AN OUTLINE OF THE VEGETATION OF NICARAGUA

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CONTENTS

I. INTRODUCTION

Plant ecology in tropical America has entered the phase of regional descriptions. There are numerous studies of the various Caribbean islands, particularly by Beard (1944b), 1946, 1949), Asprey & Robbins (1953), Stehlé (1945) and Loveless (1960). Apart from the work of Fanshaw (1952) for British Guiana, and Stevenson (1942) for British Honduras, ecological studies on the mainland have largely been confined to broad accounts similar to the many papers in *Plants and Plant Sciences in Latin America*, ed. F. Verdoorn (1945), a few regional forest studies, and some detailed descriptions of particular vegetation types. The flora of mainland tropical America is still not well known, and in Nicaragua the only flora (Goyena 1909) was written when the botany of Central America was very poorly known. Other purely botanical publications on Nicaragua are few and include the account by Aston in Verdoorn (1945), which is largely confined to a description of the major crops, and the report by Salter (1956) which lists some timber species. There are, however, important botanical sections in the regional geographical accounts by Denevan (1960) and Radley (1960).

The author arrived in Nicaragua in October 1956 under the United Nations Expanded Technical Assistance Programme and first commenced a series of ecological land surveys for agricultural development. The methods used have been described in Whyte & Taylor (1959) and Christian & Stewart (1952). A comprehensive approach is adopted and the various aspects of the environment, the climate, geology, geomorphology, soils and vegetation, are considered as components of a 'land type'.

The results of these surveys have since been published (Taylor 1959, 1961), but do not include more than brief summaries of the vegetation. From 1959 until his departure in April 1961 the author was largely engaged in aiding the Nicaraguan Government in commencing a zonal development programme on the North Atlantic coast, but during this period short visits were made to other areas of the country. During this work the author has received considerable assistance, most particularly from Sr Juan B. Salas of the Ministry of Economy, Sr Antonio Molina, Curator of the Herbarium, Zamorrano, Honduras, and from numerous staff members of the Nicaraguan Government, particularly from the Instituto de Fomento Nacional, the Ministerio de Economia, the Ministerio de Agricultura and the Servicio Geologico Nacional.

General description

Nicaragua is the largest of the five independent republics of Central America. It straddles the Central American isthmus between latitudes 10° 45′ N and 15° 15′ N, and has an area of approximately 148 000 km². The country was first discovered by Europeans in 1502 when Christopher Columbus landed at Cabo Gracias a Dios. The first conquistador arrived in 1522 and by 1527 the country was under complete Spanish control. Spanish rule continued until 1821 when the kingdom of Guatemala, with Nicaragua as one

FIG. 1. Physiographic regions of Nicaragua and localities cited in the text.

province, was proclaimed. This was succeeded in 1823 by the Central American Federation. Then followed a turbulent period until 1828 when the five member states of the Federation each proclaimed their independence.

No exact figure is available of the population of Nicaragua before Spanish settlement, but Denevan (1960) made an estimate of 600 000 to 700 000, but due to wars and exportation of slaves this was reduced to 30 000 in 1545. No census was taken until 1778 when a population of 106 926 was recorded and the December 1960 estimate was that the population was slightly in excess of 1 500 000.

Physiography and geology

For many purposes Nicaragua is divided into three regions. The Pacific region consists of two well-marked physiographic zones, the Pacific coastal ranges and valleys and the Central Depression of Nicaragua with which is associated a string of volcanoes; also generally included are the lower-lying eastern slopes of the central cordilleras. The Central Highland region is dominated by three ranges: the Cordillera Segoviana, Cordillera Isabelia and Cordillera Dariense, all running in an east–west direction parallel to the prevailing east–west air movement. The Atlantic region consists of numerous low-lying forest-covered ranges mostly of even height and frequently flat topped, which descend gradually to extensive alluvial plains and swamps.

The main geological features of Nicaragua have been described in Sapper (1937) and the Pacific region has been mapped by Zoppis & Giudice (1958). This map shows that the coastal range consists of Cretaceous and Tertiary sediments, mostly sandstones, together with tuffaceous schists, limestones and breccias, but covered in part by very deep deposits of recent volcanic ash.

The Central Depression is likewise mostly covered by young volcanic ash, but on its western boundary this plain consists of Quaternary alluvium derived by erosion from the central cordilleras. The Central Highland region is geologically less well known, but its main features are clear. The Cordillera Segoviana consists of coarse granite, probably of Palaeozoic age. Between this range and the Rio Coco is an area of small steep ridges composed of acidic metamorphics. To the south of the Rio Coco, Tertiary volcanics predominate although there are small areas of Tertiary sediments, mostly conglomerate or sandstone, and of Tertiary and Quaternary alluvium. The Tertiary volcanics are largely andesitic but there are areas of moderate extents covered by acidic lavas, rhyolite, dacite and porphyry, as well as areas of diabasics, basalts and other basic volcanics. The Atlantic region is the poorest known. There is an extensive area on the North Atlantic coast covered by a series of marine sediments mostly of Pleistocene age, as well as large areas covered by Quaternary alluvium, but the greater part of this region is covered by Tertiary volcanics. There are also areas of Tertiary sediments which have never been mapped.

The Pacific region has high temperatures and moderate to high rainfall, but with a very strong seasonal drought. The Atlantic region has a climate typical of the humid tropic lowlands but with a mean annual rainfall ranging from 2000 to 6000 mm. The Central Highland has a sub-tropical climate. In all regions the climate is dominated by moist air masses moved across the country by the north-east trades. The total rainfall and its seasonal distribution in any area is determined largely by the effect of topography on these air masses although there is also moderate precipitation derived from air masses moving in from the Pacific Ocean. This causes widespread light rain towards the end of the wet season, but even close to the Pacific coast its effect is small compared to the short but heavy showers from Atlantic air masses. Numerous rainfall records are available sufficient to produce a rainfall map (Fig. 2), although most records are of short duration. Data from selected stations are shown in Table 1. Throughout this report months with mean rainfalls of less than 100 mm are referred to as dry.

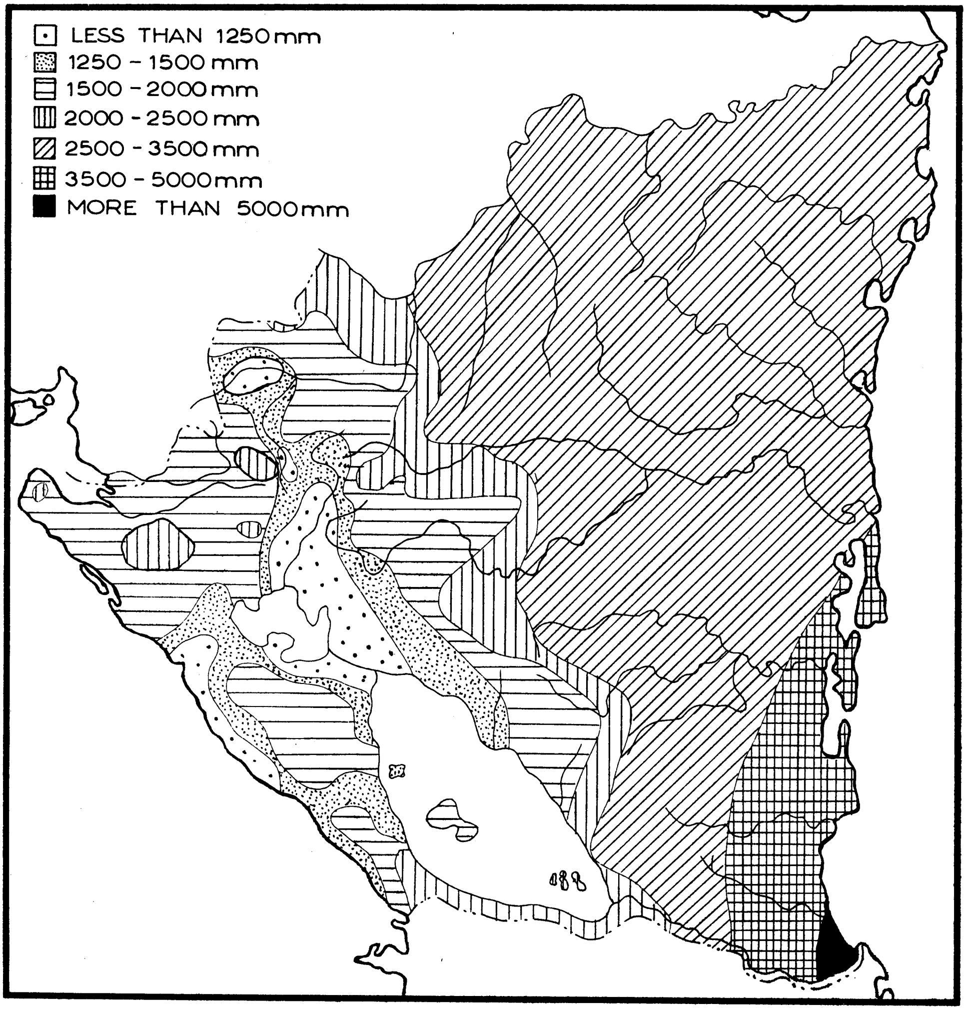

FIG. 2. Mean annual rainfall in Nicaragua.

Table 1. *Selected rainfall records in Nicaragua in millimetres*

	San Juan del Norte	Blue-fields	Puerto Cabezas	San Miguelito	Chichi-galpa	San Marcos	Granada	Managua	Tipitapa
January	466	267	201	60	1	16	6	2	4
February	271	101	85	25	1	5	2	0	1
March	117	69	61	11	3	7	6	2	3
April	170	75	50	19	25	8	21	16	4
May	396	322	204	157	255	208	152	144	108
June	611	479	457	419	343	308	284	226	192
July	823	639	442	424	193	156	165	135	123
August	605	522	391	321	273	178	170	120	112
September	335	319	401	381	414	301	276	230	199
October	545	320	374	359	499	413	289	293	229
November	879	351	343	151	84	74	75	43	59
December	805	372	281	105	7	35	23	11	13
Annual	6003	3846	3290	2432	2098	1709	1469	1222	1047

Soils

In the ecological land surveys considerable attention was paid to the soils and to their distribution. This information has been extended by general reconnaissance in other areas to produce a soil map (Fig. 3). In describing the soils the terminology suggested by Bramao & Dudal (1958) has been adopted and the following groups have been recognized:

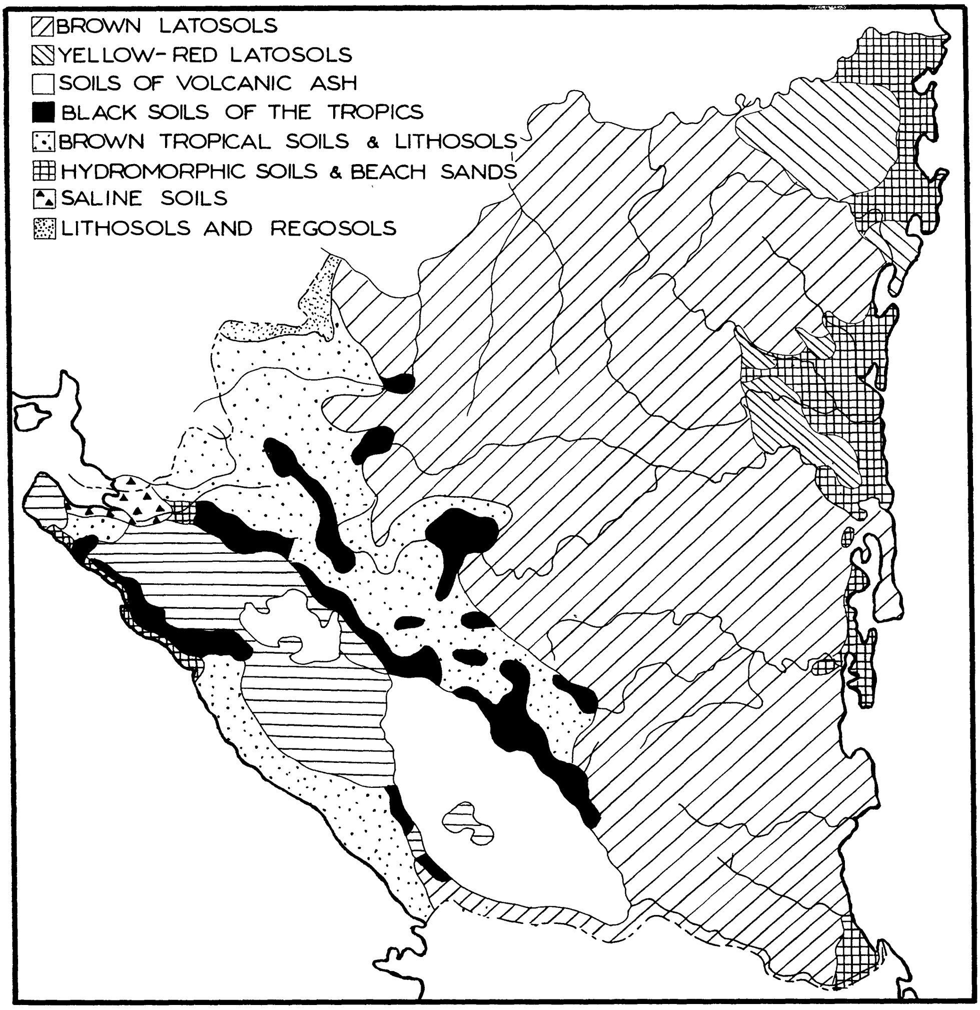

FIG. 3. Distribution of the predominant soil groups in Nicaragua.

Latosols. Brown latosols are predominant in the area corresponding to Rain forest, Seasonal Evergreen Rain forest and Submontane Rain forest. These soils have clay loam or clay topsoils and a dark brown subsoil which may be mottled at depth. They occur not only on the abundant basic volcanic rocks of this area but also on acidic schists. In this same area there are small occurrences of dark red latosols and latosolic red loams formed on the basic rocks as well as yellow latosols formed on acidic volcanics.

A further group of latosolic soils, the yellow-red latosols, are formed on the Pleistocene sediments of the North Atlantic coast. In these soils gravel loams are abundant but clay loams and clays also occur. The profile has a well-marked colour sequence passing from a black or dark brown shallow topsoil, to brown, and then rapidly to a yellow horizon below which there is a deep subsoil which may be red, grey or mottled depending on drainage conditions.

Soils of volcanic ash (*andosols and regosols*). These soils, limited to the Pacific region, are formed from wind-borne volcanic ash largely of silt size. The soil profiles are extremely variable depending on the history of deposition in the site, and although most profiles are dominated by silt loams, brown or grey-brown in colour, many other layers are frequently encountered including layers of clay or clay loam, deposits of volcanic tuffs, breccias, sand, pumice, etc.

Black soils of the tropics (*grumosols*). These soils have a deep heavy clay topsoil, largely montmorillinitic, black in colour, but occasionally dark grey or brown. The topsoil is usually 1 m in depth but in places exceeds 2 m, is very sticky when wet and cracks very deeply on drying. Occasionally lime concretions have been observed in lower levels of this layer. The subsoils are mostly grey, or bluish-grey, gravelly clays. Grumosols are mostly found on older deposits of Quaternary alluvium but also on flatter areas of basic Tertiary volcanics and Tertiary sediments.

Brown tropical soils. These soils, which may be related to Mediterranean brown soils, occur on most well-drained uneroded moderate and gentle slopes in the area of semi-evergreen and deciduous forest. They are characterized by a dark brown or black topsoil with a coarse granular structure and a blocky subsoil mostly brown in colour but sometimes yellow-brown or red-brown.

Hydromorphic soils (*hydrosols*). This group includes a wide variety of soils including humic gley soils, ground-water latosols, muck soils and peat soils. Their main features are controlled by the duration and extent of flooding on each site and by the composition of the ground-water.

Alluvial soils. These immature soils consist of superimposed layers of successive alluvial deposits and are extremely variable depending on the nature of the deposit and the amount of leaching that has subsequently occurred.

Saline soils. Associated with the salt meadow communities on the Gulf of Fonseca there are small areas of solonetz and semi-solonetz soils formed under conditions of occasional flooding by sea water coupled with high evaporation. The topsoils are very shallow grey silts or silty loams which have a surface layer of salt crystals during the dry season. The subsoil consists of a red or orange layer, often consolidated, below which is a permanently waterlogged layer, blue-grey in colour.

Lithosols. These immature soils occur on steep slopes throughout the country particularly in the Central Highlands.

Regosols. Apart from regosols formed from volcanic ash, other regosols occur on volcanic sands, beach sands and silica sands derived from weathered granite.

II. ZONAL FORMATIONS

Five zonal formations occur each within a particular range of climatic conditions. The formations are mapped in Fig. 4 and their environmental relationships and structure are summarized in Table 2. The most important factor controlling the distribution of these communities is the length and severity of the dry season. Annual rainfall is far less important but is responsible for many cases of considerable height differences between stands of the same formation. The effect of temperature, correlated with elevation, is the main factor responsible for differences between the Lower Montane Rain forest and Lowland Rain forest. Elsewhere its main effect is on floristic composition, but at elevations of 1200 m and above in drier areas is responsible for reduction in height of the forests. As no area of greater elevation than 1700 m was examined it is possible that Montane Rain forest does occur in Nicaragua but its absence below 1700 m indicates that the more

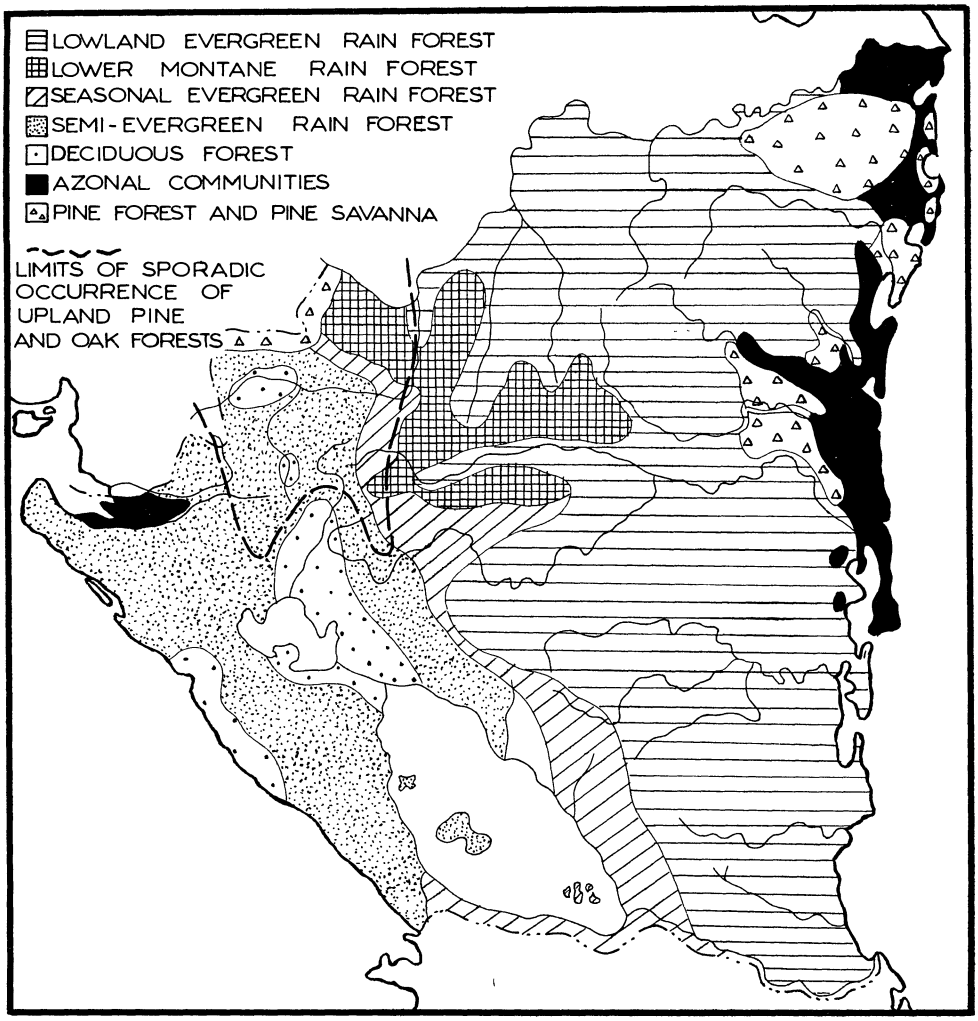

FIG. 4. Distribution of the major vegetation zones in Nicaragua.

continental climate has resulted in a far higher limit of montane zones than in the Caribbean Islands. Whilst vegetation differences due to differing soil conditions within a formation are slight, the predominant soils of the different formation are distinct; but this is due to a simultaneous effect of climate. In general the nomenclature of Beard (1944a) has been followed, but as Beard's descriptions are based largely on formations in the Caribbean Islands there are differences in the environmental limits, and associated minor differences in structure. This is best shown in Table 3 where the deciduous forests are compared. The term 'Seasonal Rain forest' of Beard (1944a) has been retained although it is very close to 'Lowland Evergreen Rain forest' as pointed out by Richards (1957). Seasonal forest is of a somewhat lower height, has only three tree layers and trees of the upper layer tend to have spreading crowns similar to the typical 'umbrella' shapes of the semi-evergreen forests.

Table 2. *Comparison of the environment and structure of zonal formations in Nicaragua*

	Formation				
	Lowland Evergreen Rain forest	Lower Montane Rain forest	Seasonal Evergreen Rain forest	Semi-Evergreen forest	Deciduous forest
Mean annual rainfall (mm)	2000–6000	Above 2000	1800–2600	1250–2500	Below 1250
Dry months	3	3	3–5	5–6	6–7
Elevation	Mostly below 600 m	Mostly above 600 m	Below 1200 m	Below 1600 m	Below 800 m
Predominant soils	Latosols	Latosols	Tropical brown soils latosols + grumosols	Tropical brown soils, grumosols, andosols + regosols	Lithosols, grumosols, regosols and tropical brown soils
Height (m)	35–45	25–40	25–35	25–35	25
Number of tree layers	4	3	3	2	2
Upper tree layer	Essentially evergreen	Evergreen	Small percentage of deciduous species	Up to 75% deciduous	Mostly deciduous
Lower tree layers	Evergreen	Evergreen	Evergreen	Mostly evergreen	Mostly deciduous
Lianas	Abundant	Common	Abundant	Occasional	Rare
Epiphytes	Abundant	Abundant	Abundant	Common	Common

The plant names quoted in this report are based on collections now held at the Herbarium, Zomorano, Honduras, and by the Forest Service, Managua, Nicaragua, and numbers quoted refer to Taylor–Salas collections. The flora of Nicaragua is very rich

Table 3. *Comparison between structure and climatic limits of Deciduous Seasonal forest in Nicaragua and Little Tobago*

	Nicaragua	Little Tobago
Mean annual rainfall (mm)	1250–1000	1300–800
Months with less than 100 mm rainfall	7–6	5
Months with less than 25 mm rainfall	5	2
Forest height (m)	25	20
Maximum diameter of trees (cm)	150	50
Upper tree layer	Mostly facultatively deciduous	Mostly obligately deciduous
Lower tree layer	Mostly facultatively deciduous	Mostly evergreen
Lianas	Rare	Somewhat rare
Epiphytes	Common	Somewhat rare
Buttressed trees	Occasional	Absent
Spiny or thorny trees	Common	Occasional

and species collected probably now exceed 10 000, so the following lists must of necessity be limited and are restricted to the dominant layer. More detailed lists will be available in mimeographed form from the Instituto de Fomento, Managua, in an expanded version of this paper.

Lowland Evergreen Rain forest. Most of the area of this formation is still covered by mature forest. Although mahogany and cedar have been extracted over a very large area this has had little effect on the overall composition of the forest and the extensive uncut areas are so little seen by man that they must be regarded as primary. Near the coast and along all large rivers there is a wide belt of secondary forest and low regrowth and in these areas three groups of secondary successions have been recognized. Firstly, where shifting cultivation is on a lengthy rotation the regrowth is of very mixed composition with *Vochisia hondurensis* Sprag., *Xylopia aromatica* (Lam.) Mart. and *X. frutescens* Aubl. common; secondly, with a shorter fallow *Cecropia peltata* L. and *Ochroma lagopus* Sw. are common in a mixed stand or may form almost pure stands; thirdly, on regularly farmed fertile alluvial soils the regrowth is dominated by the tall (20 m) bamboo *Guadua amplexifolia* Presl.

Striking features of the mature forest are its very mixed floristic composition and the wide range of most species. Many species show certain site preferences but are rarely restricted to such sites, so that the forest composition gives the impression of continuous variation but with considerable emphasis on accidental establishment. In the canopy layer the following species have been recorded:

Most common

Andira inermis (Swartz.) H.B.K.
Carapa nicaraguensis C.DC.
Dialium guianense (Aubl.) Steud.
Dipteryx panamensis (Pitt.) Record.
Luehea seemanii Tr. & Pl.
Terminalia amazonia (Gmel.) Exell.

Common

Astronium graveolens Jacq.
Brosimum terrabanum Pitt.
Calophyllum brasiliense Camb.
Cedrela odorata L.
Ceiba pentandra (L.) Gaertn.
Cordia alliodora (Ruiz & Pavon) Cham.
C. collococca L.
Dalbergia retusa Hemsl.
Ficus glabrata H.B.K.
Guarea guara (Jacq.) P. Wilson
Hieronyma alchorneoides Alemao
Licania hypoleuca Benth.
L. platypus (Hemsl.) Fritsch.
Nectandra glabrescens Benth.
Swietenia macrophylla King
Tabebuia guayacan (Seem.) Hemsl.
Terminalia chiriquensis Pitt.
Virola kotschnyi Warb.

Occasional

Achras calcicola Pitt.
Albizzia caribaea (Urb.) B. & R.
Amanoa potamophila Croiz.
Anacardium excelsum (Bert & Balb.) Skeels.
Belotia panamensis Pitt.
Bravaisia integerrima (Spreng.) Standl.
Brosimum utile (H.B.K.) Oken.
Calocarpum viride Pitt.
C. shankii Standl. & L. Wms.
Campnosperma panamensis Standl.
Cedrela mexicana Roem.
Clusia flava Jacq.
C. rosea Jacq.
Erythrina glauca Willd.
Ficus padifolia H.B.K.
Goethalsia meiantha (D. Sm.) Burret
Guarea aligera Harms.
Hura crepitans L.
Hymenaea courbaril L.
Ilex guianensis (Aubl.) Kuntz.
Lecythis costaricensis Pitt.
Licaria cervanteseii (H.B.K.) Kosterm.
Lonchocarpus spp.
Lysiloma seemanii Britt. & Rose
Manilkara spectabilis (Pitt.) Standl.
Minquartia guianensis Aubl.
Mosquitoxylon jamaicense Krug. & Urban
Nectandra gentlei Lindl.
Ocotea nicaraguensis Miq.
Ormosia schippii Pierce
Pentaclethera macroloba (Willd.) Kuntz.
Platymicium pleiostachyum Benth.
Podocarpus sp. cf. guatemalensis
Poulsenia armata (Miq.) Standl.
Prioria copaifera Griseb.
Pterocarpus officinalis Jacq.
Quercus oleoides Cham. & Schl.
Schizolobium perahybum (Vell.) Blake
Sloania picapica Standl.
Spondias mombin L.
Symphonia globulifera L.f.
Tetragastis stevensonii Standl.
Trichilia tuberculata (Tr. & Pl.) C.DC.
Trophis macrostachya D. Sm.
Virola sebifera Aubl.
Vitex cooperi Standl.
Zanthoxylum microcarpum Griseb.

Despite the large number of species in the canopy layer the flora of other layers is much richer. No one of the thousands of species present is ever frequent but the families Lauraceae, Rubiaceae, Melastomaceae, Apocynaceae, Palmae and Leguminosae are particularly common.

Lower Montane Rain forest. Although much of the eastern extension of this formation is still primary the more western areas have been used for agriculture or grazing with only small stands of mature forest remaining. Species invading abandoned crop land are most commonly *Cecropia peltata* L., *Croton panamensis* M. Arg., *Zexmania frutescens* (Mill.) Blake, *Lippia myriocephala* Schl. & Cham. and *Senecio panamensis* Steetz., but such regeneration is usually very mixed in composition and includes many species of the mature forests, particularly *Inga* spp.

The composition of the mature forest is very mixed but less so than the Lowland Rain forest. Only one species, *Chaetoptelea mexicana*, ever predominates in any stand. The species are distributed independently, with many showing altitudinal preferences resulting in an altitudinal zonation but with no sharp transitions. Of the more common species *Styrax polyanthus*, *Guarea brevianthera* and *Nectandra reticulata* are rare at elevations below 1200 m and *Chaetoptelea mexicana*, *Ficua glabrata*, *Mastichodendron capiri* and *Juglans olanchanum* are rare above this elevation. No attempt will be made here to list the lower-storey trees, which are very numerous, particularly members of the Lauraceae, Leguminoseae and Rubiaceae. Tree species recorded in the canopy layer are as follows:

Common

Astronium graveolens Jacq.
Calocarpum mammosum (L.) Pierre
Calophyllum brasiliense Camb.
Cedrela odorata L.
Chaetoptelea mexicana Liebm.
Ficus glabrata H.B.K.
Guarea brevianthera C.DC.
Ilex carpinterae Standl.
Ilex hondurensis Standl.
Juglans olanchanum Standl. & L. Wms.
Litsea glaucescens H.B.K.
Mastichodendron capiri (A.DC.) Cronquist
Nectandra nervosa Mez. & Pitt.
N. reticulata Meism.
Quercus aaata C. H. Muller
Sapium macrocarpum M. Arg.
Styrax polyanthus Perk.

Occasional

Achras calciocla Pitt.
Beilschmiedia austin-smithii (Standl.) C. K. Allen
Belotia mexicana (D.C.) Schum.
Brosimum costaricanum Liebm. & Dansk.
Calocarpum viride Pitt.
Carpinus caroliniana Walt.
Clusia flava Jacq.
Cordia alliodora (R. & P.) Cham.
C. heterophylla R. & S.
Cupania dentata D.C.
Dalbergia sp.
Dialium guianense (Aubl.) Steud.
Engelhartia nicaraguensis A. Molina
Ficus costaricana (Liemb.) Miq. Ann.
F. hemsleyana Standl.
F. involucrata (Liebm.) Miq.
Heliocarpus appendiculatus Turcz.
H. donnell-smithii Rose
Liquidambar styraciflua L.
Lonchocarpus lucidus Pitt.
Matudaea trivervia Lundl.
Meliosma glabrata (Liebm.) Urb.
Mosquitoxylon jamaicense Krug. & Urb.
Persea americana Mill.
P. schiedeana Nees.
Quercus brenessi Trel.
Spondias mombin L.
Swietenia macrophylla King.
Symphonia globulifera L.f.
Symplocos laconensis Lundel.

Seasonal Evergreen Rain forest. Only in the area lying to the east of Lake Nicaragua is there any extensive occurrence of mature stands of this formation; elsewhere these have been replaced by extensive pasture lands and regrowth from pasture. In floristic composition the formation is transitional between Lowland Evergreen Rain forest and semi-evergreen forest with the major variation in its composition being correlated with altitude. Although none of the common species are restricted to this formation many are of far less frequent occurrence elsewhere, particularly *Bombax barrigon*, *Cassia grandis*, *Hymenaea courbaril*, *Nectandra salicifolia* (H.B.K.) Nees and *Platymiscium pleiostachyum*. The regrowth stands are similarly intermediate in composition between regrowth in rain forest and semi-evergreen forest areas but *Miconia argentea* (Swartz.) DC. and *Citharexylum caudatum* L. are characteristically very common.

Semi-evergreen Seasonal forest. No primary stands of this formation remain, mature secondary forests are not common, and the area originally covered by this formation is now a patchwork of numerous secondary communities. The composition of the different stands mainly depends on the stage and type of succession concerned. Most successions have developed as a result of an invasion of woody species on pasture land. Where grazing has not been heavy the first stage is usually of mixed composition but where both fire and grazing have been long continued thorny species such as *Acacia costaricensis* Schenck *A. farnesiana* (L.) Willd. and *Pithecolobium dulce* (Roxb.) Benth., or at higher elevations *Acacia pennatula* (S. and C.) Benth. are common. On young volcanic areas *Cochlospermum vitifolium* and *Tecoma stans* (L.) H.B.K. are frequent. On abandoned cultivation the successions are quite different, with *Guazuma ulmifolia*, *Luehea candida* common throughout, *Bursera simaruba* and *Lysiloma* spp. common in drier areas, and *Gliricidia sepium* in wetter areas.

As the succession progresses it becomes more mixed in composition with the following species common: *Bursera simaruba*, *Calycophyllum candidissimum* in drier zones, *Cassia grandis* in wetter zones and *Bombacopsis quinatum*, *Bombax barrigon* and *Pithecolobium saman* on low-lying sites. Tree species exceeding 30 m height of common and occasional occurrences in this formation are as follows:

Albizzia caribaea (Urb.) B. & R.
Andira inermis (Swartz.) H.B.K.
Astronium graveolens Jacq.
Bombacopsis quinatum (Jacq.) Dug.
B. fendleri (Seem.) Pitt.
Bombax barrigon (Seem.) Dcne.
Brosimum alicastrum Swartz.
B. costaricanum Liebm.
B. terrabanum Pitt.
Calocarpum mammosum (L.) Pierre
Cedrela odorata L.
C. mexicana Roem.
Ceiba pentandra (L.) Gaertn.
Chlorophora tinctoria (L.) Gaud.
Couroupita nicaraguensis DC.
Cynometra hemitomophylla (D.Sm.) B. & R.
Enterolobium cyclocarpum (Jacq.) Griseb.
Ficus costaricana (Liebm.) Miq. Ann.
F. glabrata H.B.K.
Guarea excelsa H.B.K.
Heliocarpus appendiculatus Turcz.
Hura crepitans L.
Hymenaea courbaril
Ledembergia macrantha Standl.
Licania arborea Seem.
Luehea seemanii Tr. & Pl.
Mastichodendron capiri (A.DC.) Cronquist
Pithecolobium saman (Jacq.) Benth.
Platymiscium pleiostachyum Benth.
Pseudosamanea guachapele (H.B.K.) Harms.
Sciadodendron excelsum Griseb.
Simaruba glauca DC.
Spondias mombin L.
Sterculia apetala (Jacq.) Karst.
Swietenia humilis Zucc.
Tabebuia chrysantha (Jacq.) Nichl.
T. pentaphylla (L.) Hemsl.
Terminalia chiriquensis Pittier

Deciduous Seasonal forest. The area of this formation is also largely replaced by a complex of secondary communities. The predominant species are frequently the same as those of similar successional stages to semi-evergreen forest but apart from a greater degree of deciduousness and lower height there are characteristic differences in the more common associated species. Trees of more than 10 m height occurring in this formation are as follows:

Most common

Bursera simaruba (L.) Sarg.
Caesalpinia coraria (Jacq.) Willd.
Calycophyllum candidissimum (Vahl.) DC.
Guazuma ulmifolia Lam.
Gyrocarpus americanus Jacq.
Haematoxylon brasiletto Karst.
Luehea candida (DC.) Mart.
Lysiloma kellermani B. & R.
L. seemannii B. & R.
Phyllostylon brasiliensis Cap.

Albizzia caribaea (Urb.) B. & R.
Astronium graveolens Jacq.
Bombacopsis quinatum (Jacq.) Dug.
Bursera graveolens (H.B.K.) Tr.
Cedrela mexicana Roem.
Ceiba pentandra (L.) Gaertn.
Chlorophora tinctora (L.) Gaud.
Cochlospermum vitifolium (Willd.) Spreng.
Cordia alliodora (R. & P.) Cham.
C. nitida Vahl.
Enterolobium cyclocarpum (Jacq.) Griseb.
Gliricidia sepium (Jacq.) Steud.
Guaiacum officinale L.

Acacia glomerosa Benth.
Acrocomia vinifera Oerst.
Alvaradoa amorphoides Liebm.
Apoplanesia paniculata Presl.
Andira inermis (Swartz.) H.B.K.
Antrophora williamsii Jtn.
Apeiba aspera Aubl.
Bombax barrigon (Seem.) Dcne.
Brosimum alicastrum Liebm.
B. costaricanum Liebm.
Bursera excelsa (H.B.K.) Engl.
Caesalpinia eriostachys Benth.
Capparis cynophallophora L.
Cassia grandis L.f.
Cecropia peltata L.
Ceiba aesculifolia (H.B.K.) B. & R.
Celtis iguanaea (Jacq.) Sarg.
C. shippii Standl.
Coccoloba caracasana Meissn.
Cordia garascanthus L.
Crataeva tapia L.
Dalbergia hypoleuca Pitt.
Diospyros nicaraguensis Standl.
Erythrina berteroana Urb.
Eugenia nicaraguensis Amsh.
Ficus glaucescens (Liebm.) Miq.
F. involucrata (Liebm.) Miq.

Common

Lonchocarpus phaseolifolius Benth.
L. minimiflorus D. Sm.
Myrospermum frutescens Jacq.
Pisonia aculeata L.
P. micranthocarpa D. Sm.
Pithecolobium saman (Jacq.) Benth.
Plumaria rubra L.
Simaruba glauca DC.
Tabebuia chrysantha (Jacq.) Nickl.
Thouinidium decandrum (Humbl. & Bonpl.) Radlk.
Trichilia trifida L.
Ximenia americana L.

Occasional

Ficus ovalis (Liebm.) Miq.
Guettarda macrosperma D. Sm.
Heliocarpus appendiculatus Tunz.
Hippomane mancinella L.
Hura crepitans L.
Hymenea courbarii
Juliana astringens Sehl.
Licania arborea Seem.
Lonchocarpus latifolius (Willd.) H.B.K.
L. phlebophyllus Standl. & Steyrm.
Luehea seemanii Tr. & Pl.
Mastichodendron capiri (A.DC.) Cronquist
Platymicium pleiostachyum Benth.
Pseudosamanea guachapele (H.B.K.) Harms.
Pterocarpus hayesii Hemsl.
Sapindus saponaria L.
Sapium thelocarpum Schum. & Pitt.
Sapranthus nicaraguensis Seem.
Sciadodendron excelsum Griseb.
Spondias mombin L.
Sterculia apetala (Jacq.) Karst.
Swietenia humilis Zucc.
Tabebuia pentaphylla (L.) Hemsl.
Triplaris americana L.
Vitex gaumeri Greenm.
Zanthoxylum culantrillo H.B.K.

Although many of these trees are restricted to this formation others have a far greater range and nine species also occur in the canopy layer of the Lowland Rain forest. Of these widespread species *Ceiba pentandra* is striking, being common in the wettest zones of rain forest as well as in deciduous forest with as little as 1000 mm of mean annual rainfall.

III. AZONAL FORMATIONS

Riverine and swamp formations

In all zones of the country the combined effects of increased water supply and poor aeration on low-lying sites markedly affects both the structure and floristic composition of the vegetation. In the drier zones swamp communities are best described as a single environmental sequence with the most widespread being a mixed forest community, the *Enterolobium cyclocarpum–Ceiba pentandra* riverine forest. In structure this is a Semi-evergreen Seasonal forest and has only a small percentage of deciduous trees even when it occurs surrounded by Deciduous forest. Most of the species of the surrounding seasonal forests also occur in the riverine forest, but certain species, such as *Enterolobium cyclocarpum*, *Ceiba pentandra*, *Astronium graveolens*, *Sterculia apetala* and *Albizzia caribaea* are particularly common in the upper, and *Inga spuria* in the lower, tree layer.

Many of the tree species of this forest are common in all areas of its occurrence, but other species show distinct climatic preference, for example *Anacardium excelsum* (B. & Balb.) Skeels, *Nectandra globosa* and *Couroupita nicaraguensis* are particularly common in these stands in the Semi-evergreen Rain forest zone but are rare in stands in the Deciduous forest zone. A further group of tall trees typified by *Pseudosamanea guachapele*, *Pithecolobium saman*, *Apoplanesia paniculata*, *Licania arborea* and *Pterocarpus hayesii* while occurring in stands of riverine forest in wetter areas are much more common in the drier climatic zones.

In extensive low-lying areas with poor drainage the *Enterolobium cyclocarpum–Ceiba pentandra* riverine forest is replaced by a tall swamp forest although there is no sharp demarcation between the two communities. This swamp forest is usually over 25 m high and occasionally reaches a height of 40 m. It has a moderately dense, even canopy layer and a rather open lower tree layer at 10–15 m. This forest although including many facultatively deciduous species is largely evergreen with little leaf fall even at the end of the dry season. Although many species of the surrounding seasonal forest may occur, the canopy layer is always largely composed of the following six species: *Anacardium excelsum*, *Couroupita nicaraguensis*, *Luehea seemanii*, *Terminalia chiriquensis*, *Guarea excelsa* and *Pithecolobium saman*. Species of less frequent occurrence include *Enterolobium cyclocarpum*, *Pterocarpus hayesii*, *Brosimum costaricanum* and *Sterculia apetala*, although these are common in the transition zone to riverine forest. The lower tree layer is also of mixed composition with *Coccoloba caracasana* Meissn., *Inga spuria*, *Anona reticulata* L. and *A. glabra* L. being very common. Where the effect of seasonal inundation is most marked the vegetation consists of a woodland, 10–15 m in height, with only one tree layer in which *Bravaisia integerrima* (Spreng.) Standl. is predominant. Many species may occur in association with this community but only *Coccoloba caracasana*, *Anona* spp. and *Cecropia peltata* are in any way common. There is no sharp break between this community and the taller swamp forest, the broad transition zone being occupied by communities intermediate in structure and floristic composition. Although pure *Bravaisia integerrima* swamp woodlands have only been observed in the seasonal forest zone, these mixed transitional communities also occur in the area of Lowland Evergreen Rain forest.

In areas subject to sudden floods, usually with considerable depth of inundation for short periods, a swamp forest occurs with *Erythrina glauca* Willd. predominant. This community is rather rare in the seasonal forest zone and far larger stands are found on the Atlantic coast in the rain forest zone.

In the Evergreen Seasonal Rain forest zone the riverine forests are of very mixed composition with most species of the upland forest occurring but with *Sloanea terniflora* (M. & S.) Standl., *Nectandra globosa*, *Ceiba pentandra*, *Terminalia chiriquensis*, *Licania arborea*, *Homalium eurypetalum* Blake and *Clusia rosea* common in the upper tree layer, and *Trophis racemosa* and *Inga spuria* in the lower layer. In addition, there are several species which are common in these riverine forests but have not been observed in the surrounding Upland Evergreen Seasonal forests; these include *Pithecolobium saman* and *Coccoloba caracasana*.

Numerous communities occur in the rain forest zone and it is considered most convenient to describe these as five environmental sequences, the various stages of which grade into one another as the environment gradually changes. In this description the term 'Swampy Rain forest' is used to cover structural forms which have only three tree layers in contrast to the four tree layers of the normal Lowland Evergreen Rain forest. Swamp forest is used in accordance with the terminology of Beard (1944a), while swamp woodland is used for any low single tree-layered swamp community.

Anacardium–Bravaisia *sequence*. This sequence was seen only on the western boundaries of the rain forest zone growing on alluvium mainly near the headwaters of small streams. The first stage is common and consists of a swampy rain forest 35 m in height with many species of the climax forest present but with a tendency for *Anacardium excelsum* to become dominant. Other common species include *Terminalia chiriquense*, *Ceiba pentandra* and *Carapa nicaraguensis*. With deterioration in aeration this is replaced by a tall swamp forest 25 m in height with both *Bravaisia integerrima* and *Anacardium excelsum* abundant. These two communities are obviously analogous to *Anacardium–Bravaisia* communities in the seasonal forest zone, but due to climatic differences they differ in the associated species and in having a more complex structure.

Calophyllum–Symphonia *sequence*. This sequence was only seen on the North Atlantic coast on lower-lying sections of the Pleiocene sediments. The soils are hydromorphic, ranging from organic loams to peaty loams. In such sites the first stage of the sequence is a tall swampy rain forest of mixed composition, but *Calophyllum brasiliense* is very common; the stage is a swamp forest, 20–25 m in height, with *C. brasiliense* and *Symphonia globulifera* both abundant. In the lower-lying areas *S. globulifera* tends to replace *Calophyllum brasiliense*. Stands of this sequence are frequently found as small 'islands' surrounded by pine savannas, and during particularly dry years fires enter during the dry season even though there is a surface water table for long periods during the wet season. As a result of these fires, trees such as *Xylopia frutescens* and *Vochisia hondurensis* are very common round the edges of the stands. The next stage in the sequence is a palm swamp mostly about 8 m in height dominated by *Acoelorrhaphe wrightii* (Griseb.) Wendl. with occasional tall trees mostly *Pinus caribaea*. This palm swamp is a stage in the degeneration of swamp forest by fire to savanna and there are occasional stands of swamp forest where fire has penetrated which have *Acoelorrhaphe wrightii* abundant in the lower layer. Further effects of fire result in the production of a short herbaceous swamp 50–150 cm in height with *Cyperus polystachus* Rottb. and *Rhynochospora cephalotes* (L.) Wahl. abundant.

Pterocarpus *sequence*. This sequence has only been seen on the southern half of the Atlantic coast where it is very frequent. It only occurs on low-lying alluvium with rapid fluctuations in the level of the water table even during the wet season. It thus covers many small areas fed by smaller streams and responding quickly to changes in rainfall. In contrast the *Carapa–Campnosperma* sequence is associated with large rivers or extensive flood plains. The first stage is a mixed swamp rain forest 35 m in height with *Pterocarpus officinalis* the most frequent species, but often with *Carapa nicaraguensis* and *Dalbergia retusa* very common. This community does not differ greatly from the *Carapa nicaraguensis* swampy rain forest and many stands of intermediate composition can be found. The second stage is a swamp forest, 30 m in height, with *Pterocarpus officinalis* abundant in the upper layer and with a moderately open lower tree layer containing a few palms. The third stage is a dense palm woodland 10–12 m high consisting of only one tree layer and very sparse ground layer. Due to difficulties of entry only one stand of these palm swamps was seen, consisting of *Bactris* sp., but from aerial observation it appears that more palm species are involved. The transition between the last two stages of this sequence is gradual. Instead of having a gradual reduction in height of the upper layer of the swamp forest as occurs in other swamp sequences, the trees of this remain approximately the same height throughout the transition zone, but the canopy becomes more and more open, with the end point being marked by the presence of a solitary tree nearly 30 m in height surrounded by low palms.

In Taylor (1954) a structurally identical sequence of communities was described for very similar environmental conditions in New Guinea, with the end stage being dominated by the sago palm *Metroxylon rumphii*. The two sequences were associated with similar land forms, both occurring in areas with rapidly fluctuating water tables and were so similar in structure that the pattern of the Nicaraguan sequence could not be distinguished by aerial reconnaissance from the New Guinea sequence. Such a structural resemblance in two widely separated regions of the tropics indicates that these structural forms are a definite response of the vegetation to the environment and it is highly probable that similar sequences occur elsewhere in the tropics.

The foregoing communities of the *Pterocarpus* sequence are associated with fluctuating freshwater swamps, but *Pterocarpus officinalis* swamp forest also occurs associated with mangrove communities. In such sites the forest forms a well-defined belt inland from mangrove forest in areas with considerable fluctuation in water level which may be occasionally salty. In such sites *P. officinalis* forests have been associated with a belt of swamp forest dominated by *Prioria copaifera*, but the ecological relationships of the two communities have not been worked out.

Carapa–Campnosperma *sequence*. This sequence is associated with low-lying areas having mineral hydromorphic soils and high water tables for long periods. The tallest stage of the sequence occurs on sites which are well aerated for a moderate period during the drier months and is a mixed swampy rain forest 30 m high with *Carapa nicaraguensis* often abundant but with *Virola kotschnyi* and *Pterocarpus officinalis* very common. In the second stage, a swamp forest, *Campnosperma panamensis* is the most abundant species, but *Carapa nicaraguensis* is common. In both these stages *Pachira aquatica* is common in the lower tree layer and it is probable that in some areas the sequence terminates in a *P. aquatica* swamp-woodland. *Campnosperma* swamp forest also occurs inland from the mangrove forests on the North Atlantic coast where there is a surface water table for a large part of the year, but with poor aeration even at the end of the dry season. A single stand of a low swamp woodland 3–4 m in height dominated by *Anona glabra* was seen in an area flooded by brackish water. This community was very open and the tall sedge *Cladium jamaicensis* Crantz was abundant. This stand was near a village and it is probable that it is a secondary community following on the destruction of a swamp forest, but it could also represent the effects of severe floodings and thus be the last stage of the sequence.

Erythrina–Pachira *sequence*. This sequence covers a very extensive area on the lower reaches of the Rio Coco, but elsewhere is of rare occurrence. On the levee bank near the mouth of the Rio Coco the vegetation is a swamp forest completely dominated by *Erythrina glauca*. On somewhat higher reaches the *Erythrina* community is mixed with elements of the *Carapa* swampy rain forest which itself occurs further upstream. On the levee banks near the mouth of the river the soil is a grey alluvial clay with brown mottlings developing during the dry season. Inland from this bank the soil rapidly develops a surface layer of peat which at 100 m from the river is over 2 m in depth. This soil change is accompanied by an equally rapid change in vegetation, the *Erythrina* swamp forest giving way to a swamp woodland 10 m in height completely dominated by *Pachira aquatica*. This woodland is dense with low-branching trees and abundant thorny lianas. The ground layer is completely absent and the only firm foothold is obtained from the somewhat spreading tree roots. Although extensive areas of herbaceous swamps were seen from aerial photographs to lie well inland from the levee bank, the attempt to visit these communities was abandoned due to the very slow rate of crossing the swamp woodland. From aerial reconnaissance these herbaceous swamps were seen to have a sharp transition with the swamp woodland and were estimated to be at least 2 m in height. In the centre of the area, pools with floating vegetation were observed.

Mangroves

Mangrove communities in tropical America have been described by many authors, particularly for Florida by Davis (1940). The pioneer *Rhizophora* family, mature *Rhizophora* association, *Avicennia* association, and *Conocarpus* association as described by Davis are all present in Nicaragua in similar sites but the *Laguncularia* association is much better developed and forms a well-marked zone behind the *Rhizophora* zone both on the Atlantic and Pacific coasts. Mostly the associations consist of a single species with only occasional occurrences of other mangrove trees and with rather sharp transitions. An exception to this is a few stands of the *Avicennia nitida* and the *Laguncularia racemosa* associations on the South Pacific coast where *Avicennia bicolor* Standl. is an abundant associate species. When present, the lower tree layer is composed of the same species as in the upper layer. The ground layer is likewise composed of seedlings of the mangrove trees but at the higher levels a few patches of sedges may occur, mostly *Cyperus esculentus* L., *C. uniloides* R. Br. and *Eleocharis caribaea* (Rottb.) Blake, or of species typically found as beach pioneers. The typical mangrove fern *Acrosticeum aureum* also occurs but is normally an indicator of secondary conditions. On the Atlantic coast *Avicennia* and *Laguncularia* associations may reach heights of over 25 m but on the Pacific coast these same associations rarely exceed 15 m. Floristic differences between the communities of the two coasts are slight, the major differences being the absence from the areas visited on the Atlantic coast of stands of *Conocarpus* association, although the species does occur.

Salt meadows

The Rios Real and Negro flowing into the Gulf of Fonseca on the Pacific coast have formed a delta which is very low lying and is occasionally flooded by salt water. Apart from the two main rivers the delta is crossed by a whole series of small channels which have such a regular cross-section that they appear to be man made. These channels are lined by narrow bands of mangroves, firstly of *Rhizophora mangle* and beyond this a second narrow band of either *Conocarpus erecta* or *Avicennia nitida*, but the great bulk of the delta area is covered by numerous herbaceous or savanna communities. There are also small areas completely bare of any vegetation. The most extensive community is the *Eragrostis–Crescentia* savanna which has a low continuous ground layer and a scattered layer of small trees 6 m in height. *Eragrostis* sp. (4387) is dominant but *Andropogon brevifolius* Sw. is common as are several species of *Aristida* and *Paspalum*. Associated herbs are not abundant, the most common being *Cuphea carthaginensis* (Jacq.) Macbr., *Waltheria americana* L., *Malachra fasciata*, *Mimosa pudica* L. and *Jussiaea suffruticosa* L. The tree layer is composed of species found in the disclimax Jicaro savanna, the most frequent being *Crescentia alata*, *Pithecolobium dulce* and *Coccoloba floribunda*, but many other species occur. This savanna community covers the greater part of the slightly higher areas of the delta, the soils are solonetz frequently with a sandy topsoil, and during the dry season salt crystals are conspicuous on the soil surface.

The *Fimbristylis–Crescentia* savannas occupy similar sites to the *Eragrostis–Crescentia* savannas, but extend into lower-lying areas and tend to occur on silty solonetz soils. The tree layers of the two communities are identical, but in the *Fimbristylis–Crescentia* savannas grasses are rare in the ground layer, which is dominated by sedges, particularly *Fimbristylis spadicia*, several species of *Cyperus*, and *Eleocharis* sp. (4391). A modification of this community is the *Malachra–Crescentia* savannas which have a similar tree layer, but although *Fimbristylis spadicia* is common the ground layer is dominated by *Malachra fasciata* Jacq., with *Lippia nodiflora* (L.) Hitchc. and *Ruellia nudiflora* (Englm. & Gray) Urban common. As these three savannas may occupy identical sites it is highly probable that the differences between them are due to occasional fires lit to improve the slight grazing value of the area.

On the lowest-lying areas of the solonetz soils on the delta the topsoil is peaty and covered by a pure stand of *Fimbristylis spadicia* without any trees; intermediate sites have a similar herbaceous community but with *Eloecharis* sp. (4391) co-dominant. Surrounding the occasional bare areas where soil salt concentrations are apparently too high for any plant growth, there is a narrow transition zone where the normal salt-meadow savannas are replaced by a herbaceous community consisting solely of low, creeping succulents with *Sesuvium portulacastrum* L. dominant. Two transitional savanna communities occur between the normal salt-meadow savannas and the mangrove communities surrounding the stream channels, with *Avicennia nitida* or *Conocarpus erecta* dominant in the tree layer.

It is apparent that the high salt concentration in the solonetz soils seriously affects the vegetation, and as apart from mangrove no single stand of woodland could be seen on the delta area, it is highly probable that savanna is the true climax; but it is also apparent that fire and grazing have caused considerable changes in the floristic composition. Such salt-meadow communities are not unknown in the tropics. They have been described for the Gulf of Carpentaria, Australia, in Anon. (1954) and somewhat similar although less well-developed communities have been described by Davis (1940) for Florida. However, Richards (1957, p. 305), in his summary of the literature, states that in tropical America salt marshes are not known closer to the equator than Florida. The conditions necessary for the formation of these communities are a considerable excess of evaporation over precipitation, at least for a long period each year, yet with sufficiently large rivers to permit delta formation. These climatic conditions apply in the Gulf of Fonseca but also to most of the Pacific coast of Central America. However, delta formation in the Gulf of Fonseca is particularly favoured, partly because the rivers concerned drain an area of actively eroding volcanoes, and also they discharge their sediments into the relatively sheltered waters of the almost enclosed gulf. It is quite probable that Richard's tentative conclusion does apply in the better botanically explored Caribbean area where rainfall conditions are generally less suitable, but it is still possible that similar communities could occur on the Pacific coast of tropical Mexico.

Beach communities

As communities of tropical beaches have been well described from many areas, only a brief outline of the Nicaraguan communities will be given. The communities exhibit the typical zonation with an open pioneer community, closed herbaceous pioneer zone, a bush zone, shrub zone and finally a woodland which merges with the climax community. Structurally there is little difference between the formation of the two coasts, but there are very considerable floristic differences, particularly in the later stages, as the Atlantic beaches have a far richer flora which is undoubtedly due to the wetter climatic conditions.

A somewhat unusual feature of the Nicaraguan littoral formations is the presence of a pioneer community dominated by *Ipomoea pes-caprae* (L.) Roth on the beaches of the two large freshwater lakes. Lake Nicaragua, with a mean elevation of 25 m and area of 8000 km^2, has a total dissolved solid content of only 0·07%, largely sodium bicarbonate and Lake Managua, with an area of 1000 km^2, has a total dissolved solid content of 0·02%. Narrow sandy beaches occur rarely on Lake Managua but are common on the western shore of Lake Nicaragua. Where not disturbed by human activity these beaches are covered by pioneer communities, with *I. pes-caprae* dominant. *Canavalia rosea* is a common associated species but the other species present are typically those found in near-by wet pastures.

The dominance of *Ipomoea pes-caprae* on these freshwater beaches indicates that it is not an obligate halophyte and therefore its pan-tropic dominance of beach communities is most likely related to its ability to colonize shifting sand rapidly. The presence of this species also raises the question as to its dispersal, for it is unlikely to have been present and remained unchanged in isolation since the lakes were separated from the ocean in the early Tertiary, nor could it have arrived by distribution by water currents since then.

I. pes-caprae also dominates the pioneer zone of both Pacific and Atlantic beaches. It is associated with the sand-binding species *Canavalia maritima* (Aubl.) Thouars., *C. rosea* DC., *Jouvea pilosa* (Presl.) Scribn. and *Sporobolus virginicus* (L.) Kunth, and with numerous herbs, more particularly *Sesuvium portulacastrum* L., *Euphorbia brasiliensis* Lam., *E. buxifolia* Lam., *Eustoma exaltatum* (L.) Griseb., *Fimbristylis spadicea* (L.) Vahl., *F. spathacea* Roth, *Isocarpha oppositifolia* (L.) R. Br. and *Talinum paniculatum* (Jacq.) Gaertn.

On the Pacific beaches the bush zone is poorly developed or often absent and is dominated by *Caesalpinia crista* L. in association with *Batis maritima* L., *Bromelia pinguin* L., *B. wercklei* Mez., *Croton punctatus* Jacq., *Crotalaria retusa* L. and *Opuntia elatior*, most of which have thorns or prickles. In contrast the bush zone on the wide sloping Atlantic beaches is normally over 20 m in width and dominated by *Coccoloba uvifera* (L.) Jacq. and *Chrysobalanus icaco* L., with rare associated species.

The shrub and woodland zones of the two coasts are also completely different. On the Pacific coast the most common species are *Coccoloba floribunda*, *Conocarpus erectus*, *Crataeva tapia* L., *Hippomane mancinella* L. and *Prosopis juliflora* DC., while on the Atlantic beaches *Chysobalanus icaco*, *Coccoloba uvifera*, *Citharexylum caudatum*, *Hibiscus tiliaceus* L. and *Phyllanthus acidus* (L.) Skeels. are most common. In both areas the beach woodlands are of mixed composition but the flora of the Atlantic beaches is far richer, and despite the large lists of species made it was remarkable that no single species could be regarded as being in any way common on both coasts.

IV. DISCLIMAX COMMUNITIES

Upland pine and oak communities

Nicaragua is the southern limit of the genus *Pinus* in North America, and the communities described below are closely related to the important pine forests at lower elevations in

Mexico and Central America. Within Nicaragua 1500 km^2 is covered by upland pine forests including a very large stand on the Cordillera Segoviana and small scattered stands elsewhere. There is a strong correlation between the distribution of these forests and the soil parent material as the pines show very marked preferences for areas of silicious rocks. The underlying rock of the Cordillera Segoviana is a course granite, to the south of this is an area of silicious schists with many pine stands and elsewhere the pines commonly occur on acidic Tertiary volcanics, largely rhyolite. Despite this preference for acidic rocks, pine stands are not the exclusive vegetation on such sites nor are they restricted to such areas. In the granite ranges pines cover almost all the area but scattered small stands of mixed hardwood forest also occur. On other acidic rock types mixed hardwood forests are usually at least as frequent as pine forest. Moreover, pine forest stands, mostly of small extent, have been found growing in many localities on the common andesite and basalt of the Tertiary volcanics, and a single stand has been seen growing on dibasics. Pines occur frequently on Tertiary alluvium derived from acidic rocks but also are found on old alluvium derived from basic volcanics. Soil conditions show a similar variation; the pine forest soils are largely acidic and sandy but small areas of forests occur on all major soil groups of the Central Highlands, with the exception of young alluvial soils derived from basic volcanics. Pine forests are frequent on steep but also occur on gentle slopes and small plains, but no pine forests were seen on poorly drained areas.

The pines show definite limits in regard to elevation with some variation between the three different species concerned. *P. oocarpa* Schiede occurs only at elevations from 600 to 1700 m, *P. pseudostrobus* Lindl. from 1200 to 1700 m and *P. caribaea* Mor., while it occurs at sea level in the pine savanna zone, is only known in the Central Highlands at elevations from 400 to 900 m. It is not believed that these altitudinal limits are due solely to temperature effects, as the species concerned have a far greater altitudinal range in other Central American countries. Rather it is believed that they are also due to correlated rainfall differences and human factors. *P. oocarpa* occurs in a wide range of rainfall conditions and although it is more frequent in the drier areas with rainfalls as low as 1000 mm it also occurs in areas where the rainfall is in excess of 2400 mm but has not been observed in areas with as few as three dry months. *P. caribaea* and *P. pseudostrobus* are not known in Nicaragua from sites having less than 1500 mm mean annual rainfall.

The geographical limits of these upland pine communities are of considerable interest. The eastern limit is fairly sharp and is at present some 50 km inside the zone of settlement in the area. However, Denevan (1960), as a result of a considerable review of colonial documents, concludes that this eastern pine limit corresponds fairly closely with the limit of dense settlement at the time of the Spanish conquest and that the new area of settlement is of very recent origin. The western limit of the pine zone corresponds closely with the altitudinal break associated with the Nicaraguan depression, and the southern limit closely corresponds to the low, but not wide, valley of the Rio Grande de Matagalpa. This barrier is not as great as the distance separating the isolated stands of pine on volcanoes Casita and San Cristobal from the main pine area and is apparently partly due to scarcity of suitable conditions on the southern side of the valley. These mountains are, however, of suitable height and contain areas of acidic rocks although not as commonly as areas further north. The explanation, therefore, seems to lie with a combination of factors, including the time element, the barrier, the low density of acidic rocks and most probably the lower population in the past of the area concerned.

Both Taylor (1959) and Denevan (1960) consider that these pine communities are disclimax. Because of the close correspondence shown by the pine communities for areas of settlement and the fact that for every particular combination of conditions of the physical environment that is occupied by pine forest an almost identical combination can be found, often adjacent, being occupied by a mixed hardwood forest. One community must be secondary, and this is certainly the pine forest, for the hardwood forest has been observed repeatedly to be able to invade pine given fire protection, while pines cannot directly invade hardwood stands. This is partly due to the slower growth of pine but most importantly is due to the intolerance of shade shown by the seedlings of *P. oocarpa* and *P. caribaea* whose responses to shade were closely observed. This conclusion then permits an interpretation of the relationships of the numerous associated oak communities which similarly could not be explained on the basis of any preference for particular combinations of the physical environment (see Fig. 5).

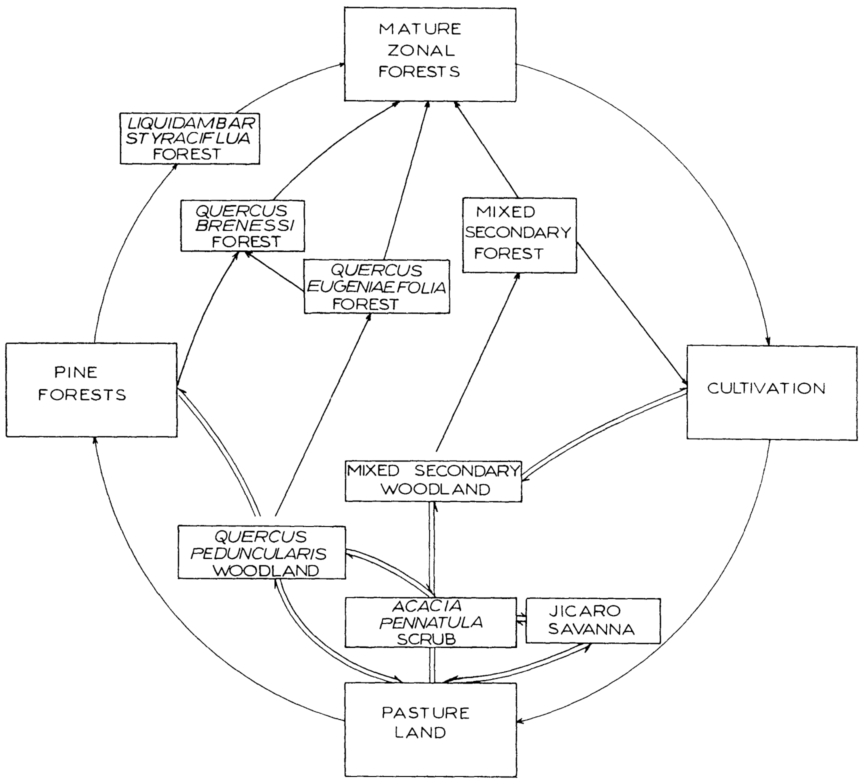

FIG. 5. Interrelationships of vegetation types in the Nicaraguan Central Highlands.

The typical pine forests are tall, 25–30 m, and rather dense, they may have a lower tree or shrub layer but frequently they have only the tall pine layer and a moderately dense ground layer, predominantly of grass. In 90% of the stands *P. oocarpa* is dominant, but at lower elevations *P. caribaea* may be dominant or co-dominant and at higher elevations *P. pseudostrobus* may be co-dominant or rarely locally dominant. In the tallest tree layer associated hardwood species are usually extremely rare but are occasionally common in narrow zones where pine forests adjoin mixed forests. When a lower tree layer occurs this may be dense or open, with usually *Quercus peduncularis* abundant and with *Lysiloma* *multifoliolatum* B. & R. and *Acacia pennatula* common. Numerous other species occur, the more frequent of which are as follows: *Amauria grandiflora* M. Arg., *Arbutus xalapensis* H.B.K., *Byrsonima crassifolia* (L.) DC., *Cecropia peltata*, *Coccoloba browniana* Standl., *Genipa americana* L., *Oreopanax peltatus* Linden, *Miconia argentea*, *Pisidia grandiflora* (D. Sm.) I. M. Jtn., *Trema micrantha* and *Triplaris melaenodendron* (Bertol.) Standl. & Steyrm. The shrub layer is usually absent but develops rapidly with a few years' protection from fire, the most common species are: *Archibaccharis asperifolia* (Benth.) Blake, *Buddleia americana* L., *Calea integrifolia* (DC.) Hemsl, *Cestrum panamense* Standl., *Conostigia xalapensis* (Bonpl.) D. Don., *Eupatorium odoratum* L., *Melanthera hastata* Michx., *Mimosa albida* Humb. & Bonpl., *Myrica cerifera* L., *Psidium guajava* L., *Solanum hispidum* Pers., *Vernonia leiocarpa* DC. and *V. patens* H.B.K. These shrubs are not resistant to regular burning so that the shrub layer only occurs when fires are infrequent but the lower tree layer if well developed can resist fire and is therefore more common. In many cases these lower layers remain when the upper pine layer dies through old age or is removed by logging. Moreover, seedlings of *Quercus peduncularis* appear to be able to withstand somewhat more severe burning cycles than the pine seedlings. For these reasons *Q. peduncularis* communities have often replaced pine forest and now occur as a band around many pine stands or occasionally as small stands isolated from any pine forest. If a heavy burning cycle is continued this community is replaced by a low shrub with *Acacia pennatula* dominant and ultimately if the annual burning of the area is assisted by grazing and more clearing by open pasture. This is the main succession at present operating in the pine area due to increased human activities in the past 50 years. There are, however, examples of the reverse where the burning cycle has been somewhat slackened. Also in a few small areas the burning cycle has apparently been recently abandoned completely and a succession has initiated leading towards a climax mixed forest, but the form this succession takes depends on the stage from which it commences and to lesser extent on the physical environmental conditions.

When this succession to climax forest commences from the pine forest stage, the pines do not regenerate due to the dense shade of the lower layers and on their death they are replaced by a somewhat mixed forest usually with *Quercus brenessi*, *Q. aaata* or *Terminalia chiriquensis* very common. On more eroded soils in the drier areas *Liquidamber styraciflua* is abundant at this stage. These forest communities reach heights in excess of 35 m and are only gradually replaced by a more mixed community with the death of the taller trees. If the fire cycle is interrupted on a site dominated by *Quercus peduncularis*, other oak species usually become frequent, including *Q. eugeniaefolia* Liebm., *Q. matagalpana* Trel., *Q. sapotaefolia* Liebm. and *Q. oleoides* C. & S.; of these *Q. eugeniaefolia* may dominate the stand, particularly if the burning cycle is again resumed. However, if fires are stopped at the *Acacia pennatula* stage, the succession to mixed forest follows the normal course of the zonal successions.

The ground layer in all pine and oak communities is quite variable, but is dense whenever the canopy is fairly open. The most frequent species is the aggressive exotic grass *Hyparrhenia rufa*, but many areas are characterized by native species.

In the drier zones *Andropogon condenstatus* H.B.K. is most abundant in association with a group of numerous other grasses, including *Arundinella deppeana* Nees., *Eragrostis lugens* Nees., *Muhlenbergia implicata* (H.B.K.) Kunth., *Pennisetum bambusiforme* (Foum.) Hemsl., *Pereilema crinitum* Presl., *Sporobolus poiretii* (Roem. & Schlt). Hitchc. and *Trachypogon angustifolius* (H.B.K.) Nees. In wetter areas *Paspalum virgatum* L. is sometimes abundant or more rarely the introduced grass *Panicum purpurescens*. In all areas tussocks of *Andropogon bicornis* L. are conspicuous but never abundant. Numerous herbs are associated with this grass layer, the more conspicuous being *Canavalia villossa* Benth., *Stylosanthes guyanensis* (Aubl.) Swartz. and *Salvia purpurea* Cav.

Pine savannas

An extensive area of pine savannas occurs on the North Atlantic coast. This approximates very closely to the area of Pleistocene sediments with its associated red-yellow latosols and hydromorphic soils, but this same area also includes small stands of rain forest. Some small stands of pine savanna also occur near by on basic Tertiary volcanics with brown latosols. The mean annual rainfall of the pine savanna area ranges from 2600 mm to over 3500 mm, with no part having more than three dry months. Radley (1960) states that the dry season along the Rio Coco might be more prolonged, but he did not have access to the rainfall records of Bilwaskama. The area is sparsely settled but fires in the dry season have been so extensive that almost the whole area is burnt annually, and stands that escape burning for more than 3 years are extremely rare.

The pine savanna has a dense ground layer from 30 to 80 cm in height and a tree layer, mostly 25 m in height, which is usually very open but may be moderately dense. Occasionally an open lower tree layer or bush layer is present. The tall tree layer consists of a single species *Pinus caribaea*. The lower tree layer, when it occurs, consists largely of *Byrsonima crassifolia* (L.) DC. and *Curatella americana* L., more rarely of *Clethra hondurensis* Britt. or *Quercus oleoides* Cham. & Schl. The scattered bushes are commonly *Miconia albicans* (Sw.) Tr., *Henriettella seemanii* Naud., *Psidium oerstedianum* (Berg.) Ndzu., *P. guineense* Swartz., *P. rotundifolium* Standl. and *Calliandra houstoniana* (Mill) Standl. The ground layer is very variable, depending both on site conditions and the frequency of burning, with more frequent burning grasses are replaced by sedges. The more abundant species are *Rhynchospora mexicana* Steud., *Thrasya campylostachya* (Hack.) Chase, *Axonopus blakei* Hitchc. and *Paspalum humboldtianum* Fluegge.

Associated with the savannas are various transitional communities. Where fire is invading rain forest the ground layer may exceed 3 m in height, with *Tripsacum fasiculatum* Trin. often abundant. There is also an area of roughly 5000 ha near Miguelbegan where pines, 35 m in height, are growing with an understorey, at 25 m, composed of rain forest species without young pines and apparently representing an invasion of the savanna by rain forest due to accidential cessation of burning in the past. A small area at Bilwaskama has been protected from fire for the last 15 years and the savanna has been replaced by a dense pine stand, over 15 m height, below which has developed a dense layer of small broad-leaf trees which has prevented germination of further pine seedlings. Many intermediate transitional communities also occur.

The author believes that the pine savannas are a fire-caused disclimax and that the climax vegetation is a tall rain forest, or a swamp forest on the lower-lying areas. The reasons for this are that the climate is well suited for rain forest, as indicated by a quick glance at rainfall figures and by the presence of luxuriant rain forest in strips throughout the savanna area; and that the soil, although poor, can well support rain forest. This last statement is disputed by Radley (1960) who maintains that rain forest never occurs on the typical savanna soils despite reference to such occurrences in Taylor (1959) at Miguelbegan and for similar conditions in Honduras by Arnold (1953); other occurrences have since been noted, the largest lying midway between Slima Sia and Bilwaskama.

This conclusion is further supported by the presence of transitional communities which can only be interpreted as stages of a succession from savanna to rain forest following cessation of burning and the observable inability of *Pinus caribaea* to germinate in the shade of a layer of hardwood trees.

Any conclusion on the time and method of formation of these savannas must be largely conjectural. Probably the first savannas were formed soon after the arrival of the first agricultural people in the region and in the course of a few hundred years reached roughly their present limits. Probably the savanna commenced as garden clearings and extended due to lateral spread as grass fires extended into the rain forest. Such a method of spread has been often suggested for tropical savannas and just as frequently denied, as for example by Taylor (1954) for New Guinea where the lateral spread of fires was prevented by a poorly burning belt of hydrophilous grass and herbs surrounding the grasslands. Such a belt does not occur on the Nicaraguan savannas and on the contrary, fires were directly observed to enter considerable distances into the forest during 1958, when the dry season was particularly severe, and for shorter distances in subsequent years.

On the basis of these conclusions the Nicaraguan Government commenced in January 1959 a fire control programme to convert 300 000 ha of pine savanna to dense pine forest. By April 1961 the protected area was covered by an average of over 4000 pine seedlings per ha and gave every evidence that it would follow the course of the succession outlined.

Jicaro and roble savannas

Savannas characterized by the jicaro tree *Crescentia alata* H.B.K. are of common occurrence in the zone of Semi-evergreen and Deciduous Seasonal forest. They cover extensive areas on large plains but also occur on quite steep slopes. The typical soils are grumosols but the same savannas occur fairly commonly on tropical brown soils, lithosols and both young and old alluvial soils, as well as occasionally on other soils. They have not been seen in areas with 4 dry months or less but are common in zones with 5–7 dry months and mean annual rainfalls ranging from 1000 to 2000 mm. The ground layer is dense and mostly belongs to the *Aristida–Bouteloua* pasture group, but there are moderate areas of other pasture types. The tree layer varies greatly but in the characteristic savanna is very open, 6–8 m in height, with *Crescentia alata* abundant. However, more mixed savannas are more common, with thorny trees being frequent. Most species of the surrounding seasonal forest occur but *Acacia costaricensis*, *A. farnesiana*, *Guazuma ulmifolia*, *Haematoxylon brasiletto*, *Pithecolobium dulce* are very frequent, and in a few stands *Curatella americana* and *Byrsonima crassifolia* are abundant.

These savannas are mostly burnt every year. As a result of the differing effects of grazing and burning great variations can be seen in the communities and all stages both of succession and regression from the typical savanna to climax forests can be readily seen. Such savannas are common in Central America and southern Mexico and there is little doubt that at least all the Nicaraguan stands are disclimax. As a result of the detailed land surveys carried out it was found that there was not a single combination of physical environmental conditions occupied by savanna that could not also be found to be occupied by a closed forest community. In view of the heavy burning practised, there can be no doubt that this is the factor responsible for the tall forests being replaced by savanna. In many regions of the world grumosols carry savanna vegetation and the alternating waterlogging and desiccation of these soils could well be thought to be responsible for the low savanna growth, but even though mostly the Nicaraguan grumosols carried savanna, numerous but small stands of forest could also be found.

In the Semi-evergreen Rain forest area near Lake Nicaragua there is a related group of savannas characterized by the roble tree, *Tabebuia pentaphylla*. This area differed from the environment of the jicaro savannas in having only a 4 month dry season and mean annual rainfalls of 2000–2500 mm. The trees of this savanna are almost entirely *T. pentaphylla*, usually well below 6 m in height even though the same species exceeds 30 m elsewhere. These savannas are also considered disclimax for the same reasons as the jicaro savannas.

Pastures

Introduced pastures are common throughout the more densely settled regions. The main species are *Hyparrhenia rufa* (Nees.) Stapf in all well-drained areas with more than 5 months' dry season, and *Panicum maximum* Jacq. and *P. purpurascens* Radl. in poorly drained or high-rainfall areas. Several distinct native pasture groups also occur in different zones of the country. On young volcanic areas the native pastures have been united into the *Panicum–Trachypogon* pasture group with many different pasture types largely depending on the effect of cultivation, burning and grazing. The most complex is a mixed sward with as many as twenty grasses common in a few hectares, with the following species being most prominent: *Trachypogon angustifolius* (H.B.K.) Nees., *Pennisetum setosum* (Sw.) L. Rich. and *Paspalum humboldtianum* Fluegge. Less complex pasture types in this group are dominated by *Eragrostis ciliaris* (L.) Link, *Panicum ghiesbreghtii* Fourn., *P. fasiculatum* Sw., *Leptochloa filiformis* (Lam.) Bean, or by the introduced species *Cynodon dactylon* (L.) Pers.

Elsewhere in the area of seasonal forests the pastures on well-drained sites belong to the *Aristida–Bouteloua* group which has been subdivided into five pasture types. Each type is of very mixed composition, and includes a large number of herbs, but usually one or two of the following species are dominant, *Aristida ternipes* Cav., *A. laxa* Cav., *Bouteloua alamosana* Vasey, *B. disticha* (H.B.K.) Benth., *Fimbristylis annua* (All.) R. & S., or *Paspalum* sp. (4090). On low-lying sites the characteristic dominants are *Oryza latifolia* Desv., *Fimbristylis spadicea* (L.) Vahl., *Eleocharis geniculata* (L.) R. Br. and *Panicum aquaticum*. Associated with these pastures are many of the species of better-drained pastures, but also a lengthy list of characteristic species, including many sedges.

In areas with less than 4 dry months there are several other pasture groups. The most important species is a tall (2 m) tussock-forming grass *Paspalum virgatum* L. which sometimes forms almost pure stands.

V. SUCCESSIONAL COMMUNITIES

Volcanic successions

Successions on volcanic sands: deep surface deposits of volcanic sand are today only important around Vulcan Cosiguena and Vulcan Cerro Negro. In 1835 Vulcan Cosiguena had a violent Pelean-type eruption with a subsequent lahar flow, while Cerro Negro has had a series of less violent eruptions during the last 30 years.

Around Vulcan Cosiguena the vegetation now includes open pasture land, bushland scrub and low woodland, with some forest communities on low-lying sites, and there are fairly extensive areas of derived savanna. It is apparent that scrub, dominated by *Lippia cardiostegia* Benth., 3 m in height, would cover most of the coarse sand deposits if fire and grazing were prevented, but much of this area is now covered by a low bushland, less than 1 m in height, with *Hyptis suaveolens* (L.) Poitt. and *Baltimora recta* L. dominant and with *Sida acuta* Berm., *S. spinosa* L., *Waltheria americana* and *Lantana camara* common. In places this bushland is replaced by a mixed pasture sward with *Eragrostis* *ciliaris*, *Oplismenus burmanii* (Retz.) Beauv. and *Andropogon brevifolius* the most common species.

In small areas where there has been some accumulation of finer material a low woodland occurs, 5–8 m in height with the most common trees being *Karwinskia calderonii* Standl., *Stemmadenia obovata* (Hook. & Arn.) Schum., *Pithecolobium dulce*, *Acacia farnesiana*, *Pisonia macranthocarpa* D. Sm., *Tecoma stans* and *Achatocarpus nigricans* Tr. & Pl.; but more usually this is replaced by a derived savanna with *Coccoloba floribunda* and *Pithecolobium dulce* abundant in the tree layer. Forests occur in areas where there has been a considerable accumulation of fine material washed from higher slopes, coupled with a supply of sub-surface water. Mostly these forests are 15–20 m in height and of mixed composition with *Lysiloma seemannii*, *L. kellermanii*, *Bursera simaruba*, *Gyrocarpus americanus*, *Cecropia peltata*, *Sapium thelocarpum*, *Bombacopsis quinatum* and *Caesalpinia eriostachys* common. In areas with short seasonal flooding the forests are taller with *Guarea excelsa* and *Enterolobium cyclocarpum* abundant in the upper layer.

Around Cerro Negro there has been little accumulation of fine material and areas of deep sand are still bare of vegetation, but where the sand deposits are somewhat shallow there are a few small areas of scrub dominated by *Lippia cardiostigia*. Mostly the change from bare areas to woodland is rapid, apparently coinciding with the point where the tree roots can tap water held by the old soils buried beneath the sand deposits. These woodlands are quite similar in composition to those around Vulcan Cosiguena, the most common trees being *Bursera simaruba*, *Lysiloma kellermanii*, *Tecoma stans*, *Byrsonima crassifolia*, *Stemmadenia obovata*, *Pisonia macranthocarpa* and *Cochlosperum vitifolium*.

Despite the effects of burning at Cosiguena, it is apparent that the type of vegetation is directly dependent on the water-holding capacity of the soil. This in turn is correlated closely with the amount of finer materials in the soil, for there is negligible accumulation of organic matter.

Accordingly the development of the plant succession depends on external factors, in particular on the rate of deposition of fine volcanic ash. Cosiguena is isolated from the main string of volcanoes and does not receive very large quantities of airborne ash so that despite a lapse of 125 years the communities are very similar to those around Cerro Negro, which although younger are close to active volcanoes. Even though this process results in a succession of communities which eventually will proceed from bare areas to a climax mixed forest this succession does not fit the classical concept of plant successions where each community changes the environment and is then replaced by a more advanced stage. The changes in the environment are determined largely by an external factor, *i.e.* the supply of volcanic dust, and while the community present reflects the actual environmental conditions it does not in itself change the environment and so is not responsible for the progress of the succession.

Successions of lava flows. Many of the volcanoes have emitted lava flows mostly predating Spanish settlement, but the most recent, a large flow around Vulcan Masaya, is reported by Zoppis (1957) to have been emitted in March 1772. This lava flow covers all low-lying land within 3 km of the crater and a tongue of lava 2 km in width extends 14 km in the direction of Lake Managua. Moderate areas are still almost bare of vegetation and the remainder of the flow is covered by a sequence of communities correlated with soil conditions with the most advanced stage being a 20 m high seasonal forest. The lava is extremely scoriaceous and has a most irregular surface so that any rain falling on the almost bare area drains away extremely rapidly. On the almost bare areas the vegetation consists of rare lichens on the crumbly lava blocks; scattered shrubs in crevices; and small herbaceous societies wherever a shallow layer of soil has accumulated. The shrubs are from 1 to 2 m in height but are species which normally reach tree size, most commonly *Plumeria acutifolia*, less frequently *Ficus ovalis* and *Byrsonima crassifolia*. The herbaceous societies are mostly dominated by *Commelina diffusa* Burm. f. but occasionally *Andropogon condensatus*, *Anthephora hermaphrodita* (L.) Kuntz., *Cyperus rotundus*, *Digitaria sanguinalis* (L.) Scop. are dominant. These herbaceous communities are very temporary and in time the supporting lava crumbles and the soil material is washed down into the crevices. The small shrubs apparently have germinated in such sites but their root systems have penetrated deep into the lava flow.

In zones where the process of filling up the crevices is nearly complete, the vegetation consists of a single continuous tree layer 6–10 m in height and a dense layer of herbs and bushes wherever there is soil on the surface. The tree layer is mixed in composition, with *Plumeria acutifolia* still the most abundant species and with *Ficus ovalis* and *Byrsonima crassifolia*, *Bursera simaruba*, *B. graveolens*, *Cochlospermum vitifolium* and *Simaruba glauca* common. In the bush layer the leaf succulents *Agave americana* L., *Bromelia pinguin* and *B. wercklei* are very common. The herbaceous layer is dominated by the grasses *Hyparrhenia rufa* and *Andropogon condensatus*. The soil at this stage contains a moderate percentage of sand and gravel derived from the lava but the greater part is of silty texture derived from wind-borne volcanic ash. At later stages under tall forest communities, similar to the climax forests, there is little surface lava and the surface soil is almost entirely derived from ash.

This sequence of communities is correlated with differences in the depth of the lava field and accordingly with the time necessary for sufficient soil to accumulate to fill the crevices mostly by deposition of wind-borne dust. Thus although the various stages observed must closely follow the stages that have occurred in any one site, the succession is in fact a series of fairly stable communities that reflect the environment in which they grow, and although this environment changes, these changes are mainly due to outside sources. It is rather interesting that the almost bare areas have altered so little in 189 years.

The area concerned has an annual rainfall of approximately 1300 mm, high temperatures all the year round, and despite a 6 months' severe dry season should be considered as quite favourable for rapid development of plant successions. That this does not happen is due to the nature of the material concerned, which is so porous and well drained that it does not permit the accumulation of organic matter or soil material on its surface.

With the exception of a small bare area on a flow of Vulcan Telica all other lava flows have now at least a 15 cm cover of deposited volcanic ash and support forest similar to the normal zonal communities.

Sulphur-fume communities. Small fumaroles devoid of sulphur fumes occur on many volcanoes and these are surrounded by a narrow band of low herbs often with *Desmodium triflorum* (L.) DC. dominant. However, the cone Santiago, part of Vulcan Masaya emitted continuously an enormous cloud of gas from 1946 until March 1960, which consisted principally of water vapour but also contained a small quantity of sulphur dioxide. The effect of this gas in the immediate vicinity of the crater was slight as most of the cloud ascended rapidly. However, the winds constantly blew the gas cloud in one direction, and at 15 km distance it passed over a high ridge (950 m) of young volcanic soils previously cultivated for coffee. In a period of a few years coffee production stopped, the coffee trees and then the coffee shade trees died. In 1957 the treeless area extended as a band on the higher points of the ridge for 6 km, in places exceeded 2 km in width. Almost all the affected area was covered by a low bushy growth 1–2 m in height, with the bush height being constant in any one site giving the effect of wind-shearing. The dominant species was *Melanthera hastata* Michx. but *Lantana camara*, *Lippia cardiostigia*, *Verbesina sublobata* Benth. and *Weddelia acapulcensis* H.B.K. were common; however, the striking feature of the whole area was its relative uniformity and paucity of species.

Around the edges of the typical bush community and in wind-protected gullies there was a short transition zone in which a few trees survived, most commonly *Ficus involuta* (Liebm.) Miq. Beyond this was a narrow zone of the typical shade trees of coffee plantations and beyond this again coffee plantations giving almost normal yields. The rapid transition from affected areas was typical of the zone and corresponded with a very constant wind direction. Only an arc extending from due west of the volcano to S. 65° W. was affected and only on very rare occasions did the fumes reach outside this area. In March 1960 the fumes suddenly stopped but when the area was revisited in March 1961, the only change was a slight increase in the general height of the bush communities.

Hydroseres

Hydroseres occur in all regions of the country but the actual course of the succession in any particular site is influenced primarily by the nature of the site including whether the water is moving or not, the nature of the substrata, etc. Zonal climate is important in early stages through its effect on site conditions, and in later stages by its direct effect.

Completely submerged vegetation is only important in areas where the water is deep and quiet. Common species are *Chara vulgaris* L. and *Hydrocharis morsus-ranae* L. Small societies submerged for long periods occur in smaller rivers; these include many hydrophilous grasses and sedges as well as *Aster spinosus* Benth. and *Najas guadalupensis* (Spreng.) Morong.

Free-floating communities are common in pools, lakes and river backwaters, common dominants include *Lemna minima* Phil., *L. perpusilla*, *Marsilia mexicana*, *Pistia stratiotes* L., *Hymenachne amplexicaulis* (Rudge) Nees., *Eichornia azurea*, *E. crassipes*, *Pontederia rotundifolia* L. and *Utricularia obtusa* Swartz. These free-floating communities are often of a temporary nature but they may be associated with *Nymphaea ampla* (Salisb.) DC. or *N. blanda* Nez., or on the lakes, *Cabomba aquatica* Aubl. in the more advanced stage of the hydrosere.

The next stage of the succession is a society with the plants rooted under water but having emergent stems; common dominants are *Typha angustifolia* L., *Cyperus articulatus* L., *C. giganteus* Vahl., *C. polystachyes* Rottb., *Eleocharis geniculata* (L.) R. Br., *Rhynchospora cyperoides* (Sw.) Mart., *Panicum frondescens* and *Setaria geniculata*. Around small pools such societies are of very mixed composition with many associated species including *Aeschynomene sensitiva* Sw., *Jussiaea linifolia* Wahl., *J. peruviana* L., *J. suffruticosa* L., *Heliotropium indicum* L., *H. procumbens* Mill., *Ipomoea reptans* (L.) Poir., and *Aciotis paludosa* (Mart.) Tr. The next stage is sometimes dominated by tall herbaceous species including many species of *Calathea* and *Heliconia* as well as *Thalia geniculata* L. Such communities are very common in the rain forest zone but do occur, although less frequently, in all zones. The succession then passes into the communities previously described as azonal.

An important variation of the hydrosere occurs on areas devasted by flash floods. The first stage is usually dominated by hydrophilous herbs but trees are soon established. Three distinct successions were observed with *Salix chiliensis* dominant in the Atlantic region, and in the Pacific region *Astianthus viminalis* (H.B.K.) Boil. as dominant on rocky areas and *Triplaris malaenodendron* (Bertol.) Standl. & Steyrm. on clay soils.

SUMMARY

A detailed land survey covering both vegetation and soils was carried out in Nicaragua and it was found that the five zonal vegetation formations were closely correlated to the length of the dry season. Numerous swamp and riverine communities were detailed, together with their environmental relationship as well as communities on mangrove areas, beach sands and a large group of salt-meadow communities. Pine and oak forests, pine savannas and two other savanna types were also described and their environmental relations discussed, the conclusion being reached that in each case the community concerned was disclimax. The various pasture types found were described and placed into major pasture groups. The course of plant succession on various volcanic deposits was outlined with the conclusion being reached in two cases that the rate of the succession was largely independent of the effect of vegetation. An outline was also given of the main hydroseres.

REFERENCES

Anon. (1954). Survey of the Barkly region, 1947–48. *C.S.I.R.O. Land Res. Ser.* No. 3. Melbourne.

Arnold, B. (1953). *Studies on the Brus Lagoon area, Honduras.* O.N.R. Report, Dept. of Geogr., Univ. of California.

Asprey, G. F. & Robbins, R. G. (1953). The vegetation of Jamaica. *Ecol. Monogr.* **23,** 359–412.

Beard, J. S. (1944a). Climax vegetation in tropical America. *Ecology*, **25,** 127–58.

Beard, J. S. (1944b). The natural vegetation of the island of Tobago, British West Indies. *Ecol. Monogr.* **14,** 135–63.

Beard, J. S. (1946). The natural vegetation of Trinidad. *Oxf. For. Mem.* No. 20.

Beard, J. S. (1949). The natural vegetation of the Windward and Leeward Islands. *Oxf. For. Mem.* No. 21.

Bramao, D. L. & Dudal, R. (1958). Tropical soils. *Proc. Ninth Pac. Sci. Congr.* 1957, **20,** 46–50.

Christian, C. S. & Stewart, G. A. (1952). General report on a survey of Katherine-Darwin region, 1946. *C.S.I.R.O. Land Res. Ser.* No. 1. Melbourne.

Davis, J. H. (1940). The ecology and geologic role of mangroves in Florida. *Publ. Carneg. Inst. Wash.* No. 517, 303–412.

Denevan, W. M. (1960). The upland pine region of Nicaragua. M.A. thesis, University of California.

Fanshaw, D. B. (1952). The vegetation of British Guiana—A preliminary review. *Imp. For. Inst. Oxford, Inst. Pap.* 29.

Goyena, M. R. (1909). *Flora Nicaraguense.* Managua.

Loveless, A. R. (1960). The vegetation of Antigua, W. Indies. *J. Ecol.* **48,** 495–527.

Radley, J. (1960). The physical geography of the east coast of Nicaragua. M.A. thesis, University of California.

Richards, P. W. (1957). *The Tropical Rain Forest.* Cambridge University Press.

Salter, E. A. (1956). *De la Flora Nicaraguense.* Bluefields, Nicaragua.

Sapper, C. (1937). Mittelamerika. *Handbuch der Regionalen Geologie*, Band 4a. Berlin.

Stehlé, H. (1945). Forest types of the Carribean Islands, Part 1. *Carib. For.* **6** (suppl.), 273–408.

Stevenson, N.S. (1942). Forest associations of British Honduras. *Carib. For.* **3,** 164–71.

Taylor, B. W. (1954). The vegetation of the Buna-Kokoda area, Papua. Ph.D. sup. pap., University of Sydney.

Taylor, B. W. (1959). *Ecological Land Use Surveys in Nicaragua*, vol. I. Instituto de Fomento Nacional, Managua.

Taylor, B. W. (1961). *Ecological Land Use Surveys in Nicaragua*, vol. II. Instituto de Fomento Nacional, Managua.

Verdoorn, F. (1945). *Plants and Plant Science in Latin America.* Waltham, Mass.

Whyte, R. O. & Taylor, B. W. (1959). *A Comprehensive Approach to Land Classification.* FAO publication, FAO/59/4/2422.

Zoppis, L. & Giudice, D. (1958). Geologia de la costa Pacifico de Nicaragua. *Bol. del Serv. Geol. Nat. de Nicaragua*, **2,** 19–68.

Zoppis, R. (1957). El volcan Masaya de Nicaragua. *Bol. del Serv. Geol. Nat. de Nicaragua*, **1,** 45–64.

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