter cover, and browse damage to seedlings and resprouts. Two of the largest and two of the smallest gaps were resurveyed after two years. Differences between gaps in mixed forest and mbau forest were tested by Students' *t*-test.

Two sampling techniques were used to determine the density and composition of soil seed banks:

1. Plots were searched for large seeds ($\geq$ 5 mm, longest dimension). Leaf litter, humus, and superficial soil was sifted on a total of 99 one meter square plots in mixed and mbau forest. Seeds were placed in flats in the sun and were watered for six months.
2. For smaller seeds, a volume of soil (300 cm^2 x 7 cm) was spread in the sun on sterilized sand to form germination beds. These beds were on a platform to discourage predators and covered with fine mesh mosquito netting to avoid contamination. A trellis of palm fronds provided light shade. Twenty samples each were taken from mixed forest, mbau forest, and secondary forest. Half the samples were taken at the wettest time of year (November) and half at the driest time (February). Germinations were monitored for four months in each case.

Another pair of seed beds was maintained, one in the open and one under the shade of the forest canopy. As seeds of gap-colonizing species became available they were set into small cleared plots so that germination and growth could be observed. The group of plots in the large clearing of the base camp received partial shading from a trellis of palm fronds. These plots and those in the forest shade were unmanipulated except for occasional weeding.

The composition of secondary forest of two different ages and histories was studied on sites previously used for slash and burn agriculture (S in Figure 2). The younger secondary forest had developed on sites abandoned 15 years earlier and subjected to only one planting and harvest cycle after the mature forest was cleared. Original cover had been mixed forest with several islands of mbau forest. In the older, 40 year-old, secondary forest, woody vegetation had become re-established after the village and gardens of the town of Biane were abandoned. The original vegetation was mixed forest and it is likely that, after clearing, most of the Biane area sampled had been subjected to two or more planting cycles.

Twelve plots, 25 m x 25 m each, were located at both sites. All stems >10 cm dbh were identified (or a specimen collected) and the diameter measured. All stems > 2.5 cm dbh and $\leq$ 10 cm dbh were recorded in 15 m x 15 m subplots, one in each of the larger plots. The plot sizes were the same as those used for composition studies of both mixed and mbau forest (described in chapter 1). This permited direct comparisons between secondary and primary forest sites. Analysis was by 1-way ANOVA with preplanned comparisons.

RESULTS

There were significantly (P < .01) more gaps in mixed forest than in mbau forest (Table 1). Mean size of individual gaps, whether measured at ground or canopy level, was not significantly different at a probablility of 0.05. Site means for canopy gap size were consistently larger in mixed forest but due to large variances, the two forest types only differed at a probability of 0.1.

Given that there were more gaps in mixed forest and that there was no significant difference in gap size, the expectation is that for any given area of forest, a larger proportion would have been disturbed by treefalls in mixed forest than in mbau forest. There was, in fact, a significant difference (P < .05) in total gap area per plot when open canopy area was compared between the two forest types but when ground disturbance areas were compared the difference was only significant at a probability of P < 0.1 (Table 1).

Variances for gap size and disturbance area measurements were very high at all sites in both forest types, (see standard deviations, SD, Table 1). This indicates that treefall disturbance was highly irregular relative to the sample size (plot size = 2.5 ha). There was indication that even at a much larger scale, gap occurrence would have remained irregular. Nomadic hunters reported a large blowdown in mixed forest which, upon inspection, was estimated to have leveled from 70 to 100 ha of forest. Even the older hunters had never seen a blowdown of this scale. The periodicity with which such blowdowns occur is

Table 1. Size and frequency of treefall gaps, on 2.5 ha plots, in mixed and mbau forest types of the Ituri Forest, Zaire.[a]

		Mbau forest sites[b]			Mixed forest sites			Comparisons[c]		
								sites within forest		among
		M	E	S	Z	N	K	mbau	mixed	forests
gap frequency #/25000 m^2	$\bar{x}$	4.0	2.8	2.3	6.3	6.5	2.8	NS	P<.05	P<.01
	SD	1.41	0.96	0.96	0.96	3.70	0.96			
ground gap size m^2	$\bar{x}$	124.8	99.3	241.0	203.8	218.8	168.5	NS	NS	NS
	SD	93.31	81.66	273.61	148.27	140.90	87.28			
canopy gap size m^2	$\bar{x}$	58.5	68.8	106.0	111.0	147.3	133.8	NS	NS	(P<.1)
	SD	50.69	53.80	113.12	85.58	65.30	51.71			
ground plot area opened m^2	$\bar{x}$	496.5	210.8	440.8	965.3	1083.3	416.3	NS	NS	(P<.1)
	SD	538.25	161.50	573.11	773.99	850.01	199.5			
canopy plot area opened m^2	$\bar{x}$	202.5	104.3	164.3	589.3	618.8	349.3	NS	NS	P<.05
	SD	285.46	67.09	250.53	532.30	358.3	171.5			

[a] n = 12 plots in each forest type (three sites with four plots each). A total of 30 ha was surveyed in each forest type.

[b] Mbau forest sites : M = Mangbara, E = Eboyo, S = Sambo. Mixed forest sites : Z = Apanzoki, N = Ndaki, K = Kadiketu.

[c] Analysis by 1-way ANOVA with preplanned comparisons; probabilities of < 0.1 and > 0.05 are shown in parentheses; probabilities > 0.1 are not significant (NS).

unknown.

The range of gap size and disturbance area did not differ significantly among the three sites in either forest type (Table 1). Gap frequency, on the other hand, did vary significantly within mixed forest sites ($P < .05$). The four plots at the Kadiketu site had relatively few gaps as compared to plots at the other mixed forest sites.

Notes were made on some variables likely to affect the diversity of microsites available for plant germination and growth in all gaps encountered in the plots (Table 2). There were no significant differences between the two forest types in the percent of gaps originating from branchfalls, single treefalls, or multiple treefalls. In both mixed and mbau forest approximately half of all disturbances were from single treefalls. Nor was there a significant difference between forest types in the percent of treefall gaps with at least one upturned rootmass. In both cases slightly more than one fourth of all gaps had rootmasses with exposed mineral soil.

Further observations on differences between gaps in mixed forest and mbau forest were made in the 41 gaps studied more intensively. Spherical densiometer readings of percent open sky did not differ significantly for the two forest types (mbau forest mean = 15.2%, SD = 8.46; mixed forest mean = 18.8%, SD = 7.57). Two similar samples were taken in the large blowdown (> 70 ha). Both had much higher mean readings (> 50% open sky) than any of the other treefall gaps.

Certain species occurred regularly as newly germinated

Table 2. Percent of gaps with specific characteristics relevant to seedling microsites.[a]

gap characteristic		Forest Type Mbau	 Mixed	t value	significance[b]
branch-fall	$\bar{x}$	37.2	24.9	1.456	NS
	SD	3.91	8.79		
single tree-fall	$\bar{x}$	51.8	54.0	0.619	NS
	SD	3.69	0.23		
multiple tree-fall	$\bar{x}$	11.0	20.9	1.346	NS
	SD	1.58	9.25		
upturned rootmass	$\bar{x}$	25.7	31.9	0.430	NS
	SD	23.08	19.41		

[a] Analyses, using mean values from each site (four plots per site, three sites per forest type), were by Students' *t* test using arcsine transformed values. Standard deviations (SD) were calculated from arcsine transformed values.

[b] NS = not significant, $P > 0.1$.

seedlings in treefall gaps. The 18 most common species were found in from five to 32 of the 41 gaps surveyed (Figure 3, Table 3). Of these 18, four species germinated in at least 29 of the gaps (Table 3). In most cases there were no mature individuals of the same species adjacent to the gap (exceptions: six gaps with *Musanga cecropioides* adjacent and one gap with *Ricenodendron heudelotii* adjacent). These 18 species accounted for 94% of all tree seed germinations in treefall gaps, even after excluding from the calculation all seedlings with a mature individual of the same species on the perimeter of the treefall.

The 18 common gap species were poorly represented in the canopy of the mature forest. Of stems greater than 10 cm dbh, they composed 2.8% in mixed forest and only 0.6% in mbau forest. They were an even smaller component of the understory of mature forest.

Along with the 18 shade-intolerant gap species, 38 other tree species occurred as new seedlings in gaps (Figure 3). Some of these appeared to be shade- intolerant species as are the 18 gap species. Mature individuals were rare or absent from undisturbed forest but were common in the canopy of secondary forest less than 50 years old (*Erythina sp., Barteria nigritans, Dacryodes sp.*). Also found as seedlings in gaps were some understory species (*Garcinia smeathmanii, Hunteria congolana, Pancovia harmsiana, Trichilia rubescens*) and some canopy species of the mature forest (*Monopetalanthus microphyllus, Irvingia gabonensis, Donella pruniformis, Dialium corbisieri*). The seedlings and saplings of these latter two groups could be found in undisturbed forest as well.

Figure 3. The frequency with which individual species occur as seedlings in treefall gaps.

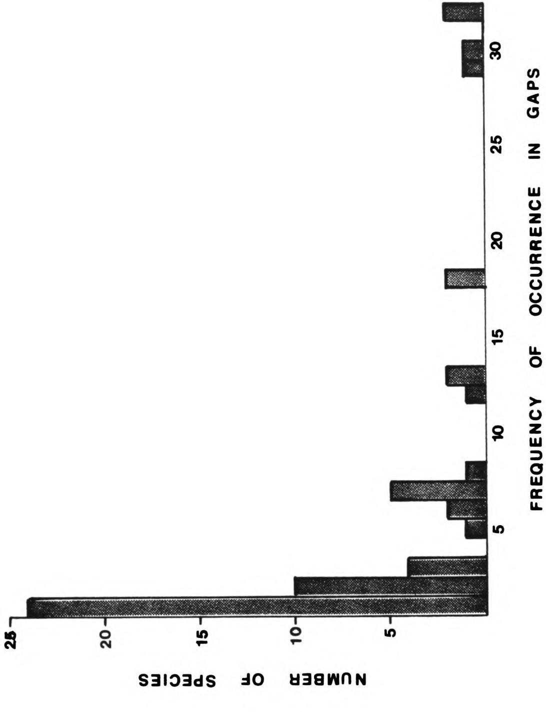

NUMBER OF SPECIES
25
20
15
10
5
FREQUENCY OF OCCURRENCE IN GAPS
5
10
15
20
25
30

Table 3. Occurrence of common gap-regenerating tree species in the treefall gaps surveyed, with their principal mode of seed dispersal, in the Ituri Forest of Zaire.

species	family	number of gaps (n=41)	dispersal agents[a]
Musanga cecropioides	Moraceae	32	b, p, m
Macaranga monandra	Euphorbiaceae	32	b?
Ricinodendron heudelotii	Euphorbiaceae	30	m
Macaranga spinosa	Euphorbiaceae	29	b?
Alstonia boonei	Apocynaceae	18	w
Trema orientalis	Ulmaceae	18	b
Albizia gummifera	Mimosaceae	13	?
Fagara macrophylla	Rutaceae	13	b
Canarium schweinfurthii	Burseraceae	12	b, h
Bridelia sp.	Euphorbiaceae	8	b?
Cola lateritia	Sterculiaceae	7	p?
Ficus capensis	Moraceae	7	p
Uapaca guineensis	Euphorbiaceae	7	p?
Croton mubango	Euphorbiaceae	7	m
Harungana madagascariensis	Guttiferae	7	b?
Erythrophleum suaveolens	Caesalpiniaceae	6	?
Phyllanthus sp.	Euphorbiaceae	6	m
Anthocleista schweinfurthii	Loganiaceae	5	p?

[a] b = bird
p = arboreal primate
m = terrestial mammal (duiker, elephant)
w = wind
h = humans

Except for the 18 gap species, all other species were rare as germinating seedlings in treefall gaps. Four of the 38 occurred in three gaps, ten in two gaps, and 24 in one gap (Figure 3). Not included here are *Brachystegia laurentii* and *Gilbertiodendron dewevrei*. These were found in gaps but always within approximately 10 meters of the crown of a mature individual of the same species. These two species are found abundantly in all size classes under undisturbed canopy of mixed forest (*B. laurentii*) or mbau forest (*G.dewevrei*).

Only the 18 gap species were common enough as seedlings to be used to contrast treefall gaps in mixed and mbau forest with regard to species composition of germinating seeds. Of the 41 gaps surveyed, four were in transition forest. Only those clearly in mixed or mbau forest were appraised (Table 4).

All 18 gap species were found as seedlings in both mixed and mbau forest gaps. No species was restricted by conditions peculiar to gaps of only one of the forest types.

The two smallest gaps surveyed (< 50 m^2) had no germinations (gap # 33) or only one germination (gap # 35). There was a bias towards sampling larger gaps as the aim of the survey was to identify tree species germinating in gaps. The 37 fully-analyzed gaps were grouped into three size classes. All but two of the 18 gap species were found as seedlings in at least one gap of each size class (Table 4). The two exceptions were among the least common of the 18 gap species; *Croton mubango* was found in only six gaps and *Alstonia boonei* was found in only five. Most of these species were

Table 4. Pioneer species germinations in gaps of different size in mixed and mbau forest types of the Ituri Forest, Zaire.[a]

pioneer species	Gap size (m^2) and forest type[b]					
	<250		≥250 <500		≥500	
	mbau	mixed	mbau	mixed	mbau	mixed
Musanga cecropioides	4	2	6	6	5	6
Macaranga monandra	3	1	6	7	5	6
Ricinodendron heudelotii	3	2	4	7	5	7
Macaranga spinosa	4	2	5	6	4	6
Alstonia boonei	1	0	3	2	5	5
Trema orientalis	2	0	1	3	4	5
Albizia gummifera	1	1	1	2	3	3
Fagara macrophylla	0	1	2	2	2	3
Canarium schweinfurthii	1	0	2	3	2	1
Bridelia sp.	1	0	3	2	0	2
Cola lateritia	1	0	0	2	1	3
Ficus capensis	1	1	1	0	1	3
Uapaca guineensis	0	1	0	2	1	2
Croton mubango	0	0	0	1	1	4
Harungana madagascariensis	2	0	1	1	1	1
Erythrophleum suaveolens	2	0	0	1	2	0
Phyllanthus sp.	1	0	2	0	1	2
Anthocleista schweinfurthii	0	0	1	0	3	1
number of gaps	n=7	n=3	n=6	n=9	n=5	n=7

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[a] A total of 37 gaps were included in the analysis, 18 from mbau forest and 19 from mixed forest. Gaps from transition forest were excluded.

[b] Ground measurement of gap area.

found in the smaller gaps (< 250 m^2) as well as the larger ones. This is remarkable considering that the smaller gaps provided much less total surface area for colonization.

The occurrence of mature individuals of the five gap species found most commonly as seedlings in gaps, *Musanga cecropioides, Macaranga monarda, Macaranga spinosa, Ricinodendron heudelotii*, and *Alsonia boonei*, was considered an indication of past treefall disturbance in primary forest. All canopy-level individuals of these gap species were recorded for the 2.5 ha plots (Table 5). These species have different growth rates but, judging from disturbances of known age where the species are found, these mature individuals of pioneer species represent disturbances of from 10 years (*M. cecropioides, Macaranga spp.*) to probably more than 30 years of age (*A. boonei, R. heudelotii*).

The number of mature light-dependent trees did not differ significantly between the two forest types at a probablility of .05; however, a trend toward more such trees in mbau forest was apparent at a probability of 0.1 (Table 5). When sites within a single forest type were compared there was a significant difference in mbau forest between the Eboyo and Sambo sites ($P < .05$). (These data were not taken at the Mangbara site).

The five pioneer species were not equally represented as mature individuals in the two forest types. The fastest growing ones (*Musanga cecropioides, Macaranga spp.*) accounted for most of the

Table 5. Frequency of old gaps and mature pioneer trees in 2.5 ha plots in mixed and mbau forest types of the Ituri Forest, Zaire. [a]

		Mbau forest sites[a]		Mixed forest sites			Comparisons[c]		
							sites within forest		among
		E	S	Z	N	K	mbau	mixed	forests
number of old gaps	$\bar{x}$	5.8	6.3	11.8	8.0	12.3	NS	NS	P<.01
	SD	1.26	3.95	3.50	2.94	2.22			
mature pioneer trees	$\bar{x}$	15.5	5.5	9.3	5.8	2.8	P<.05	NS	(P<.1)
	SD	10.34	2.08	5.80	2.50	2.99			

[a] n = 12 plots in each forest type (three sites with four plots each). A total of 30 has was surveyed in each forest type. Pioneer trees surveyed included *Musanga cecropioides*, *Macaranga spp*, *Ricinodendron heudelotii*, and *Alstonia boonei*.

[b] Mbau forest sites : E = Eboyo, S = Sambo.
Mixed forest sites : Z = Apanzoki, N = Ndaki, K = Kadiketu.

[c] Analysis by 1-way ANOVA with preplanned comparisons; probabilities of < 0.1 and > 0.05 are shown in parentheses; probabilities > 0.1 are not significant (NS).

mature pioneer individuals recorded in mbau forest (94% or 79 of 84 individuals). In mixed forest, the slower-growing pioneer species (*Ricinodendron heudelotii, Alstonia boonei*) were a larger proportion of the mature pioneer species in the canopy (53% or 36 of 68 individuals).

The number of old gaps was significantly greater in mixed forest than in mbau forest (Table 5, $P < .01$). When the sites within a single forest were compared, no significant difference was found ($P > 0.1$). The old gaps, recognized as decaying logs under residual canopy gaps, were used as an approximation of the frequency of intermediate-aged disturbances (5-15 years of age).

The difference in density of surviving sapling and pole-size individuals in mixed and mbau forest treefalls was only significant at a probability of < 0.1 (Table 6; mbau forest mean = 2.70, SD = 1.15; mixed forest mean = 1.52, SD = 0.53). If the only species considered are those reaching maturity at canopy height, then the density of surviving juveniles > 2.5 cm diameter was significantly greater in mbau forest gaps than in mixed forest gaps (Table 6; mbau forest mean = 2.52, SD = 0.98; mixed forest mean = 1.19, SD = 0.51). Gaps in transition forest and the smallest treefall gaps were omitted from the calculations. The highest densities of remaining saplings and poles was found in the two smallest gaps (< 50 m^2), both in mbau forest, (means = 11.11 and 12.24 surviving individuals per 100 m^2) presumably because less damage is caused by a falling branch than by an entire living tree.

The two-year growth data for seedlings of gap-species (i.e.

Table 6. Density per 100 m^2 of surviving saplings and poles in treefall gaps.[a]

		Mbau forest (n = 8 gaps)	Mixed forest (n = 5 gaps)	t value	significance[b]
all species	$\bar{x}$	2.70	1.52	2.134	(P<0.1)
	SD	1.15	0.53		
potential canopy species	$\bar{x}$	2.52	1.19	2.782	P<.05
	SD	0.98	0.51		

[a] All stems > 2.5 cm dbh and $\leq$ 20 cm dbh included in survey.

[b] Probability > .05 in parentheses.

pioneers) and released shade-tolerant saplings in gaps were difficult to summarize because of the great variability between species and among individuals within species. The cause of variability in growth rate within individuals of the same species arises, no doubt, from the many uncontrolled factors, including size at first measurement, browse damage, shading from adjacent vegetation, position within gap, genetic variability, etc.

Four gaps were revisisted after four years, two medium-sized gaps in transition forest (500 m^2 and 290 m^2) and two large gaps (2600 m^2 in mixed forest and 2250 m^2 in mbau forest). The large gap in mbau forest received frequent okapi (*Okapia johnstoni*) damage and none of the marked pioneer seedlings, primarily of the 18 gap species, were present after two years. Some new ones had apparently seeded in and three of these had basal diameters > 3 cm. Height had been stunted by repeated browsing. Released seedlings and saplings of caesalpiniaceous dominants were free from browse damage. Recorded diameter increments on light-released saplings were 15 mm (*Gilbertiodendron dewevrei*, from 22.6 to 24.1 cm dbh) and 7 mm (*Brachystegia laurentii*, from 6.2 to 6.9 cm dbh). Released seedling of *G. dewevrei* (< 1 m height when first measured) grew a mean of 31.5 cm in height (n = 4, SD = 13.63).

The large gap in mixed forest was not frequented by okapi. Individuals of some pioneer species were very prominent after two years. The greatest diameter increment was in *Musanga cecropioides* (+86 mm, +100 mm, and +92 mm, measured above the incipient aerial roots; original basal diameter measurements had been 20 mm, 50 mm, and

81 mm respectively). The fastest growing pioneers were those receiving maximum sunlight. They were in the center part of the gap and had germinated on upturned rootmasses above the surrounding vegetation and debris. Other measured pioneer species that were located after 2 years (n = 8) varied in basal diameter increment from 5.2 mm (*Canarium schweinfurthii*) to 31.4 mm (*Croton mubango*).

No pioneer species was refound in one of the two medium sized gaps. In the other, of three pioneer seedlings found in 1981, two had died after two years. The remaining one, *Macaranga spinosa*, had only increased 4 mm in basal diameter. Two released seedlings of dominant species showed growth equal to or better than the pioneer species. A *Gilbertiodendron dewevrei* seedling had a basal diameter increment of 4.5 mm (from 17.1 to 21.6 mm) and a *Brachystegia laurentii* seedling had a basal diameter increment of 3.8 mm (from 11.6 to 15.4 mm).

Eight of the 18 common gap species have seeds large enough to have been picked out from soil samples searched for large (> 0.5 cm length) seeds (*Ricinodendron heudelotii, Albizia gummifera, Canarium schwienfurthii, Cola lateritia, Uapaca guineensis, Croton mubango, Erythrophleum suaveolens*, and *Phyllanthus sp.*). One viable seed of *Ricinodendron heudelotii* and one of *C. schweinfurthii* were found and subsequently germinated. Two seeds of *E. suaveolens* were found which failed to germinate in five months but which appeared to be viable when cracked open. Seven other viable seeds, of six species, were found as well (Table 7). Not included in the survey results were the numerous seeds of *B. laurentii* which were just ripe and falling

Table 7. Large viable seeds (> 5 cm length) found in the litter and uppermost soil layer of mbau forest and mixed forest.

	Mbau forest	Mixed forest
area sampled	61 m^2	38 m^2
species found	*Ricinodendron heudelotii* *Canarium schweinfurthii* *Erythrophleum suaveolens* two unknowns	*Klainedoxa gabonensis* *Tabernaemontana sp.* *Strombosiopsis tetrandra* one unknown

to the ground during one sample period.

The total area searched for large seeds was 99 m^2 (Table 7), about half the size of an average gap. Although not very many seeds of large-seeded light-dependent trees were found, this density corresponds with the findings in actual treefall gaps. Most gaps contained only one to two seedlings of *Ricinodendron heudelotii* whereas many seedlings of a small-seeded species such as *Musanga cecropioides* or *Macaranga spp.* are likely to be present.

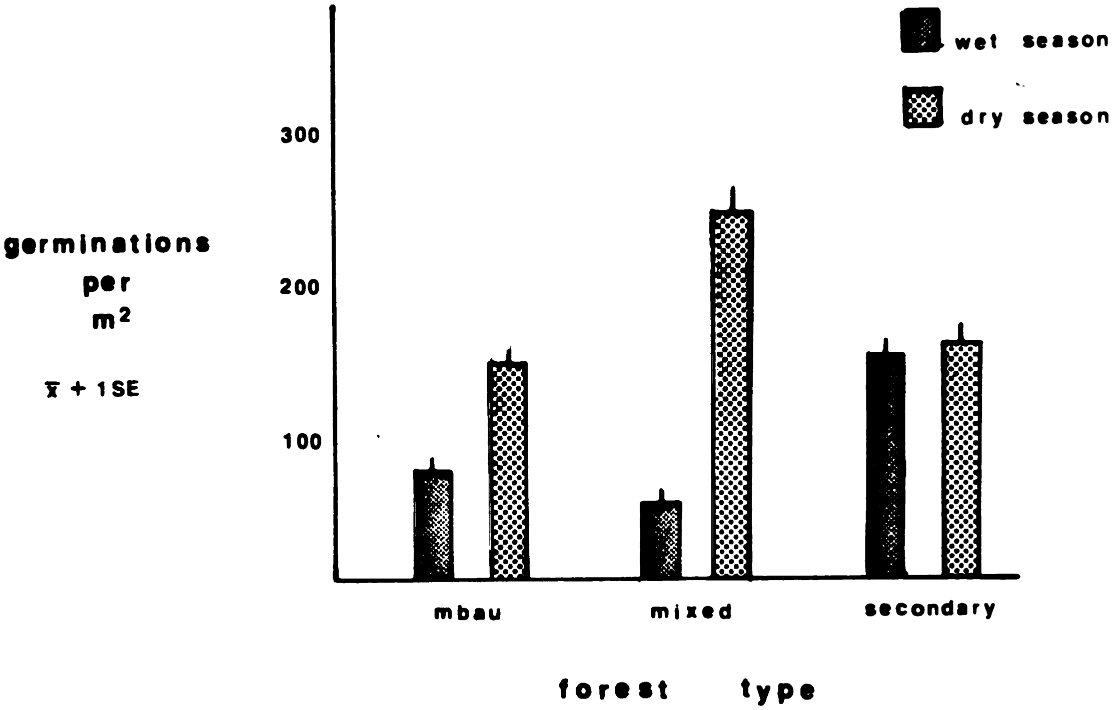
Relative to large-seeded species, during both wet and dry seasons, woody species with small seeds (generally < 3 mm length) were well represented in the soil seed banks of all three forest types (Appendix A). Four of the eighteen most common gap species were found in these samples (*Musanga cecropioides, Trema orientalis, Macaranga spp. Phyllanthus sp.*). Of these, the two most abundant, *M. cecropioides* and *T. orientalis* were found in soil collected both during the wet and the dry season and in soil from both mixed and mbau forest (Table 8). Small-seeded woody species maintained a mean density of 50 seeds per square meter for both collecting periods in all three forest types (Figure 4). In the two primary forests *M. cecropioides* was the most abundant species in the seed bank with a mean density of 82 seeds per square meter (averaged over collection periods and the two forest types). Seedlings of this species and the other small-seeded species are generally restricted to exposed mineral soil in treefall gaps. This microsite, including upturned rootmasses, accounts for only a small proportion of the area affected by treefall disturbance.

Table 8. Number of seed germinations in soil samples from three forest types during a wet and dry season, 1982-1983.

	Number of germinations[a]					
	Mbau forest		Mixed forest		Secondary forest	
	wet	dry	wet	dry	wet	dry
Musanga cecropioides	15	23	7	54		
Trema orientalis	4	11	5	17	44	37
Ficus exasperata	2					
Ficus sp.	1		1			
Macaranga sp.						1
Phyllanthus sp.		1		1		
unknown		7	1			1
unknown			1			
total	22	30	15	72	44	39

[a] For both seasons, 10 soil samples were taken from each forest type. Each sample was a volume of soil, 300 cm^2 x 7 cm.

Figure 4. Abundance of viable seeds of small-seeded woody species in the soils of three forest types during the wet and dry season (1982-1983).


wet season
dry season
300
200
100
germinations
per
m²
x̄ + 1SE
mbau
mixed
secondary
forest type

Seeds of three of the gap species were available in large enough quantities to allow preliminary observations on germination response under different conditions. Seeds of *Phyllanthus sp.* and *Ricinodendron heudelotii*, both large-seeded, and those of the small-seeded *Musanga cecropioides* were planted in sub-canopy and open germination beds. *Phyllanthus* seeds and *Ricinodendron* are antelope dispersed. Seeds regurgitated during rumination were collected from captive antelope pens. *M. cecropioides* seeds are much smaller and are commonly dispersed by primates after passage through the digestive track. The whole fruit was mashed into a slurry with water and spread into plots.

After eight months, 18 of 118 *Phyllanthus* seeds planted in the open produced seedlings while none of the 59 planted in the shade germinated. The first seeds in the open plots germinated after 1 1/2 months and seeds were continuing to germinate after seven months. Many of the seeds had "disappeared", however, possibly due to predation. Eight months after planting, all but eight seeds had disappeared from the shade plots and these were found to be rotten when broken open.

None of the 143 *Ricinodendron heudelotii* seeds placed in shade beds germinated during 1 1/2 years of observation. Thirty of the ungerminated seeds appeared to be viable when broken open a year after planting (the embryo was firm and white). Of approximately 500 seeds placed in the open germination beds, 38 had germinated after a year and a half. As with *Phyllanthus*, germinations were not synchronous but occurred irregularly throughout the observation period with the first germinating two months after planting and others germinating during the last months of observation. Of the ungerminated seeds remaining in the plots, more than 90% appeared to be viable when hammered open.

The slurry of *Musanga cecropioides* seeds was spread over two plots each in the open and shaded germination beds. In each location, one of the plots had been cleared and scraped to mineral soil and the other plot was covered with dead fallen leaflets of *G. dewevrei*. The total number of seeds planted was not counted but numbered in the 100s for each plot. After six months in the shaded beds, no germinations had occurred on the litter-covered plots. During the sixth month of observation,though, three seedlings germinated on the bare mineral soil. In the open beds, one germination occurred after six months in the litter-covered plot; many (>50) germinations occurred in the bare mineral soil plot.

Using standard diversity indices to compare secondary forest with the two types of primary forest, it is apparent that, for stems > 10 cm dbh, both 15 year-old and 40 year-old forests are more diverse than, or at least comparable in diversity to, mixed forest. The two secondary forests are considerably more diverse than mbau forest. The Simpson's diversity indices ($Ds = [\ 1-\ (\Sigma ni(ni-1)\ /\ N(N-1))]$) for 15 year-old and 40 year-old forests are 0.92 and 0.95 respectively. The Ds values for mixed forest and mbau forest are 0.89 and 0.37 respectively. In the case of Simpson's diversity indes, greater diversity causes the value to approach unity. The value of the Shannon diversity index ($H' = -\Sigma\, pi\log pi$ where $pi = ni/N$) is also higher for more diverse communities. The H' values for the 15 year-old and 40 year-old forests are 1.37 and 1.68 respectively. The H' values for mixed and mbau forest are only 1.35 and 0.45 respectively.

A statistical comparison of the diversities of secondary and primary forest was made by comparing species richness (number of species per plot) and stem density (number of stems per plot) for all forest types (Table 9). Four different diameter classes are considered independently. The 15 year-old secondary forest was significantly less species rich than the 40 year-old secondary forest for two of the diameter classes, the sapling class ($P < .01$, all stem > 2.5 cm dbh ≤ 10 cm dbh) and the tree class ($P < .05$, all stems > 25 cm dbh ≤ 50 cm dbh). The species richness of the pole-size class (> 10 cm dbh ≤ 25 cm dbh) and large tree size class (> 50 cm dbh) were not significantly different between the two forests. Tree species in the largest size class included those which were not cut when the forest was originally cleared (two species in two plots of the 15-year forest, three species in one plot of the 40-year forest).

The mixed forest was significantly richer in species than 40 year-old secondary forest for the pole-size class ($P < .05$) but for other size classes there is no significant difference. The 40-year forest is significantly richer than mbau forest (Table 9, $P < .01$ or $.001$) for all size classes except the large tree class (> 50 cm dbh).

There is no significant difference in stem densities between 15 year-old and 40 year-old forests (Table 10) except for the pole size class which was denser in 40 year-old forest ($P < .05$). Four of the 15 year-old forest plots had suffered extensive elephant damage in the previous two years. It appeared that most of the pioneer species broken had resprouted, often with several stems.

Table 9. Species richness of different diameter classes in 15 year-old secondary forest, 40 year-old secondary forest, and mature mixed and mbau forests.

			Number of species per plot				Comparisons[a]		
diameter class	plot size (m^2)		15-year forest	40-year forest	mixed forest	mbau forest	15-year vs. 40-year	40-year vs. mixed	40-year vs. mbau
>2.5 cm		$\bar{x}$	14.90	18.75	19.42	12.50	P<.01	NS	P<.01
≤10 cm	225	SD	4.68	5.07	3.58	3.61			
		plots	n=12	n=12	n=12	n=12			
>10 cm		$\bar{x}$	8.33	9.83	12.25	3.54	NS	P<.05	P<.001
≤25 cm	625	SD	4.33	3.13	3.98	1.93			
		plots	n=12	n=12	n=24	n=24			
>25 cm		$\bar{x}$	2.83	4.25	3.79	1.50	P<.05	NS	P<.001
≤50 cm	625	SD	1.40	2.05	1.86	0.98			
		plots	n=12	n=12	n=24	n=24			
		$\bar{x}$	1.17	1.75	1.75	1.17	NS	NS	NS
>50 cm	625	SD	0.84	1.22	1.11	0.48			
		plots	n=12	n=12	n=24	n=24			

[a] Analysis by 1-way ANOVA with preplanned comparisons.

Table 10. Stem densities of different diameter classes in 15 year-old secondary forest, 40 year-old secondary forest, and mature mixed and mbau forests.

			Number of stems per plot				Comparisons[a]		
diameter class	plot size(m^2)		15-year forest	40-year forest	mixed forest	mbau forest	15-year vs. 40-year	40-year vs. mixed	40-year vs. mbau
>2.5 cm		$\bar{x}$	27.08	32.50	60.75	43.00	NS	P<.001	P<.05
≤10 cm	225	SD	9.55	6.79	11.62	10.28			
		plots	n=12	n=12	n=12	n=12			
>10 cm		$\bar{x}$	17.00	13.67	21.54	11.96	NS	P<.001	NS
≤25 cm	625	SD	9.41	3.92	5.56	4.38			
		plots	n=12	n=12	n=24	n=24			
>25 cm		$\bar{x}$	4.67	7.75	6.00	4.83	P<.05	NS	P<.05
≤50 cm	625	SD	3.03	5.28	2.89	2.39			
		plots	n=12	n=12	n=24	n=24			
		$\bar{x}$	1.67	2.25	2.29	3.42	NS	NS	P<.05
>50 cm	625	SD	1.16	1.29	1.52	1.74			
		plots	n=12	n=12	n=24	n=24			

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[a] Analysis by 1-way ANOVA with preplanned comparisons.

Both mixed forest and mbau forest had a greater density of sapling size stems in the understory ($P < .001$ and $P < .05$, respectively) than did 40 year-old forest. Mixed forest also had a denser pole size class ($P < .001$) than did the 40 year-old forest. Mbau forest was significantly sparser in the tree size class ($P < .05$) but significantly denser in the largest size class ($P < .05$) than the 40 year-old forest.

The basal area of all species > 10 cm dbh did not differ significantly between the 40 year-old secondary forest (mean = 29.6 m^2 ha^{-1}, SD = 7.62) and the two mature forests (mixed forest mean = 30.4 m^2 ha^{-1}, SD = 8.016; mbau forest mean = 34.08 m^2 ha^{-1}, SD = 11.2).

There was very little overlap between the secondary and mature forests in terms of which species account for the basal area. Shade-intolerant species dominated in the secondary forests, although there remained the few remnant mature forest trees, mentioned earlier, which were not cut when the forest was cleared. Many of the gap species were important in the canopy of secondary forest, in particular, *Musanga cecropioides, Macaranga spinosa* and *Phyllanthus sp.*.
The 18 gap species alone were responsible for 77% (SD = 19.6) of the basal area in 40 year-old forest where they were 54% of all stems > 10 cm dbh. In the 15 year-old forest they comprised 76% of stems > 10 cm dbh.

The important species contributing to basal area in mature forest were shade-tolerant species whose seedlings and saplings were represented in all size classes of the understory. *G. dewevrei* accounts for 88.5% (SD = 15.05) of the basal area in mbau forest. *B. laurentii*, *C. alexandri*, and *C. michelsonii* combined account for 60.7% (SD = 20.31) of the basal area in mixed forest.

The dominant species of the mature forest were strikingly rare, even as juveniles, in the secondary forest. They were absent from the sapling and pole size classes (Table 11). The combined density of *G. dewevrei*, *B. laurentii*, *C. alexandri* and *C. michelsonii* was significantly lower for these size classes in 40 year old forest than in either of the mature forest types ($P < .01$ and $P < .001$). Nor were these species any more frequent as juveniles in the 40 year-old forest than in the 15 year-old forest (Table 11). In fact, although there were no significant differences, the mean density of these species was higher in the younger forest where many of them may have been sprouts from undamaged root stock. (The younger forest had only been burned once).

Smaller seedlings were not systematically censused in the secondary forest but special note was taken of seedlings of *G. dewevrei* and *B. laurentii*. Where these were seen, they were always closely associated with a parent tree which had not been cut during cultivation. The seedlings formed a narrow seedling shadow reflecting the limited range of the characteristic ballistic dispersal. The mature forest species appearing in the understory of secondary forest and not associated with remnant parent trees were animal dispersed. These included species such as *Dacryodes sp.*, *Anonidium manii*, *Celtis mildbraedii*, *Dialium sp.*, *Chlorophora excelsa*, and *Parinari excelsa*. All of these species are

Table 11. Comparative density of sapling and pole-size individuals of mature forest dominants in the subcanopies of secondary and mature forests.[a]

diameter class	plot size(m^2)		Number of stems per plot 15-year forest	40-year forest	mixed forest	mbau forest	Comparisons[b] 15-year vs. 40-year	40-year vs. mixed	40-year vs. mbau
>2.5 cm		$\bar{x}$	1.33	0.92	5.67	7.33	NS	P<.01	P<.001
≤10 cm	225	SD	2.10	1.78	4.16	4.89			
		plots	n=12	n=12	n=12	n=12			
>10 cm		$\bar{x}$	1.00	o.58	7.92	8.92	NS	P<.001	P<.001
≤25 cm	625	SD	1.76	1.24	3.91	4.34			
		plots	n=12	n=12	n=24	n=24			

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[a] Includes combined density of *Gilbertiodendron dewevrei*, *Brachystegia laurentii*, *Cynometra alexandri*, and *Cleistanthus michelsonii* for each forest type.

[b] Analysis by 1-way ANOVA with preplanned comparisons.

infrequent in the mature forest relative to the shade-tolerant dominants.

DISCSUSSION

Species diversity relative to size and frequency of treefall gaps

The first hypothesis proposed in this study was that the more diverse mixed forest has more frequent and larger disturbances than mbau forest. The results were somewhat equivocal. There are likely to be more treefall disturbances for any given area of several hectares in mixed forest than for a similar sized area in mbau forest. The disturbed proportion of the total area, however, was not predictably greater in mixed forest than mbau forest due to gap size variability and the irregularity of gap occurence in both forests.

If individual sample plots were larger, for instance 1-3 km^2 per plot, this would reduce the inter-plot variability in total area disturbed, at least if gaps of only up to approximately 1000 m^2 were encountered. These larger plots, however, would still not allow adequate sampling for the blow down scale disturbances. In fact, it is unlikely that any size plot would be adequate because of the time factor. Large blowdowns are not only rare in space but also in time. This does not preclude the possibility that they have had an influence on the distribution of forest types.

It is possible that an area with very few recent treefalls may have had many in the past. The fact that old gaps with decaying logs were more numerous in mixed than in mbau forest supports the hypothesis of greater overall disturbance in mixed forest. It is particularly interesting that the mixed forest site with the fewest recent treefalls, Kadiketu, had the most old gaps. This suggests a possible cyclical occurrence of gaps at a time interval of > 15 years. Such patterns were not seen, or looked for, elsewhere but they merit further investigation.

The five most common pioneer species were more frequent as mature individuals in mbau forest than in mixed forest (although only at $P < 0.1$). This result appears to be in conflict with the presence of more old gaps in mixed forest. It is curious that only the fastest growing pioneer species, in particular *Musanga cecropioides*, were represented in the mbau forest canopy, whereas the slower growing pioneers were more common in mixed forest. A possible explanation for this is a difference in the nature of canopy closure of gaps in the two forest types. The dominant and emergent trees in mixed forest have broad shallow crowns which often are not contiguous, allowing light to reach subcanopy layers. Subcanopy size classes are denser in mixed forest than mbau forest (Table 10, see also chapter 1). It may be that shade-intolerant gap-species are able to maintain themselves as pole-size individuals in mixed forest but not mbau forest. In mbau forest the dominant, *G. dewevrei*, has deep narrow crowns which are generally contiguous. The subcanopy layers are relatively sparse and composed mainly of shade-tolerant species.

This interpretation points to the importance of canopy structure to the maintenance of species diversity. The perpetuation of species richness in the upper canopy depends on the species richness of shade suppressed understory layers because the understory is the major source of future canopy level crowns. In the Ituri Forest the difference in diversity between mixed and mbau forest understories may be more closely tied to differences in canopy structure than to differences in gap dynamics.

Species diversity relative to the variety of gap microsites

The second hypothesis proposed was that treefalls in the mixed forest provide a greater diversity of microsites for seedling establishment and growth than mbau forest. None of the measured variables thought to affect microsite differed significantly between the two forest types (number of gaps with upturned rootmasses, overhead cover, and number of gap-forming trees).

The litter was different in the two forest types as a result of differences in species composition. Mbau forest gap litter was composed primarily of *G. dewevrei* leaves and branches whereas litter from this species was essentially absent from mixed forest. These differences did not have a measurable influence on germination of pioneer species. Similar species colonized gaps in both forest types. Although gap size and shape undoubtedly determined whether or not individual seedlings would be likely to reach maturity, above a certain minimum area (approximately 100 m^2), gap size did not influence which species germinated.

There was no evidence that tree species had specialized in any more than a general way to specific sites within gaps or to specific "kinds" of gap. For instance, small-seeded species did not root through thick litter but they were found germinating not only on root masses but also spots of bare soil and rotting wood. Also, released dominants grew better than shade-intolerant pioneers in small gaps, but, except for young seedlings, they were also able to grow in the full sunlight conditions of large gaps.

In terms of affecting forest composition, the important conditions in treefall gaps may not be those at ground level, which are pertinent primarily to germinating pioneers, but rather those at mid-level which are pertinent to released canopy species. Overall, pioneer species make a very small contribution to canopy diversity. Released saplings and poles are probably less microsite sensitive and may be able to benefit from a range of increased availability of light. Although the density of potential canopy species was greater in the understory of mbau forest, the species richness of this layer was greater in mixed forest (see chapter one). The factors affecting the diversity of the suppressed subcanopy layers may be more immediately relevant to the maintenance of canopy diversity than variations in seedling microsites provided by treefall gaps of different sizes or shapes.

In terms of autecological studies pertinent to forest diversity, it is likely to be more productive to investigate tolerance ranges for different species rather than microsite specializations. Particularly interesting are ranges of tolerance to shade and sunlight for different sizes or ages of any given species as these factors affect the relative abundance of canopy species as suppressed individuals in the understory.

Contribution of gap-dependent species to overall forest diversity

The third hypothesis proposed was that gap-dependent species account for a greater proportion of all tree species present in mixed forest than in mbau forest. The 18 species which regenerate in and commonly restricted to gaps occur in both forests but are relatively unimportant in both. Both forest types are dominated by shade-tolerant species, *G. dewevrei* in mbau forest and *B. laurentii*, *C. alexandri*, and *C. michelsonii* in mixed forest; however, the relative abundance of the shade-tolerant dominants is less in mixed forest, both in terms of density and basal area, than in mbau forest.

The decreased importance of shade-tolerant dominants in mixed forest was not matched by an increased importance of the common gap-dependent species. Instead, a group of species of uncertain shade tolerance was more prominent in mixed than in mbau forest. These species were not common in the understory of mature forest but this fact is not an adequate indication of their shade intolerance as they were also rare in the canopy. The conditions under which these tree species usually germinate and establish remain obscure, except that they do not behave like pioneer species as they were not common in early secondary forests. It is not even clear that these species will show similar physiological responses to a given set of environmental conditions.

The scattered individuals of mature forest species found as juveniles under the canopy of 40 year-old forest belonged to this group. All the species found had animal-dispersed seeds whereas the seeds of the shade-tolerant dominants in mature forest were heavy and normally received no further dispersal than the forceful expulsion from their pods.

This difficult-to-classify group of species may correspond to Whitmore's (1982) "broad class of species of intermediate tolerance", or late secondary species. The fact that these species are more abundant and diverse in mixed forest than in mbau forest may be related not only to the frequency of gaps in mixed forest but also to the forest structure itself. The upper canopy (35-45 m) is more open and heterogeneous in mixed forest than mbau forest. It may be that *B. laurentii*, due in part to the geometry of its crown, is less likely to exclude species of intermediate tolerance which can not survive under a closed canopy of *G. dewevrei*.

Distribution of forest types relative to major past disturbances.

The fourth hypothesis proposed was that one of the two forest types is composed of species more resilient to large scale disturbance than the other forest type. Presumably the species association of one forest type can invade and establish more rapidly than the species association found in the other.

If we consider a major disturbance to be one that kills all living trees over an area of several hectares or more, then tree species that disperse diaspores over large distances will have the best chances for establishment. Mixed forest contains a greater proportion of animal and wind-dispersed tree species than mbau forest. Thus, the forest that would eventually replace early secondary species after a major disturbance would more closely resemble mixed forest. Because of their poor dispersal capabilities, however, mixed forest dominants, including *Brachystegia laurentii*, *Cynometra alexandri*, and *Cleistanthus michelsonii* would be conspicuously absent.

None of the shade-tolerant dominants from either forest type are adapted to colonize large disturbances. These species have primarily ballistically dispersed diaspores. In a 40 year period, seedlings of the shade-tolerant dominants from mature forest had not invaded the secondary growth on abandoned garden sites more than several meters beyond the crown edge of remnant mother trees. Nevertheless, the three dominant canopy species in mixed forest have larger crowns and smaller seeds than the mbau forest dominant and they would, therefore, be likely to move into a disturbance from its border more quickly than *Gilbertiodendron dewevrei.*

It is tempting to hypothesize that prehistoric disturbance is responsible for the current distribution of the two forest types in the Ituri region, or at least, for the distributions of the forest dominants. *Gilbertiodendron dewevrei*, *Brachystegia laurentii*, *Cynometra alexandri*, and *Cleistanthus michelsonii* may be slowly spreading from isolated forest pockets left in the wake of large scale major disturbance. In the case of mixed forest, in the central Ituri Forest, the three latter shade-tolerant species are now co-dominant. On the other hand, in some areas a single dominant species may act as a slowly-moving invasive front (see Louis 1947 for *G. dewevrei* and

Eggeling 1947 for *C. alexandri*). The transition zone where species' fronts meet today may be dynamic and subject to change according to local disturbance patterns.

An extensive burned charcoal layer, at 20 cm depth, was found in the study area and was dated at 2,290 ±90 years B.P. (Beta Analytic Inc., Coral Gables, FL). This is evidence for past disturbance. There is, as yet, however, no palynological data to support a "refugium-expansion" explanation for forest type distributions in the Ituri watershed. A field study that might reveal a relationship between species distributions and pre-historical fire would involve mapping the extent of the burned charcoal layer in conjunction with maps of dominant forest species.

In summary, some support was found for three of the four hypotheses proposed in this paper. Their ability to adequately explain the difference in species diversity between the two forest types, however, is uncertain. The more diverse mixed forest had more frequent though not consistently larger treefall disturbances than the mbau forest. No difference in microsite availability within treefall gaps was found between the two forest types. The five most common tree species found as seedlings in treefall gaps were not more frequent as mature individuals in mixed forest than mbau forest and they accounted for only a small proportion of the trees present in either forest. The mixed forest contained a greater proportion of well-dispersed tree species indicating that it may be more resilient to major disturbance than mbau forest. Well-dispersed species would be relatively rapid colonizers, but the majority of canopy-level individuals in both forest types is accounted for by only a few poorly-dispersed species which are not good colonizers.

Although the less complete dominance by a single shade-tolerant species in mixed forest may be due, in part, to the more frequent treefall disturbance in this forest type as compared to mbau forest, this study suggests that other factors are also important. Differences in density and regularity of the upper canopy affect the species richness of suppressed subcanopy layers which, in turn, determine the diversity of species able to be released by small canopy gaps.

If the less frequent treefall disturbance in mbau forest is due to the forest structure itself, then normal disturbance rates may be important to the maintenance of diversity within each forest type but not to major changes in forest composition. This is because the characteristic structure of mbau forest is due to the established single species dominance by *Gilbertiodendron dewevrei*. That *G. dewevrei* stand structure might engender low disturbance rates is suggested by its aerodynamically smooth canopy surface and the species' tap root (Putz 1984). A variable disturbance rate at the transition zone between mixed and mbau forest might affect the rate of advance or retreat of *G. dewevrei* but only the rare large-scale disturbance would make major changes in species diversity and then only by changing dominance patterns and restructuring the forest.

Normal disturbance rates, as measured in this study, may be relatively trivial patterns, as far as forest composition and diversity are concerned, imposed on a more fundamental pattern of recovery from ancient disturbance. Although there is ample evidence for Holocene changes in the extent of African rain forest (Hamilton 1982, Livingstone 1980a, 1980b), how these climatically-mediated shifts are reflected in modern forest composition at any given point has not been clarified. But, to the extent that interpretations can be drawn from a larger time scale, our understanding of dominance and diversity in African equatorial forests would be greatly enhanced.

FOOTNOTES

[1] The Ituri Forest is generally included in tropical rain forest maps as the northeastern edge of the Guineo-congolese forest block (Richards 1952, Walter 1973, White 1983). It fits the general structural and climatic definition of rain forest as used by Richards (1952) and Whitmore (1984). Although very few climatic data have actually been collected in the Ituri region, Bultot (1971) inferred, from patterns at surrounding stations (observations 1930-1959), that mean annual precipitation was between 1700 and 1800 mm with a rainless period of no more than 40 days. The driest period is from mid-December to the end of February, during which time the monthly precipitation may fall below 100 mm.

[2] "Mature", here, means "climax" as used by Lorimer (1980) to describe an all-aged forest of Southern Appalachia, "capable of self perpetuation in the absence of severe disturbance". The dominant canopy trees of both Ituri forest types occur as seedlings, saplings and poles under the forest canopy (see chapter one).

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CHAPTER III

REGENERATION PATTERNS OF DOMINANT TREES IN LOW AND HIGH DIVERSITY TROPICAL FORESTS

INTRODUCTION

Humid evergreen and semi-evergreen forests throughout the tropical zone are noted for high tree species diversity relative to temperate forests (reviews in Unesco/UNEP/FAO 1977, Hall & Swaine 1981, Leigh 1982, and Whitmore 1984). Large numbers of tree species are found to coexist in even relatively small forest sample areas. The co-occurrence of many tree species is remarkable in view of the fact that most mature trees, regardless of species, have similar resource requirements (Hubbell 1980, Whitmore 1982). As pointed out by Connell (1978) and Hubbell (1980), this homogeneity of resource base makes it unlikely that tropical forest diversity can be explained by niche differences among different species of mature tree. The ecology of juvenile stages has, therefore, been invoked as being critical to an understanding of species richness. Two general hypotheses have been proposed: 1. The regeneration niche hypothesis (Grubb 1977) and 2. The seed and seedling predation hypothesis (Janzen 1970, Connell 1971).

In this paper predictions generated from these hypotheses are examined in a comparative manner, using experiments and observations in both a species-rich and a species-poor tropical forest. Field work was conducted between January 1980 and June 1983 in the Ituri Forest of northeastern Zaire (Figure 1). The base of operations was at Epulu in a transition zone between single-species dominant mbau forest and mixed forest (Figure 2). The rationale and assumptions of the comparative approach are explained after discussion of both hypotheses and presentation of predictions derived from them.

Regeneration Niche Hypothesis. Grubb (1977) suggests that plant species diversity is tied to differences in species' requirements for regeneration. He considers all stages of the regeneration cycle to be potentially important including flowering, pollination, seed-set, dispersal, germination, establishment and the further development of the immature plant. Grubb predicts that in species-rich tropical communities available regeneration niches have been partitioned such that species have narrowly defined regeneration niches. Recently these ideas have been applied specifically to tropical forests through the concept of "gap-partitioning" or the partitioning of establishment sites by tropical tree seedlings (Hartshorn 1978, 1980; Denslow 1980; Orians 1982, Pickett 1983).

There have been numerous studies of germination requirements and seedling morphology of tropical tree species (Guevara & Gomez-Pompa 1972, Ng 1978, Hall & Swaine 1981, Putz 1983, Uhl & Clark 1983) and the phenology of flowering and pollination syndromes (Janzen 1967, Heithaus et al 1974, Stiles 1975, 1978, Frankie 1975, 1976). These studies have added greatly to our knowledge of regeneration of tropical trees, but they do not directly test the hypothesis that tree species richness in

Figure 1. The Ituri Forest, Zaire.

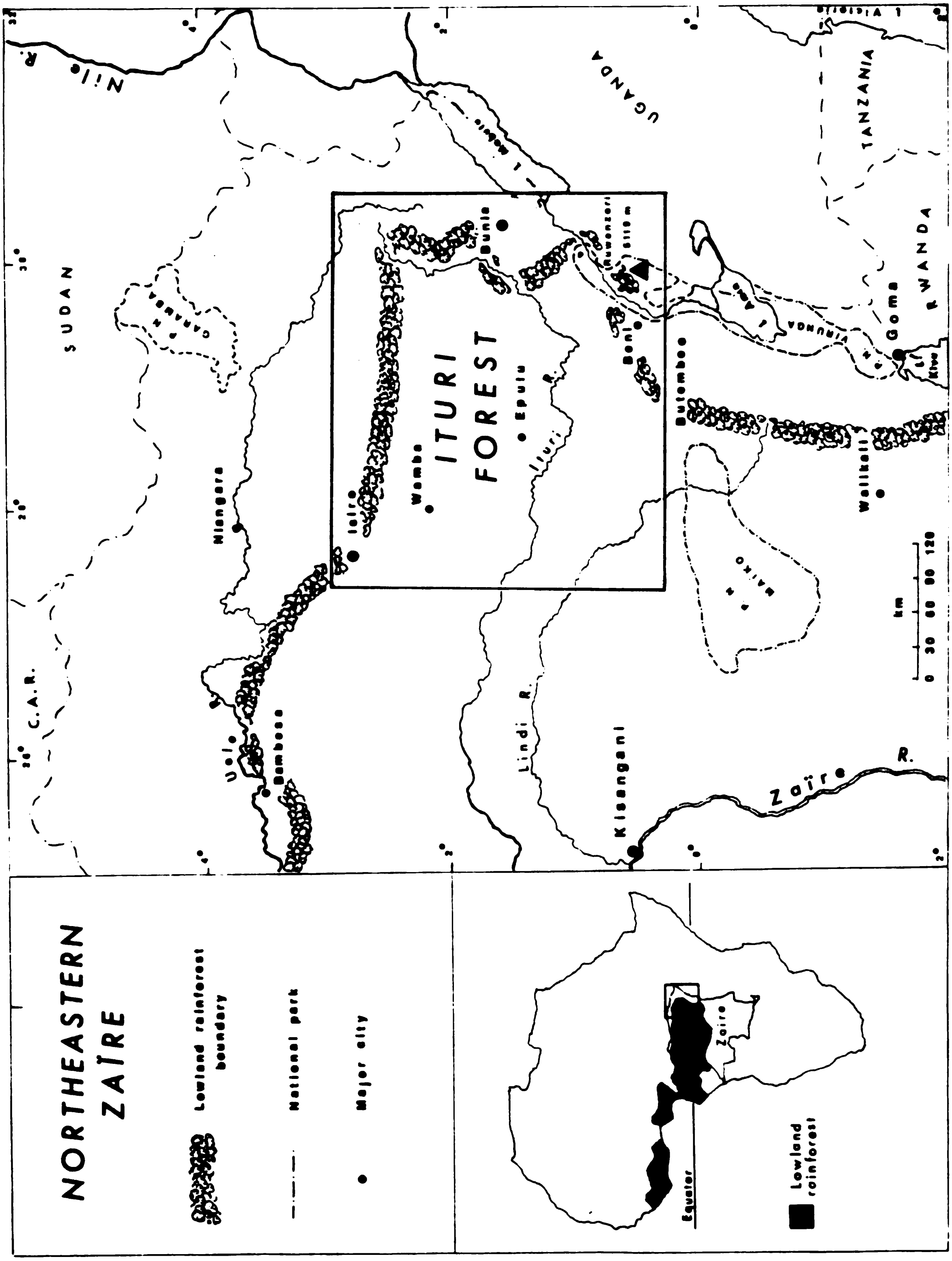
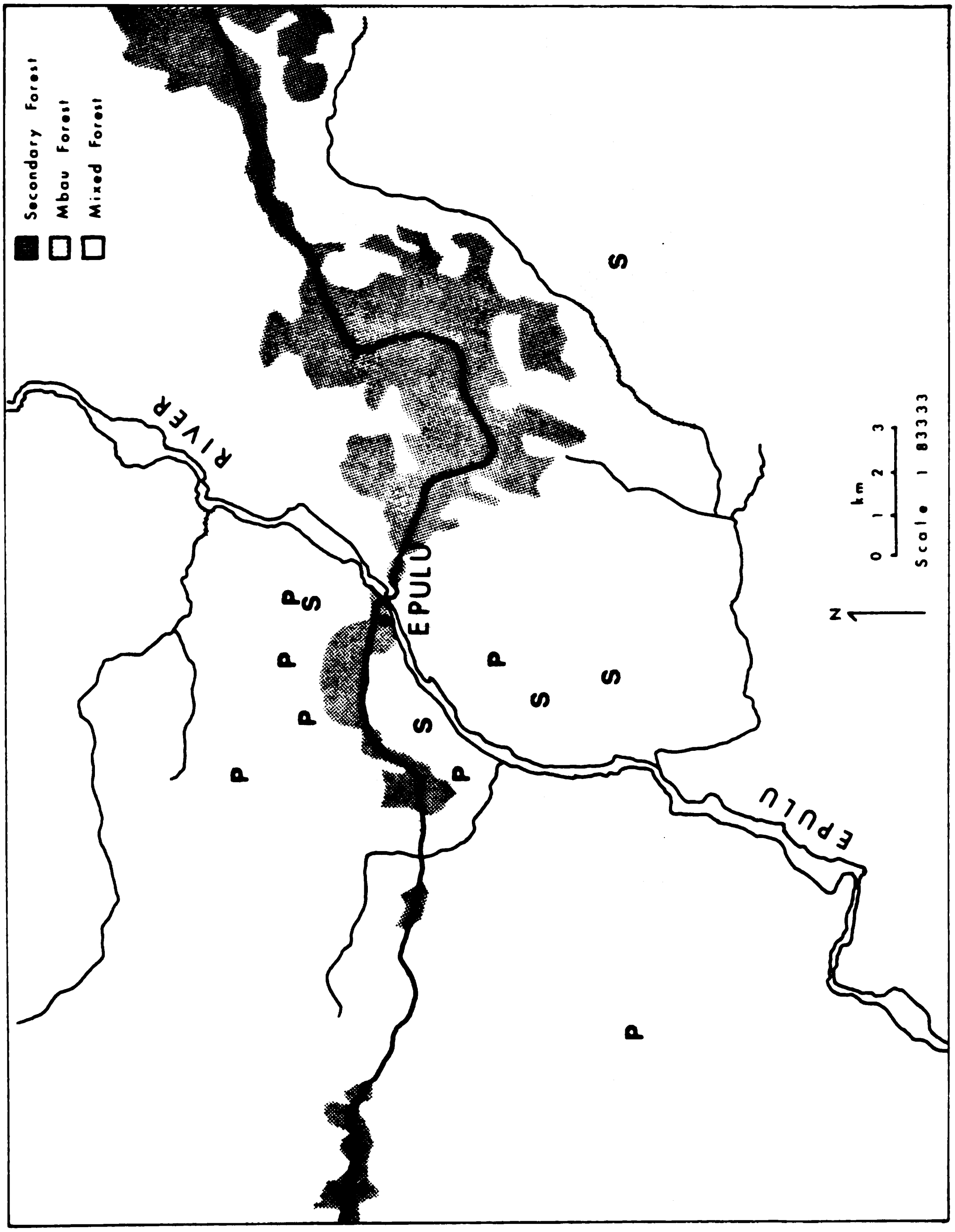

NORTHEASTERN ZAÏRE
Lowland rainforest boundary
National park
Major city
Lowland rainforest
Equator
Zaïre
SUDAN
C.A.R.
UGANDA
TANZANIA
RWANDA
P.N. Garamba
P.N. Maiko
P.N. Virunga
Nile R.
Uele
L. Mobutu
L. Idi Amin
L. Victoria
L. Kivu
Ruwenzori 5119 m
Bunia
Beni
Butembo
Goma
Walikali
ITURI FOREST
Epulu
Wamba
Isiro
Niangara
Bambesa
Ituri R.
Lindi R.
Zaïre R.
Kisangani
km
0 30 60 90 120
24°
26°
28°
30°
4°
2°
0°

Figure 2. The central Ituri Forest study site, with locations of forest types and research areas.

Plot locations:

P ... Phenology studies

S ... Seed-transplants


■ Secondary Forest
□ Mbau Forest
□ Mixed Forest
EPULU RIVER
EPULU
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tropical forests is maintained by partitioning of the regeneration niche.

Using a comparative approach, I predict that in mature species-rich tropical forest coexisting species will have discrete and narrow regeneration capabilities. These syndromes are expected to contrast with a relatively wider, less-specialized regeneration niche for the dominant species in mature species-poor tropical forest.

Seed/seedling predation hypothesis. According to this hypothesis, as stated by Janzen (1970) and Connell (1971), diversity is promoted by the fact that seeds and juveniles suffer particularly high mortality near the parent tree. This hypothesis, dubbed the "escape hypothesis" by Howe and Smallwood (1982), allows that species specific predation may increase either because of the greater concentration of seeds under the parent or because of the nearness of a conspecific adult. In both cases the expected result is elimination of all juveniles under the parent and increasing probability for survival and establishment at greater distances from conspecific adults. This process leads to the coexistence species. Numerous field studies conducted during the 1970s gave conflicting results (reviewed in Howe and Smallwood 1982, Connell et al. 1984, Clark & Clark 1984). Two of the recent studies demonstrated that the process of greater mortality near the parent or adult conspecifics does indeed frequently occur (Augspurger 1983, Clark & Clark 1984).

It has been pointed out that the expected pattern of predation may occur during juvenile stages but, nevertheless, not make a major contribution to the species richness of mature trees (Hubbell 1980). This would be the case in a non-equilibrium community where the presence of many species results from disturbance (past or ongoing) or slow climatic change (Connell 1978).

Our comparative approach simultaneously tests the seed-predation hypothesis and its importance to the maintenance of species richness. It is predicted that in species-rich tropical forests seed and seedling mortality will be very high close to the parents and less severe distant from adult conspecifics. If this process is important to the maintenance of species diversity, a contrasting pattern will occur in species-poor forests. Juvenile mortality near parents will be less devastating and may not differ significantly from mortality distant from parents.

If the comparative approach is going to be informative it is essential that there be no other overriding causes determining the differences in species richness between the two contrasted forests. Neither forest should be successional and both forests should occur on equivalent sites without marked differences in topography, soils, or water regime. In northeastern Zaire these conditions hold for the single species dominant mbau forest and the species-rich mixed forest.

In their ecological classification of the forests of central Africa, Lebrun and Gilbert (1954) identified an order of forests which was evergreen, dense and equatorial (Gilbertiodendretalia Dewevrei). These forests are widespread on deeply weathered, well-drained latosols. Two of the characteristic species are *Gilbertiodendron* *dewevrei* (DeWild.) Leonard and *Brachystegia laurentii* (DeWild.) Louis ex Hoyle. The former is the dominant of the monodominant mbau forest, accounting for more than 90% of the canopy-level stems and is well represented in all the juvenile size classes (Louis 1947, Gerard 1960, chapter one, this study). According to Gerard mbau forest is found on a wide variety of soils in the Uele region (3°N, 24°E). Vegetation and soil maps drawn for northeastern and eastern parts of the evergreen forest zone confirm that mbau forest is not linked to any outstanding site characteristic and co-occurs with mixed forests on many soil types (Pecrot & Leonard 1960; Evrard et al. 1960; see also chapter one, this study).

The second characteristic species, *B. laurentii*, is the most important of several co-dominants in the mixed forest, but never accounts for more than 40% of the canopy-level stems in our study area (chapter one, this study). It too is shade tolerant with juveniles in all size classes (Germain & Evrard, 1956). Two other co-dominant species in mixed forest also have shade tolerant seedlings and saplings, *Cynometra alexandri* (Eggeling 1947) and *Cleistanthus michelsonii* (pers.obs.). All three mixed forest species are important elements in forests on a variety of soils.

Our study area contains large blocks of both mixed and mbau forests (Figure 2). They form a ragged mutual border with island inclusions of several hectares to several km^2 of one forest type within the other. Soil samples from both forest types were analyzed for texture and macronutrient availablility but failed to reveal any significant differences in substrate between mbau and mixed forests (chapter one, this study). Both forests occur on gently rolling topography. The prevalence of canopy species regeneration in the understory suggests that both forest types are mature with a basically self-replacing species composition.

The mixed and mbau forests in northeastern Zaire meet the conditions of being neither successional nor edaphic formations; however, before we can test the two diversity hypotheses comparatively we must establish that opposing predictions would necessarily be made in each forest type. Diversity differences between the two forest types are striking (Table 1). Simpson's diversity indices (Ds), which measure both richness and equitability, are significantly different (P<.01) when calculated for stems >10 cm dbh in both forest types. Mixed forest has significantly more tree species per half hectare than mbau forest. *Gilbertiodendron dewevrei* accounts for a significantly greater percentage of the stems in mbau forest than *B. laurentii* does in mixed forest. These differences in diversity give strong reason to infer that if any single process is operating to maintain species richness in mixed forest, it would be inoperative in mbau forest.

Comparisons between the two forests are rendered more meaningful by the fact that species with similar morphological and ecological attributes exist in each forest type and can be compared. *Gilbertiodendron dewevrei*, the dominant in mbau forest, which is essentially absent from mixed forest except for rare stands, is of the same tribe, Amherstiae (Caesalpiniaceae), as *Brachystegia laurentii*, the most abundant canopy tree in mixed forest. The next

Table 1. Species diversity of mixed and mbau forest types of the Ituri Forest, Zaire, calculated for stems > 10 cm dbh.[a]

	Mixed forest	Mbau forest	Probability
Ds[b]	.89	.37	P<.01
species richness in 0.5 ha	65	18	P<.01
dominance[c] (% stems)	28	79	P<.01

[a] Data collected from 24 $625m^2$ plots in each forest type. Analysis by Student's *t* test.

[b] Simpson diversity index; greatest possible value (species richness and equitability) = 1.

[c] Percent of all stems accounted for by the dominant species in each forest type.

most common species in mixed forest, *Cynometra alexandri* (Table 2), although of another tribe, is also caesalpiniaceous and has a flower and a fruit morphology similar to that of *G. dewevrei* and *B. laurentii*. The comparisons presented here consist of contrasting observations or experimental results obtained of the two mixed forest species with those obtained of *G. dewevrei* in the mbau forest. A third mixed forest co-dominant *Cleistanthus michelsonii* was excluded from the study although it also is well represented in all size classes (Table 2). It belongs to a different family, Euphorbiaceae, and has very different reproductive characteristics. Presumably, if single-dominance arises from specific characteristics of the dominant canopy species, this will be more apparent when this species is contrasted with canopy species which do not attain comparable dominance but which, nevertheless, resemble the single-dominant speices in reproductive ecology and morphology.

The outstanding diversity differences between the two forests and the morphological similarity of some of the component species in each community allow a comparative examination of the two diversity hypotheses. Predictions for each forest type are:

	PREDICTIONS	
HYPOTHESES	MIXED FOREST	MBAU FOREST
1. regeneration niche	narrow regeneration niche, (evidence of specialization)	broad regeneration niche
2/ seed/seedling predation	high mortality near parents	good survival near parents

Table 2. Size class distribution of three co-dominant canopy species in mixed forest.[a]

size class[b]	Average number of individuals per hectare *Cleistanthus michelsonii*	*Cynometra alexandri*	*Brachystegia laurentii*
saplings	55.6	18.5	178.0
poles	25.3	15.3	86.0
trees	10.0	8.0	39.0
large trees	4.7	11.0	11.0

[a] Data collected from 24 625m^2 plots in each forest type.

[b] size classes:
saplings, stems > 2.5cm dbh ≤ 10 cm dbh;
poles, stems > 10 cm dbh ≤ 25 cm dbh;
trees, stems > 25 cm dbh ≤ 50 cm dbh;
large trees, stems > 50 cm dbh.

in mortality distant
from parents

The work of Rankin (1978) set a precedent for studying the "escape hypothesis" in single-species-dominant tropical forest. In the mora forests of Trinidad she substantiated prediction 2 for the dominant *Mora excelsa.* There was low predation on seeds and a high level of seedling establishment under parents in the single species dominant forest. Due to the high density of *M.excelsa* adults it was impossible to experimentally remove seeds to greater and greater distances from the parent in mora forest and simultaneously be moving them farther from adult conspecifics. For this reason experimental seed-predation plots were either located under adult conspecifics or removed to an alternate forest type. The same experimental procedure was used in the Ituri Forest study because of the high density of *G. dewevrei* in mbau forest.

There is an additional reason for this design in the Ituri Forest. All three caesalpiniaceous species produce mast seed crops. That is, they fruit synchronously, flooding the environment temporarily with a single species' seeds. The seeding periods of the three species themselves do not overlap. It was possible, therefore, to test predation on seeds at low overall seed density in the environment and distant from adult conspecifics by removing the seeds to the alternate forest type: *C. alexandri* and *B. laurentii* seeds were removed to the mbau forest and *G. dewevrei* seeds were removed to mixed forest.

The mast fruiting pattern itself suggests a third hypothesis related to the "escape hypothesis". It has been suggested that where there is a high density of a given tree species, and relatively low populations of potential seed predators, the tree species can escape decimation of its seed crop by mast fruiting (Janzen 1974, 1976; Boucher 1981). Predator satiation can occur in such a situation long before the seed resource has been destroyed. Such community-level predator satiation requires that the density of seeds be high over a large area. Seeds removed from the high density area would, presumably, be destroyed. Patterns of predation revealed by seed-transplants allow an evaluation of this mechanism for juvenile survival under adult *G. dewevrei.* A third prediction generated from this hypothesis is outlined as follows:

	PREDICTIONS	
HYPOTHESIS	MIXED FOREST	MBAU FOREST
3. predator satiation	heavy predation on *G. dewevrei* seeds when artificially introduced into environment devoid G.dewevrei seeds	low percentage of *G. dewevrei* seeds destroyed by predation in mast fruiting area

METHODS

The predictions from the regeneration-niche hypothesis are less specific than predictions from the second and third hypotheses and are not amenable to direct experimental testing. Instead, systematic observations were made on the following aspects of the regeneration niche: flowering and fruiting phenology, pollination and seed dispersal. The species observed were *Gilbertiodendron dewevrei* (mbau forest), *Brachystegia laurentii* (mixed forest), and *Cynometra alexandri* (mixed forest). Predictions from the predation and predator-satiation hypotheses were tested with a series of seed-transplant experiments carried out over two years. Seed-predators were identified and populations of one important predator group (rodents) were assessed. Survivorship of newly germinated seedlings was monitored.

Flowering and fruiting phenology

Canopy level trees of *G. dewevrei* and *B. laurentii* were monitored. The nearest canopy tree of a given species at every 10 m interval along a transect was permanently marked for a total of 65 *B. laurentii* in mixed forest and 62 *G. dewevrei* in mbau forest (P in Figure 2), although one marked *G. dewevrei* was not refound in 1982 and 1983.

The method used for assessing flowering level was similar to that used by Gerard (1960). Ground counts of floral bracts reflect flower density because floral bracts fall regardless of whether or not pollination occurs and, being very coriaceous, they persist on the forest floor for more than a month. At the end of the flowering period all fallen floral bracts were counted within a 1 m^2 plot two paces from the base of each tree in an easterly direction. The direction was adjusted to be under the tree crown in the case of *B. laurentii* which frequently had asymmetrical and noncontiguous crowns.

At the end of the fruiting period, an estimate of fruits matured was made by counting all seeds and new seedlings within a radius of 2 1/2 meters of each marked tree. The number of propagules present may have been greatly reduced through predation; therefore, a count was also made of the empty pods on the ground. Pods fall soon after dehiscence and the size and depression marks indicate whether or not seeds matured. All evidence of seed predation was noted.

Pollination studies.

Pollination experiments were aimed at determining whether or not xenogamy (out-crossing) was essential or if geitonogamous pollinations (between flowers on a single tree) could result in successful fertilization. These manipulations were accomplished only on one species, *G. dewevrei*. This species was the easiest to work with because, being the most abundant, it had the greatest number of accessible crowns. It also had the largest flowers of all three caesalpiniaceous species. A technique that yielded satisfactory results involved bagging all experimental flowers prior to anthesis. Fine cotton weave facing-material was used for the bags. Tanglefoot was generously applied to the stem to discourage ants from making holes in the bags. Stamens of all flowers to be out-crossed were clipped, but only after anthesis. It was clear, by inspection, that a single flower, at least when bagged, did not deposit pollen on its own stigma. All manipulations were made soon after dawn, the apparent time of anthesis. Ten infloresences were bagged on three trees.

Observations were made of flower visitors at *G. dewevrei* crowns convenient for observation.

Seed Dispersal.

The three main caesalpiniaceous species have ballistic seed dispersal with no special adaptations for dispersal by animals. Dispersal distance is largely determined by the force of propulsion from the dehiscing pod, the mass of the seed, and interference in the canopy. The distribution of seedlings around isolated mature individuals is a good reflection of seed-dispersal distance. By using isolated trees, interference from other canopy-level trees was avoided. Four *B. laurentii* trees and four *G. dewevrei* trees were located which had been left standing when garden plots were cleared around them. At the time of the study they had been isolated in forest regrowth vegetation for 16 to 18 years. The radius of each crown was measured as was the distance of all seedlings in a 4 m wide unidirectional belt transect from the base of each trunk.

Seed-transplants.

Each of the caesalpiniaceous species has a separate fruiting season and, therefore, predation experiments were necessarily done with one seed species at a time: in 1981, *C. alexandri* followed by *G. dewevrei* and in 1982, *G. dewevrei* followed by *B. laurentii*.
The methods used were modified as additional information was acquired and, in consequence, the experimental designs were varied for each of the four seed transplant periods (Table 3). In each case the design

Table 3. Experimental designs and treatments applied to seed-transplant plots in the Ituri Forest, Zaire, 1981 and 1982.

			Treatments				
			A	B	C		
year	starting month	species	background seed density and distance from adult conspecifics	seed-predator exclosures	site factors	experimental design	seeds per plot
1981	Aug.	*Cynometra alexandri*	mast (mixed forest) and no-mast (mbau forest)	antelope exclosure and open plot	leaf litter and no litter	2 grids of 28 plots each	60 (mixed) 70 (mbau)
1981	Sept.	*Gilbertiodendron dewevrei*	mast (mbau forest) no-mast (mbau forest) and no-mast (mixed forest)	antelope exclosure and open plot	no-mast in both forest types	3 lines of 10 paired plots each.	30
1982	Oct.	*Gilbertiodendron dewevrei*	mast (mbau forest) no-mast (mixed forest) and intermediate site	all-mammal exclosure and open plot		lines of plots (5,2,2). Ten plot pairs.	15
1982	Nov.	*Brachystegia laurentii*	mast (mixed forest) no-mast (mbau forest) and intermediate site	all-mammal exclosure and open plot		lines of plots (2,3,2). Ten plot pairs.	50

was factorial and the experimental units were 1 m^2 plots. Seeds were placed in them and subjected to various treatment modifications. Seed disappearance, evidence of seed-predation, and germination were recorded in each plot at one to two week intervals until at least two weeks after full expansion of the eophylls of surviving seedlings.

The treatment which most directly applies to prediction 2 (treatment column A, Table 3) had two components: 1. natural seed density on the forest floor and 2. distance from adult conspecifics, at the location where an experimental plot was placed. In 1981, for *C. alexandri*, these two components varied together: plots were either in a mast-fruiting area where there were both *C. alexandri* adults and seed-rain or they were in the other forest type (mbau) where neither was present. That same year during *G. dewevrei* seed fall, a stand of mbau forest was found that was not in fruit and did not have fruiting *G. dewevrei* near-by. This permitted partial testing of the two components separately. Plots with *G. dewevrei* seeds could be located under adult conspecifics where there was no background seed fall.

In 1982, the two components were not tested separately, but "intermediate sites" were added. The intermediate site for *G. dewevrei* seeds was mixed forest where it bordered on mast-fruiting mbau forest. In most areas these borders were quite abrupt. For *B. laurentii*, the intermediate site was an island of mbau forest (less than 1 km^2) which was surrounded by mixed forest with mast-fruiting *B. laurentii* trees. Thus, in both cases, plots in the intermediate site were in a no-seed area where, nevertheless, adult conspecifics and seeds were present in large numbers at less than a 200 meter distance. The site with high conspecific seed density and proximity to parents was, for *G. dewevrei*, mbau forest where *G. dewevrei* was mast-fruiting and, for *B. laurentii*, mixed forest where *B. laurentii* was mast-fruiting. The opposite conditions for each were in the alternate forest type.

As an attempt to identify the effect of seed-predators, plots were placed in exclosures (treatment column B, Table 3). In 1981 the only prior information on predators came from an analysis of forest antelopes' rumens (J. Hart, 1985). The antelope ate seeds of all three caesalpiniaceous species. Meter-high wattle fences were erected around those plots which were to have antelope excluded. The 1981 observations revealed that rodents were significant predators as well. Enough 5 mm wire mesh was acquired to make 10 all-mammal exclosures for the 1982 seed-transplant plots.

Although soils were similar in mixed and mbau forests there remained a possibility that other site factors, rather than or in addition to differential seed predation, could affect seed and seedling survival in mast and no-mast sites. Most obvious were differences in leaf litter. When seeds of mixed forest species were removed to mbau forest in order to remove them from conspecific seeds and adults, an additional treatment effect was a change in litter type. In mbau forest the litter is composed of large coriaceous *G. dewevrei* leaflets. Leaf-litter in mixed forest is more heterogeneous and generally composed of smaller leaves and leaf-parts. In 1981 an added factor in the design of *C. alexandri* seed-transplants was litter removal (treatment column C, Table 3). By the fortuitous finding of a non-fruiting mbau stand during *G. dewevrei* seed fall in 1981, all site factors, not just litter, could be controlled for *G. dewevrei* seed-transplants by having two no-mast sites, one under non-fruiting conspecific adults and one in mixed forest. A site factor was not included in the 1982 designs.

Seed plots were set out one to two weeks before peak seed fall for each species. The number of seeds placed in each plot varied with the species and from year to year (last column, Table 3). *Brachystegia laurentii* and *C. alexandri* have smaller seeds than *G. dewevrei* (Table 4) and, therefore, more of them were required per plot to approximate a comparable "reward" for a seed predator. It is estimated that the 1982 seed plots represent, over the 1 m^2 area, a seed density two to three times greater than would be expected under the canopy of a heavily fruiting tree at peak seed fall.

The actual field design varied with each seed-transplant experiment (Table 3). In 1981, the *C. alexandri* seed plots were set up as two grids of 28 plots each, one grid in mixed forest (mast) and one grid in mbau forest (no-mast). Plots were 3 m apart. Within each grid the four possible combinations of treatments were randomly assigned.

A short-coming of the grid design was that all plots were concentrated in a single area of each forest type. Predators could be concentrated in a given area due to some factor other than seed fall. This problem was alleviated for *G. dewevrei* seed-transplants in 1981 by locating paired seed-plots along transects, each plot-pair 15 m

Table 4. Seed characteristics of the three dominant caesalpiniaceous tree species of the Ituri Forest, Zaire.

Species	seed diameter[a]	wet weight[b]	dry weight
Gilbertiodendron dewevrei	5.5 cm	30.4 gm (SD=4.11)	18.2 gm (SD=2.15)
Brachystegia laurentii	2.5 cm	3.5 gm (SD=0.13)	2.8 gm (SD=0.13)
Cynometra alexandri	2.5 cm	2.0 gm (SD=0.08)	not recorded

[a] The approximate shape of all three species is a flattened disc; the measurement was of the longest dimension.

[b] Both wet and dry wieghts were calculated as the means from five lots of ten seeds each for *G. dewevrei* and *C. alexandri*, and from three lots of 50 seeds for *B. laurentii*.

apart last, for a total of ten pairs in each of three environments. The three environments were mast-fruiting mbau forest (heavy seed-fall), no-mast mbau forest (no seed fall), and mixed forest (no seed-fall). Within each environment the paired treatments were antelope exclosure versus no exclosure.

Plots were spread out over an even larger area in each forest type in 1982. For *G. dewevrei* seed-transplants there were five transects, with five unenclosed plots 15 m apart per transect in the mast environment (mbau forest). There were two transects each in the no-mast and intermediate environments (mixed forest), with five plots per transect. The mast and no-mast environments both had five additional all-mammal exclosure plots. Plots were laid out in a similar manner along transects for *B. laurentii* seed-transplants. There were 25 plots in three transects in the no-mast environment (mbau forest) and an additional two all-mammal exclosure plots. There were ten plots in two transects, for both the intermediate environment (mbau forest island) and the mast environment (mixed forest). An additional three plots in the intermediate site and five plots in the mast site were covered by all-mammal exclosures.

The number of *G. dewevrei* seeds falling to the mbau forest floor near plots was monitored in 1981 and 1982. In 1981 all naturally fallen seeds were counted in a third 1 m^2 plot between each set of paired plots. Additional seeds falling into the plot were recorded. In 1982, before seeds were placed into the test plots, the natural background seedfall was estimated from five 1 m^2 seed counts near each plot location.

Seed-predators.

For trapping purposes, in 1982 one hundred piles of *G. dewevrei* seeds and 43 piles of *B. laurentii* seeds were set out in a variety of habitats. As soon as seeds disappeared from a pile or other evidence of predation was seen, a snap trap baited with the test seed species was set by the pile. More seeds were added to the piles as seeds disappeared. Traps were checked daily for approximately three weeks.

Four species of forest antelope were in captivity at the Epulu base camp, *Cephalophus dorsalis, C. monticola, C. leucogaster*, and *C. nigrifrons*. All four species were offered *B. laurentii* and *G. dewevrei* seeds so that their handling of the seeds could be observed.

Small rodent populations in mixed and mbau forest were sampled with peanut-baited snap traps in order to determine if rodent communities in the two forest types had similar of species composition and density and if there was an increase in rodent density in either forest type during the fruiting season of the dominant trees. This was done by means of two replicate grids of snap traps (36 traps, 5 paces apart, 6 rows of 6 traps each) checked daily. The environments thus sampled were:

A. mbau forest just after *G.dewevrei* seed fall	Nov.3-15, 1982
B. mbau forest when there are no *G.dewevrei* seeds falling or on ground	March 19-30, 1983
C. mixed forest at end of *B.laurentii* seed fall	Jan.18-27, 1983
D. mixed forest when there are no *B.laurentii* seeds falling or on ground	Apr.6-15, 1983

Seedling survivorship.

Seedling survivorship of *G. dewevrei* and *B. laurentii* was studied in three ways: 1. estimation of the density of surviving seedlings from the 1982 seed crops, 2. calculation of the total understory seedling density, and 3. measurement over two years of survivorship and growth of suppressed seedlings of unknown age. Methods were as follows.

1. In January 1983, about three months after the end of seed-fall, all newly germinated *G. dewevrei* seedlings were counted in six 50 m x 6 m plots. The plots were in areas of mbau forest where no rodent trapping had been undertaken. No census of *B. laurentii* survival from the 1982 seed crop was made; however, a sample was made of *B. laurentii* survival from the 1980 seed crop. All new seedlings were counted in eight 3m x 2m mixed forest plots. These plots included those set up to study suppressed seedlings (described below under 3.).

2. The density of all seedlings of *G. dewevrei, B. laurentii* and *C. alexandri* less than 0.5 m in height was recorded by complete seedling counts in 24 randomly located 6.25 m^2 plots in mixed and mbau forest (12 plots in each forest type). Seedlings >0.5 m in height but <2.5cm dbh were similarly measured in 25 m^2 plots (12 in each forest type). Larger size classes were measured in 225 m^2 plots (stems < 10 cm dbh) or in 625 m^2 plots (stems > 10 cm dbh). There were 24 plots of the two larger plot sizes in each forest type (see chapter one).

3. In order to monitor growth and mortality of shade tolerant seedlings on the forest floor, all seedlings of *G. dewevrei* and *B. laurentii* in seven 3 m x 2 m plots were marked with aluminum tags in 1981; all leaves and leaf scars were counted. The plots were at 10 m intervals along a transect which ran from mbau forest into mixed forest. The seedlings were checked at least twice each year. Height increment and new leaves were recorded for surviving seedlings. New seedlings were marked, their height measured, and leaf number recorded.

RESULTS

Phenology.

Flowering of *G. dewevrei* and *B. laurentii* is irregular from year to year. Also, trees may flower but fail to produce mature fruit (Table 5). With all mbau forest sites considered together, 1981 and 1982 were mediocre flowering and fruiting years for *G. dewevrei* relative to 1983 when all marked trees produced a dense carpet of floral bracts. The two years during which data were collected for *B. laurentii* were markedly different. The first, 1981, was low for both flowers and fruits, whereas 1982 was an improved flowering year and a very successful fruiting year.

The censusing technique did not permit comparisons of reproductive effort between *G. dewevrei* and *B. laurentii*

Table 5. Percent of marked *Brachystegia laurentii* and *Gilbertiodendron dewevrei* producing flowers and fruits, 1981 - 1983.

species[a]	year	flowering level[b]			fruiting level[b]		
		none	low	high	none	low	high
Brachystegia laurentii	1981	47	31	22	89	11	0
	1982	18	25	57	1	14	85[c]
Gilbertiodendron dewevrei	1981	21	31	49	41	48	11
	1982	5	48	47	36	39	25
	1983	0	0	100			

[a] n = 65 *B. laurentii* trees and n = 62 *G. dewevrei* trees (1982 and 1983, only 61 *G. dewevrei* trees).

[b] flowering level:
none = no floral bracts in sample;
low = >0 <50 floral bracts per m^2;
high = $\geq$50 floral bracts per m^2.

fruiting level:
none = no seeds or mature pods under crown;
low = 1-15 mature pod valves and/or 1-15 seeds under crown;
high = >15 seeds under crown.

[c] This high percentage is probably an artifact of seed dispersal from adjacent trees.

because species differences in crown structure affect the density of fallen floral bracts and dispersal differences affect the density of fallen seeds. Nevertheless, the data do allow within-species comparisons. Trees in any given area tend to be synchronous with respect to their reproductive state. Defining a stand as synchronous where 3/4 or more of the marked trees were either reproductive (>50 flowers per m^2) or non-reproductive (including low reproductive effort, <50 flowers per m^2), it was found that collectively, over three years, there were 24 synchronous and five asynchronous stands (Table 6). The synchrony was most pronounced for *G. dewevrei.*

Individuals that flowered out of synchrony with the rest of the stand had low reproductive success. Flowering trees were considered to be isolated (asynchronous) when 3/4 or more of the other marked trees in the stand did not flower. In all there were nine asynchronous *B. laurentii* trees (out of 65 trees observed over two years) and two asynchronous *G. dewevrei* trees (out of 62 trees observed over three years). Four of these individuals showed no signs of successful pollination (one *G. dewevrei* and three *B. laurentii*). Aborted pods were found under eight others (two *G. dewevrei* and six *B. laurentii*) and only three had fallen pods with the marks of mature seeds (one *G.dewevrei* and two *B. laurentii*). Of these latter only one still had a surviving seed under it (*G. dewevrei*). This low reproductive success may have been due to reduced pollination in asynchronous trees and/or to increased pre- and post-dispersal predation.

Supra-annual flowering schedules may indicate that an

Table 6. Synchrony of flowering between trees within stands.

Species	number of stands	number of years	synchronous[a]	asynchronous[a]
Brachystegia laurentii	4	2	5	3
Gilbertiodendron dewevrei	7	3	19	2

[a] Synchronous stands were sampling sites in which 75% or more of the marked trees were either reproductive or non-reproductive. If less than 75% were of the same reproductive state the stand asynchronous.

individual tree lacks the energetic resources for two consecutive years of reproductive effort. A chi-square test for two independent samples was used to test the null hypothesis that the flowering status of a tree in a given year is independent of its previous year's flowering record. The null hypothesis cannot be rejected for *B. laurentii* (Table 7a). The second year, 1982, was an overall "good" flowering year. Even trees that flowered in 1981 apparently were not significantly less likely to flower in 1982 than those which did not flower in 1981.

In the case of *G. dewevrei* the null hypothesis is rejected (Table 7b). If a tree does not flower in year one it is more likely to flower in year two than an individual that flowered in year one. It is noteworthy, however, that 1983 was a uniformly high flowering year and all trees observed had a dense carpet of flowers and bracts beneath the canopy no matter what the previous year's flowering record had been. Conceivably there are very poor years for reproduction as well, when no trees flower regardless of the previous year's record.

Pollination experiments.

The only experimental flowers whose ovaries developed were those that had had xenogamous pollen transfers (Table 8). Considering that fresh pollen was always abundant and close at hand for geitonogamous transfers but scarce for out-crossing, these results are strong evidence that xenogamy is essential to fertilization in *G. dewevrei*.

The most common morning flower-visitors in *G. dewevrei*

Table 7. Reproductive status of individual trees on consecutive years.[a]

a. *Brachystegia laurentii*

flowering level, year 2	flowering level, year 1[b]	
	0-low	high
0-low	20	8
high	31	6

$X^2 = 1.49$, NS

b. *Gilbertiodendron dewevrei*

flowering level, year 2	flowering level, year 1	
	0-low	high
0-low	10	22
high	51	39

$X^2 = 6.1$, $P<.05$

[a] Analysis was by a chi square test for two independent samples. $P>.05$ is not significant (NS).

[b] Flowering level was high at ≥50 pairs of fallen floral bracts per m^2, and 0-low at <50 pairs of a fallen floral bracts per m^2.

Table 8. Record of ovary maturation subsequent to hand pollination of *Gilbertiodendron dewevrei*, 1982

	ovaries pollinated	ovaries matured
cross pollinations	35	12
geitonagamous crosses	20	0

crowns were sunbirds. The olive sunbird, *Cyanomitra olivacea*, and the violet-tailed sunbird, *Anthreptes aurantium*, frequented the trees observed. The honeybee, *Apis mellifera*, was not attracted to *G. dewevrei* flowers, the only showy part being a single deep red standard petal which often dropped coincident with sunbird visitation. The relatively large space (1-2 cm) between anthers and stigma makes it unlikely that honeybees or other small insects could effect pollination.

Pollination experiments were not possible for the other two caesalpiniaceous species but both *B. laurentii* and *C. alexandri* infloresences were intensely visited by honeybees. The flowers are smaller and more compact, making pollination by insects likely.

Seed Dispersal.

Considering that both *B. laurentii* and *G. dewevrei* are self-dispersed by the explosive force of the dehiscing legume, it is not surprising that the lighter seeds (Table 4) of *B. laurentii* generally land farther from the parent tree. Of the four reproductively mature and isolated *G. dewevrei* individuals examined, the farthest dispersed propagules, as evidenced by surviving seedlings, were six meters beyond the edge of the crown. The mean maximum dispersal beyond crown edge for the four trees was 3.25 m (SD=2.5). Of the four *B. laurentii* individuals whose seedling shadows were measured, the greatest dispersal distance beyond the edge of the crown was 39 m and the mean maximum distance was 33.25 m (SD=6.898). The dispersal distance of *B. laurentii* propagules was significantly greater than that of *G. dewevrei* (Student's *t* test, P<.001). It appears that *Cynometra alexandri* seeds disperse even farther. Despite efforts to find adequately isolated *C. alexandri* trees in secondary forest, the seedling shadow of any one tree overlapped with the seedling shadow of another. This was in spite of the fact that the trees were 100 m or more distant from each other.

Seed-Transplants.

Mortality due to predation was greatest prior to and just subsequent to germination. Seeds that germinated and successfully reached the stage of having at least one normally-expanded seedling leaflet were counted as having survived the seed stage. All three caesalpiniaceous species have epigeal seedlings with exposed spreading storage cotyledons. Freshly fallen seeds sown in plots begin to germinate in four days or less. At this point the radicle has emerged from the seed coat. One to two weeks after the emergence of the radicle, the hypocotyl lengthens in undamaged seeds and the cotyledons are lifted off the ground. During the elongation of the hypocotyl, the seeds appear to have the same range of predators as prior to germination. Destructive predation can still be heavy at this time and continue right up to the extension and expansion of the eophylls. The cotyledons are not caducous and remain attached to seedlings after expansion of seedling leaves unless removed by predators or knocked off. Presumably loss of cotyledons is less disastrous at this point. After expansion of eophylls, which occurs several days after the extension of the hypocotyl, seedlings become considerably less vulnerable to predators although new seedling leaves of all three species were nipped to some extent.

There were three visible types of predator damage on all three species at seed-transplant piles. These were identified with rodents, ungulates (duikers), and insects.

1. Rodent damage. Tooth marks were visible on cotyledons. Fine shavings from the gnawing of cotyledons were evident. In the case of *G. dewevrei*, parts of seeds rather than whole seeds were missing and only one to several seeds were gnawed overnight.

2. Duiker damage. Several to many seeds were missing during a 24 hour period, and usually only seed coats and radicles were left. If cotyledon parts were left, they had broken edges but no tooth marks. In the case of *B. laurentii* and *C. alexandri* many entire seeds completely disappeared overnight. Furthermore, duiker tracks were often found in conjunction with this type of damage. These criteria are consistent with the remains found in the captive-duiker pens after feeding trials.

Rodent and duiker damage were readily distinguished in the field in the case of *G. dewevrei* seeds; however, their damage to the smaller seeds of *B. laurentii* and *C. alexandri* was more confusing as even rodents may have carried whole seeds away. Where seeds were entirely missing from plots duiker and rodent damage could be confounded. Shavings and partly eaten seeds were nevertheless often left as evidence of rodent culpability. The reliability with which the signs of these two groups of mammalian predators could be distinguished at *G. dewevrei* piles is demonstrated by trapping results (Table

9). More rodents were caught at piles which had previously been identified as showing "rodent-type" damage than at piles identified as showing "large-mammal-type" damage (P<.001, chi square test for two independent samples). This is in spite of the fact that damage to seed piles would continue after the traps were in place.

3. Insect damage. This was best observed in the field in the case of *G. dewevrei* seeds. Initially beetle damage appeared as oviposition holes through the seed coat but as the infestation progressed, piles of frass appeared on the outside of the seed. Heavily infested seeds either did not germinate or there was no further growth after the radicle protruded. Neither lifting of the hypocotyl nor leaf expansion occurred. Less heavily infested seeds where only the cotyledons were damaged but the rest of the embryo left unharmed could successfully germinate but the resulting seedling was smaller with the cotyledons shrunken, blotchy, and riddled. *Gilbertiodendron dewevrei* and *B. laurentii* seeds showing oviposition holes were kept in ventilated jars until beetles began to emerge. Two curculionid species emerged from the *G. dewevrei* seeds. These were the same beetles which were found to be active around seeds on the forest floor. One bruchid species emerged from the *B. laurentii* seeds.

A number of other insects were found in or on seeds. Among the largest were lepidopteran larvae and orthopterans. These insects were relatively rare, and solitary. In the case of *G. dewevrei* their damage was generally small relative to the size of the seed; however, these external feeders could, conceivably, have entirely consumed the smaller seeds of the mixed forest species.

Table 9. Type of seed damage and rodent-catch at piles of *Gilbertiodendron dewevrei* seeds where associated traps were baited with *G.dewevrei* seeds.

type of damage recorded	total number of piles	piles where no rodent was caught	piles where rodent(s) were caught	total number of rodents caught
rodent	20	6	14	26
large mammal	13	12	1	3
unknown	10	9	1	1
rodent and large mammal	6	3	3	3

Mortality due to fungal attack was rare, but was likely the cause of some seed loss in one *C. alexandri* seed plot and two *B. laurentii* seed plots. No mortality having fungal pathogens as a primary cause was noted for *G. dewevrei* in either 1981 or 1982. Gerard (1960), on the other hand, reported thick mycelial proliferation over some *G. dewevrei* seeds in mbau forest 400 km northwest of Epulu.

Seed-transplant experiments.

Cynometra alexandri (1981). After ten days 50% or more of the total mortality recorded at seven weeks had already occurred. The early mortality occurred during the seed stage or after the emergence of the radicle and appeared to have been caused mainly by rodents and ungulates.

Survivorship to the seedling stage, seven weeks after the seeds were sown into the plots, was analyzed with a three-way factorial analysis of variance (Table 10 a & b). Clearly the most important main effect was forest type, with more than 40 percentage points difference in seed survival between the two environments (Table 10a). There was much higher survival for the seeds in mixed forest where there was already a background of *C. alexandri* seed-fall than for seeds placed in mbau forest where *C. alexandri* seeds and adults were absent.

Greater survival occurred inside the exclosures where duikers were excluded. There also was a significant interaction between forest type and litter (i.e. A x C, Table 10b). This results from the

Table 10. Survival of *Cynometra alexandri* seeds and seedlings in seed-transplant plots, seven weeks after seeds were set out (1981).

a. Percent survival of *C. alexandri* seeds and seedlings. Each value is the mean from seven replicate plots, the standard deviation is in parentheses.

Treatment : A	C	B	
		enclosed	open
mixed forest (mast)	litter	54.3 (13.0)	45.7 (9.6)
	no litter	56.1 (11.1)	53.1 (7.8)
mbau forest (no mast)	litter	8.6 (10.2)	1.9 (2.1)
	no litter	3.7 (2.8)	2.1 (2.7)

b. Three-way ANOVA table. P<.05 is not significant (NS).

source of variation	df	SS	F	
A. forest type	1	32,593	3227	P<.001
B. antelope exclosure	1	345	34	P<.001
C. litter	1	19	1.8	NS
A x B	1	9	<1	NS
A x C	1	168	16.6	P<.01
B x C	1	101	10	P<.05
A x B x C	1	3409	337.6	P<.001
Error within subgroups	48	487		

increased survivorship in mbau forest but decreased survivorship in mixed forest under the conditions of litter being present. One possibility is that the large dark mbau leaflets tended to camouflage or actually cover the seeds. The significance of the two-way interaction (A x B x C, Table 10b) might be related to the fact that the effect of the mbau forest litter varied according to the predator. Inside exclosures, where the main predators were rodents, litter was associated with lower seed mortality; however, outside exclosures where the duikers, as well as rodents, were predators, the litter effect was absent. Relative to the main effects, litter had a minor impact on predation levels.

Brachystegia laurentii (1982). Considering only the open plots, mortality of *B. laurentii* seeds was found to be significantly different in the three environments tested (P<.001, Kruskal Wallis test, Table 11). The highest survival occurred in the intermediate site where 64.2% of the seeds produced viable seedlings. Rodent activity was lower in the intermediate site than in the mast site as evidenced by lower rodent catches from the seed-piles where traps were put out. In 97 trap days in mixed forest (mast area) during *B. laurentii* seed-fall, four rodents were caught in snap traps baited with *B. laurentii* seeds. Despite more than twice as many trap days (226) in the small island of mbau forest, still only four rodents were caught.

Omitting the intermediate site, a chi-square test for two independent samples showed that there was significantly greater survival of *B. laurentii* seeds in the mast area than in the no-mast

Table 11. Survival of *Brachystegia laurentii* seeds and seedlings in seed-transplant plots, seven weeks after seeds were set out (1982).

a. Mean number of *B.laurentii* seeds surviving to seven-week seedling stage. Standard deviation in parentheses. The number of seed-transplant plots is reported as n = x and the original number of seeds per plot was fifty.

Treatment : A B

	enclosed		open	
	mean	%	mean	%
mixed forest (mast)	29.6 (15.1) n = 5	59.2	23.6 (10.0) 2 sites, n = 10	47.2
mbau forest near mast area (intermediate site)	41.3 (4.0) n = 3	82.7	32.1 (11.2) 2 sites, n = 10	64.2
mbau forest distant from mast area	37.5 (10.6) n = 2	75.0	3.1 (5.8) 3 sites, n = 25	6.2

b. Differences in seed and seedling survival according to treatment. The null hypothesis is that there is no difference.

Treatment		Significance level	Statistical test
A	forest type (open plots only)	P<.001	Kruskal-Wallis
A	forest type (intermediate site excluded) (open plots only)	P<.001	chi square test for two independent samples
A x B	exclosures in both forest types (intermediate site excluded)	P<.01	chi square test for two independent samples

area ($P<.001$) with 47.2% survival in the former and only 6.2% survival in the latter. As in the *C. alexandri* seed-transplants, the exclosures had a positive impact on survival in all environments (Table 11). With *B. laurentii*, however, the impact of the exclosures was much greater. All mammals were excluded from the screen exclosures whereas the 1981 *C. alexandri* exclosures only excluded antelope.

Insects were the principal predators able to penetrate the all-mammal exclosures. Mortality within these exclosures was, therefore, a measure of the impact of insects. Comparison between mast and no-mast areas shows significantly greater mortality due to insects in the mast area with 40.8% mortality in the former and 25% in the latter ($P<.01$, chi-square test for two independent samples).

In the absence of a direct measure, mortality due to mammals can be estimated by subtracting the percent mortality under the exclosure cages from the percent mortality in the open seed piles. This gives 68.8% mortality due to mammals in the no-mast area as opposed to only 12% in the mast area.

Gilbertiodendron dewevrei (1981). In 1981, seeds were transplanted into mixed forest, no-mast mbau forest (non-fruiting), and mast mbau forest. In the mast mbau forest, the natural density of seeds on the ground was 11.2 seeds per m^2 (s_x=3.1) when seeds were originally sown into plots. Accumulation of seeds in empty plots over the next two weeks averaged one seed per m^2 per week and dropped to half that rate over the subsequent three weeks.

Seed predation was markedly different in the two mbau forest sites. Very few seeds showed evidence of mammal damage in the mast site. Of the original 30 seeds per plot, a mean of 28 (SD=1.97) remained on the enclosed plots and 29 (SD=0.97) on the open plots. In the no-mast mbau forest, on the other hand, ten days after the seeds were placed, all but three of the 600 seeds had disappeared. In most cases there were bits of seed coat and cotyledons with rodent toothmarks left at the sites. Evidence of predation in the mixed forest (no-mast) was similar to that in the non-fruiting mbau forest. Ten days after sowing in mixed forest plots, the seeds at 11 of the plots had disappeared and only scraps of seed remained.

The seed disappearance patterns were even more pronounced after three and a half weeks (Table 12). No viable seeds or seedlings remained in either of the no-mast environments. The majority of the original seeds were still present on the plots in the mast environment and there was no significant difference between the number left in the enclosed as opposed to the open plots (Student's *t* test).

This apparent difference between mast and no-mast environments was, however, spurious as regards actual seed survival. All *G. dewevrei* seeds remaining in the mast forest were rotten and riddled with beetle emergence holes. Any viable seeds would have long since germinated. In fact none of the 1,800 seeds used in the 1981 *G. dewevrei* seed transplant experiments produced a surviving seedling.

Gilbertiodendron dewevrei (1982). On open plots of the 1982 *G. dewevrei* seed transplants, mortality was very high in both the mast (mbau forest) and the no-mast (mixed forest) areas. As with *B. laurentii* seed-transplants, greatest survival occurred at an

Table 12. Survival of *Gilbertiodendron dewevrei* seeds and seedlings in seed-transplant plots, three and a half weeks after seeds were set out (1981).

a. Mean number of *G.dewevrei* seeds or seedlings remaining in plots. For all values n = 10 plots and originally there were thirty seeds sown into each plot. Standard deviation in parentheses.

Treatment : A	B enclosed total seeds	 viable seeds	 open total seeds	 viable seeds
mbau forest (mast area)	26.6 (3.0)	0	27.9 (3.4)	0
mixed forest (no-mast area)	0	0	0	0
mbau forest (no-mast area)	0	0	0	0

b. Differences in seed and seedling survival according to treatment. The null hypothesis is that there is no difference.

treatment	significance level	statistical test
A. forest type	not significant	by inspection
B. antelope exclosure	not significant	by inspection
A x B exclosures in both forest types	not significant	by inspection
Differences in actural number of seeds remaining in plots. (i.e. not completely eaten or removed).		
A. forest type	highly significant	by inspection
B. antelope exclosure (mast area only)	not significant	Student's *t* test

intermediate site where there was no seed-fall but where a concentration of conspecific seeds and adults was nearby.

Due to variability in density of seed-fall in mbau forest, two environments were recognized as separate treatments: 1. heavy seed-fall (all plots in areas averaging > 1 seed per m^2) and 2. light seed-fall (many plots in areas averaging < 1 seed per m^2). The two treatments from the no-mast (mixed) forest were: 1. near *G. dewevrei* seed-fall (intermediate site) and 2. distant from seed-fall. The null hypothesis that there is no difference in the average number of seeds which survive the seed-stage in the four environments is rejected (Table 13, P<.01, Kruskal Wallis test). As with the *B. laurentii* seed-transplants, the treatment result that deviated the most from the others is the intermediate site having the highest survival rate of 33%.

When the intermediate site was removed from analysis and survival was contrasted at the mast (light seed-fall) and no-mast (distant) areas, no significant difference was found (Table 13, Mann-Whitney U test). Despite the similarly severe seed/seedling mortality, the causal agents were different in the two environments. This was clear from the difference in survival under all-mammal exclosures (Table 13). In the mixed forest (no-mast) where all mammals were prevented access to the *G. dewevrei* seeds, there was high survival (93%). There continued to be high mortality (13% survival), in the mbau forest, even in the exclosures, due to insect predation. Thus the null hypothesis of similar mortality under mammal-proof exclosures in the two environments is rejected (P<.004, Mann-Whitney U

Table 13. Survival of *Gilbertiodendron dewevrei* seeds and seedlings in seed-transplant plots, five weeks after seeds were set out (1982).

a. Mean number of *G.dewevrei* seeds surviving to the five-week seedling stage. Standard deviation in parentheses. The number of seed-transplant plots is reported as n = x, and the original number of seeds per plot was 30.

Treatment :	A	B			
		enclosed		open	
		number	%	number	%
mbau forest (mast area)	heavy seed fall			0.2 (0.4) 1 site, n = 5	1.3
	light seed fall	2.0 (2.3) n = 5	13	1.65 (2.8) 4 sites, n = 20	11
mixed forest	distant from mast	14.0 (1.7) n = 5	93	1.0 (1.6) 2 sites, n = 10	6.7
	adjacent to mast (intermediate site)			5.0 (3.5) 2 sites, n = 10	33

b. Differences in seed and seedling survival according to treatment. The null hypothesis is that there is no difference.

Treatment	Significance level	Statistical test
A forest type (open plots only)	P<.01	Kruskal-Wallis
A forest type (intermediate site excluded) (open plots only)	NS	Mann-Whitney U-test
A x B exclosures in both forest types (intermediate site excluded)	P<.01	chi square test for two independent samples

Test).

The large size of *G. dewevrei* seeds made it possible to visually determine the cause of seed damage. For this reason data in addition to the mammal exclosure results can be used in comparing causes of mortality between the two principal environments. There was a much larger sample size when observations made at the open seed piles were included. The results were consistent with the exclosure results (Table 14). The following hypotheses are rejected: 1. mortality due to insect damage and 2. mortality due to mammal damage were the same for seeds set out in the two environments, mbau forest with seed-fall and mixed forest without seed-fall (chi-square test for two independent samples, P<.001 in both cases). Insect predation was intense in the mast area whereas a much greater percentage of *G. dewevrei* seeds succumbed to mammal predators when the seeds were placed far from mast areas.

Trap-grids

The trap-grid data must be interpreted cautiously for a number of reasons. One reason has to do with the experimental design itself. Each day of an assessment period was meant to represent the same trapping effort: 36 traps per grid with two grids in a single habitat type. In actuality rain or falling twigs and seeds would often spring traps during the 24 hours between checking periods. For graphing purposes, trap nights were defined as the number of traps found still set or with a caught rodent after a 24 hour period. When sprung traps resulted in a trapping effort for a single night of less than 20 traps,

Table 14. Percent total seed mortality due to insects or mammals at seed-transplant plots (*Gilbertiodendron dewevrei*, 1982). Original seed number was 300 seeds in each forest type.

	mammal	insect	unaccounted for
mbau forest (mast area)	3.4	95.0	1.6
mixed forest (no-mast area)	97.0	0.7	2.3

that night's catch was combined with the subsequent night's results, until twenty trap nights or more effort were achieved. This avoided artificially low data points. Unfortunately there was no way to be certain whether or not a trap was sprung immediately after being set or just before being checked. This makes data from rainy periods, such as the first days of trapping in no-mast mixed forest, difficult to interpret.

Another reason for caution in interpretation of the data is that the rodents may not have responded to the peanut bait in the same way at different periods. When traps were put out during a mast period they were presumably being put into a background of food abundance, whereas during a no-mast period the peanuts may have been appearing in an environment where there was a shortage of rodent food.

The two primary rodent species caught with peanuts on the trap grids, *Hylomyscus stella* and *Hybomys univittatus* (Table 15), were also the primary species caught at seed-piles using *G. dewevrei* and *B. laurentii* seeds as bait. They accounted for 28 out of 33 rodents caught in traps baited with *G. dewevrei* seeds and six out of nine rodents caught in traps baited with *B. laurentii* seeds. In fact all species caught in traps baited with Caesalpiniaceous seeds were also caught with peanut bait. Therefore, the relative rodent densities estimated by the trap grids are relevant to seed predation of these two caesalpiniaceous tree species.

There were fewer species of rodents caught in mbau forest during both mast and no-mast periods (three species and two species respectively) than were caught in mixed forest (six species during both

Table 15. Rodents caught on trap grids during mast and no-mast seasons in mbau and mixed forest. Peanuts used as bait (1982 & 1983).

a. Rodent species caught in each forest type.

environment	number of trap nights	species	number of individuals per species	total
MBAU FOREST				
mast period	605	*Hylomyscus stella*	23	
		Praomys jacksoni	3	
		Hybomys univittatus	1	27
no-mast period	640	*H. stella*	12	
		H. univittatus	2	14
MIXED FOREST				
mast period	644	*H. stella*	15	
		H. univittatus	8	
		Deomys ferrugineus	5	
		P. jacksoni	3	
		Lophuromys luteogaster	1	
		Grammomys rutilans	1	33
no-mast period	411	*H. stella*	9	
		H. univittatus	8	
		P. jacksoni	6	
		D. ferrugineus	4	
		Malacomys longipes	2	
		Malacomys verschureni	1	30

b. Number of rodents caught over first ten days of trapping in each forest type. Standard deviation in parentheses.

fruiting condition	forest type mbau		mixed	
mast	14 11	(2.12)	11 22	(7.78)
no-mast	5 9	(2.83)	16 14	(1.40)

mast and no-mast, Table 15). This is consistent with expectations due to the higher shrub and tree diversity and greater microhabitat diversity of the mixed forest.

In order to compare rodent densities it was assumed that a greater number of rodents caught on trap grids reflected a greater density of rodents. The experimental design suggested use of a two-way ANOVA to test the hypothesis that there was no differences in numbers of rodents caught over ten days and nights in the four environments (mixed forest vs. mbau forest and peak fruiting season vs. post fruiting season, Table 15b). In actuality, due to the low replication and the high variance for mixed forest during the peak fruiting season (SD=7.78), a non-parametric test was considered more appropriate. A chi-square test, however, failed to reveal any significant differences between the environments with respect to the number of rodents caught.

If the mast periods are eliminated from consideration, a comparison of the "normal" or no-mast rodent population in the two forest types can be made. A Student's *t* test was used to test the hypothesis that rodent catches were the same both in mixed forest and mbau forest during the non-fruiting seasons of *B. laurentii* and *G. dewevrei*. In this case the null hypothesis can be rejected, but only if we accept a probability level of $P<0.1$. Rodents occur at lower density in mbau forest.

Since snap traps were used, all rodents caught were killed. It was expected that, without significant immigration, all the rodents in the immediate area of a grid would be "trapped out". For this reason it is interesting to examine a plot of rodents caught over time (cumulative trap nights, Figure 3). The two curves which conform most closely to the expected "trap out" pattern are those for the no-mast periods in both mbau and mixed forest (Figure 3). In both cases there was an initial decline in the number of rodents caught followed by a low-level catch which never reached the original capture rate. By the end of the trapping period, in both forest types (all four trap grids), the catch was down to zero rodents per day.

In mbau forest, during the seed-fall of *G. dewevrei*, and in mixed forest, during the seed-fall of *B. laurentii*, the pattern was more erratic (Figure 3). In the mixed forest, the curve shows an initial decline but there continue to be surprisingly high catches on trap nights 5,6,7 and 10. In the mbau forest, even the initial decline in rodent catch is absent. One grid had the highest catch on trap night 5 and the other on trap night 8. In neither of the forest types, and on only one grid in mixed forest, was the rodent catch on the final trapping night zero. These patterns suggest that immigration of rodents into the trapping areas did occur during mast periods.

Seedling survival.

The understory surveys, made in mbau forest several months after seed-fall, showed high overall seedling mortality for *G. dewevrei* in 1982. The average density of surviving seedlings in March 1983 was 0.02 seedlings per m^2 (Table 16). This was only 1/40th the mean number of all small size *G.dewevrei* seedlings in the understory (0.8 seedlings per m^2 <0.5m in height). Slightly larger seedlings were even denser (1.07 seedlings per m^2, >0.5m in

Figure 3. Rodents caught on successive nights in snap traps in mixed and mbau forests. Mean and range are from two trap grids.

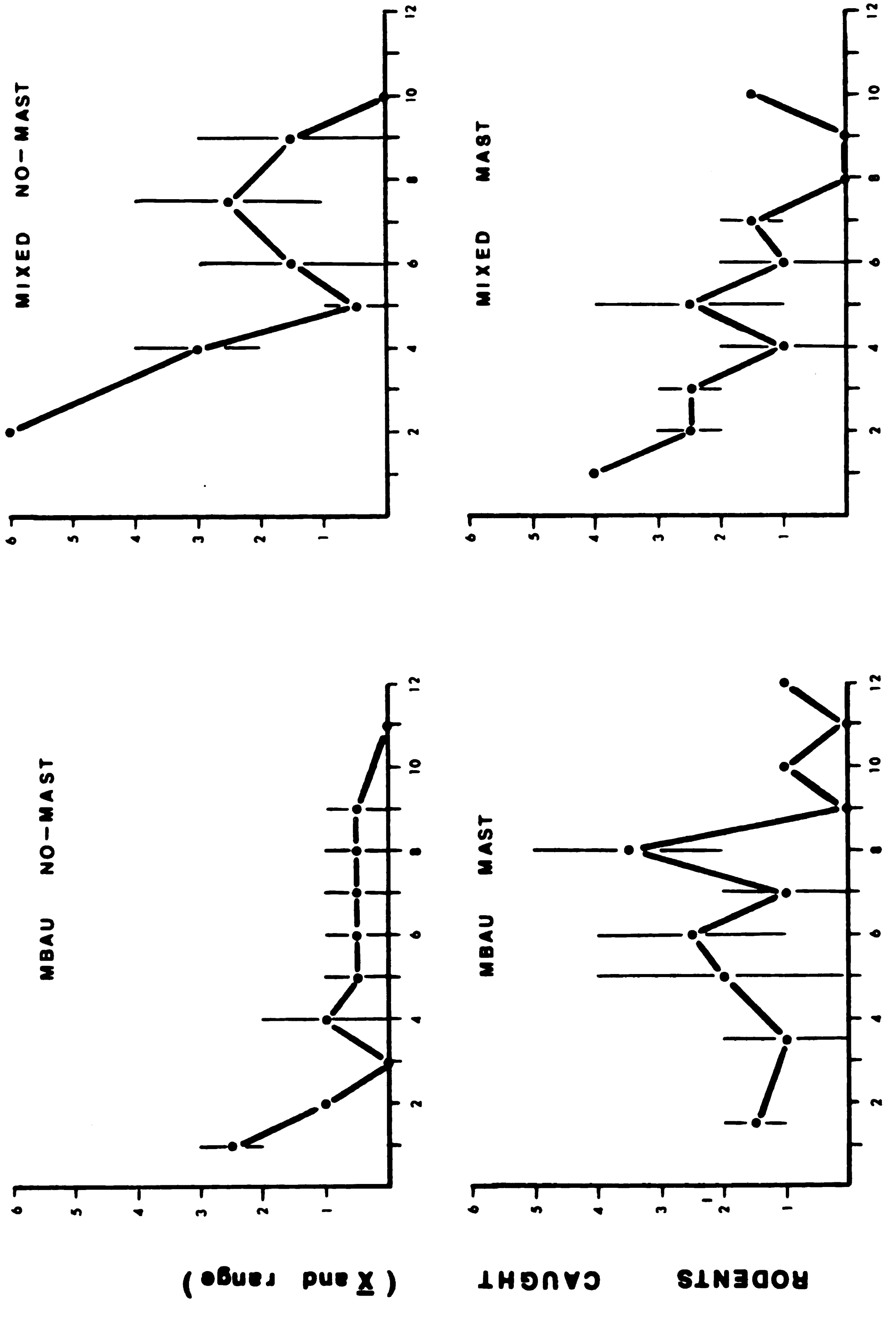

MBAU NO-MAST
MIXED NO-MAST
MBAU MAST
MIXED MAST
RODENTS CAUGHT (X̄ and range)
SUCCESSIVE TRAP NIGHTS
1
2
3
4
5
6
2
4
6
8
10
12

Table 16. Density of seedlings in the forest understory.

Gilbertiodendron dewevrei			*Brachystegia laurentii*		
density (m^{-2}) in mbau forest			density (m^{-2}) in mixed forest		
1st year	2nd year to <0.5m high	≥0.5m <2.5m high	1st year	2nd year to <0.5m high	≥0.5m <2.5m high
0.022	0.8	1.067	13.74	1.55	0.147
(0.022)[a]	(0.43)	(0.86)	(11.03)	(1.2)	(0.23)

[a] Standard deviation in parentheses.

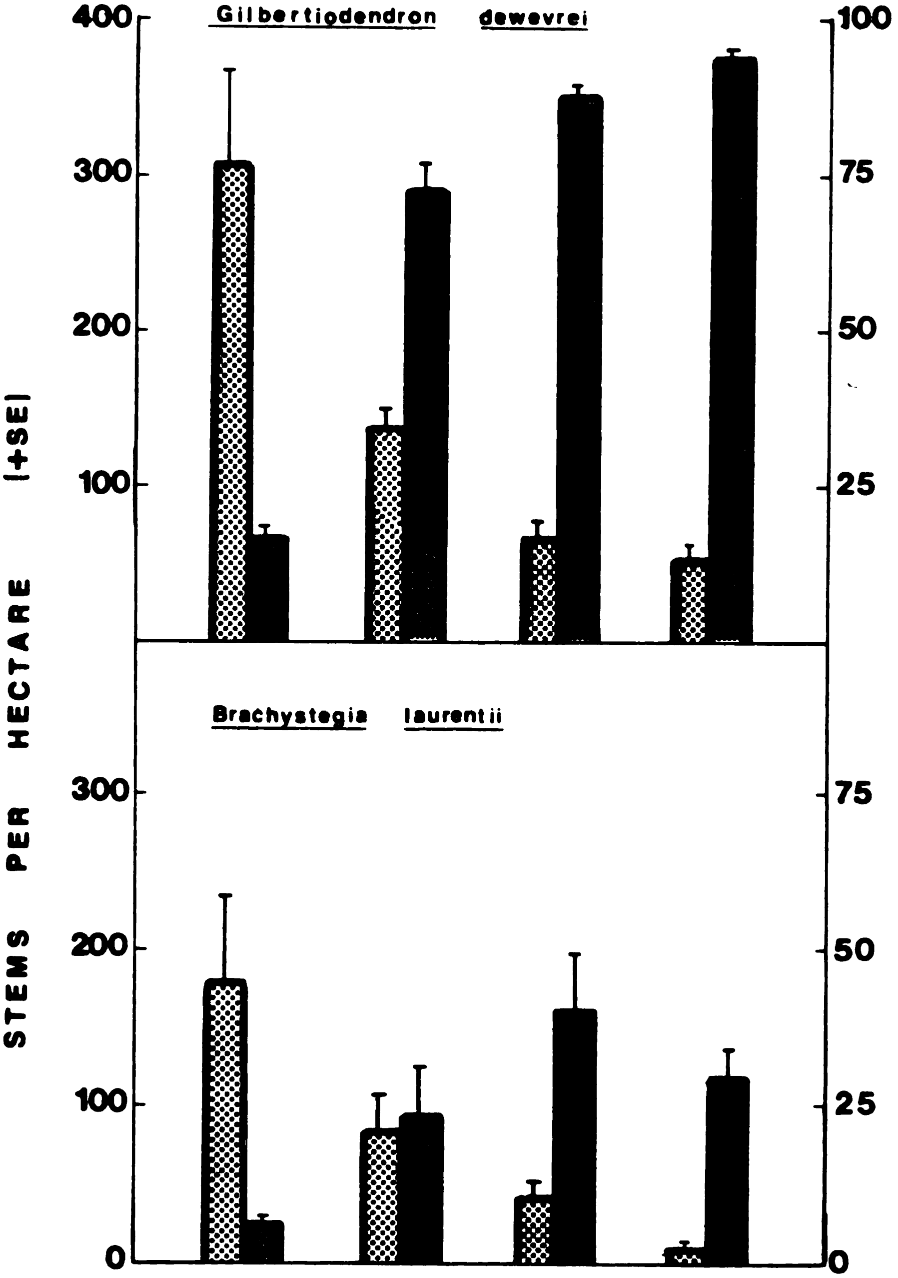
height <2.5cm dbh, Table 16).

An estimate of *B. laurentii* seedling survival from a single year's seed-fall shows an overall higher density than was measured for *G. dewevrei* with 13.7 seedlings per m^2 (Table 16). This was more than eight times the density of small size *B. laurentii* seedlings in the understory when first year seedlings were not included (1.55 seedlings per m^2 < 0.5m in height). Slightly larger seedlings were even sparser (0.147 seedlings per m^2 > 0.5m in height and < 2.5 cm dbh). Thus, *G. dewevrei* and *B. laurentii* exhibited opposite trends in density with increasing seedling size (Table 16). Larger seedlings of *G. dewevrei* were the densest seedling size class whereas larger seedlings of *B. laurentii* were the sparsest seedling size class.

When progressively larger size classes were surveyed similar trends were found (Figure 4). In mixed forest *B. laurentii* showed a greater reduction in number of stems in the larger size classes than did *G. dewevrei* in mbau forest. Whereas *B. laurentii* diminishes in importance in the largest size class (>50 cm dbh), accounting for a smaller proportion of all species present, *G. dewevrei* accounts for a consistently larger and larger percent of all stems in the increasingly larger size classes.

The two-year monitoring of seedlings was more productive for *G. dewevrei* than for *B. laurentii*. By counting leaves and leaf-scars, life-time leaf production could be reliably determined for small seedlings of *G. dewevrei* which are stouter and more woody

Figure 4. The importance of *Brachystegia laurentii* in mixed forest and of *Gilbertiodendron dewevrei* in mbau forest for different size classes, expressed as mean stem density and as mean percent of all species.


Gilbertiodendron dewevrei
Brachystegia laurentii
STEMS PER HECTARE (+SE)
PERCENT ALL STEMS (+SE)
400
300
200
100
0
100
75
50
25
0
>2.5
≤10
>10
≤25
>25
≤50
>50

than *B. laurentii*. *Brachystegia laurentii* seedlings frequently lost whole segments of stem, thus reducing the size of the living plant being maintained in the understory and also erasing the record of leaf emergence. *G. dewevrei* seedlings also maintain active meristems low on the stem and frequently began a second axis of growth but terminal portions were not lost.

A total of 124 *G. dewevrei* seedlings less than one meter in height were monitored. Considering that *G. dewevrei* seedlings are 0.3 to 0.35 m in height (to first node) immediately after germination and full expansion, the observed seedlings had not, for the most part, doubled their germination size (mean height at end of observation = 54.7 cm; SD = 13.76). The marked seedlings were considered to be the suppressed seedling bank which had survived without any canopy opening.

Periodicity of leaf production was estimated so that seedling's leaf + leaf scar number (= leaf index) could be converted into an age estimate. These estimated indicated how long each seedling had survived in the shaded understory. Although it would have been preferable to have started with first year seedlings, observations of new seedlings in the shaded understory (made in conjunction with seed predation studies) revealed that leaf production during the first two years of seedling life was no greater than during subsequent years. During the first year, with few exceptions, two opposite eophylls were produced; the vast majority of unreleased seedlings produced a single additional leaf or no new leaves during the second year.

In two years 16% of the marked *G. dewevrei* seedlings died. Of the remaining seedlings, 10% produced no leaves, 45% produced only one leaf and 22% produced two leaves. Only 6% produced more than two leaves. The mean annual leaf production by the marked understory seedlings was 0.63 leaves (SD=0.612, Table 17). The average periodicity of leaf production, therefore, was 1.58 years between leaves. There was no single season which corresponded to a leaf flush in the understory.

The mean leaf index figure for all marked seedlings was 7.2 (SD=3.04). Multiplied by the periodicity of leaf production, this converted to a mean age of 11.4 years for small, unreleased seedlings of *G. dewevrei* in the mbau forest understory. Inspection of the distribution of seedlings along a gradient of increasing leaf index indicated a range in ages (Figure 5). There appeared to be three peaks, possibly caused by the intermittent, supra-annual, nature of mast seed production. When the plots were last monitored (April 1983) the ground was covered by a thick fall of *G. dewevrei* flowers. If, as the flower density suggests, 1983 was a successful year for seedling production, the mean age of unreleased seedlings will have shifted downwards in all plots.

DISCUSSION

Re-examination of the three hypotheses

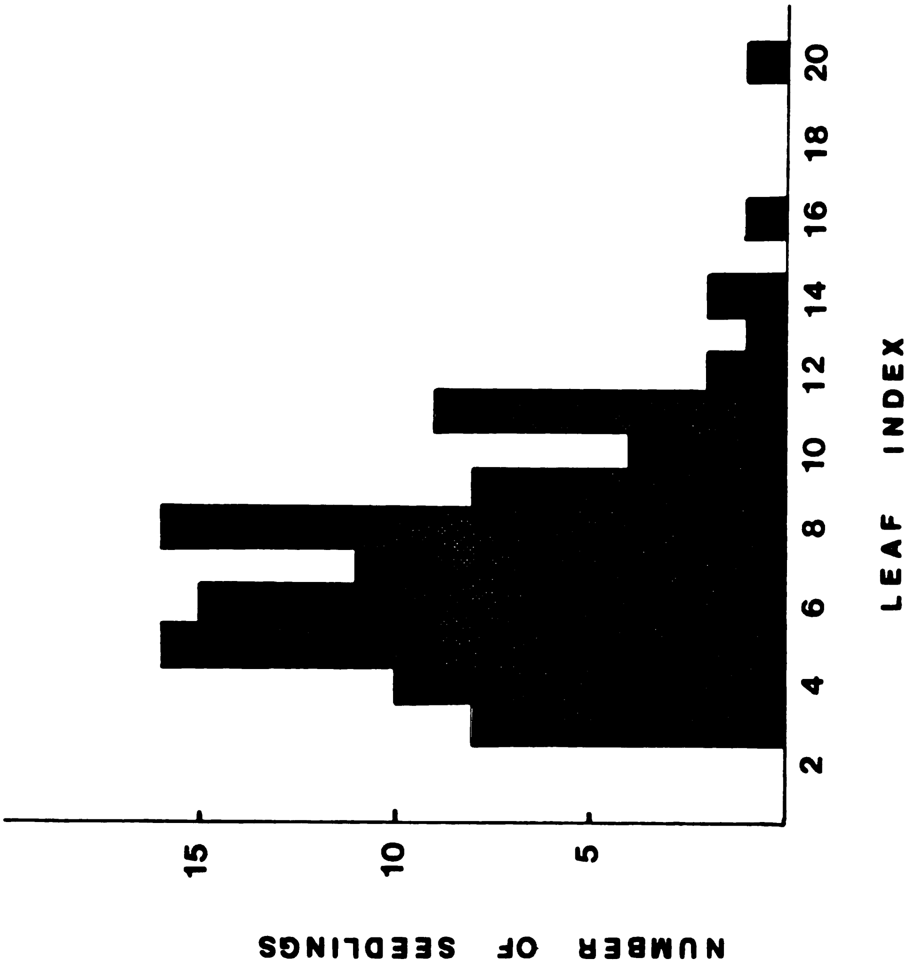
1. *The "regeneration niche" hypothesis* was invoked to predict that the dominant species, *Gilbertiodendron dewevrei*, occurring at high density in the low-diversity forest, would have a

Table 17. Growth and survival of small *Gilbertiodendron dewevrei* seedlings in the shaded forest understory. Originally 124 seedlings were marked and observed.

	no new leaves	one new leaf	two new leaves	dead
Year 1	31	68	12	13
Year 2	64	37	3	7

mean annual leaf production per seedling = 0.63 leaves year^{-1}
SD = 0.612

Figure 5. Leaf index (leaves and leaf scars) of *Gilbertiodendron dewevrei* seedlings <1 m in height in the shaded forest understory.


NUMBER OF SEEDLINGS
15
10
5
2
4
6
8
10
12
14
16
18
20
LEAF INDEX

broader regeneration niche than the related species, *Brachystegia laurentii* and *Cynometra alexandri*, which are found only at lower densities in a species-rich tropical forest.

A number of previous studies have suggested that the coexistence of tropical tree species may be possible through the partitioning of establishment sites in gaps (Orians 1982) or between gaps (Hartshorn 1980, Denslow 1980). As was clear from the seed predation experiments and forest survey plots, all three caesalpiniaceous species of the Ituri germinate and persist for several years beneath unbroken forest canopy. They were found as advanced regeneration in the vicinity of conspecific mature individuals. None of the three caesalpiniaceous species has specialized to particular sites for germination and early establishment but, rather, all utilize the universally available shaded forest floor.

Other aspects of the "regeneration niche" were examined for evidence of greater specialization by the mixed forest species. Observations of reproductive phenology showed a tendency toward synchrony in stands of both *G. dewevrei* and *B. laurentii*; however, fewer *G. dewevrei* trees flowered asynchronously. *G. dewevrei* was also more predictable in that if a tree failed to flower one year it was more likely to be reproductive the next.

Comparative data for pollination systems are lacking; however, it is doubtful that *B. laurentii* or *C. alexandri* would have more specialized syndromes than that of *G. dewevrei* which is obligately out-crossed and sunbird pollinated, and whose flowers last only a single day. This is an interesting contrast to the expectation

Janzen had for mast-fruiting tropical tree species on poor soils (1974). He predicted that the flowers should last more than one day and be available to a wide variety of pollinator life forms.

All three caesalpiniaceous species have the same general self-dispersal system. It is, however, most restricted in the case of *G. dewevrei*, both in terms of the average distance from the parent that a seed falls and, because of the greater weight of the seeds, the likelihood for accidental dispersal by mammals.

In summary, for all aspects of regeneration considered, from flowering to establishment, we failed to find any evidence suggesting that *G. dewevrei* has a broader regeneration niche than related species in species-rich tropical forest. On the contrary, *G. dewevrei* has a more clearly defined and predictable flowering pattern, a specialized pollination system, and relatively less flexible seed dispersal possibilities.

2. *The seed and seedling predation hypothesis* can only be evaluated from the data presented if the disappearance of seeds from plots can be reliably interpreted. For statistical analysis disappearance was treated as mortality. If a fraction of these missing seeds had been removed and left to germinate the implications for the parent tree would be very different. Large rodents are known to be both seed predators and seed dispersers in South American tropical forest (Smythe, 1978). Scatter-hoarding behavior is apparently common among South American pacas and agoutis and often results in seed dispersal.

The litter found at seed-transplant plots of all three caesalpiniaceous species of this study suggested that rodents often ate right at the site. For *G. dewevrei* this was almost always the case or else the seed was gnawed into smaller pieces to be carried away. Probably only the largest rodent in the Ituri Forest, *Cricetomys emini*, could carry whole *G. dewevrei* seeds in its mouth. We have no direct observations of its eating *G. dewevrei* seeds but it seems likely that it would considering the diversity of other rodents using *G. dewevrei* seeds as food. *C. emini* is not known to scatter-hoard; however, it does carry seeds into its burrow to eat. The chamber of these burrows is generally greater than a half meter underground (pers. obs.). A *G. dewevrei* seed left uneaten in such a chamber would dry out or rot.

The thin papery seed coat and rapid germination of all three caesalpiniaceous species make them unsuitable for hoarding. None of them have arils or edible fruit parts to entice removal of the seed without damage to the embryo but, due to the smaller size of *B. laurentii* and *C. alexandri* seeds, accidental dispersal by mammals is more likely than with *G. dewevrei*. Occasionally a rodent may transport a seed to a safer environment in which to eat but then, for some reason, abandon the seed.

Larger mammals do not appear to be better seed dispersers than rodents. The litter left by duikers feeding on the caesalpiniaceous seeds indicated that the seeds were slightly chewed and then swallowed into the rumen. This was, indeed, the behavior observed in the captive duiker pens when seeds were provided. As in the case of rodent predation, the seeds are destroyed. Dispersal is a very unlikely outcome, especially dispersal more than a meter or two from where the seed landed when catapaulted from the tree crown by the splitting pod.

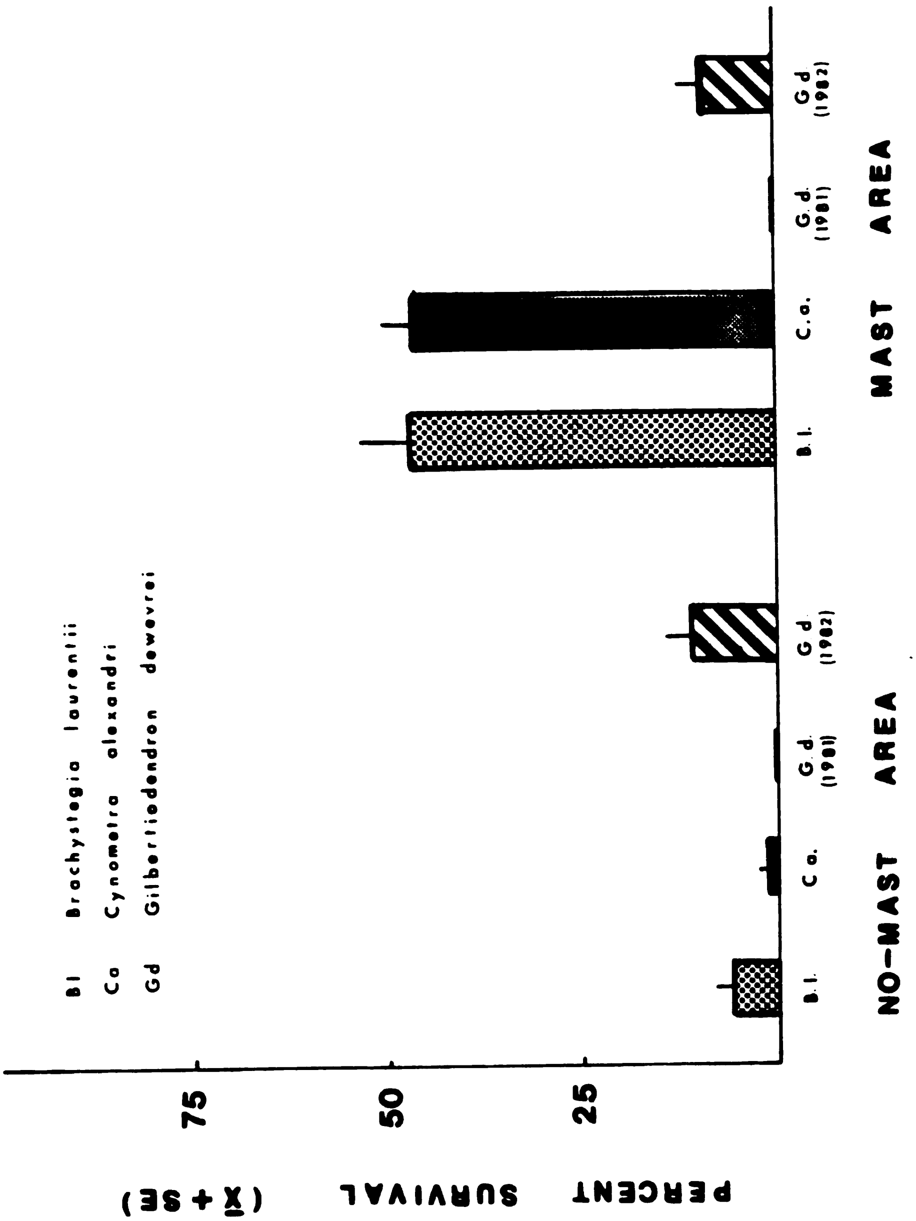
In the case of *G. dewevrei*, the only likely agents of accidental dispersal are the largest mammals. Humans eat and transport *G. dewevrei* seeds. Hunter-gatherers and agriculturalists, however, have probably only immigrated into the dense evergreen forest during the past few centuries (Hart & Hart, in press). Their contribution to dispersal is recent. Elephants also eat *G. dewevrei* seeds. It may be that they toss them or occasionally carry them significant distances. Such dispersal events must be very rare and difficult to quantify.

The interpretation of seed disappearance as seed mortality seems justified. Any visitation of seed plots by elephants would have left ample evidence. Removal of seeds by smaller mammals likely entailed seed destruction.

The seed and seedling predation hypothesis suggests that juveniles of *G. dewevrei* in the low-diversity forest would escape heavy predation in the vicinity of the parent tree, whereas juveniles of mixed forest species in the high-diversity forest would suffer greater predation near parents than distant from parents. Seed transplant experiments did not substantiate this pattern.

Mortality was similar for both mixed forest species, *B. laurentii* and *C. alexandri* (summarized in Figure 6). On open plots (no exclosure) the greatest mortality occurred in the no-mast area distant from conspecific seeds and seedlings. Survival was significantly improved near a concentration of conspecific seeds and

Figure 6. Percent survival of mixed and mbau forest species as seeds or seedlings in mast and no-mast areas.


PERCENT SURVIVAL (X̄ + SE)
75
50
25
Bl Brachystegia laurentii
Ca Cynometra alexandri
Gd Gilbertiodendron dewevrei
B.l.
C.a.
G.d. (1981)
G.d. (1982)
NO-MAST AREA
B.l.
C.a.
G.d. (1981)
G.d. (1982)
MAST AREA

adults. *Gilbertiodendron dewevrei*, the dominant species in the single-dominant forest, sustained high levels of seed predation both near and distant from fruiting conspecifics (Figure 6). Contrary to expectations of the seed/seedling predation hypothesis, *G. dewevrei* suffered more, not less, seed-predation under parent trees whereas the mixed forest species experienced less seed predation in the vicinity of parent trees.

It was possible to determine that the main environmental factor influencing predation on any single group of seeds set out was the presence or absence of a mast seed crop in the area. Litter had a negligible impact on seed predation in *C. alexandri* seed-transplants. The type and severity of damage suffered by *G. dewevrei* was similar in non-reproductive mbau forest with typical mbau forest litter (1981) and in mixed forest with typical mixed forest litter. The results from the no-mast mbau forest further indicate that the presence of adult conspecifics was less critical than the overall density of conspecific seeds in the environment. This is further supported by the fact that asynchronously reproductive trees had poor reproductive success.

During seed-fall in mbau forest the density of *G. dewevrei* seeds is much greater and more even than the density of *B. laurentii* or *C. alexandri* seeds in mixed forest during their respective seasons of seed-fall. This is due to the greater synchrony and dominance of *G. dewevrei* trees. It is surprising, in light of the predation hypothesis, that seed-fall in mixed forest should have a greater positive impact on survival of *B. laurentii* and *C.*

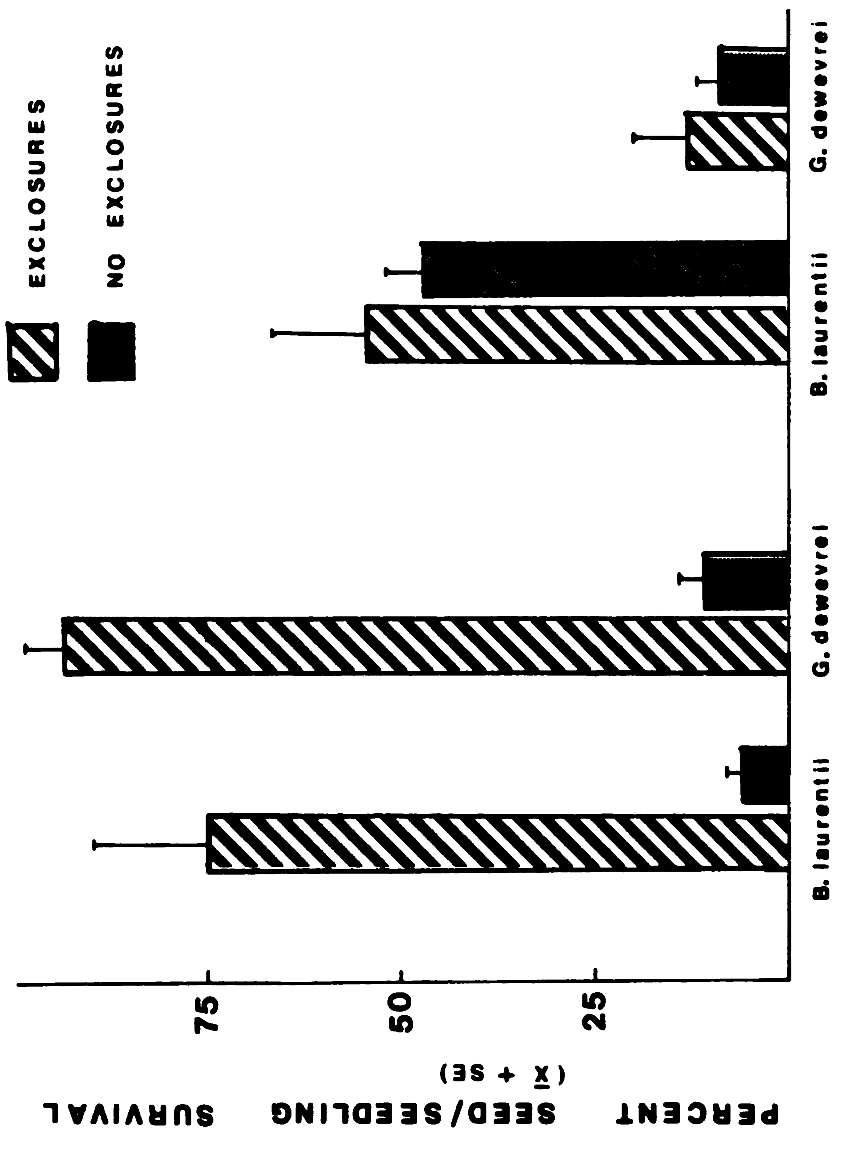
alexandri juveniles than the impact of mast seed-fall in mbau forest on *G. dewevrei* juveniles.

3. *The predator satiation hypothesis* suggests that seeds removed from an area of mast-fruiting conspecifics will suffer increased predation. Community-level predator satiation would only be expected for mast-fruiting species. But, as stated above, the predator satiation prediction was not fulfilled for *G. dewevrei*, the species with the most pronounced mast-fruiting syndrome. Seed-predation was equally severe both within and distant from mast-areas. Predator satiation was more effective in the case of *B. laurentii* and *C. alexandri*, both of which occur at lower densities than *G. dewevrei*.

Seed survival in mammal exclosures and intermediate seed-transplant plots offered some insight into the mechanisms resulting in these predation patterns (Figure 7). In both cases the exclosures produced the most dramatic increase in seed survival in the no-mast areas. An additional 69% of *B. laurentii* seeds and 82% of *G. dewevrei* seeds survived under exclosures in no-mast areas as opposed to only an additional 12% and 4%, respectively, in mast areas. This suggests that mammalian predators were responsible for a greater proportion of the mortality occurring in no-mast areas than in mast areas.

This corroborates observations that beetle seed predators were most abundant in mast areas, and particularly in mbau forest. The curculionid species which specialize on *G. dewevrei* seeds were, alone, able to demolish most of the seeds in mast areas. It may be

Figure 7. Percent seed survival with and without mammal exclosures in mast and no-mast areas.


EXCLOSURES
NO EXCLOSURES
PERCENT SEED/SEEDLING SURVIVAL
($\bar{X}$ + SE)
75
50
25
B. laurentii
G. dewevrei
B. laurentii
G. dewevrei
NO-MAST AREA
MAST AREA

that if the experimental design had included a plot in mast areas which excluded insects but not mammals, there would have been high seed survival.

Mammalian predators may be satiated in the mast areas of all three caesalpiniaceous species, leaving the vast majority of seeds untouched. The survival of the remaining seeds, then, depends on the density of insect predators or fungal pathogens. In our study fungal pathogens were relatively unimportant and insect predators were unevenly distributed. Species-specific insect predators were concentrated in mast areas and, in both 1981 and 1982, those specializing on *G. dewevrei* in mbau forest had, by far, the most devastating effect on seed survival.

Results at intermediate area seed-transplant plots indicate that mammals may have been migrating into mast areas even though their proportionate impact on seed survival was much less in mast areas. Intermediate seed-transplant plots were located in no-mast areas but within 50-100 meters of a seed-fall area. Of all plots without exclosures, the greatest seed survival occurred in intermediate areas for both *G. dewevrei* and *B. laurentii*. For *B. laurentii* seeds, 17% more seeds survived in intermediate area plots than in mast area plots and 58% more than in no-mast plots. For *G. dewevrei* seeds, 24% more survived in intermediate area plots than in mast area plots and 22% more than in no-mast plots.

Both mammalian and insect predators were less common at the intermediate plots. In the case of the species-specific insect predators, the small anomalous piles of seeds may have been too distant from the main concentration of seeds to be found. As for the scarcity of mammals, the trap-grid results support the interpretation of their absence as emigration from these areas into the adjacent mast areas.

Visual interpretation of the graphed results from the trap grids (rodent catch over time) suggests that there was greater movement of rodents during mast periods than no-mast periods. Although there was a lower population of rodents in mbau forest than in mixed forest during no-mast seasons, this was not the case during their respective mast seasons. At the time of mast seed-fall, the numbers of rodents caught showed no significant difference between mbau and mixed forest.

In summary, if the only predators threatening the seeds had been mammals, there would have been dramatically improved survival of seeds placed in mast areas due to predator satiation. Even though mammalian seed predators migrated into seed-fall areas they had only a small impact on the total crop of casealpiniaceous seeds. This translated into greater seed survival for *B. laurentii* and *C. alexandri* in mixed forest but not for *G. dewevrei* in mbau forest. In the latter, the reduced predation pressure from mammals was more than compensated for by concentrated populations of stenophagous beetle seed predators.

Several paradoxes emerge from this discussion of the three hypotheses. The mechanisms proposed to enhance either species diversity or single species dominance were indeed discovered to be operative in the Ituri Forest, but the diversity-promoting processes were found in the least diverse community and the dominance-promoting process was found in the community with the least dominance (Table 18).

Table 18. The predicted and actual Ituri Forest communities where effects of three processes pertinent to species diversity were recorded.

Process	Predicted effect[a]	Community with effect predicted	 actual
specific seed-predators cause massive mortality under parent trees	promote species coexistence (Janzen 1970, Connell et al. 1984)	mixed forest	single-dominant mbau forest
non-specific seed-predators "switch" to abundant species	promote species coexistence (Connell et al. 1984)	mixed forest	single-dominant mbau forest
community-level predator satiation	maintain dominance (Janzen 1974, 1976, Boucher 1981)	single-dominant mbau forest	mixed forest

[a] Citations are to articles stating or supporting the prediction.

Specific seed predators cause massive seed mortality to *G. dewevrei* seeds under *G. dewevrei* adults. It has been suggested that such a predation pattern would promote species co-existence (Janzen 1970, Connell et al. 1984); however, *G. dewevrei* is strongly dominant in mbau forest. Nonspecialized feeders feed heavily on the seeds of *G. dewevrei* as the seeds become abundant. It appears, for instance, that rodents migrate into mbau forest during the mast-fruiting season. It has been proposed that prey "switching", by concentrating predation on the most abundant species, would lead to species co-existence (Connell et al. 1984). *G. dewevrei*, however, continues to monopolize the canopy, co-existing only with species which are at very low density. There is decreased predator-caused mortality on *B. laurentii* and *C. alexandri* seeds in areas of mast seed-fall. It has been suggested that such community-level predator satiation would lead to dominance by the mast-fruiting species (Janzen 1974, 1976, Boucher 1981). The mixed forest where predator-satiation apparently occurs, however, is more species-rich than mbau forest where predator-caused mortality to the seeds of the dominant is equally high in mast and no-mast areas.

Although the hypothesized processes are real and occurring in the Ituri Forest communities, they have not had a controlling influence on the species diversity of adult trees. Based on the mortality patterns during the early juvenile stages, a very different community composition for mature individuals is predicted than actually occurs. How is it that *G. dewevrei* can suffer such devastating seed mortality and still make up 90% or more of the stems in the canopy level size class? One possibility is that the mortality results from the seed transplants under-represented overall *G. dewevrei* seed and seedling survival. Post-germination surveys, however, confirmed that there was indeed extremely high mortality to seeds in the *G. dewevrei* mast areas. Another possibility is that 1981 and 1982 were anomalous or, at least, that there are occasionally years with considerably higher survival of *G. dewevrei* seedlings. This remains a possibility, but it is interesting that the apparent age distribution of small seedlings in the understory ranges from first year seedlings to seedlings of over 15 years in age. *G. dewevrei* seedlings, relative to *B. laurentii* seedlings are very persistent in the shaded understory, appearing to accumulate from year to year.

The presence of *G. dewevrei* in all subcanopy size classes suggests that it is able to take advantage of small canopy openings and to withstand repeated canopy closure. Although *B. laurentii* is present in all size classes in mixed forest, it does not have the pattern of progressively greater importance, measured as percent of all stems, which *G. dewevrei* exhibits for increasingly large size classes in mbau forest. This pattern in *G. dewevrei* may be indicitive of slower growth and an ability to withstand protracted shading in all sub-canopy size classes.

Gilbertiodendron dewevrei exhibits many characteristics of the stress-tolerator syndrome as described by Grime (1979) and, when contrasted with *B. laurentii*, it shows relatively more of these characteristics in a more pronounced manner. Observations on small suppressed seedlings in the understory showed longer leaf life and slower growth for *G. dewevrei* as compared to *B. laurentii*. The reason for such low confidence in determining the age of *B. laurentii* seedlings was their more rapid leaf production and shedding at several nodes simultaneously. According to Grime's schema, morphogenetic responses to stress which are slow and small in magnitude are typical of the "stress-tolerator" whereas the more rapid changes (leaf-area, root-shoot ratio, etc.) are typical of the "competitor". The stress which apparently gives *G. dewevrei* its understory advantage relative to other species, is inflicted by parent individuals, the deep even canopy of contiguous *G. dewevrei* crowns typical of mbau forest.

If this interpretation of *G. dewevrei* dominance is correct, then this is a life history pattern which would not be expected to be successful in chronically disturbed tropical forests (cyclone belt, steep slopes). It would also be expected that after major disturbance or climatic amelioration establishment of such a single-dominant forest would be slow relative to a more diverse mixed forest. The encroachment of this single-dominant forest is necessarily slow due to the feeble dispersal of propagules and the lengthy seed-to-canopy generation time. The mixed forest, on the other hand, contains numerous animal dispersed species and even the caesalpiniaceous species which dominate the canopy disperse farther than *G. dewevrei*. Many canopy- level species in mixed forest are shade-tolerant as juveniles, suggesting that the species composition of the mixed forest may be self-replacing over many generations. However, transition zones between mixed forest and mbau forest may be dynamic, with progressive shifts in species composition as *G. dewevrei* invades the mixed forest understory or disturbances make major changes in the light environment of advanced regeneration.

The "regeneration niche" hypothesis was earlier rejected as a useful paradigm in understanding diversity differences between mixed and mbau forest. It was pointed out that related species in both forest types have similar establishment requirements despite their marked differences in dominance. This is true in that all three caesalpiniaceous species germinate and persist for some time in the shaded understory beneath parent trees. However, if a long term perspective is taken, what may be a key difference between the mixed and mbau forest species is quite consistent with the "regeneration niche" hypothesis. Preliminary data suggests that *G. dewevrei* may be able to tolerate shady subcanopy conditions considerably longer than *B. laurentii* or *C. alexandri.* The mbau forest dominant may be buffered against high seed mortality by the fact that any seedling which survives the early predation threats has a substantially better chance of persisting until a canopy gap provides light for growth. The distinctive dimension of *G. dewevrei*'s "regeneration niche" is seen in the accumulation of aging seedlings and saplings in a basically undisturbed forest understory.

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