To the Graduate Council:

I am submitting herewith a dissertation written by Stanley Opunabo Abell entitled "Comparative Ecological Studies on the Effects of Disturbance on Rainforest Structure and Species Diversity." I have examined the final copy and this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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The Graduate School

COMPARATIVE ECOLOGICAL STUDIES ON THE EFFECTS OF DISTURBANCE ON RAINFOREST STRUCTURE AND SPECIES DIVERSITY

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Stanley Opunabo Abell
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DEDICATION

I dedicate this piece of work to my son, Somieye and my mother, "Nane," who bore the brunt of my long stay in college and whose patience and silent suffering encouraged, sustained, and motivated me all through my academic odyssey.

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ABSTRACT

The tropical rainforest ecosystems of the world are currently being altered (or destroyed) at a rate never before recorded for any forest ecosystem. Recent estimates put the destruction rate at 2% per year, which is equivalent to 11 million hectares. The primary reason for the destruction include rapid population increases, economic development, and agriculture-related activities. Unfortunately most policy planners in the countries in which these endangered ecosystems are located are presently too concerned with short-term economic interests to worry about long-term ecological consequences such as loss of soil fertility and genetic impoverishment.

Compared to other forest ecosystems, very little is known about the rainforest; for example, of an estimated three million species of plants and animals in the tropics, only 500,000 have been described. There is, therefore, an urgent need for studies which will elucidate the complex interactions which occur in disturbed and undisturbed rainforest ecosystems.

The specific objectives of this study were: (1) to examine the effects of partial and complete forest disturbance on litter and understory biomass production, (2) to evaluate differences in species diversity between

moist evergreen and semideciduous rainforests, (3) to evaluate the relationship between rainforest species diversity and precipitation, (4) to determine the effects of slash-burning on rainforest soil fertility, pH, cation exchange capacity, movement of macroelements such as carbon, nitrogen, phosphorus, and potassium, and the cumulative impact of the changes on forest regeneration and succession, and (5) to compare the results obtained to similar results obtained elsewhere in Asia and South America.

To accomplish these objectives, forest stands at different successional stages were sampled, and their floristic richness, species diversity, importance values, understory biomass and litter accumulation rates were compared. In the fire study, results from early (December) and late (March) burned plots were compared with those from an unburned control.

Data from the above evaluations were obtained by random sampling. In the species diversity study six 25 x 25 m plots were used to sample all trees with gbh 15 cm or more. In the litter and biomass studies, five 1 meter square plots were utilized. The plots were located in an (1) undisturbed "virgin" forest, the so-called Strict Nature Reserve or SNR, a (2) 30-year old secondary forest, and a (3) 30-year old partially cut forest, the so-called tropical shelterwood system, or TSS. Understory biomass and species' presence data from early and late burned and control plots, and understory biomass and litter data from a Strict Nature Reserve, a Tropical Shelterwood System and a 30-year-old secondary forest, were collected monthly and compared. Variations in soil element concentrations caused by fire were laboratory analyzed and compared. Representative plant specimens collected during the species diversity study were mounted and preserved for herbarium use. Climatic data relevant to the study area were obtained from various Nigerian government agencies and published sources.

A number of observations were made: (1) Most Nigerian rainforest species are represented by only a few individuals per hectare. (2) Single-species dominance as noted in temperate deciduous forests are rare, while multiple-species dominance with combinations of Diopyrus, Cola, Celtis, Drypetes and Sterculia were more common. (3) Extremes in moisture conditions reduce plant species diversity components and intermediate moisture conditions give rise to maximum species diversity. (4) High species diversity is a function of high species eveness or equitability. (5) Moisture availability is the major factor that controls litter and biomass production patterns. (6) Moisture (in the form of rainfall) exerts a positive influence on biomass production and a negative influence on litter accumulation. (7) Fire in general altered and reduced plant species distribution by direct destruction of seeds, roots and other plant organs, but early burning in December improved soil fertility by increasing the concentrations of nitrogen, phosphorus and exchangeable magnesium, and (8) early burning and complete protection from fire encouraged plant species growth and regeneration, while late burning encouraged forest reversion to grassland.

The major conclusion drawn from the above results is that, in order to maintain continued high species diversity and prevent the extinction of important plant species in the Nigerian rainforest, changes must be made in present forestry and cultural practices. The present practice of leaving disturbed forest to naturally regenerate itself is inadequate and needs to be supplemented by artificial regeneration practices, especially agroforestry. Forest clearing for agricultural, industrial and urban development should be confined to secondary forests, while primary forests are set aside as parks and reserves to serve as outdoor scientific laboratories and to protect representative species from total extinction. Forest reserves should be established mainly in the high species diversity areas where moist and dry rainforests interface.

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CHAPTER I

INTRODUCTION

The major ecological problem currently facing the developing countries of Africa, Asia and South America is environmental degradation resulting from population pressure on a land that has already exceeded its carrying capacity with present production facilities. Though over-population is a world-wide problem, its effect is more critical in the developing countries of the tropics that lack a strong and efficient economic infrastructure and the technological knowledge to solve the allied problems of environmental degradation. Such countries today have larger populations than they can conveniently support under existing infrastructural and social resources.

The primary effects of overpopulation in most third world countries are manifested in the rapid depletion of forest resources through the conversion of forest lands to agricultural and industrial uses, urban development and mineral exploitation. These activities have cummulatively caused a near total destruction and serious species depletion in the few remaining rainforests of the tropics. Sommer (1976) and Perssons (1974) suggested that the entire tropical biome, comprising about 9.35 million km^2, is being depleted at a rate of 100,000 to 150,000 km^2 per year. These estimates, which were cautious to the extent that they represented minimal estimates, led to the calculation that each minute was seeing the disappearance of at least 20 hectares of forest. At this rate of destruction, the entire tropical biome could disappear in about 45 years. But, the rate of disappearance is likely to increase due to greater demands for wood. The amount of wood cut world-wide in 1974 totaled about 2,500 million cubic meters, an amount that is likely to increase to 6,000 million cubic meters by the year 2000 (Pringle 1976).

Southern Nigeria once contained extensive areas of virgin rainforest (Schimper 1903), but today most of these forests have been destroyed by population pressure and economic developments such as mining, road construction and urban expansion. The few isolated stands of undisturbed rainforest that still survive are presently confined to the Strict Nature Reserves (SNRs), but these too are increasingly coming under the demands of an ever-increasing human population.

The history of forest destruction in Nigeria correlates positively with increases in population since the end of the Second World War (Oguntala pers. comm.). Hall (1977) estimated that only a fraction of the 180,000 km^2 of land climatically suitable for rainforest development in Nigeria presently contain any form of high forest vegetation. Ola-Adams and Iyamabo (1977) reported approximately 26,000 hectares of rainforest are cleared annually in Nigeria, and Umeh (1975) predicted that by the year 2000 A.D. the destruction rate of the Nigerian rainforest will increase to about 129,000 hectares annually.

In 1979, the Nigerian Federal government under President Shehu Shagari launched a "Green Revolution" program which was supposed to make the country self-sufficient in food production by the year 1985. Under this program, 12 of the 19 states of the federation located in the rainforest zone were each expected to clear 40,000 hectares of forestland for crop production. This will amount to the destruction of approximately half a million hectares of forest.

Data from U.S. Landsat photographs have also shown that only 96,000 km^2 of Nigeria is covered with forest vegetation. This is about 10% of the country's land surface area of 983,213 km^2 and was below the 25% minimum forest cover recommended by the United Nations. Of this 10% 1,929 square kilometers (2%) can be described as rainforest, and only 87 km^2 is designated as Strict Nature Reserve (Bamgbala and Oguntala unpublished).

Concomitant with contraction of the Nigerian rainforest is the reduction and possible extinction of many plant species. Many rainforest plants have never been taxonomically classified and their pharmaceutical utility has never been investigated. Their loss, therefore, will be irreparable.

The threat presently facing the Nigerian rainforest can be summed up by quoting from an excerpt from West Africa magazine (September 1, 1980):

> Nigeria's forest could be totally destroyed by 1995. The agents of destruction have been identified . . . high demand for land . . . and domestic uses of forest products. . . . Many extensive areas known for their vegetation density about 40 years ago in Western Nigeria and Benin Forests have virtually disappeared, and apart from very remote parts of the Cross River State, it is doubtful if true rainforest can be found anywhere in Nigeria today.

Few research studies have been done in Nigerian rainforests to compare the structural attributes and species diversity of natural and modified rainforest ecosystems. Vital data on the functional dynamics of the Nigerian rainforest are also lacking. In southwest Nigeria, few structural and functional dynamic studies have been done (Evans 1939; Richards 1939; Hopkins 1965a, 1965b; Ola-Adams and Iyamabo 1977; Oguntala 1970, 1979). The effects of fire management on rainforest soils (Hopkins 1966, Nwoboshi 1970), litter fall pattern and mineralization in monoculture plantations (Egunjobi and Faseun 1972) have also been studied. But no study has yet been conducted on species diversity of the different rainforest zones and the many forest reserves in southern Nigeria. Data are also lacking on the effects of deforestation and slash-burn agriculture on understory biomass production and soil structure and chemistry. There is, therefore, an urgent need for studies on the Nigerian rainforest, especially now that the few remaining natural forests are being rapidly depleted of their species due to human population growth and related problems.

The specific objectives of this study were: (1) to examine the factors causing rainforest perturbation and destruction and to determine the relationship between species diversity, disturbance intensity, and climatic factors such as rainfall, temperature and humidity; (2) to determine the effects of slash-burning on rainforest soil fertility, pH, cation exchange capacity changes, movement of macroelements such as carbon, nitrogen, phosphorus and potassium, and the cumulative effects of these on regeneration and succession; (3) to determine the biomass and litter accumulation rates of different forest types as affected by varying intensities of fire; (4) to calculate the species diversity of the two main forest types (semi-deciduous and moist rainforests) in the many forest reserves in southwest Nigeria; and (5) to compare the results with those from similar studies elsewhere in Asia and South America.

To accomplish these objectives, forest stands at different successional stages were studied and their species composition, species diversity, absolute and relative tree stem densities, absolute and relative tree dominance, importance value, stand litter accumulation rates and understory biomass were compared. In the fire study results from early (December) burned and late (March) burned plots were compared to an unburned control plot. Floristic elements and soil structural and chemical changes resulting from fire were noted.

It is hoped that the data provided in this study will contribute to the intelligent management of the African rainforest in general and encourage its future utilization on a renewable and sustained-yield basis.

CHAPTER II

REVIEW OF LITERATURE

Although tropical rainforests are perhaps the most complex ecosystem, comparatively few studies have been done on them. Increased understanding of their structural and adaptive characteristics is essential to solve the numerous applied problems resulting from their degradation.

To date few functional and structural studies have been done on the Nigerian rainforest. Most of the early studies concentrated on phenology, species enumeration and lifeform description and therefore of limited applicability in predicting destructive trends and formulating conservation strategies. On the global level many studies have been done under the International Biological Programme (IBP). Regional studies have also been done under the Man and the Biosphere (MAB) Program in the Ivory Coast (Huttel 1967), Manaus, Amazonia (Klinge 1973), Thailand, Kampuchea, and Malaysia (Ogawa et al. 1965, Hozumi et al. 1969a, b), Panama (Golley et al. (1969), and Puerto Rico (Ovington et al. 1970). The majority of these studies emphasized allometric methods (Kittredge 1944), in which dry weights of sample trees were related to tree size by linear regression after logarithmic transformation. The same method could not be used in this study because of the large-scale destruction that would be involved.

The role of fire in rainforest ecosystem modification is another important ecological factor that has been studied (Ahlgren and Ahlgren 1960, DeBell & Ralston 1970, Grier 1975). Corresponding studies in tropical settings are few and emphasis have been on grassland ecosystems (Guilloteau 1956, Trapnell 1959, Rains 1963.

Speciation and Evolution of Tropical Species

The floristic and structural complexities of tropical rainforests have long evoked speculations as to their origin. Most geneticists (Simpson 1953, Grant 1963, Stebbins 1966, Lerner 1968) agree that the likely effect of the stable tropical climate on the evolution of tropical plants is that it enhanced stabilizing selection instead of disruptive selection. Their theory is based upon the assumption that stable or uniform climate will eliminate from a population all species with genotypes least adapted to the norm and more adapted to the extremes. Thus with time, only species whose frequency of occurrence fall near the mean will flourish (Dillon 1970).

Federov (1966) and Ashton (1969) have stated that genetic drift deriving from isolation and self-fertilization are the main driving force behind the evolution of tropical plant species. Dobzhansky and Parlovsky (1953) demonstrated in their studies with *Drosophila* that rapid and continuous evolution could occur in small partially isolated populations even if environmental parameters remained constant. Ashton (1969) argued that because spatial isolation and self-fertilization are more common in tropical rainforest, a restriction is placed on gene recombination. This, according to Heslop-Harrison (1964), caused the populations to be distributed among homozygous pure lines. This also supports Federov's (1966) contention that factors such as small population sizes of tree species, isolation, absence of seasonal rhythm, irregularity of flowering and difficulty in cross-pollination in tropical rainforest environment, all add to create favourable conditions for speciation in which the role of genetic drift prevails over that of natural selection. Under these conditions, Federov concluded, mutant genes accumulate and contribute to rapid evolution of new species.

Compared to the South American and Asian rainforest, the African rainforest is less diverse in plant, birds and insect species (though not mammals, Bourliere 1973) (Richards 1963a, Carcassan 1964, Chapman and White 1970). Richards (1952) and Martin (1968) attribute the cause of this species poverty to historical factors such as climatic changes of the Pleistocene.

The present extent of the African rainforest consists of two main blocs, the so-called Guinea bloc in West Africa and the much larger bloc of the Zaire basin. During the Pleistocene era the African rainforest shrank to its smallest size, but isolated patches of forest survived as refugia and served as reservoirs from which the forest later re-established itself. (For detailed information on the effects of Pleistocene on the African rainforest see Richards 1963a, Monreau 1966, Bigalke 1978, Kayanja 1979, Hall and Monreau 1970, Kingdom 1971, 1973, Hamilton 1974, 1976, Livingston 1975, Hall 1978, and Grubb 1979).

While there are some disagreements about number and location of the African Pleistocene refuges, there is general concensus concerning four principal localities. These are: (1) the upper Guinea refugium, (2) the Cameroon-Gabon refugium, (3) the Eastern Zaire refugium, and (4) the East African Mountain System refugium. The Upper Guinea refugium comprises parts of eastern Liberia and western Ivory Coast. This refugium is reported to be exceptionally rich in endemic species of both plants and animal (Bigalke 1978, Kingdom 1971, Grubb 1979). The second refugium, the Cameroon-Gabon refugium, extends into eastern Nigeria and parts of the Congo. This refugium has been reported to have the richest flora on the African continent (Tappen 1960).

Richards (1963b) attributed this richness to species isolation caused by the Cameroon mountains which limited man's destructive access. The third refugium, located in northern and eastern Zaire, contains the largest number of mammals in Africa (Bigalke 1978, Kingdom 1971, 1973). Of the four refugia, the East African refugium is the least diverse consisting mainly of montane species (Monreau 1966, Chapman and White 1970).

At present there are few studies on the distribution of species in the African rainforest; only two taxa, Diospyros (White 1962) and Euphorbiaceae (Leonard 1965), have been thoroughly studied. White (1962) showed that, of the 31 taxonomically isolated forest species of Diospyros, four were endemic to the Guinea forest bloc. These figures illustrate the poverty of the West African rainforest which, as earlier indicated, may be the result of high human population density and uniform physiography of the region (Wild 1968, Faden 1974).

Succession, Diversity and Stability Relationship

The theory of succession explains the predictability and regularity with which plant species are in time replaced by others. The earlier theories (Clements 1916, Cowles 1899, Braun Blanquet 1932), postulated that successional species modified their habitats and made them less fit for themselves but more fit for other species that eventually replaced them. Species replacement during succession continued until the site is completely occupied by climax species which maintained themselves perpetually barring major perturbation.

Succession has been related to various ecosystem properties such as productivity (Connell and Orias 1964) and stability (Odum 1969). The relationship between species diversity (during succession) and stability was first mentioned by MacArthur (1955) who stated that species diversity and stability increased during succession, reaching its highest at climax. This view was supported by Monk (1967), McCormick (1968) and Holland (1971). But other ecologists contended that species diversity does not necessarily increase with succession but, depending upon the nature of external factors impinging on the system, may either increase or decrease (Margalef 1958, Whittaker 1965, Pielou 1966).

Many of the reports which support diversity increases with succession and its maximum manifestation during climax failed to make provision for the different attributes of diversity (such as richness and apportionment), all of which may vary along the same gradient (Odum 1969). Despite this, results from most diversity-succession studies on vascular plants have tended to confirm the hypothesis that diversity increases through succession. Studies by DeSelm and Shanks (1967) in a temperate forest area of Tennessee, however, reported a rapid plateauing in diversity during early wet secondary succession. Golley (1965), on the other hand, reported fluctuations in variety at 11-year intervals which he attributed to difficulty in invasion by new species.

The term "stability" as generally used in ecological literature may refer to stability of numbers, of relative abundance patterns, of dominance, and of species composition. In this study the term is used to mean the ability of a system to return to its ground state or original position after external perturbation.

Experimental demonstration of diversity-stability relationship has been provided by Hurd et al. (1971), Hurd and Wolfe (1974), Mellinger and McNaughton (1975) and McNaughton (1977), who treated abandoned hayfields with inorganic fertilizers to stimulate plant productivity. In these experiments they showed that the new primary productivity of the old communities did not change after the nutrient enrichment, whereas that of the younger and less diverse communities showed substantial increases. The fertilizer also caused significant declines in the evenness of plant species abundance on the old field, although there was no effect on the younger plant community.

These experiments, therefore, suggest that while diversity and stability may be associated under certain conditions, no obligate relationship exists between the two in successional ecosystems.

Reasons for High Species Diversity of Tropical Regions

Tropical regions have been reported to contain a large number of congeneric (or closely related) species (Richards 1969). Six hypotheses have been postulated to explain this high species diversity (Pianka 1966). The first of these hypotheses, the available time theory, assumes that all communities diversify with the passage of time, and that older communities, as a result, contain more species than younger ones. Evidence that tropical communities have been in existence longer than their temperate counterparts has been provided by Axelrod (1952) and Muller (1968) who traced the existence of tropical regions to the Cretaceous Period. This theory attributes the impoverished state of temperate and arctic regions to the effects of Pleistocene glaciation (Fisher 1960), and the species richness of the tropics to the lack of a corresponding large-scale destruction. Simpson (1964), however, disagreed, arguing that temperate zones have probably been in existance as long as tropical ones, and Newell (1962), in support, stated that temperate zones in intermediate latitudes were not critically affected during the Pleistocene era because their floras and faunas were only merely laterally shifted away from the path of destruction.

Proponents of the second theory, the theory of spatial heterogeneity, assume that there exists a general increase in environmentl heterogeneity as one proceeds towards the tropics, and that the more complex and diverse a physical environment becomes, the more complex and diverse the animals and plant communities supported by it (Fisher 1960, Simpson 1964, Sanders 1968). Implicit in this hypothesis is the assumption that as habitat heterogeneity increases, utilizable resources also increase, enabling the invasion and existence of species whose resource utilization (niche breath) are similar to the species already present (Case and Gilpin 1974, Roughgarden 1974, McMurtrie 1976).

The third hypothesis, the competition hypothesis, states that there is greater competition for resources in the tropics which gives rise to finer restrictions (or niches) in food and habitat requirements and enable the co-existence of many species (Dobzhansky 1950, Williams 1964, May and MacArthur 1972). Thus species overlapping on one niche dimension can coexist if they separate on some other dimension (May and MacArthur 1972).

Experimental demonstration of this hypothesis was provided by Paine (1966, 1974) who studied intertidal invertebrates co-existing as sessile adults along the coast of Washington State. Paine found that in the presence of a predatory starfish (Pisaster ochraceous) the abundance of the best competitors (Mytilis californicus) was kept sufficiently low for other species of invertebrates to remain in the community. When the starfish was removed from a section of the community, the number of prey species dropped from 15 to 8 in one year (Paine 1966). The eventual outcome of competition in the absence of predation was nearly complete dominance of the rock faces by the one or two species that could grow best under the prevailing environmental conditions. Similar situations exist in the tropics which, according to the fourth hypothesis (predation), contain more predators (and parasites). These influence the region's biotic diversity by preventing any species from building its population to levels that will enable it to monopolize available resources (Pianka 1974, Janzen 1969). The resulting reduced interspecific competition also allows the addition and co-existence of intermediate prey types which in turn support more predators in the system. Experimental support of this hypothesis has been given by Grice and Hart (1962) who showed shifts in trophic structure along latitudinal diversity gradients.

The fifth hypothesis, the productivity hypothesis (MacArthur 1969), states that greater productivity results in greater diversity, everything else being equal. Using cybernetics to explain the theory, the authors contended that under stable climatic conditions of the humid tropics only a small portion of the energy assimilated by organisms will be used in regulatory activities, leaving a high proportion available for growth and reproduction of offspring. This, according to Baker (1970) and Connell and Orias (1964), will give rise to larger populations which, in turn, means greater base for genetic variation and opportunities for mutation. Federov (1966) and Ashton (1969) showed that most tropical tree taxa are represented by only a few individuals, contradicting the implied larger populations within tropical tree genera. The most recent experimental demonstration of the productivity hypothesis was done by Grime (1973a, b, 1975, 1977), and Al-Mufti et al. (1977). These studies showed that plant community species diversity was related to standing crop biomass and litter components of the community.

The sixth and final hypothesis, the climatic stability hypothesis, is based upon the assumption that a stable climate will better enhance the evolution of finer specializations and adaptation than an erratic climate

(Klopfer 1959). This hypothesis also implies that species diversity in the tropics has reached an equilibrium state, while those in temperate and polar regions are still "biologically immature" (Fisher 1960). Given the restricted post Pleistocene time period, most of the available niches in temperate and arctic regions are yet to be filled (Baker 1970). In another study Klopfer and MacArthur (1960) provided experimental evidence to support their thesis that "niches are narrower in the tropics." Their findings indicate that non-passerines, possessing a more stereotypic behavior, are better adapted to exploit the more constant tropical environment than are the passerines whose more plastic behavior allows them to inhabit less predictable habitats. The same phenomenon applies to plants in the tropics which need no behavioral flexibility to cope with climatic variations since such variations are either absent or very insignificant.

CHAPTER III

THE STUDY AREAS

The study was conducted in the Nigerian rainforest reserves of Gambari, Shasha, Olokemeji, Idanre, Omo, Okomu and Sapoba (Figure 1). These reserves are all in south-western Nigeria, in the rainforest zones described by MacGregor (1937), Evans (1939), Richards (1939, 1952), Ross (1954), Jones (1955), Keay (1959) and Hopkins (1962). The choice of these reserves was dictated by logistic and biological considerations such as proximity and accessibility and by the intensity and frequency of disturbance.

Gambari, Shasha and Olokemeji are in the northern sections of the rainforest belt and have been variously described as dry or semi-deciduous (Keay 1959). Okomu, Omo and Sapoba are typical moist evergreen rainforests and are in the southern sections of the rainforest belt. In between these two forest types is the Idanre Forest Reserve which has climatic features common to both dry and moist rainforests. All these forest reserves have experimental subplots established in 1952 by the Forest Research Institute of Nigeria, Ibadan. These subplots, otherwise called Permanent Sampled Plots (or PSP), are protected (from external interference) and are used exclusively for ecological studies.

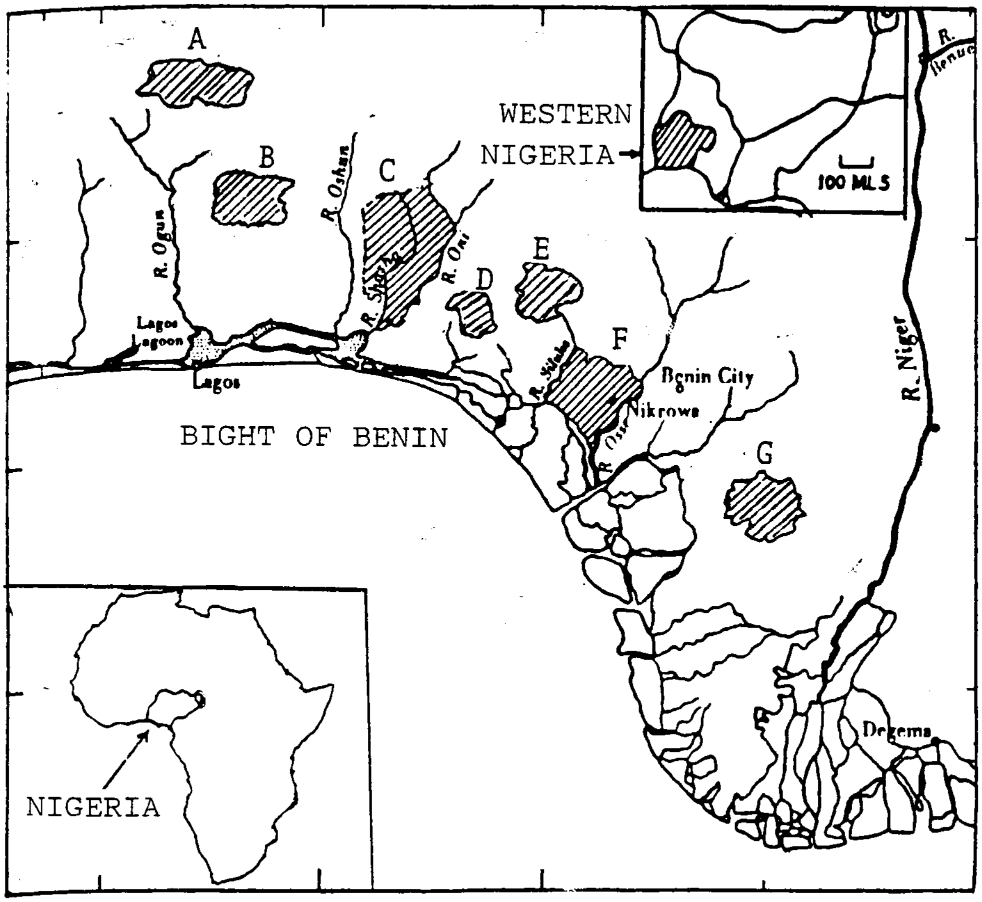


Figure 1. Map of southwest Nigeria showing the location of study sites (Richards 1939). Key: A = Olokemeji Forest Reserve (F.R.), B = Gambari F.R., C = Shasha F.R., D = Omo F.R., E = Idanre F.R., G = Sapoba F.R.

Each PSP is 4.72 ha. (12 acres) in size and is divided into 16 subplots, each 0.30 ha. (or 0.75 acres).

General Features of the Climate

Understandably, climatic data obtained from weather stations do not always reflect the climatic conditions that control plant responses to their environment. This is because climate is subject to modification by topographic factors, e.g. wind and insolation. Weather station data, however, are useful in characterizing the general climatic features of a region. Monthly temperature, rainfall and humidity measurements of representative sites in the three major forest types are given in Tables 1 and 2. Differences in the monthly values of these climatic variables exert great influence in controlling the distribution pattern of vegetation in Nigeria. Of these factors, rainfall is the most important (Ali 1975).

Another important factor that influence the regional climate of West Africa is its geographical location. West Africa's location between two large homogenous surfaces of land and water places it in the path of two large air masses whose seasonal movement directly affects the regional vegetation complex (Ojo 1977). These air masses, the tropical continental (cT) and the tropical maritime (mT) (Figure 2) alternate

Table 1. Mean monthly rainfall, temperature and humidity of study sites for the periods 1975-1980 (unpublished data of Forest Research Institute of Nigeria, Ibadan, 1980).

Forest Reserve	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
						RAINFALL (mm)							
													Annual
Sapoba F.R.	21	46	55	126	198	266	294	596	327	211	60	19	2219
Gambari F.R.	20	38	135	146	159	204	188	157	204	179	66	29	1525
Idanre F.R.	21	42	95	136	179	235	241	377	266	195	63	24	1874
						TEMPERATURE ($^{\circ}$C)							
													Monthly
Sapoba (Max.)	32	32	32	32	31	31	28	28	29	29	31	34	30.7
F.R. (Min.)	23	20	22	23	23	22	22	21	21	21	21	19	21.5
Gambari (Max.)	32	34	33	32	31	29	27	26	27	29	30	31	30.0
F.R. (Min.)	19	20	21	21	21	20	20	20	21	20	21	21	20.4
Idanre (Max.)	32	33	32	32	31	30	27	27	28	29	30	32	30.1
F.R. (Min.)	21	20	21	22	21	21	21	20	21	20	21	20	20.1
						RELATIVE HUMIDITY (% at 1400)							
													Monthly
Sapoba F.R.	76	76	77	70	85	87	89	92	86	83	86	77	82
Gambari F.R.	77	58	65	72	75	79	81	84	82	80	76	74	75
Idanre F.R.	77	67	71	71	80	83	85	88	84	82	81	76	79

Table 2. Physical and climatic data of major rainforest reserves in southern Nigeria.

Forest Reserve	Location	Altitude	Geology	Topography	Rainfall	Classification	Source
Gambari	7°25'N,3°53'E	200 m	Basement complex rocks	Gently undulating	1525	Semideciduous	Egunjobi and Fasehun (1972)
Shasha	7°05'N,4°30'E	23 m	"	"	1787	"	Ross (1954)
Idanre	6°50'N,5°10'E	-	"	"	-	Moist-semi-deciduous	Hall (1977)
Okomu	6°20'N,5°10'E	-	Tertiary sands	"	2605	"	Jones (1955)
Sapoba	6°04'N,5°32'E	83 m	"	"	2219	Moist evergreen	This study
Olokemeji	7°28'N,3°33'E	140 m	Basement complex rock	"	1232	Semideciduous	Hopkins (1966)
Omo	6°45',4°20'E	25 m	Basement complex and Mesozoic rocks		2020	Moist evergreen	Hopkins (1966) Hall (1977)

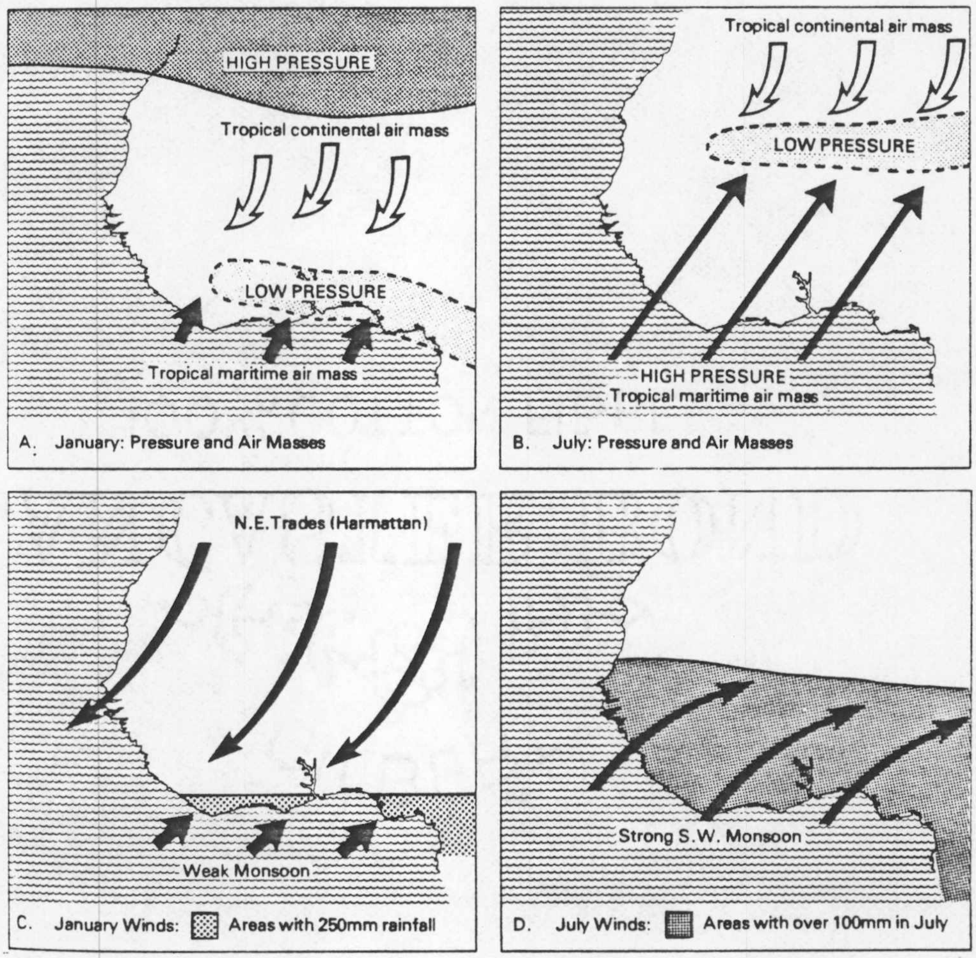
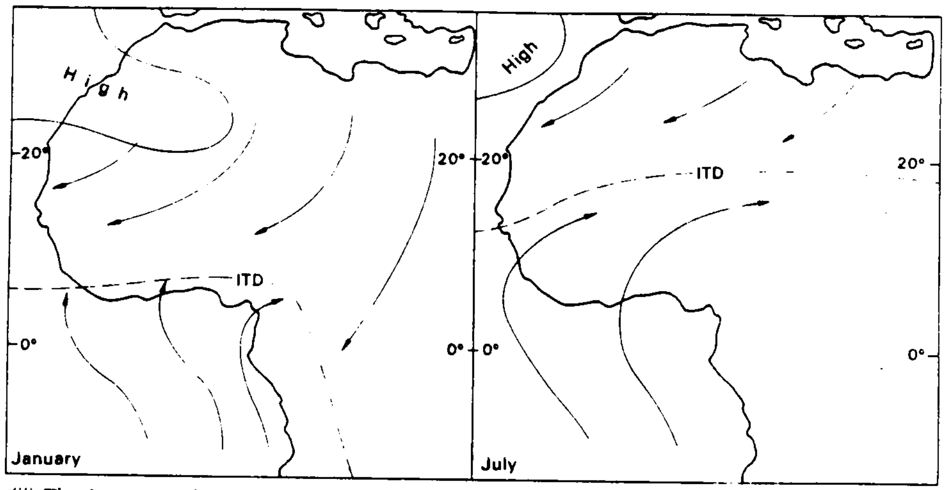


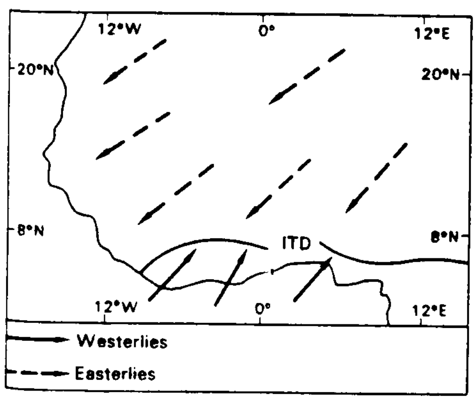
Figure 2. Maps of West Africa showing seasonal oscillation of the tropical continental and tropical maritime air masses and their influence on the regional climate (Agboola and Hodder 1979).

seasonally and are separated by a zone of turbulence called the intertropical discontinuity (ITD) (Hubert 1939, Hamilton and Archbold 1945, Sawyer 1952 and Walker 1958). The tropical maritime originates from the Atlantic Ocean, and because it is warm, it can be heavily laded with moisture. It is also the dominant wind system over most of West Africa during the rainy season when its northward movement follows the northward shift in the location of the sun, reaching its most northerly point in July or August at approximately 18° N along the Nigerian coast (Figure 3). The fluctuations in the position of the ITD over West Africa between January and July varies the depth of the warm, moist mT air mass, resulting in varying intensities of rainfall.

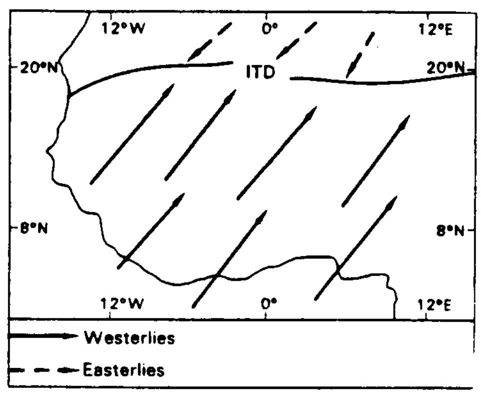
As shown in Table 1, the mean annual rainfall for the period 1975-1980 is 1874 mm for Idanre Forest Reserve which is intermediate in climatic features between the moist and the dry forest types. The mean monthly temperature over the same period is 31° C (max.) and 22° C (min.) for Sapoba Forest Reserve, 30° C (max.) and 20° C (min.) for Gambari Forest Reserve and 30° C (max.) and 20° C (min.) for Idanre Forest Reserve. The mean annual relative humidity for the period is 82% for Sapoba Forest Reserve, 75% for Gambari Forest Reserve and 79% for Idanre Forest Reserve. In all



(ii) The Intertropical Discontinuity (ITD) over West Africa in January and July.



Mean position of the surface ITD in January.



Mean position of the surface ITD in Sept

Figure 3. Maps of West Africa showing seasonal oscillation of the Intertropical Discontinuity (ITD) during the dry and rainy seasons (Ojo 1977).

forest types temperature was highest in the dry season between November and February and lowest in the wet or rainy season between March and October.

Seasonality of the Climate

Nigeria has two main climatic seasons, the wet season (April to October) and the dry season (November to March). These seasons correspond to the periods of maximum influence of the two major air masses and their associated winds. The wet season is associated with moisture-laden southwesterly winds (the tropical maritime), while the dry season is associated with the dry northeasterly winds (the tropical continental). The length of each season varies from place to place depending upon the duration and prevalence of the air masses and the depth of the ITD.

When the humid mT prevails, relative humidity is usually high and rainfall is experienced along the southern Nigerian coast. In the dry season, the dry cT, locally referred to as "Harmattan," is the dominant wind system.

The Harmattan

The harmattan wind blows towards West Africa from the north between December and January. Being from the Sahara Desert, it is an extremely dry wind. The harmattan period is characterized by sunny, rainless and cloudless days, low relative humidity and cold nights. In general, the dessicating effects of the harmattan are of great agricultural and ecological significance to the peasant farmers who use it to ensure quick drying and burning of brushwood on cleared farmlands.

Other ecological effects of the harmattan have been discussed by Schnell (1952), Phillips (1959) and Taylor (1960). For example, the harmattan is said to be responsible for the development of xeromorphic species and distinct windward and leeward biotypes on the Togo Mountains (Jenik & Hall 1966). The extreme diurnal temperature ranges that occur during the harmattan period were also shown to have a selective influence on the distribution of rare montane tree and herb species such as *Hypoestes triflora*, *Haumaniastrum alboviride* and *Senecio lelyi* (Jenik & Hall 1966).

Geology

The geology of the Nigerian rainforest zones has been described by Hopkins (1962) and Jones (1955), who identified three main rock types: (1) precambrian, (2) sedimentary, and (3) volcanic. The precambrian, old crystalline and metamorphosed rocks composed of quarzites, granite, schists and gneiss, are predominant in the northern portions of the study site and underlie the Gambari, Olokemeji, and Shasha Forest Reserves. In the south, the precambrian rocks are covered by sedimentary rocks of

Tertiary age which consist of alluvial deposits of sand, silt and clay and are sometimes referred to as "Coastal" or "Benin Sands" (Ali 1975, Oguntala 1979). The third rock type, the volcanic rocks, occur only in parts of Olokemeji Forest Reserve. They consist of volcanic materials such as basalt, dolorites, gabro and serpentine and outcrop in the south as intrusive series.

Topography and Drainage

Topography of the study area has been described by Jones (1955) and Hopkins (1962) as a gently undulating plain which reaches its highest point (369 m) at about 240 km from the Atlantic coast before gradually falling northwards and eastwards towards the River Niger. The only deviation from this undulating pattern is found in parts of the Olokemeji Forest Reserve where the undulations are more pronounced, having two prominent hills, the Ako and Abo, from which the reserve derived its name; "oke" is a Yoruba word for hill, and "meji" means two or double in Yoruba.

The study area is drained by many rivers which have their catchments in the interior of the forest zones. Prominent rivers are the Ogun, Oshun, Shasha, Oluwa, Owena, Siluko, Osse and Warri (Figure 4). They all drain directly into the Atlantic Ocean through an elaborate deltaic network. Collectively they

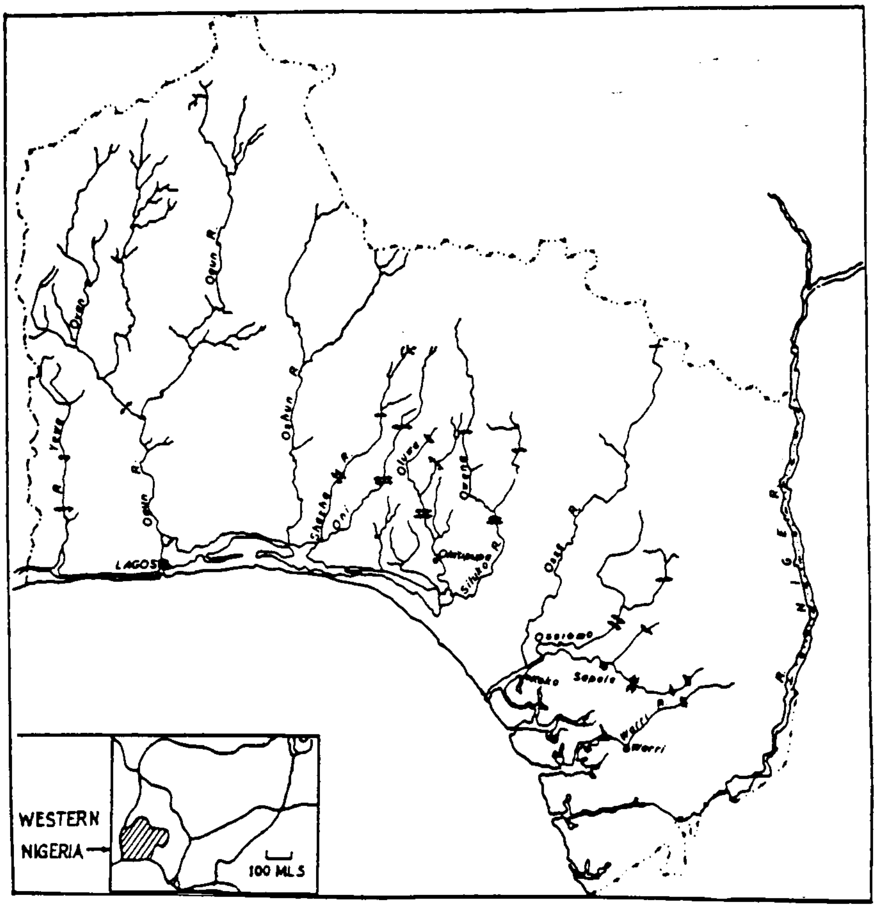


Figure 4. Map of West Africa showing the major rivers draining the study sites (Adeyoju 1969).

provide efficient drainage system for the heavy precipitation of the southern Nigerian forest zone.

Soils

Few soil studies have been done on the study site and detailed soil maps are virtually non-existent in Nigeria. The information presented here was extracted from limited published sources which include studies by Wilson and Bains (1928), Jenkins (1959), Hopkins (1962) and Aluko (1977).

The soils have been described as generally well-drained except in the swampy extreme south (Jones 1955). Parent materials consist of unconsolidated deposits of "Benin Sands" (Oguntala 1979). Gambari and Olokemeji soils are similar in structure and chemistry and belong to the Ondo Association. They are, however, different from those at Okomu, Sapoba and Omo due to differences in parent material.

Wilson and Bains (1928) described soils in the Okomu Forest Reserve as composed of "white and honey-colored clayed sands with bands and beds of fine-textured clay." Oguntala (1979) also described the soils in the Sapoba Forest Reserve as consisting mainly of "red earth deposits that are partly interstratified with clays and lignites of the Lignite Group." Aluko (1977) found an appreciable percentage of gravels in the Gambari soils, "forming hard layers where concretions occur." Wilson and Bains (1928) further described the soils in the Okomu Forest Reserve as unconsolidated, lacking cementing materials and easily broken with slight finger pressure. Oguntala (1977) described the soil in the Sapoba Forest Reserve as having an A horizon (0-11.4 cm) with very little leaf litter, dark reddish-brown topsoil, moist loose and coarse sands with little clay content, becoming more compact with depth and gradually merging into a B horizon (11.4-111.8 cm) of red clay sands, which becomes more compact with depth.

In another related study, Jenkins (1959) described a soil profile in the Olokemeji Forest Reserve as having, "an A horizon of light grey (10YR 7/2) humic loam with moderately strong angular to crumb structure, with . . . very irregular lower boundary merging into a B horizon on very pale brown (10YR 7/3) coarse and sandy loam."

The influence of parent material on soil formation in the study sites is exerted mainly throught the characteristics it imparts to the soil produced, though this too is greatly modified by rainfall. Hall and Bada (1979) observed that with increasing mean annual rainfall there is marked intensification of leaching, and a reduction in the contrast between soils derived from different parent rocks.

They also found that on any given rock type, a gradient of increasing severity of leaching produces soils with decreasing base saturation percentages (Hall and Bada 1979); and in places where the subsoil base saturation exceeds 40% ferruginous soils occur, but where it is lower than 40% ferrallitic soils occur (Ahn 1970).

Vegetation

The distribution of vegetation in Nigeria is greatly influenced by regional climate, especially the mean annual rainfall and the dry harmattan wind. Thus, in the moist and wet south, (Figure 5, zones F and G), rain-forest is the climax vegetation, while in the drier north (Figure 5, zones A to E), climax vegetation is savanna woodland (Keay 1959). Between these distinct vegetation types is a transition vegetation intermediate in character between forest and savanna (Jones and Keay 1959). MacGregor (1937) and Richards (1939) have given the 251.90 mm isohyet boundary as the line separating these two types.

The distribution of forest in Nigeria is influenced by factors such as farming, grass fires, slash-burn agriculture and edaphic characteristics. The effects of these factors, however, are localized and merely modify existing climax vegetation.

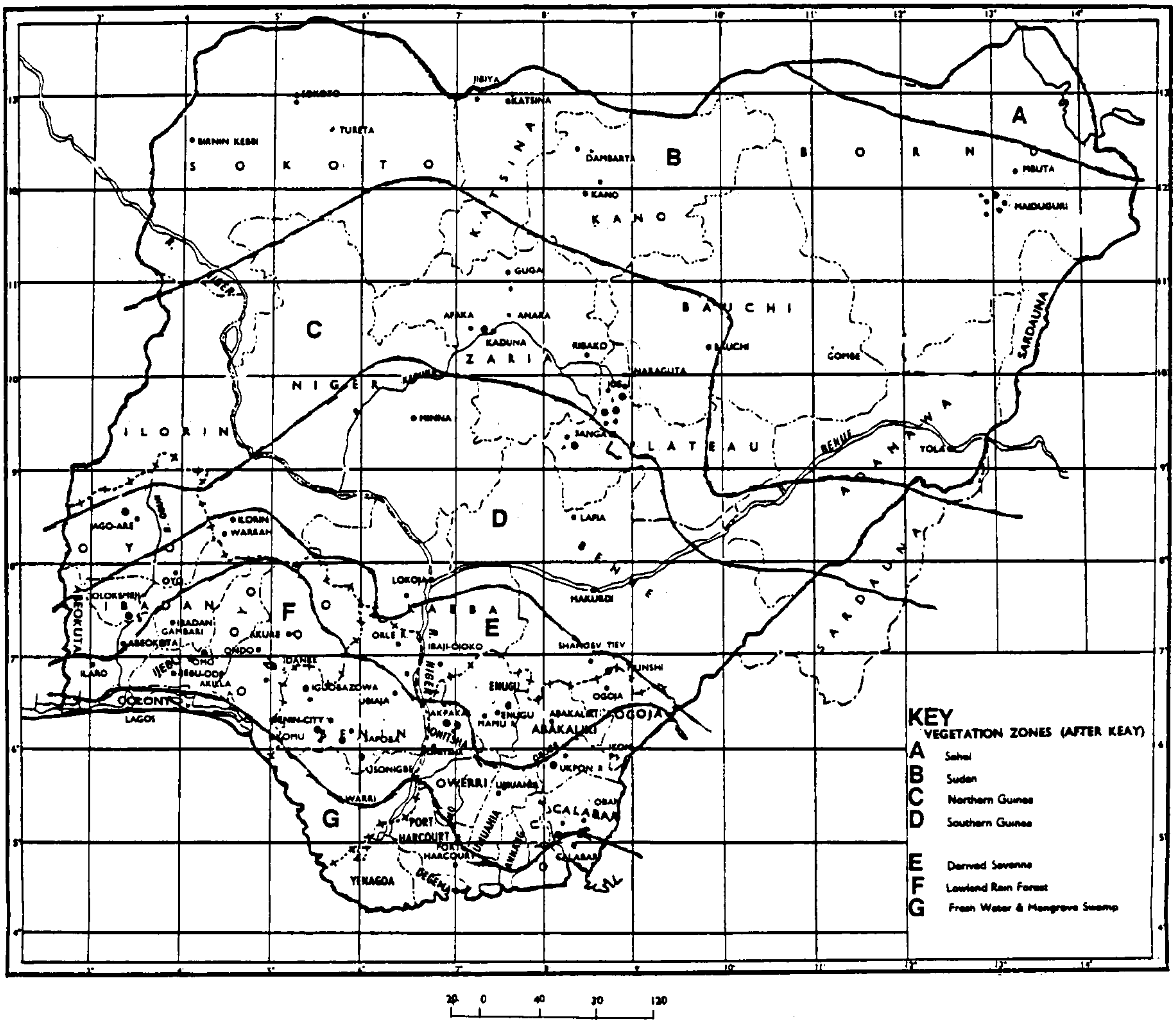


Figure 5. Map of Nigeria showing natural vegetation zones (Federal Land Survey 1965).

Nigerian rainforests are complex, multistoried and composed chiefly of plants whose origins lie within the tropics (Baur 1964). Like other rainforest ecosystems, they are floristically rich and have high species diversity. This richness, according to Richards (1952), is due to the comparative old age of the forest which caused greater plant speciation to occur. With few exceptions, the tree species are found in fairly even proportion, and no one species predominates.

The structure of Nigerian rainforest depends on the maturity of the trees and the manner in which the whole forest has been influenced by man and animals. In a relatively mature high forest there are three strata of trees. "Stratum" as used in this report means a layer of trees whose crown vary in height between certain limits. These strata, though always present, are ill-defined and are not easily recognized by casual observation because they often form continuous canopy in lateral as well as vertical contact with one another. On the other hand, some strata may be widely separated due to stand immaturity and biotic disturbance.

The shape of the tree crowns differs greatly in the different strata, depending upon the relative heights at which branching begins and on the length and angle of the main branches. Generally, the taller the tree, the wider and flatter the crown. This correlation between height and crown is less marked in the semideciduous rainforest.

The uppermost tree stratum, about 45 meters or more high, consists of relatively few species with wide-spreading and often isolated crowns; these are called emergents. The emergents make up most of the valuable timber species in Nigeria; for example, species such as Khaya ivorensis (Mahogany) are very common and highly prized. The middle stratum, 15-45 meters high, consists of a wide variety of species which have relatively small crowns and which are generally in lateral contact with each other. The third stratum, the understory, consists of trees 15 meters and below. These usually have spreading crowns, short boles and often bound together by lianas. Below the understory are the shrub and herb layers which consists mainly of young seedlings of the bigger trees. There are also synusia of saprophytes, parasites, fungi and bacteria.

Understory vegetation include taxa like Diospyrus (Ebony), Drypetes, Rinorea and Ouratea. Also well represented are the Euphorbiaceae, Rubiaceae, Annonaceae and Apocynaceae. Among the herbs, the Acanthaceae, Commelinaceae, Marantaceae, Zingiberaceae and Araceae are the most common.

The herbaceous ground flora of the Nigerian rain-forest, like its climbers and stranglers, rarely form a closed layer except in gaps and clearings where they form a luxurianth vegetation. A few grasses (Gramineae) (e.g. Leptaspis cochleata, Andropogon tectorum, Andropogon schirensis, Monocymbium sp. and Daniella sp.) also occur as ground flora, especially in the dry rainforest. Comparatively few Gramineae occur in the moist rainforest (an important distinguishing feature) except where the forest has been significantly disturbed. Some rhizomatous herbs (e.g. Dorstenia and Geophila) occur in clumps and have rhizomes adapted for propagation instead of perennation (Richards 1952). According to Raunkiaer (1934), a majority of the rainforest herbs are "herbaceous phanerophytes" as opposed to hemicryptophytes and geophytes of temperature deciduous forests.

Climbers and stranglers occur in both dry and moist rainforests though they are more profuse in the semi-deciduous forest. They range from thick woody lianas to tiny herbaceous twiners such as Strychnos sp., Acacia atacantha, Hugonia sp., Calamus deeratus, Piper guineensis, Salacia alata, Trichilia gilletii and Entada scelerata. These tend to be very dense in gaps where they form thick impenetrable tangles, the size and frequency of which is used by tropical foresters to estimate past degrees of forest disturbance.

The branching pattern of trees in the Nigerian rainforests differs markedly from those of temperate forests. For example, the network of twigs and branches characteristic of temperate region trees is rare and many species have no more than third-degree branching. Barks of the trees is generally thin, smooth and light colored. Thick bark, characteristic of temperate zone trees (e.g. the American oaks and pines), are uncommon and even trees of the emergent layer have bark that is only a few millimeters thick (Richards 1952). In contrast, taxa such as Hylodendron gabunense and Fagara sp. have very thorny trunks.

The leaves of most mature rainforest trees are of the entire sclerophyllous type and belong to the "mesophyll" size-class (Raunkiaer 1934). A typical mature leaf is deep green in color, oblong-lanceolate to elliptical in shape, with entire or finely serrated margin, and often have pulvini and pronounced "drip tip". Richards (1952) observed minor stratal differences in the leaf structure which correlated with the vertical microclimatic gradients of the various tree strata. Many juvenile plants, for example, were observed to have larger leaves than the adult of the same species; this is probably an adaptation which enable maximum use of light in the rainforest understory.

The trees of the Nigerian rainforest are frequently buttressed and/or stilt-rooted. Cauliflory, and vascular epiphytes are also common and include aroids, orchids and ferns.

The ecological functions of the pulvini and cauliflory are not yet well known. One explanation is that the pulvini are adaptations for adjusting leaf lamina towards the direction of light incidence for maximum photosynthesis; cauliflory was explained as an adaptation which enables the lower story plants (growing in semi-darkness) to display their flowers where they are easily seen and reached by shade-loving insects (Richards 1952). A second explanation for cauliflory (also given by Richards 1952) is based upon energy economics. It was argued that cauliforic plants save substantial energy by not dissipating energy to translocate photosynthetically manufactured sugar to twigs and upper branches for flower and fruit production. The evolutionary significance of this phenomenon is appreciated in terms of the limited light available for photosynthesis in the understories of mature rainforest trees.

In general, compared to the evergreen rainforests, the semideciduous rainforest is characterized by epiphytism, open forest canopies and an understory that sometimes contains grasses that wither during the dry season. The term "semideciduous" as used in this report implies that the majority of the trees, especially the larger ones, are deciduous during the dry season, while others, mostly the middle and lower stories remain evergreen. Comparatively, the emergent trees in a semideciduous forest are shorter than their moist forest counterparts (Baur 1964).

The main difference between the semideciduous and the moist evergreen rainforest is their floristic composition. For example, Sterculiaceae, a common dominant in the semideciduous rainforest is poorly represented in the moist rainforest where Meliaceae and Leguminosae dominate. Typical plants of the Nigerian semideciduous rainforest include Triplochiton scleroxylon, Sterculia rhinopetala, Brachystegia nigerica, Pterygota macrocarpa, Celtis brownii, Antiaris africana, Bosqueia angolensis, Chrysophyllum albidum, Cola sp., Trichilia prieureana, Newbouldia laevis, and Drypetes sp.. Further information on Nigerian semideciduous rainforest species and ecology may be found in Ainsley (1926), Mackay (1933), MacGregor (1937), Rosevear (1954), and Clayton (1958).

The moist rainforest, on the other hand, consists of such characteristic species as the valuable mahogany timber (Khaya ivorensis), Lovoa sp., Guarea sp., all of Meliaceae, and Leguminosae such as Gossweilerodendron *balsamiferum*, *Alstonia boonei*, *Grewia coriaceae*, *Hymenostegia afzelii*, *Annonidium mannii*, *Barteria fistulosa*, *Blighia sapida*, *Bridelia ferruginea*, *Maesobotrya staudtii*, and *Myrianthus arboreus*. Further information on the Nigerian moist forest species and ecology may be found in Evans (1939), Richards (1952), Jones (1955), Keay (1959), Baur (1964) and Lowe (1966).

CHAPTER IV

FIELD AND LABORATORY METHODS

Species Diversity Study

This study evaluated the effects of varying intensities of forest disturbance on subsequent regeneration and floristic composition. It also compared the species diversities of the semi-deciduous and moist rainforests of southwest Nigeria and attempted to find the correlation between diversity indices and climatic parameter such as rainfall, temperature and humidity.

The first part of this study was done in the Omo Forest Reserve in five random 20 by 20 m (0.04 ha.) plots chosen in (1) a natural undisturbed forest or Strict Nature Reserve, hereafter designated as SNR, (2) a 30-year-old secondary forest, and (3) a partially disturbed forest, the so-called Tropical Shelterwood System, hereafter designated as TSS. The SNR was apparently "virgin", as attested by the presence of numerous tree species valued for their wood. Inaccessibility due to isolation might explain the undisturbed nature of the SNR since there are no motorable roads close by. The TSS treatment involved the selective poisoning of all uneconomic species with sodium arsenite and cutting of climbers to open the forest and allow light penetration to encourage regeneration.

The following criteria were strictly adhered to in choosing study sites:

(1) Accessibility (by road) and the need to have sampling areas within walking distance (3 miles) from motorable roads.

(2) Avoidance of areas having extensive understory vines or other evidence of anthropogenic disturbance.

(3) Avoidance of stand edges in order to eliminate ecotone effects, and

(4) Avoidance of areas that show signs of previous litter sampling, biomass clippings, ungulate browsing or monkey and elephant activities.

Previous workers have encountered difficulties in enumerating woody species found in the Nigerian rainforest. To mitigate this problem the Forest Research Institute of Nigeria made available the services of two tree spotters and two experienced field taxonomists whose knowledge of the rainforest was very useful. Field criteria used in species identification include texture, smell and taste of freshly cut bark samples, presence or absence of latex, and characteristics of flower, fruit and leaf. Most of the trees were identified at first observation and only on two occasions did the need to consult and refer to notes and texts arise.

In each study plot an inventory of all trees over 15 cm gbh was carried out. Girth measurement was taken at breast height (4.5 ft. or 1.35 m), except with buttressed trees where it was taken 1 foot above the highest buttress. Stems that forked into two below breast height were counted as two stems and measured separately.

General listings of shrubs, herbs and climbers were made when necessary using a Spiegel relascope. Soil pits were dug in the center of each plot and soil samples were collected for laboratory analysis. Binoculars were used to study very tall trees and slide photographs were taken to document observed architectural differences between the various forest types. Collected specimens were pressed and dried, usually within 8 hours after collection, and arranged into family groups. Certification of field identification was done by Mr. Frances Onumadu of the Forest Research Institute Herbarium in Ibadan, Nigeria, according to the method of Keay et al. (1964).

The second phase of this study involved the enumeration and girth measurement of all plants $\geq$ 15 cm in six randomly chosen 25 by 25 meter plots at the Okomu, Sapoba, Shasha, Idanre and Gambari Forest Reserves. All herbs, shrubs and tree saplings $\geq$ 2 cm in height in six randomly chosen meter square plots were enumerated and recorded.

Biomass and Litter Studies

These studies were done at the Sapoba Forest Reserve instead of the Omo Forest Reserve as earlier planned because the forest officials there prohibited all forms of destructive sampling. The aim of this restriction was to preserve the research plots belonging to the United Nations' on-going "Man and the Biosphere" (MAB) studies. An attempt was made to circumvent this problem by using linear regression techniques according to methods of Swank and Schreuder (1974), Whittaker and Woodwell (1968) and Whittaker et al. (1974). Such regression analysis using allometric relationships between stem diameter and dependent variables (such as leaf and stem biomass) has been used elsewhere and shown to be an accurate method of estimating total tree biomass (Monk et al. 1970).

The aim of the biomass study was to compare the biomass of understory vegetation in four different forest types: (1) an undisturbed natural forest (SNR), (2) a 5-year-old field of the shrub, *Eupatorium odoratum*, (3) a 30-year-old TSS forest, and (4) a 50-year-old (mature) plantation of *Triplochiton scleroxylon* in the "Kennedy Field Laboratory" at Sapoba Forest Reserve. These experimental plots were originally established as single species plantations but were later left untended and used to study regeneration and invasion trends of species. At each site, all above-ground components of the vegetation (including herbs, shrubs and tree saplings below two meters) were cut each month at ground level in five one square meter randomly chosen subplots. The harvested materials were sorted into stems, leaves and floral components and oven-dried at 80° C for 48 hours and weighed to the nearest 0.05 g.

Materials for the litter study were collected from the ground in the Sapoba and Gambari Forest Reserves from: (1) an undisturbed natural forest, (2), a TSS forest, and (3) a monoculture stand of *Triplochiton scleroxylon*. The litter which included leaves, stems, twigs, fruits and flowers was collected in five randomly chosen square meter plots within an area of 100 square meters in each forest type. Litter was collected monthly between August 1980 and July 1981. They were then oven-dried to constant weight at 80°C for 48 hours and weighed to the nearest 0.05g.

The Fire Study

The fire study was done in the experimental fire plot (#254) at the Olokemeji Forest Reserve. This is an on-going experiment started by the Federal Department of Forestry, Ibadan, in 1929. The objectives of this study were

(1) to investigate the above-ground biomass accumulation and chemical and physical changes that occur in rainforest soils after slash-burning, and (2) to compare the effects of different burning regimes (late and early burnings) on soil structure and species regeneration. One plot of approximately 0.25 hectares was chosen in each of three treatments: (1) an early (December) burned plot, (2) a late (March) burned plot, and (3) an unburned control. In each plot the standing crop biomass below two meter height was harvested from five randomly located quadrats. Harvested herbage was oven-dried to constant weight at 80° C for 48 hours and weighed to the nearest 0.05 g. This process was repeated every month from August 1980 to July 1981.

Soil analysis involved the collection of soil samples from the A horizon of five randomly chosen points in each plot, using a Jarret auger. The samples were placed in bags and taken to the soil division of the Forest Research Institutes' Laboratory for analysis. Field texture of the horizons was determined according to the "feel" method described in the Soil Survey Manual (Soil Survey Staff 1951). Thickness of the A and, where possible, the B horizons, was determined using the soil corer. Mottling and other soil characteristics associated with wetness were determined in the field. Soil profile description could not be made in the conventional manner, as forest officials prohibited large-scale perturbation.

Soil pH was determined electrometrically in a 1:1 suspension of water to fresh soil and in a 1:2.5 soil:1N KCL solution (Jackson 1958). Organic carbon percentage was determined by the method of Walkley and Black, and organic carbon by multiplying organic carbon by 1.74 (Jackson 1958). Exchangeable calcium and magnesium were extracted by leaching with neutral normal ammonium acetate and determined by flame photometry, and readily available phosphorus by the molybdenum blue method of Bremner (1965). Total nitrogen was determined by the semi-micro Kjeldahl procedure described by Black (1965).

For mechanical analysis, soil samples were sieved through 2.00, 0.63 and 0.2 mm mesh screens to determine percent coarse fragments (Soil Survey Staff 1951).

Computer Methods

All species data recorded in the field were coded and transferred to computer data sheets and punched onto standard IBM data cards and stored in DEC-10 disc tapes. Subsequent data sorting and editing were performed by transferring data and programs from the DEC-10 to IBM, using the Statistical Analysis System (SAS) (Barr et al. 1976) and the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975). Calculations performed on the data set of the species enumeration include density, frequency, relative frequency, relative basal area, importance value, variance, standard deviation, range and standard error of the mean. Computations were also made for similarity index and species diversity (H') using the equation $H' = (N \log N - \Sigma_{ni} \log_{ni})/N$ where N is the total number of individuals of all species and ni is the number of individuals of the i^{th} species (Appendices F and G). The equation for the similarity index is given in the form: $2S_s/(S_1 + S_2)$, where S_s is the number of species shared by two samples, and S_1 and S_2 are the number of species in communities 1 and 2, respectively.

To explain interplot similarity between different forest reserves, cluster analyses programs (CLUSTR) (Post and Shephard 1974) were executed, based upon the importance values (IV) and relative basal area (RBA) of the most abundant species. This is essentially a hierarchical, polythetic, and agglomerative procedure which minimizes the variance within groups and maximizes that between them. The procedure combines pairs of sample plots with minimal dispersion (distance apart) until all samples are combined into a single group (Pielou cited by Schmalzer 1978).

The program language was FORTRAN run on IBM 370/3031 and 360/65 electronic digital computers at The University of Tennessee Computing Center. An initial attempt was made to ordinate the species with an ORDIFLEX program (Gauch 1977), using Principal Component Analysis (PCA), axis extraction, and reciprocal averaging techniques to show the relationship among and between species and environmental variable. A similar cluster program has been successfully employed by Schmalzer (1978) and Hinkle (1978) to study forest communities on the Cumberland Plateau of Tennessee, but because the program was originally designed to handle larger plot data set, it was modified to facilitate its adaptation to the 30 plots of this study.

CHAPTER V

RESULTS

Species Composition and Diversity

The species diversity study compared the diversity indices of forest reserves in the semi-deciduous and moist rainforests in Nigeria (Table 3). Many taxa of the Nigerian rainforest are represented by one individual while a few are represented by numerous individuals. In terms of total number of individuals, the few common species far outnumber the many rare ones (Table 4). This trend is similar to those observed in other rainforest ecosystems by Black et al. (1950), Richards (1952), Odum et al. (1960) and Federov (1966).

The highest evenness and diversity (1.69) were recorded in Idanre Forest Reserve, in the middle of the series of reserves sampled (Table 4, Appendix A). Such relatively high species diversity component values could be attributed to the forest reserve's median location between the semideciduous and the moist rainforest zones. On the other hand, lowest diversity indices were obtained from the two semideciduous forest reserves at Gambari (1.39) and Shasha (1.46). Similar relationship between environmental moisture gradient and diversity components have been reported for temperate forest ecosystems by Whittaker (1960) and Monk (1967).

Table 3. Species distribution pattern in some Nigerian forest reserves.[a]

Forest Reserve	Number of Species	Number of Individuals	Diversity Index	Forest Type
Gambari	50[b]	332[c]	1.39[d]	Semideciduous forest (dry Rainforest)
Shasha	82	615	1.46	"
Idanre	95	430	1.69	Moist-Dry Rainforest
Sapoba	85	423	1.58	Moist Rain-forest
Okomu	65	459	1.61	"

[a]Data based on species with gbh ≥ 15 cm from six 25 by 25 meter plots (total 3750 m^2).

[b]Average of all plots.

[c]Total of all plots.

[d]All plots considered as one large plot.

Table 4. Species diversity components of major rainforest reserves in southern Nigeria.

Number of Species	Number of Individuals[a]				
	Gambari F.R.	Shasha F.R.	Idanre F.R.	Sapoba F.R.	Okomu F.R.
1	20	24	37	34	16
2	8	12	15	11	8
3	1	9	7	9	6
4	2	7	3	3	2
5	1	3	6	4	4
6-10	9	9	14	11	12
11-20	4	5	6	5	9
21-40	3	3	3	3	3
41-80	2	1	-	1	1
91	-	1	-	-	-
100	-	1	-	-	-
Total	50	75	91	81	61

[a]Data based on species with gbh $\geq$ 15 cm from six 25 by 25 meter plots (3750 m^2).

A total of 165 species and 2255 individuals were recorded in the 30 experimental plots sampled during the species diversity study (Appendix A). No species diversity variation was observed between the plots as shown by their low coefficient of variation (C.V.) (Table 5). An initial attempt was made to find a correlation between basal area and species diversity but no significant relationship was established.

Species diversity variations observed in this study appear to be a function of differences in the species richness of the reserves (Table 3, Appendix A). Similar observations have been made elsewhere by Shafi and Yarranton (1973) who reported a positive relationship between richness and diversity.

The most similar reserves are those close to one another on the precipitation gradient (Table 6). The moist-dry high species number Idanre Forest Reserve showed the greatest relationship (largest coefficient) with the moist Sapoba Forest Reserve.

Classification

The hierarchical dendrogram produced from the cluster analysis showed that plots of the Gambari Forest Reserve were distinct from the other groups (Figure 6).

Table 5. Shannon-Wiener plot diversity index of the Nigerian rainforest reserves.

Forest Reserve	Species Diversity Index							
	Plot A	Plot B	Plot C	Plot D	Plot E	Plot F	Mean	C.V.
Gambari	1.27	0.99	1.28	1.32	1.07	1.23	1.19	0.285
Shasha	1.29	1.23	1.25	1.34	1.37	1.10	1.26	0.222
Idanre	1.47	1.25	1.41	1.29	1.33	1.27	1.33	0.157
Sapoba	1.36	1.31	1.22	1.34	1.35	1.41	1.33	0.187
Okomu	1.47	1.25	1.44	1.28	1.33	1.35	1.34	0.156

Table 6. Sorenson's Similarity Indices (coefficient of community) of major Nigerian rainforest reserves.

	Semideciduous		Moist-Dry	Moist	
	Gambari	Shasha	Idanre	Sapoba	Okomu
Gambari	100	0.326	0.224	0.204	0.205
Shasha		100	0.402	0.333	0.405
Idanre			100	0.864	0.462
Sapoba				100	0.440
Okomu					100

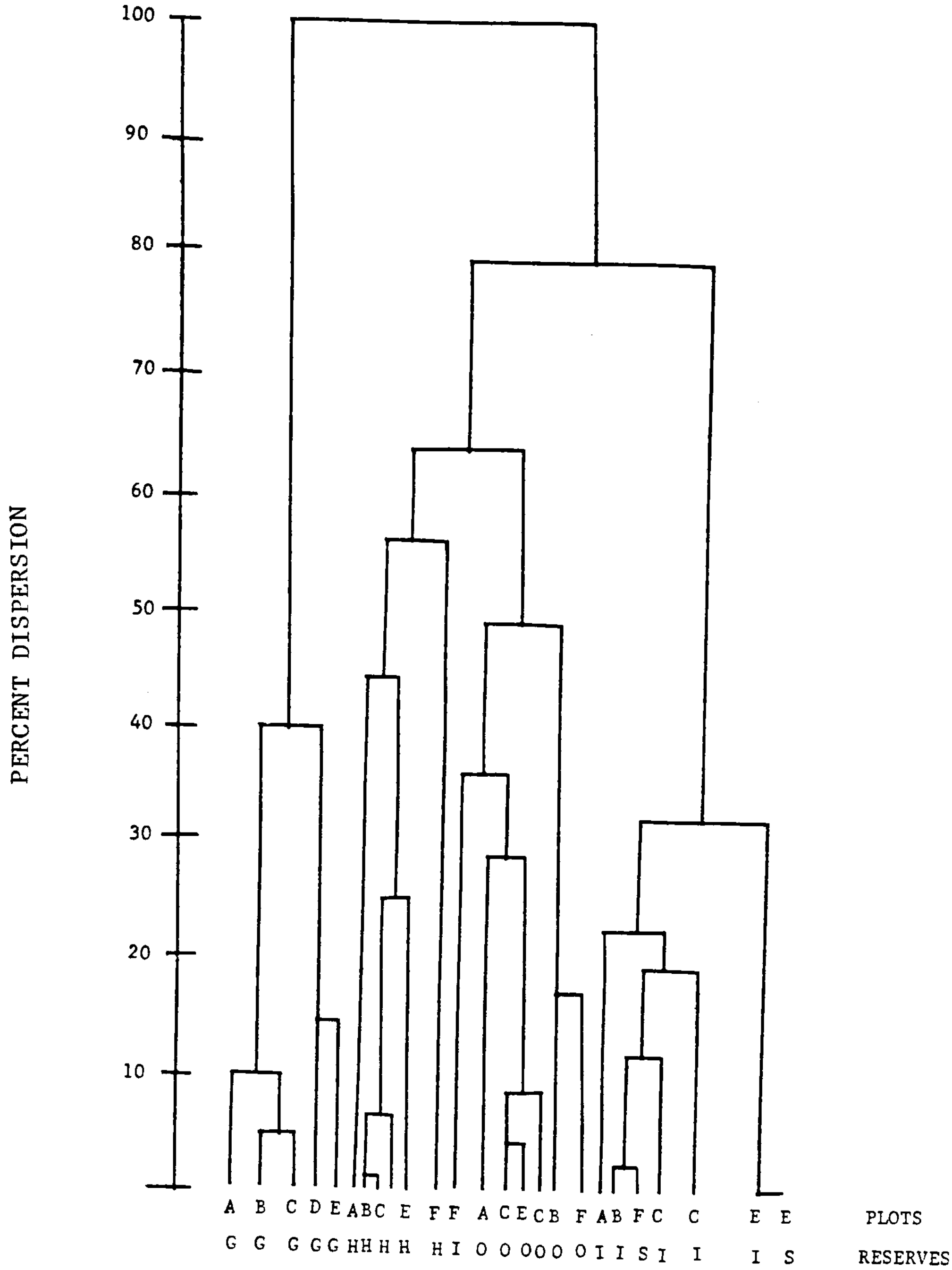


Figure 6. Dendrogram of cluster analysis of some Nigerian rainforest reserves using importance value. Key: G = Gambari, H = Shasha, I = Idanre, O = Okomu and S = Sapoba.

They also combined into two groups below the 20 percent dispersion level, an indication of the relatively high floristic homogeneity of the samples of this reserve. Plots of the Shasha and Okomu Forest Reserves also separated as distinct groups but at a higher level of dispersion. Close association was also observed between some Sapoba and Idanre plots, supporting their relatively high similarity index (Table 6).

Interplot differences between the Gambari and Sapoba-Idanre groups were explained by the distance between their groups, a relationship which reflects differences in their species composition. It was observed that while plots of the semideciduous rainforests of Gambari and Shasha stood out as separate groups, those of the intermediate Idanre Forest Reserve consisted of plots of both the semideciduous and moist rainforests.

The lack of single-species dominance, as sometimes occurs in temperate forests, makes categorization of Nigerian rainforests into community types a difficult task. *Celtis*, *Cola* and *Sterculia* species dominate in the Gambari Forest Reserve, making up 44% of the stems of the 50 species counted (i.e., ignoring the ubiquitious *Strombosia pustulata*) (Table 7).

Monthly Litterfall

Analyses of data from the litter studies showed that forest zone location affected litter production.

Table 7. Most abundant taxa of the Nigerian rainforest arranged in order of their frequency.

Taxa	Frequency	Relative Density	Relative Basal Area	Importance Value
Strombosia pustuluta	90	0.10	7.25	7.35
Diospyros dendo	80	0.06	6.00	6.06
Diospyros suaveolens	80	0.04	3.37	3.41
Guarea cedrata	73	0.04	3.47	3.51
Celtis zenkeri	60	0.02	4.20	4.22
Trichilia prieureana	60	0.02	3.36	3.38
Annonidium mannii	57	0.06	9.50	9.56
Rinorea dentata	57	0.04	0.37	0.41
Gossweilerodendron balsamiferum	43	0.03	7.88	7.91
Conopharyngia penduliflora	40	0.02	0.63	0.65
Strombosia grandifolia	40	0.03	3.51	3.54
Drypetes gilgiana	37	0.01	2.00	2.01
Pausinystalia johimbe	37	0.02	3.94	3.96
Terminalia superba	37	0.01	6.75	6.76
Sterculia rhinopetala	30	0.01	11.23	11.24
Celtis brownii	27	0.01	3.45	3.46
Cola nigerica	20	0.03	2.53	2.56
Hymenostegia afzelii	10	0.03	1.90	1.93

The quantity of litter produced was also affected by forest age, structure, and species composition.

Litter production in the semideciduous rainforest at Gambari was seasonal while that in the evergreen moist forests at Sapoba was more evenly distributed and showed less acute production peaks (Tables 8 and 9). In each forest stand the greatest production occurred during the dry season (January to April), while the lowest occurred in the rainy season (between May and October). The reason for the heavy litter fall in March may be due to the fact that heavy rains heralding the begining of the rainy start in March and wash down litter materials previously trapped in the branches of trees. Also, decomposition rate is much reduced during the dry season.

Total litter production in both semideciduous and moist rainforest was highest in the SNR, followed by the TSS, and lowest in the Triplochiton plantation. These trends, while not statistically different, may be related to the forest stand's complexity and diversity, with the most diverse of them (the SNR) producing the largest amount while the least diverse (the monoculture plantation) produced the least litter.

Comparison of the monthly rainfall, litter and biomass (Table 1, page 22; Tables 9 and 10) indicated

Table 8. Monthly litterfall (in grams) in the semideciduous rainforest at the Gambari Forest Reserve.

Month	Undisturbed SNR		30-Year-Old TSS (Partially Disturbed)		50-Year-Old Plantation (Triplochiton)	
	Total	S.D.	Total	S.D.	Total	S.D.
Jan	201.7	±1.5	193.1	±2.2	166.5	±2.4
Feb.	158.1	±1.6	147.0	±1.7	126.8	±2.6
March	218.4	±1.6	203.1	±2.2	175.1	±2.9
April	178.1	±2.1	165.6	±2.9	146.8	±1.9
May	23.5	±0.6	22.8	±0.5	20.6	±0.4
June	15.1	±0.3	13.3	±0.4	11.1	±0.2
July	14.5	±0.2	14.3	±0.3	12.5	±0.2
Aug.	12.7	±0.5	12.1	±0.2	10.4	±0.4
Sept.	15.5	±0.3	14.8	±0.5	12.4	±0.5
Oct.	21.5	±0.8	20.2	±1.1	17.1	±0.3
Nov.	10.3	±0.3	9.7	±0.1	8.2	±0.2
Dec.	13.3	±0.5	11.2	±0.6	9.2	±0.3
Yearly Total	883.4	±86.5	827.7	±81.2	717.2	±70.4

Table 9. Monthly litterfall (in grams) in the moist rainforest at the Sapoba Forest Reserve.

	Undisturbed SNR		30-Year-Old TSS (Partially Disturbed)		50-Year-Old Plantation (Triplochiton)	
Month	Total	S.D.	Total	S.D.	Total	S.D.
Jan	91.3	±3.4	83.2	±3.7	78.8	±3.1
Feb.	80.8	±4.0	63.9	±4.3	61.0	±2.5
March	100.8	±5.0	89.5	±5.0	83.0	±2.1
April	83.6	±4.1	71.6	±2.9	67.6	±5.1
May	57.4	±2.7	50.9	±1.3	50.8	±3.8
June	31.8	±1.3	27.0	±1.3	25.0	±1.0
July	34.5	±1.9	30.4	±1.8	29.7	±1.7
Aug.	26.7	±2.1	28.3	±0.7	23.6	±0.6
Sept.	32.5	±2.1	27.9	±0.9	33.3	±1.2
Oct.	53.6	±2.5	47.0	±1.3	46.8	±1.4
Nov.	27.9	±3.1	20.4	±1.1	16.9	±0.4
Dec.	28.6	±1.5	23.7	±0.7	19.0	±0.7
Yearly Total	650.1	±92.6	564.2	±24.6	535.8	±23.5

Table 10. Monthly understory biomass production (in grams) in the moist rainforest stands at the Sapoba Forest Reserve.

Month	Undisturbed SNR (200 Year Old)		30-Year-Old TSS (Partially Disturbed)		50-Year-Old Plantation (*Triplochiton*)		5-Year-Old Vegetation of *Eupatorium*	
	Total	S.D.	Total	S.D.	Total	S.D.	Total	S.D.
Jan.	12.4	±0.5	14.4	±0.6	12.7	±0.4	32.2	±0.6
Feb.	7.3	±0.3	7.7	±0.5	7.4	±0.3	15.5	±0.5
March	20.3	±0.4	23.9	±0.8	22.8	±0.7	53.1	±0.5
April	36.0	±0.6	39.8	±0.8	38.9	±1.8	86.0	±2.1
May	13.2	±0.5	15.2	±0.8	14.5	±1.1	36.1	±0.4
June	9.9	±0.3	10.6	±0.4	10.1	±0.4	25.7	±0.4
July	24.6	±0.7	27.5	±0.4	26.2	±0.7	63.0	±0.9
Aug.	39.3	±0.5	42.3	±1.2	40.2	±1.6	96.3	±0.9
Sept.	54.3	±0.1	59.6	±1.9	45.6	±2.1	140.0	±2.0
Oct.	42.8	±0.5	45.6	±2.1	43.9	±1.1	113.8	±2.0
Nov.	18.8	±0.9	21.2	±0.7	19.3	±1.2	46.9	±0.7
Dec.	23.3	±0.8	26.1	±0.8	23.9	±1.2	60.9	±1.4
Annual Total	302.4	±16.3	333.7	±15.8	265.8	±13.1	769.6	±37.9

that rainfall and litterfall are negatively correlated while rainfall and understory biomass production are positively related. These relationships might be explained by the fact that periods of heavy precipitation in the Nigerian rainforest were marked by active tree meristematic activity and reduced senescence, both of which increase biomass production and reduce litterfall. Thus moisture availability through rainfall and the lack of it during the harmattan periods were the major factors influencing tree litter production patterns in the Nigerian rainforests. Other factors such as light intensity, wind and temperature are also important (Richards 1952).

Net Primary Productivity of Understory Plants

Understory biomass production was greatest in the five-year-old *Eupatorium odoratum* vegetation (769. gm) and lowest in the 50-year-old plantation of *Triplochiton scleroxylon* (265.8 gm) (Table 10). The relatively high value in the *Eupatorium* stand was attributed to abundant sunlight which occurred in the absence of a tree canopy. More biomass (72% of the total) was produced during the rainy months, April through October (Table 10). This again underlined the importance of rainfall in rainforest phenology.

In all stands, biomass production was greatest in September, at the peak of the rainy season. But as dry season approached, biomass production fell slightly and gradually tapered off to its lowest levels in February. The so-called "August break," the brief dry spell in the middle of the rainy season, did not markedly affect the understory biomass production pattern. The lack of clear relationship between rainfall variation and understory biomass production could, in part be due to the fact that the study was done in a moist vegetation zone where the probability of acute water stress was slight.

Understory biomass and litter production patterns were similar in the different forest reserves except that in the middle and the end of the rainy season (June to September), production more or less stabilized (or oscillated) because of abundant rainfall (Figure 7). Litter production also showed a bimodal response to the double dry season.

The Nigerian Rainforest also contains typical understory taxa such as Diospyros, Rinorea and Ouratea (Table 11). Seedlings and sapplings of middle and upper story species such as Strombosia pustulata and Celtis zenkeri are also present.

Effects of Annual Burning on Soil and Species Distribution

With only a few exceptions, all species recorded in the burned plots (Table 12) were fire-resistant while those recorded in the control plots were mostly fire-

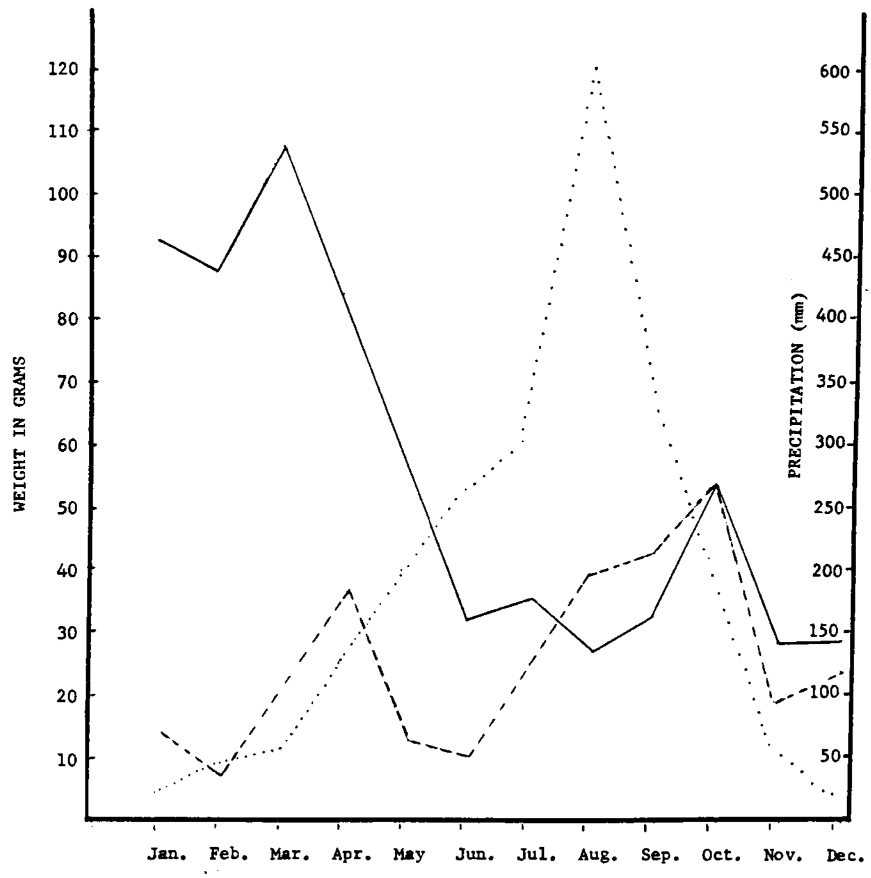


Figure 7. Graph showing the influence of precipitation (dotted line) on litter accumulation (solid line) and understory biomass production (broken line) in the moist rainforest at Sapoba Forest Reserve.

Table 11. Typical understory taxa of the Nigerian rainforests.[a]

Taxa	Taxa
Acacia atacantha[b]	Memecylon membranifolium[e]
Agelaea sp.[b]	Microdesmis zenkeri[e]
Aulacocalyx jasminiflora	Nephrolepis cordifolium[d]
Baphia nitida[e]	Olax viridis
Begonia mannii	Ouratea affinis
Calamus deeratus[d]	Palisota ambigua[d]
Celtis zenkeri[e]	P. barteria[d]
Centotheca lappacea[c]	P. hirsuta[d]
Chasmanthera dependens	Phyllanthus muellerianthus
Commelina capitata[d]	Piper guineensis[b]
Culcasia scandens	Pollia condensata[d]
Cyathula prostrata[b]	Psychotria sciadephora[e]
Desmodium adscendens[d]	Rinorea sp.[e]
Dioscorea sp.[b]	Salacia alata[d]
Diospyros dendo[e]	Scottellia coriacea[e]
D. suaveolens[e]	Smillax kraussiana[b]
Dorstenia sp.[d]	Sphenocentrum jollyanum
Entada sclerata[d]	Strombosia pustulata[e]
Geophila sp.[d]	Strychnos sp.[d]
Hugonia sp.[b]	Thalia sp.
Icacina trichantha[e]	Tetracera sp.[b]
Isachne sp.[d]	Trichilia gilletii[b]
Leptaspis cochleata[c]	Urera cameroonensis
Mariscus umbellatus	Vernonia conferta

[a]Key: b = liana, c = grass, d = herb, e = juvenile tree or shrub.

Table 12. Understory taxa in the fire-treated and control plots in the Olokemeji Forest Reserve.

Taxa	Treatment		
	Early Burn	Late Burn	Control Plot
Ageratum conyoides	x	-	x
Andropogon schirensis	x	x	-
A. tectorum	x	x	-
Aspilia africana	x	x	-
Borreria sp.	x	-	-
Butyrospermum paradoxum	x	x	-
Cassia siame	-	-	x
Crossopteryx febrifuga	x	x	-
Daniellia sp.	x	x	-
Dissotis rotundifolia	-	-	x
Erythroxylum emerginatum	-	-	x
Euphorbia hirta	x	x	x
Ficus capensis	-	x	-
Fimbristylis sp.	x	x	-
Hyparrhenia rufa	x	x	-
Manilkara obovata	x	x	-
Mariscus sp.	x	x	-
Nauclea latifolia	x	x	x
Oldenlandia sp.	x	x	x
Panicum sp.	-	-	x
Pennisetum sp.	x	-	-
Phyllanthus sp.	x	x	x
Pseudocedrela kofschyi	x	x	-
Setaria sp.	-	-	x
Solanum vebascifolium	-	-	x
Spigelia anthelmia	x	x	-
Tacca sp.	x	-	x
Torensis sp.	x	-	x

susceptible (Hopkins 1962, 1965c). There was a virtual absence of grass species in the control plot except around its edges, but the burned plots contained many grass species including Andropogon schirensis, Andropogon tectorum, Hyperrhenia rufa, Tacca leontopetaloides, Setaria sp., Panicum sp.,Daniellia sp., and Monocymbium sp.. There were also a few sedges, Fimbristylis sp. and Mariscus sp.. In the rainy season Hyperrhenia rufa dominated in terms of total abundance but in the dry harmattan months Andropogon tectorum became the most visible. These changes might be explained in terms of moisture relationships.

Monthly biomass production (Table 13) in all plots showed a seasonal trend, increasing to its highest levels during the rainy months and falling during the dry months. But on an annual basis, the late-burned (March) plot produced the greatest biomass, 12,847 gm, compared to 11,687 gm in the early-burned (December) plot and 2,898 gm in the control plot (Table 13). Late-burned and control plots also produced their greatest biomass, 2,098 gm and 564.4 gm, respectively, in October, while the early-burned plot produced its highest values in September (Table 13). These production peaks correspond to periods of maximum rainfall in Nigerian rainforests.

Table 13. Monthly understory biomass production in the fire-treated and control plots at the Olokemeji Forest Reserve.

Month	Early Burned Plot		Late Burned Plot		Protected Control Plot	
	Total	S.D.	Total	S.D.	Total	S.D.
Jan.	186.4	± 2.9	736.2	± 11.6	127.4	± 5.2
Feb.	251.1	± 3.6	800.6	± 8.6	61.5	± 2.3
March	532.2	± 8.4	996.4[B]	± 23.3	170.3	± 5.1
April	1,370.4	±23.0	945.4	± 24.9	352.4	± 3.6
May	1,215.4	±16.7	821.3	± 15.1	111.3	± 3.2
June	1,258.7	±21.6	835.5	± 23.4	99.9	± 4.0
July	1,492.1	±21.6	1,023.3	± 18.6	242.0	± 6.2
Aug.	1,710.4	±17.8	1,429.4	± 20.0	374.6	± 6.7
Sept.	1,776.2	±24.1	2,098.0	± 19.2	564.3	±10.7
Oct.	1,149.2	±14.0	1,566.7	± 19.1	390.1	± 8.7
Nov.	520.4	± 5.6	860.4	± 22.1	224.3	± 8.2
Dec.	224.7[B]	± 8.9	727.8	± 13.2	179.6	± 6.3
Annual Total	11,687.4	±594.4	12,847.7	±416.2	2,898.1	±497.9

B = month of burning

The cause of the comparatively small understory biomass produced in the protected plot is unknown. However, such factors as growth inhibition by forest floor litter, light attenuation, root competition for water and nutrient, and allelopathy may be important. In the same study site Ola-Adams (unpublished) reported an overstory-litter-production trend that is essentially the inverse of understory biomass production. Here, rainfall (soil moisture) was cited as possible cause of the inverse trend.

Results of soil chemical analyses (Table 14) indicated differences between the control plot and the mean value of the burned plots in percentage exchangeable calcium and available phosphorus. The only parameter in which the control plot had higher values than the mean of the burned plots was in nitrogen percentage. There was also a marked increase between the late- and the early-burned plots in the percentages of phosphorus, which increased from 7.20 gm in the late-burned plots to 14.52 gm in the early-burned plots. Exchangeable magnesium also increased from 3.83 gm to 4.90 percent.

Results of mechanical analyses (Table 15) showed no textural differences between burned plots and control. Differences were observed between the early- and late-

Table 14. Soil nutrients content differences between early and late burned and control plots at the Olokemeji Forest Reserve.

Analysis	Early Burned	S.D.	Late Burned	S.D.	Mean of Burned Plots	Control	S.D.
pH	6.09	± 0.57	6.31	± 0.11	6.20	6.15	- -
Organic matter (%)	3.20	± 0.24	1.28	± 0.05	2.24	2.22	- -
Nitrogen (%)	0.10	± 0.33	0.07	± 0.09	0.09	0.10	- -
Available phosphorus (meq/100g)	14.52	± 1.74	7.20	± 0.12	10.86	6.42	± 0.13
Exchangeable calcium (")	4.90	± 0.51	4.03	± 0.10	4.46	1.48	- -
Exchangeable magnesium (")	4.90	± 0.51	3.83	± 2.18	4.46	1.33	± 0.04
Exchangeable potassium (")	0.10	- -	0.12	± 0.02	0.11	0.09	- -

Table 15. Soil texture of early and late burned and control plots (expressed as percentage).

Analyses	Early Burned	Late Burned	Mean of Burned Plots	Unburned Control
Coarse sand	39.16	55.48	47.32	45.73
Fine sand	42.44	29.78	36.11	37.55
Silt	6.33	4.13	5.23	5.07
Clay	12.08	10.61	11.35	10.65
Stones (2-5 mm)	5.36	1.67	3.51	1.80
Hygroscopic moisture	0.99	0.62	0.80	0.87

burned plots. But whether or not these differences were consistent and replicable is not known.

CHAPTER VI

DISCUSSION

Species Composition and Diversity

The species inventory data of the Nigerian rainforests indicates that majority of the taxa were represented by few individuals while few taxa were represented by numerous individuals. This observation agreed with the general trend observed in other rainforests by Smythe (1970) and Janzen (1970, 1971) who explained their observation by factors such as seedling predation, allelopathy, and habitat heterogeneity. Single-species dominance is, therefore, rare in undisturbed rainforest but occur occasionally from natural coppicing and seedling establishment near seed sources (Nicholson 1965, Poore 1967).

Although the influence of soil properties on species distribution was not the aim of this study, it was observed that greater soil heterogeneity in the Nigerian rainforest increased species diversity. This supports an earlier report by Hall (1977) that soils of the Ferrallitic Soil Group support high species diversity in the Nigerian rainforest, and that certain families of plants are soil-specific. The predominance of Myrtaceae and Leguminosae in the study plots could, therefore, be explained in terms of influence of soil factors.

The relatively high species diversity calculated for the Idanre Forest Reserve, despite its relative small number of individuals (low stockings), may be due to its greater equitability (or the distribution of individuals among the species). Lloyd and Ghelardi (1964) have shown that differences in species diversity between plant communities depends upon equitability of individuals of the species among sample plots; plant communities with identical richness could, therefore, have different diversity indices, depending upon their equitability.

The results of this study indicate that, despite its greater number of individuals, the Shasha Forest Reserve had a low species equitability. For example, with 594 individuals and 75 species, the Shasha Forest Reserve had a species diversity of only 1.46, compared to 1.58 of the Okomu Forest Reserve with 416 individuals and 81 species. The Idanre Forest Reserve, on the other hand, with only 424 individuals and 91 species, had a species diversity index of 1.69 because of its higher species equitability. The conclusion drawn from this is that maximum species diversity results when the individuals of the species are evenly distributed.

The cause of differences in species diversity between the Okomu and the Sapoba Forest Reserves, which were in close proximity to one another and exposed to similar climatic influence, was unclear. One reason may be differences in prior land use; while the Okomu Forest Reserve was isolated from human settlement, the Sapoba Forest Reserve was situated very close to many small farm settlements. Given that most rural communities in Nigeria "harvest" the forest for building materials, food and firewood, human pressure was undoubtedly greater on the Sapoba Forest Reserve. The only form of disturbance exerted on the Okomu Forest Reserve derived from herbivores, including elephant, deer, and buffalo.

The extent to which time (since last disturbance) affected floristic composition was unclear. But the low coefficient of variation observed in the species diversity of the plots (Table 5, page 55) suggested that the Forest Reserves of the Nigerian rainforests were at similar stages of succession. The conclusionn from this was that the differences in species diversity between reserves may be due to the influence of rainfall, with intermediate moisture conditions, as observed in the Idanre Forest Reserve, giving rise to maximum species diversity. On the other hand, moisture extremes as observed in the semideciduous and moist rainforest (such as Gambari, Shasha, Okomu and Sapoba) gave rise to relatively low species diversity.

Classification of Nigerian Rainforests

As in other tropical forests, single-species dominance is rare in the Nigerian rainforest. For this reason, it has been difficult to interpret or classify cluster groups by the dominant species as done with temperate zone vegetation. Separation of the cluster groups (Figure 6, page 57), therefore, only showed the similarities that results from local factors such as successional seres, disturbance history and edaphic variations. Emberger et al. (1950a, b) has successfully used soil characteristics to classify rainforest in the Ivory Coast and distinguished two associations, the Heisteria parvifolia association on the Miopliocene sands and the Diospyros-Mapania association on the Precambrian schists. In rainforest classification the emphasis is, therefore, on the larger and more numerous trees. Understory vegetation plays a minor role in rainforest classification because it is mostly buffered from the direct effects of the macroclimate and thus dependent on the microclimatic factors (e.g., litter, soil, pH humidity, light and allelopathic factors) created by the larger trees. From this it could be concluded that rainforest plant communities showed the same essential features as their temperate forest counterpart.

It is not clear whether the Nigerian rainforest could be precisely classified into either the community or continum concepts of vegetation classification. Data from this study (Appendix A), however, showed that while some of the forest reserves had plant species which were characteristic of them, generally species population increased and decreased along a north-south environmental moisture gradient according to individual species moisture requirement and drought tolerance; species composition patterns thus changed only slightly along the environmental gradient because moisture factors (rainfall, humidity and evapotranspiration) varried only slightly along adjacent points on the gradient.

Monthly Litterfall

Because of its role in the maintenance of soil fertility and circulation of mineral elements between the biotic and abiotic phases of forest ecosystems, litter materials exerted an important influence on rain-forest biochemistry. In all undisturbed forest the amount of forest floor litter changes very little with time because of the existence of a near total equilibrium situation between the rate of litter production and the rate of litter decomposition (Olson 1963, Gosz et al. 1972, Reiners and Reiners 1970, Lang 1974, Minderman 1968). It is important to point out here that because all the litter materials in this study were collected on the ground at monthly intervals, the values obtained were net values from which a small amount had already decayed.

The results of this study indicated that significant variations occurred in the total litter material collected from the disturbed and undisturbed rainforest stands. Litter production was greatest in the undisturbed Strict Nature Reserve (SNR), and least in the Triplochiton plantation (Tables 8 and 9, pages 61 and 62). The tropical shelterwood system (TSS) had an intermediate value. This variation in litter production pattern reflect age-related functional attributes of the various forests, in relation to their past land use, successional status and floristic composition.

Litterfall in th semideciduous rainforest is markedly seasonal, with about 68% of the litter accumulating during the 4 months of the dry season. But in the moist evergreen rainforest, litterfall occurs more evenly throughout the year, with about 50% of the litter falling during the dry season (Tables 8 and 9, pages 61 and 62). The greater seasonality of leaf litterfall in the semi-deciduous rainforest can be attributed to its greater number of deciduous tree species, and to the effects of water stress on the trees, especially during the dry months of the harmattan period. Hopkins (1966), working in the Nigerian rainforest reported two litterfall peaks, one during the "major" dry season (between November and March) and the other during the "minor" dry season (or the so-called "August break"). The litterfall trend documented in this study agrees with Hopkins' (1966) observation. However, data published by Adis (1979) on non-seasonal central-Amazonian rainforest indicate a different trend, with more litter falling during the rainy season than during the dry season.

The seasonality of litterfall observed in the Gambari Forest Reserve agreed with trends reported by Hopkins (1965a) for the Olokemeji Forest Reserve, and by Madge (1965) for a secondary forest near Ibadan in the state of Oyo in southwestern Nigeria. Both authors agreed that precipitation is the major factor responsible for the seasonality of leaf litterfall in the Nigerian rainforest.

Observations made during this study on litterfall trend indicate that species composition is the main influence that affects variations in stand litter production; this view corroborates Jensen's (1974) findings. In the semi-deciduous rainforest, for example, typical dry rainforest taxa such as Sterculia rhinopetala and Celtis sp. shed all their leaves during the dry season (in November and December) such that forest stands containing a high proportion of these species produced much litter during this period. On the other hand, forest stands containing many evergreen species showed little variation in their litterfall pattern throughout the year.

The possible effects of wind on litterfall has also been investigated by Madge (1965) but no correlation was found. However, he noted that temperature fluctuations, which are greatest during the dry season, may influence leaf fall in the Nigerian rainforest.

Rodin and Bazilevich (1967) reported that nitrogen return to the soils of tropical rainforest is about twice that reported for temperate forest ecosystems, and that the reason for this was the lower nitrogen and phosphorus content of temperate taxa. Nye (1960) attributed the lower nitrogen content of temperate leaf litter to the fact that most temperate species translocate greater amounts of nitrogen out of their leaves prior to leaf senescence. For this reason nitrogen turnover rate is faster in tropical forest environment compared to temperate forest (Hopkins 1966, Ovington 1962).

Comparison of litter production between semi-deciduous and moist rainforest show that more litter was produced in the semideciduous rainforest. This is the reverse of what Hopkins (1966) reported for the semideciduous rainforest at the Olokemeji Forest Reserve.

But results obtained elsewhere in South America by Franken (1979) and Franken et. al. (1979) were similar to the results of this study. The smaller forest floor litter production observed in this study can be attributed to the rapid decay rates that prevailed in all moist rainforests. This view corroborates Birch's (1958) study in which he reported that alternate wetting and drying of organic matter in moist rainforest environments significantly increase litter decomposition rate. On the other hand, the larger quantities of litter reported for the semi-deciduous rainforest could be attributed to the relatively slower decay rates prevalent in the region. Litter mineralization rates are thus faster in moist rainforest environments than in semideciduous rainforests. Table 16 shows the leaf litter decomposition rates for selected tropical regions based upon results from other workers.

The estimated total litterfall during the study period is 6.4 t/ha. for the moist SNR at the Sapoba Forest Reserve and 8.7 t/ha. for the SNR at the semideciduous rainforest at the Gambari Forest Reserve. These figures fall within the range reported for other tropical regions by Jenny et al. (1949), and Mitchell (cited by Bray and Gorham (1964) who reported values ranging from 8.5 to 12.1 t/ha. and 8.3 to 14.4 t/ha. for a Colombian and a

Table 16. Litter decomposition rates in different rainforest ecosystems.

Forest Type	Location	Mean Years for leaf Decomposition	Source
Moist evergreen rainforest	Kade, Ghana	0.2	Nye (1961)
"	Yangambi, Zaire (Leopoldville)	0.3	Laudelot and Meyer (1954)
Semideciduous rainforest	Ibadan, Nigeria	0.4	Madge (1965)
Perhumid tropical forest	Colombia, South America	0.6	Jenny et al. (1949)
Subtropical forest	Chinchina, Colombis, South America	1.6	"

Malaysian rainforest, respectively (Table 17). In the Nigerian rainforest, Hopkins (1966) reported values ranging from 3.7 to 4.6 t/ha. for a semideciduous rainforest near the city of Ibadan and 7.2 t/ha. for a moist evergreen rainforest near Omo village; these figures were a little below the estimates of this study.

The greater litter mass from the SNR over the younger TSS forest reported in this study are in disagreement with data presented by Laudelot and Meyer (1954) and Hopkins (1966) who reported higher values for young secondary forests than for mature climax forests. Hopkins attributed his high values to the high percentage of deciduous taxa contained in the secondary forest he sampled, arguing that because such forests are undergoing compositional changes, their litter products are more diversified and result in "production overshoot." On the other hand, the secondary forest Laudelot and Meyer sampled was composed mainly of *Musanga cecropioides*, an ecological equivalent of the neotropic *Cecropia peltaria* and does not, therefore, represent a typical secondary forest.

Net Primary Productivity of Understory Plants

Although understory vegetation contains only a small fraction of the total forest biomass, it plays an important role in the functioning of tropical forest

Table 17. Annual litterfall in different rainforest ecosystems.

Forest Type	Location	Litterfall t ha^{-1} yr^{-1}	Source
Lowland rainforest	Colombia	8.5t ha^{-1} yr^{-1}	Jenny et al. (1949)
Young semideciduous rainforest	Zaire	12.3t ha^{-1} yr^{-1}	Laudelot and Meyer (1954)
"	Ghana	10.5 ha^{-1} yr^{-1}	Nye (1961)
Lowland rainforest	Brazil	5.6t ha^{-1} yr^{-1}	Klinge and Rodrigues (1968)
"	Malaysia	5.5-14.8t ha^{-1} yr^{-1}	Bray and Gorham (1964)
"	Nigeria	7.2t ha^{-1} yr^{-1}	Hopkins (1966)
Semi-deciduous rainforest	Nigeria	5.6t ha^{-1} yr^{-1}	Madge (1965)

ecosystems through its influence on mineral cyclying and forest regeneration (Madgwick and Satoo 1975). Understory vegetation serves as the seedling pool from which recruitments into the upper canopies are made following forest disturbance by man, animals (e.g., elephants), and wind.

These results suggest that understory biomass production in the Nigerian rainforest was controlled mainly by rainfall (moisture) and light availability. The relation between biomass production and rainfall, however, is not as definitive as between litterfall and rainfall (Figure 8, page 88). The biomass production curve (Figure 8, page 88) showed production falls in June and October. The fall in June may have been caused by the activities of phytophagous insects (which were very abundant in the study plots at this time of the year) while that in October may be attributed to the sudden shedding of leaves of deciduous species in response to the beginning of harmattan season and greater light penetration to the understory vegetation.

The reason for the low understory biomass values of the *Triplochiton scleroxylon* plantation is unclear. In related studies Webb et al. (1967) (eastern Australia) and Mangenot (1958) (West Africa) have reported failures of understory and seedling development under *Grevillea robusta* and *Scaphopetalum amoenum* due to allelopathy.

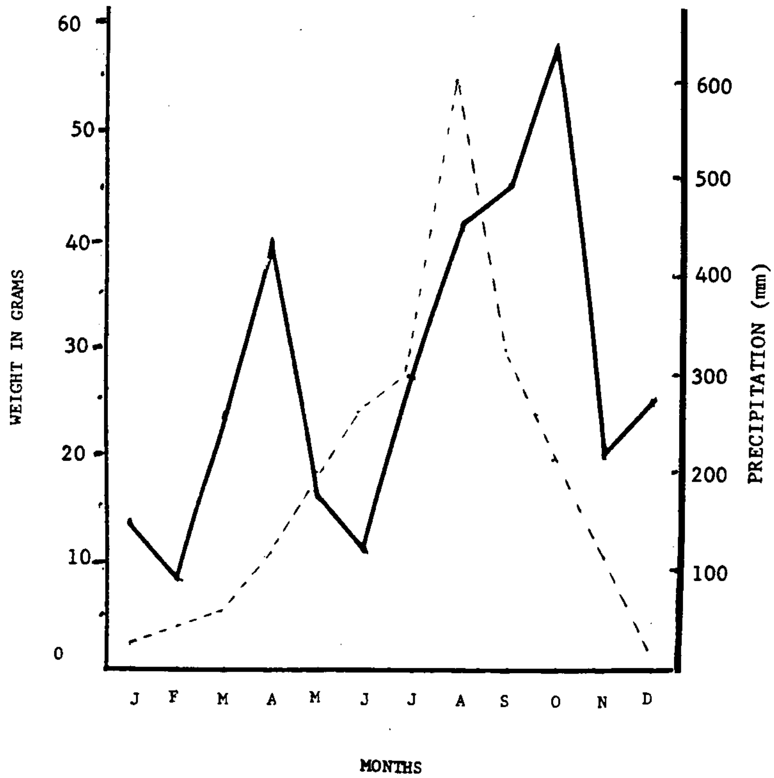


Figure 8. Graphs showing typical understory biomass production and rainfall curves in the moist rainforest at Sapoba Forest Reserve (solid line = biomass production, broken line = rainfall).

The positive relationship between biomass production and moisture availability agreed with results reported by Lieth and Whittaker (1975) who used moisture, temperature, and sunlight intensity to predict plant biomass production. Drozdov (1971), Brazilevich et al. (1971a) and Brazilevich et al. (1971b) have related biomass production to the ratio of radiation intensity and heat needed to evaporate the annual precipitation; in a related study Rosensweig (1968) reported a logarithmic relationship between net primary production of vegetation and actual evapotranspiration.

Connell and Orias (1964) reported a positive correlation between biomass and species diversity to support their productivity hypothesis. Results of this study in which the more productive Strict Nature Reserve at Sapoba had a higher species diversity index than the less productive SNR at the Gambari Forest Reserve (Table 4, page 53) corroborated their argument. Although the higher values from the less diverse *Eupatorium odoratum* stand contradict Connell and Orias' hypothesis, the *Eupatorium* stand sampled in this experiment was only five years old and lacked the complexity of any of the other older vegetation.

Effects of Annual Burning on Soil and Species Distribution

The effects of fire on forest soils are generally beneficial but uncontrolled fire of high intensity could be detrimental to soil nutrient budget and microorganisms. Fire temporaly improves soil fertility by converting standing crop biomass into mineral-rich ash which is available to the plants for growth and reproduction (Ahlgren and Ahlgren 1960). In the rain-forest zones of Nigeria prescribed burning is done annually as an integral part of the pantropic slash-burn agriculture. Such fires are set in the dry season when the understory vegetation is dry. The intensity and effects of such fires depend upon whether the fires were set in December (early burning) or in March (late burning).

The results of this study showed that the time at which the fire was set differentially affected soil chemistry (Table 14, page 72) and floristic composition on the burned sites (Table 12, 68). Early burning was found to be less destructive than late burning, and this was because at the time of early burning the understory vegetation was still succulent or wet from the previous rainy season. On the other hand, fires set in March burn at higher temperatures than those set in December since in March the understory vegetation was completely dessicated from the dry harmattan winds.

Proponents of the beneficial effects of fire argue that controlled burning stimulates seed germination and increase the concentration of nitrogen and phosphorus in soil through increased nitrogen fixation (Ahlgren and Ahlgren 1965, Gosz et al. 1973). They also argued that the detrimental effects of fire are only of short duration and that eventually the long-term benefits outweigh the short-term adverse effects. The results of this study indicated that fire improved soil fertility by increasing the concentrations of soil fertility elements such as magnesium and phosphorus (Table 14, page 72). The slightly lower concentration of phosphorus, magnesium and potassium observed in the unburned plots agreed with the findings of Lewis (1974), Grier (1975) and Clayton (1976) in a South Carolina coniferous forest. However, study done by Oguntala (1980) on the same study site showed higher values of magnesium and phosphorus in the control plots compared to the burned plots. And while this study recorded no significant variation in pH between the plots, Oguntala's (1980) study recorded much lower pH variation between the burned and the control plots.

This study also agrees with related studies done elsewhere in West Africa (Charter and Keay 1960, Hopkins 1965c) in which major chemical changes occurred in forest soils due to timing of burning. Hopkins (1965c), for example, reported that early burning and total protection from fire encouraged tree and shrub growth while late burning destroyed young seedlings and stimulated forest regression into grasslands. This view is supported by Schnell (1971) who argues that the so-called savanna (grassland) vegetation of West, East and Central Africa are not climatic cimaxes but the results of repeated annual fires.

The low organic matter concentration observed in the late burned plot could be due to the high temperature and greater combustion that accompanied late burning. Egunjobi (1974) stated that late burning encourages perennial grass establishment . The results supported this view, since more grass species occurred in the burned plot than in the early burned plot. The complete absence of grass species in the control plot could be due to competition from more shade tolerant understory species, and to growth inhibition by the larger amounts of organic litter materials in the control plot.

Comparison of the results of this study with that reported by Moore (1960) in the same study area indicate that while there have been increases, with time, in all plots in the percentage of stone, fine sand, clay, available phosphorus and exchangeable magnesium, there has also been a decrease in the percentage of coarse sand, silt, nitrogen and potassium. However, such comparison should be done with caution since the observed differences could also be due to differences in sampling procedure and analytical errors.

CHAPTER VII

SUMMARY AND CONCLUSION

This study dealt with the structural and functional changes that occur in disturbed and undisturbed rainforest ecosystems in southern Nigeria. It also evaluated the species diversity of various rainforest types and the effects of early and late burning on rainforest soil chemistry and understory species distribution. The main impetus behind the current destruction of rainforest in Nigeria has been traced to population increases and concommitant demand on forest products such as paper pulp, fuelwood, timber, and forest clearing for agriculture and urban expansion.

The following observations were made after the data were analysed. (1) Most plant species in the Nigerian rainforest are represented by only a few individuals per hectare. (2) Single-species dominance, as noted in temperate deciduous forest, is rare here, while multiple-species dominance, with combinations of *Diospyros*, *Cola*, *Celtis*, *Drypetes* and *Sterculia*, is common. (3) Extremes in moisture conditions reduce plant species diversity, and intermediate moisture conditions give rise to maximum species diversity; the most ideal location for rainforest nature reserve establishment, therefore, are the intermediate precipitation zones near the Idanre Forest Reserve. (4) High species diversity is a function of high species evenness. (5) Moisture availability (during the rainy months) and the lack of it during the harmattan months are the major factors that control the chronologic patterns of litter fall and biomass production. (6) Rainfall exerts a positive influence on biomass production and a negative influence on litter accumulation. (7) Fire, especially early burning, altered plant species distribution, increased plant species diversity, and improved short-term soil fertility by increasing soil phosphorus and exchangeable magnesium. (8) Early burning and complete protection from fire encouraged invasion of grass and, in other areas, forest reversion to grassland; therefore, late burning as executed in Nigeria in March is detrimental to soil fertility, species diversity and forest regeneration.

The major conclusion is that, in order to maintain continued high species diversity and prevent the extinction of important plant species in the Nigerian rainforest, changes will have to be made in present forestry and cultural practices. The present practice of leaving disturbed forest to naturally regenerate itself is inadequate and needs to be supplemented by artificial regeneration practices. Forest clearing for agricultural, industrial and urban development should be confined to secondary forests, while primary forests are set aside as parks and reserves to serve as outdoor scientific laboratories to protect representative plant species from total extinction. Forest reserves should be established mainly in the high species diversity areas where moist and dry rainforests interface.

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APPENDICES

APPENDIX A

ABSOLUTE DENSITY BY TAXON OF PLOTS[a] IN THE NIGERIAN RAINFOREST RESERVES.

Table 18. Absolute density by taxon of plots in the southern Nigerian rainforest reserves.

	Forest Reserve				
Taxa[b]	Gambari	Shasha	Idanre	Sapoba	Okumu
Afzelia bipindensis		2	2		
A. caudata			1	1	
Aidia genipiflora	1	2	8	1	
Albizia sp.			1	1	
Allanblackia floribunda			6	7	
Alstonia boonei			1		5
Amphimas pterocarpoides			3	3	
Angylocalyx zenkeri			4	3	5
Antidesma laciniatum	1				
Aningueria robusta	4	3			
Annonidium mannii			39	44	9
Anthonotha macrophylla		5	1		5
A. sp.					1
Antiaris africana	2	3	1		
A. welwitschii			2	3	
Baphia nitida		6	6	6	2
B. suaveolens					4
Barteria fistulosa					16
B. nigerica					2
Beilschmiedia	1				
Berlinia confusa			6	6	1
Blighia sapida	1		4	4	8
B. unijugata	3			1	1
Brachystegia nigerica	6	8			
Bridelia ferruginea					17
B. micrantha		2			
Buchholzia coriaceae		13			2
Canarium schweinfurthii		1	1	1	
Canthium glabriflorum		1			
Celtis brownii	25	5			
C. mildbraedii	7	10		1	
C. zenkeri	15	6	9	8	2
Chlorophora excelsa				1	
Chrysophullum albidum	5	2			
C. sp.	2				

(Table 18 continued)

Taxa[b]	Forest Reserve Gambari	Shasha	Idanre	Sapoba	Okomu
Cleitopholis patens		1	2	2	9
Cola acuminata		4			7
C. gigantea	10	1			
C. hispida					3
C. millenii	21				
C. nigerica		57			
C. sp.	1	1			
Coelocaryon sp.			4	5	
Coffea sp.			1	1	
Combretodendron africana			2	2	1
C. sp.			2	2	
Conopharyngia penduliflora			12	17	
Cordia millenii	21	3	2		
C. sp.			2		
Croton penduliflorus			9	8	
Cyclodiscus gabunensis			1	1	
Daniellia ogea	1		1	1	
Desplatzia dewevrei	4				
Dichapetalum sp.	1				
Discoglypremna caloneura			1	2	3
Distemonanthus benthamianus				2	1
Diospyros canaliculata		8			
D. crassiflora			3		
D. dendo		91	10	11	22
D. mesipiformis		2			
D. monbuttensis	1	4			1
D. piscatoria		15	3	1	
D. sp.			1	2	
D. suaveolens		39	16	20	10
D. undabunda		8			1
D. xanthochlamys		3			
Dracaena sp.		3			
Drypetes aframensis	2				
D. chevalieri		2			
D. gilgiana	9	24			
D. principum	1				
D. sp.		100			
Elaeis guineensis	13			1	
Enantia chlorantha		1	1	1	2
E. sp.	1				
Entandrophragma angolense		1			3
E. candolei			1	1	

(Table 18 continued)

Taxa[b]	Forest Reserve				
	Gambari	Shasha	Idanre	Sapoba	Okomu
E. cylindricum				1	
E. macrocarpa			1	1	
Eriocoelum macrocarpum	1				
E. sp.		1	1		
Euclinia longiflora		1			
E. sp.			1	1	
Fagara macrophylla		3	1	2	11
Funtumia africana			5	5	
F. elastica	2		2		2
Garcinia cola			1		
G. sp.		1	1	1	1
Glyphaea lateriflora	6				
Gossweilerodendron balsamifrum			17	25	2
Grewia coriaceae					21
Guarea cedrata		7	26	33	16
G. thompsonii			2	4	10
Hannoa klaineana	2		5	6	
Hexalobus crispiflorus					1
Holoptelea grandis	1				
Homalium alnifolium		2	5	5	
Hylodendron gabunense		1	30	37	
Hymenostegia afzelii					42
Hypodaphnis zenkeri			1	1	
Irvingia gabonensis			1	1	1
Klainedoxa gabonensis			2	2	
Kyaya ivorensis			5	3	12
Lannea microcarpa					7
L. sp.			3	3	
Lophira alata					1
Lovoa trichilioides			5	5	10
Lychnodiscus reticulatus	1				
Maba sp.	1				
Macrolobium sp.			9	4	
Maesobotrya staudtii					4
Maesopsis eminii		1			
Mansonia altissima		3			1
Mareya micratha			1	1	
Memecylon sp.		1			
Microdesmis puberula		2	2	2	
Monodora myristica	2		3	3	
M. tenuifolia		6			

(Table 18 continued)

	Forest Reserve				
Taxa[b]	Gambari	Shasha	Idanre	Sapoba	Okomu
M. xemtaiodes			1		
Musanga cecropioides		1			
Myrianthus arboreus					13
Napoleona vogelii	2	2			
Nauclea diderrichii			1	1	
Newbouldia laevis	7				3
Octhocosmus africanus			1	1	
Octolobus argustatus			7		
Oricia suaveolens	7				
Oxyanthus speciosus	1				
Pancovia sp.		1			
Pausinystalia johimbe		1	6	8	13
Pentaclethra macrophylla			8	9	
Phyllanthus discoideus		3	1		
Picralima sp.	6	11	6		
Piptadeniastrum africana	1		1	1	1
Polyalthia suaveolens				1	5
Pterygota macrocarpa	13	4			
Pterocarpus osun			1	1	
Rauvolfia vomitoria		1	1		13
Rinorea dentata		19	14		7
R. poggei			2		
Rothmania coriacea				2	2
R. hispida		4	1		3
R. whitfieldii		2	1	1	
Scottellia coriacea		5	3	3	9
Spathodea campanulata	1	1			
Staudtia stipitata		1	1	3	1
Sterculia oblonga	1	1	1		7
S. rhinopetala	48	7			
Stereospermum sp.		1			
Strombosia grandiflora			19	19	1
S. pustulata	43	31	17	16	39
Tabernaemontana penduliflora		12			
T. pachysiphon		1			
Terminalia superba	1	4	2	1	13
Tetrapleura sp.				1	
Tetrorchidium didymostemon			6	6	
Treculia africana			1	6	
Trichilia prieureana	16		5	6	8
T. heudelotii		4	1	1	2
Triplochiton scleroxylon	2	2			

(Table 18 continued)

Taxa[b]	Forest Reserve Gambari	Shasha	Idanre	Sapoba	Okomu
Unknown sp. (A)			2	1	
Unknown sp. (B)		1			
Unknown sp. (C)	6		3	3	
Unknown sp. (D)		3	1	1	
Unknown sp. (E)	1		1	1	
Uvariopsis dioica			8	9	
Vitex rivularis		2	1	1	1
Voacanga africana		4			
Xylopia quintasii		1		1	3
Total taxa	50	75	91	81	61

[a]Data based on species with gbh ≥ 15 cm from six 25 by 25 meter plots (total 3750 m^2).

[b]Nomenclature according to Hutchinson and Dalziel (1954).

APPENDIX B

RARE TREE TAXA OF NIGERIAN RAINFOREST[a]

Anthonotha boonei
Baphia pubescens
Beilschmiedia sp.
Canthium glabriflorum
Chlorophora excelsa
Dichapetalum sp.
Drypetes principum
Enantia trifolium
Entandrophragma cylindricum
Erythrina sp.
Euclinia longiflora
Garcinia kola
Hexalobus crispiflorus
Lophira alata
Lychnodiscus reticulatus
Maba lancea
Maesopsis eminii
Memecylon sp.
Monodora xemtaiodes
Musanga cercropioides (secondary species, not rare)
Nesogordonia papaverifera
Oxyanthus speciosus
Pancovia sp.
Randia cladantha
Stereospermum sp.
Tetrapleura tetraptera

[a]Species with gbh $\geq$ 15 cm in six 25^2 meter plots.

APPENDIX C

ABSOLUTE DENSITY AND BASAL AREA BY TAXON OF PLOTS IN THE STRICT NATURE RESERVE AT THE OMO FOREST RESERVE.

Taxa	Total No. Present		Area[a]
Albizia sp.	2		3340.3
Barteria sp.	2		194.6
Blighia sapida	1		166.4
Canarium sp.	1		629.6
Celtis zenkeri	17		4784.7
Chorophora excelsa	2		41.8
Cleitopholis patens	4		1135.6
Conopharyngia penduliflora	1		995.6
Cordia sp.	1		703.8
Diospyros sp.	26		4428.7
Discoglypremna caloneura	2		611.4
Enantia chlorantha	2		635.3
Fagara macrophylla	1		83.6
Ficus sp.	1		1792.3
Musanga cercropioides	7		8449.7
Ochthocosmus africanus	1		166.4
Octolobus argustatus	6		898.5
Pausinystalia johimbe	1		1097.9
Picralima sp.	3		365.9
Rinorea dentata	14		1981.1
Scotellia coriacea	2		671.3
Sterculia rhinopetala	14		5874.5
Strombosia pustulata	9		3839.1
Xylopia quintasii	1		192.0
Total	121	Total BA	43,171.9

[a]Basal area of trees ($\geq$15 cm gbh) in five 20 x 20 meter plots.

APPENDIX D

ABSOLUTE DENSITY AND BASAL AREA BY TAXON OF PLOTS IN THE SHELTERWOOD SYSTEM (TSS) AT THE OMO FOREST RESERVE.

TAXA	Total No. Present		Basal Area[a]
Baphia nitida	1		21.6
Brachystegia sp.	1		124.3
Canthium sp.	1		20.4
Celtis zenkeri	10		1002.7
Cleistopholis patens	1		107.8
Cola sp.	1		6829.2
Cordia sp.	1		568.7
Coryanthe sp.	1		20.3
Diopyros sp.	77		1780.3
Discoglypremna caloneura	1		17.9
Enantia chlorantha	2		40.0
Hexalobus crispiflorus	1		580.0
Hylodendron gabunense	3		357.1
Octolobus argustatus	19		359.4
Picralima sp.	17		546.4
Pycnanthus angolensis	1		37.5
Scottellia coriacea	1		55.9
Strombosia pustulata	11		337.5
Tabernaemontana penduliflora	3		61.2
Total	155	Total B.A.	12,984.3

[a]Basal area of trees (≥ 15 cm gbh) in five 20 by 20 meter plots.

APPENDIX E

ABSOLUTE DENSITY AND BASAL AREA BY TAXON OF PLOTS IN THE 30-YEAR-OLD SECONDARY FOREST AT THE OMO FOREST RESERVE.

Taxa	Total No. Present	Basal Area[a]
Afzelia sp.	1	19.1
Bridelia micrantha	2	119.2
Celtis zenkeri	7	155.7
Cleistopholis patens	7	1042.0
Combretodendron africana	1	24.9
Cordia millenii	7	291.3
Diospyrus sp.	2	112.7
Discoglypremna caloneura	2	52.7
Fagara macrophylla	8	213.9
Funtumia africana	2	43.6
Guarea cedrata	1	31.9
Khaya ivorensis	1	50.6
Macaranga barteri	26	688.9
Musanga cecropioides	3	314.9
Myrianthus arboreus	1	23.8
Nauclea diderrichii	1	38.9
Octolobus argustatus	1	19.6
Phyllanthus discoideus	3	54.8
Pycnanthus angolensis	3	16.8
Randia sp.	4	77.0
Ricinodendron heudelotii	2	145.6
Sterculia rhinopetala	4	72.3
Strombosia pustulata	1	31.9
Terminalia superba	1	38.6
Terminalia ivorensis	1	111.4
Trichilia sp.	3	76.0
Total	95	3,868.3

[a]Basal area of trees (≥15 cm gbh) in five 20 by 20 meter plots.

APPENDIX F

COMPUTER PROGRAM USED TO CALCULATE THE SIMILARITY INDEX

```
      DOUBLE PRECISION FN1,FN2
      DIMENSION A(500),B(500)
      WRITE(5,100)
100   FORMAT(1H ,'ENTER FILE NAMES (2A10)')
      READ(5,200)FN1,FN2
200   FORMAT(2A10)
      OPEN(FILE=FN1,UNIT=1,ACCESS='SEQIN')
      OPEN(FILE=FN2,UNIT=21,ACCESS='SEQIN')
      DO 5 I=1,500
      READ(1,210,END=991)A(I)
210   FORMAT(4X,A3)
      ICK=I
5     CONTINUE
991   S1=ICK
      DO 10 J=1,500
      READ(21,210,END=992)B(J)
      JCK=J
10    CONTINUE
992   S2=JCK
C**********************************************************************
      REWIND 1
      REWIND 21
      DO 15 K=1,ICK
      READ(1,210)A(K)
      REWIND 21
      DO 20 KK=1,JCK
      READ(21,210)B(KK)
      IF(A(K).EQ.B(KK))IC=IC+1
20    CONTINUE
15    CONTINUE
      C=IC
      CCS=(2. * C) / (S1 + S2)
      WRITE(5,150)C,S1,S2,CCS
150   FORMAT(1H ,'C=',F4.0,5X,'S1=',F4.0,5X,'S2=',F4.0,5X,'CCS=
     + F10.3)
      STOP
      END
```

APPENDIX G

COMPUTER PROGRAM USED TO CALCULATE THE SHANNON-WIENER DIVERSITY INDEX

```
      DOUBLE PRECISION FN1
      WRITE(5,100)
100   FORMAT(1H ,'ENTER FILE NAME')
      READ(5,200)FN1
200   FORMAT(A10)
      OPEN(FILE=FN1,UNIT=1,ACCESS='SEQIN')
      READ(1,300)TN
300   FORMAT(3X,F4.0)
      RLOGTN=ALOG10(TN)
      P=TN*RLOGTN
17    READ(1,300,END=991)SN
      RLOGSN=ALOG10(SN)
      SUM=SUM + (SN * RLOGSN)
      GO TO 17
991   HPR = (P - SUM) / TN
      WRITE(5,150)HPR
150   FORMAT(1H ,5X,'SPECIES DIVERSITY =',F12.5)
      STOP
      END
```

VITA

Stanley Opunabo Abell, born in Degema, Nigeria, on May 10, 1952, spent his childhood on the island of Abonnema. He attended Nyemoni Elementary School and graduated in 1962. He started grammar school at the Baptist High School, Port Harcourt in 1966 but later transferred to the Baptist Academy, Lagos, where he graduated in 1970. In his senior year at the Baptist Academy he was appointed director of students cafeteria (Food Prefect) and later elected deputy president (Senior Prefect) of the Student Union.

He attended the Federal School of Science, Victoria Island, Lagos, Nigeria, and graduated in June 1973. While at the Federal School of Science he was elected the Speaker of the Student Union.

He worked briefly as a research assistant to the Rivers State Ministry of Agriculture in Nigeria but later earned a scholarship to read animal science and agronomy in the United States. He attended the University of Georgia in Athens where he received a Bachelor of Science in Agriculture in June 1976. In 1979, he received a Master of Science degree in Biology and Agronomy from Middle Tennessee State University, Murfreesboro. In the same year he was admitted into the University of Tennessee, Knoxville, for a Ph.D. in

Ecology. He returned to Nigeria in 1980 to do the field work for his doctoral research.

He is a member of the Smithsonian Institute, American Association for the Advancement of Science, Ecological Society of America, American Forestry Association, Sierra Club and the Gamma Beta Phi and Beta Beta Beta Biological honor societies.