

A PHYTOSOCIOLOGICAL STUDY OF THE NORTHERN RUPUNUNI SAVANNA,
BRITISH GULANA.

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ment of the requirements
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Science.

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I N T R O D U C T I O N

Savannas are one of the largest and least known vegetation types on the surface of the earth. They are so poorly known that they have neither been adequately mapped nor has their area been measured. However, the total area of savannas in the world may be almost 7 million square miles. In South America, they cover an area probably larger than any other type of vegetation on the continent. Savannas occupy over 20% of the area of Brazil, as much as 100,000 square miles in Venezuela, and not much less in Bolivia and Columbia (vide Shantz, 1954).

Although savannas are larger in extent than the Tropical Rain Forests, they have attracted less attention. With the accelerating population increase in the world, savannas will become increasingly important for food production and settlement. It is therefore necessary that the savannas of the world are carefully studied to ascertain their ecological structure and productive potential and to ensure their wise use.

This study concerns only a part of one small savanna and a cursory comparison with two others. It must be emphasised that any results and statements here refer only to the area studied and are not universally applicable. Apologies are offered for two omissions. Firstly, a section on the origin and causes of savanna has been omitted as these aspects were not studied. Secondly, although it is hoped that this study has been put in context, the extrapolation of its results to other areas has been scrupulously avoided, consequently leading to some inconclusiveness. No apologies are needed for posing

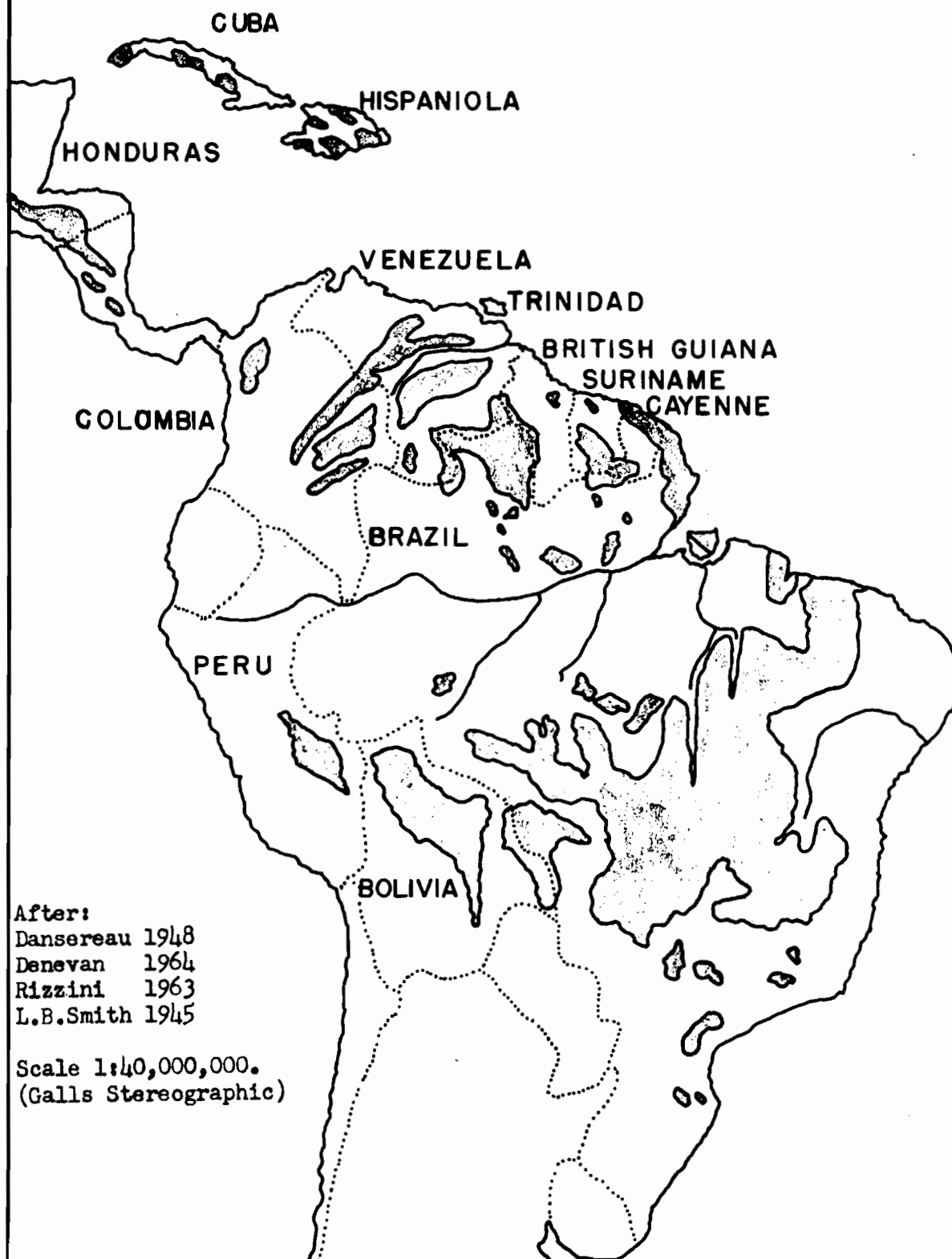
more questions than have been solved.

The aim of this study is threefold. Firstly, as the title indicates, it is a phytosociological study of a savanna. Although most attention has been directed towards the vegetation, animals and environment, as prime components of the ecosystem are treated in some detail. The Rupununi savannas are so intrinsically interesting, that digressions away from the topic of the vegetation are made where appropriate.

Secondly, this is one of the few instances where the quantitative ecological methods of the Wisconsin school have been applied to the tropics. It is thought that with modification, they will prove to be more useful than other methods hitherto applied.

Thirdly, this study has been a part of a research training for tropical ecology in general, and phytosociology in particular.

TENTATIVE SKETCH MAP
OF SOME OF
THE SOUTH AMERICAN SAVANNAS



After:
Dansereau 1948
Denevan 1964
Rizzini 1963
L.B.Smith 1945

Scale 1:40,000,000.
(Galls Stereographic)

L I T E R A T U R E R E V I E W

It is difficult to convey the state of botany in the tropics to anyone unfamiliar with the literature. The added difficulties which attend work in the tropics are to a certain extent outweighed by its virgin nature and unlimited scope. Corner (1946) writes: "To bring tropical botany to the present level of temperate botany, there is needed yet in the tropics a hundred times as many botanists as the world has ever known." Advice is rarely lacking but often frustratingly stultifying. It ranges from the pragmatic: "Draw everything, photograph everything, note everything" (A.H. Church in Corner, 1946) to the almost unobtainable, "know your plants. . . at the outset". (Bews in Tansley & Chipp, 1926). The former advice gives rise to the familiar surprise at the knowledge of tropical Foresters etc. Uncommunicated information, however profound, is useless. The latter advice may convert a few doughty souls to taxonomy, but deters many. The ability to distinguish taxa is more valuable than the ability to recall names. Keying plants can never be new to botany but plants can be studied with a field name or number and determined by experts later. If taxonomy should precede ecology, there would be no tropical ecology yet. Logic must occasionally be left to logicians so that the simplest is studied before the richest as Van Steenis advises. (1937 in Richards 1952).

The literature in general is extensive, although much is hard to obtain. The Interlibrary Loan Scheme has become an important research asset, but many magazines are non-circulating, as are older works, and

photocopying is expensive.

Tropical South American botany is still in the exploratory stage started by the great Naturalist-Travellers in the 1800's. Their works are often the best or only studies available. The progress of Tropical South American botany has been recorded by Gleason (1932a). Of the early Naturalists, Humboldt and Bonpland, (1819), Schimper (1888), Belt (1888), Sachs (1879), Martius (1840), Spruce (1908), Wallace (1878) and Bates (1863) remain authorities. Savannas have never been studied so ably or in so much detail since Warming (1892) wrote on a Brazilian Campo Cerrado at Lagoa Santa.

Fanshawe and Swabey (1948) have written about the Botanists of British Guiana. The table summit of Mount Roraima (9094 ft.) attracted Botanists from the time of Rudge (1805) and Meyer (1818) to the 1963-64 Bangor University expedition to Roraimas sister peak Kukenam. The Schomburgk brothers advanced the knowledge of the Guiana flora considerably by their extensive travels and assiduous collecting. (1848, 1876, 1922, and with Bentham 1839 and Hooker 1840). They wrote vivid and accurate descriptions of the Rupununi savannas. Other Botanists, such as Appun (1871) and ImThurn (1888), were less prolific, though invaluable. Jenman wrote tantalisingly brief descriptions of the savannas of Guiana in 1882 and 1888.

More recently, the botany of British Guiana has been studied by the Forestry Department, (Anderson, Hohenkirk, in Fanshawe and Swabey 1948), by the Geological Survey, (Bartlett, Stockdale) and even the Veterinary Service, (Fraser 1946). William Beebe (1925) established a research station in British Guiana after the Great War, giving rise to Graham's pioneer Flora (1933) and attracting the famous Botanists

Gleason (1932) and Hitchcock (1936). The Oxford University Expedition Society was the starting point of Richards Ecological studies, (Davis & Richards, 1933, 1934, Richards, 1952) and Saniwiths (1929) taxonomic interests.

The Rupununi savannas were the subject of the excellent observations of Myers (1936). This work is compared with other savanna studies by Beard (1953). These savannas are also being studied from different aspects by other McGill University expeditions, such as Waddell (1963) on the Anthropogenic factor; others on soils, Geomorphology and Climate.

There are few accounts of savanna ecology. The Suriname school under Lanjouw (1936, 1954) produces the "Vegetation of Suriname", periodically. Heyligers (1963) and Donselaar (1964) have presented phytosociological studies after the Braun-Blanquet system on the Intermediate type of savannas in Suriname. Adjanihoun (1936) used these methods on savannas in the Lower Ivory Coast. Blydenstein (1962) applied North-American phytosociological techniques to the Llanos. These four papers indicate the quickening pulse of savanna research.

Other savanna work is being done in Brazil and has been excellently documented in "Simposio sobre o Cerrado", produced by the University of Sao Paulo in 1963, and reviewed by Ferri, (1963). The Brazilian savannas are being studied from many aspects, and ^{such studies} are based on appreciable field work with less unfounded speculation and extrapolation than has previously bedevilled the savanna controversy.

Venezuela is the second center, after Brazil, of savanna research in South America. The work of Lasser (1955), Ramia (1959a), Tamayo (1956), and Aristeguieta (1959) is referred to, concerning the problems of the Llanos. Some of their work is summarised in "Sabanias",

volume 3 of the Ministry of Agriculture publication, "Reconocimiento Agropecuario", (1961). Takeuchi, (1960 a & b) worked in the Rio Branco savanna between the Llanos and the Rupununi.

Trinidad has long been a center of tropical botany, formerly from the Imperial College of Tropical Agriculture, now the University of the West Indies. The most recent study is that of Richardson (1963) on the Aripo savanna. He compares his observations with those of Marshall (1934), Myers (1933) and Beard (1946, 1953, 1955). Cayenne, (French Guiana) has not produced many savanna studies. Lanjouw, (1936) reported that the French Guiana savannas were similar to those he studied in Suriname. Benoist (1925) briefly described the French Guiana savannas, and was followed much later by Rue (1958) and Hooek (1960).

Taxonomic studies have been published by Maguire (1948, 1953 ff.) of the active New York Botanical Gardens. Harrison, (1958) from Kew, produced the first detailed list of plants from any British Guiana savanna, that of Ebini. Rizzini (1963) and Hoehne (1939, 1940, ff.) are working on the Brazilian Flora and Pittier (1926, 1947) on the Venezuelan Flora.

The literature on savannas other than in South America has not been consulted in detail. Apart from Adjanchoun (1962) of the Ivory Coast, most African studies are descriptive, but hard to compare. A few Botanists have studied both South American and African or other savannas. Chevalier, (1925, 1928, 1929, 1931, 1933), Schnell (1945, 1952), Aubreville, (1947, 1949, 1953, 1961, 1962), Troll (1936, 1950, 1956, 1959), Cole (1958, 1959, 1960, 1963), and Lauer (1952) have worked on savannas on both sides of the Atlantic.

A sound and rapid entry into the literature is afforded by

Verdoorn (1945) (vide Smith, A.C. and Smith L.B.) into Latin American Vegetation, by Roseveare (1948) into Latin American Grasslands, and by the Simposio sobre o Cerrado (1963) into savannas. These three works contain excellent bibliographies which ramify to most publications. This can be extended to world savannas by reference to Hills (1960) and Beard (1953). The literature of each topic is reviewed at the beginning of the appropriate section.

DESCRIPTION OF THE REGION

LOCATION

Savannas were studied in three areas of North Eastern South America:

1. The Far-Interior savanna of the Rupununi, British Guiana.
2. The Intermediate savanna of Ebini, British Guiana.
3. The Island savannas of Trinidad. (O'Meara, Aripo and Piarco)

1. RUPUNUNI

The Rupununi savannas of South Western British Guiana are an extension of the vast Rio Branco savanna of North Eastern Brazil. The Kanuku mountains divide the Northern from the Southern savanna. Only the Northern Rupununi savanna, an area of about 2,000 square miles, was studied. It extends from latitude $3^{\circ} 30'$ to 4° North, and from longitude 59° to $59^{\circ} 40'$ West (approximately). The respective geographical boundaries are the Kanuku mountains to the South and the Pakaraima mountains to the North, with the Rupununi river to the East and the Ireng and Takutu rivers of the Brazilian border to the West. The administrative center, Lethem, is about 250 miles west of the Surinam border and 110 miles S.S.E. of the Venezuelan border.

Geology:

The Northern Rupununi savanna is part of the Precambrian shield extending from the Orinoco to the Palaeozoic Geosyncline of the Amazon basin. (McConnell, 1961). The Northern savanna may

depth of
 have been eroded to a/2,000 ft. by a vast east-west flow into the Caribbean leaving the Pakaraimas and Kanukus elevated above the plateau. The present underlying rocks, designated the Takutu formation, may be a series of red and grey shales and sandstones of the mesozoic (McConnell, 1961) which have occasionally been found as outcrops in the Takutu, Rupununi and Riwa River banks. (Bleakley, 1957). This formation is presently overlain by deep quaternary sediments of sands and clays, with fluviatile and possibly lacustrine deposits. (Stark et al, 1959). The few flat topped hills and ridges may be former river terraces or lake beaches. (Bleakley, 1957).

The Pakaraima mountains to the north are composed of pre-cambrian rhyolites with granitic intrusions and gabbroic and doleritic dykes. They are partially covered with quartzitic sandstones. The Kanuku mountains to the South are composed of a granitic gneiss extending into the Southern savannas. (Barran, 1956, Loxton et al, 1958). Differences in geology have been suggested as the causes of savannas by Waibel (1948).

Geomorphology:

The Northern Rupununi savanna is on the north-south watershed between the Amazon (Atlantic) and Essequibo (Caribbean) Rivers. Most of the drainage is into the Ireng-Takutu-Rio Branco system but the western side drains into the Rupununi-Essequibo system. Formerly, most of the drainage was to the west and there is evidence that the Takutu and Ireng rivers joined the Rupununi river. Now the Amazon system is actively capturing the drainage possibly due to a slow westward tilting of this part of the shield. (Loxton et al, 1958).

The present divide is the hingeline.

To the north lies a large shallow depression from Good Hope to Annai at the base of the Pakaraimas which rise steeply upwards. This depression, the Northern Flats, is flooded in the wet season joining the Ireng and Rupununi Rivers. The Kamuku mountains are skirted by a slightly elevated erosion surface (Stark, 1959) extending to the Northern Flats. This raised surface is composed of undulating lateritic gravel ridges on sand and permits free drainage. The shallow depressions between ridges however are less well drained. In addition the Northern Flats are poorly drained. Defective drainage has been named as a cause of savannas by Bennett and Allison (1928), Michelmores (1939), Beard (1914). Cole (1963) suggests that differences in Geomorphology lead to the varying distribution of savannas.

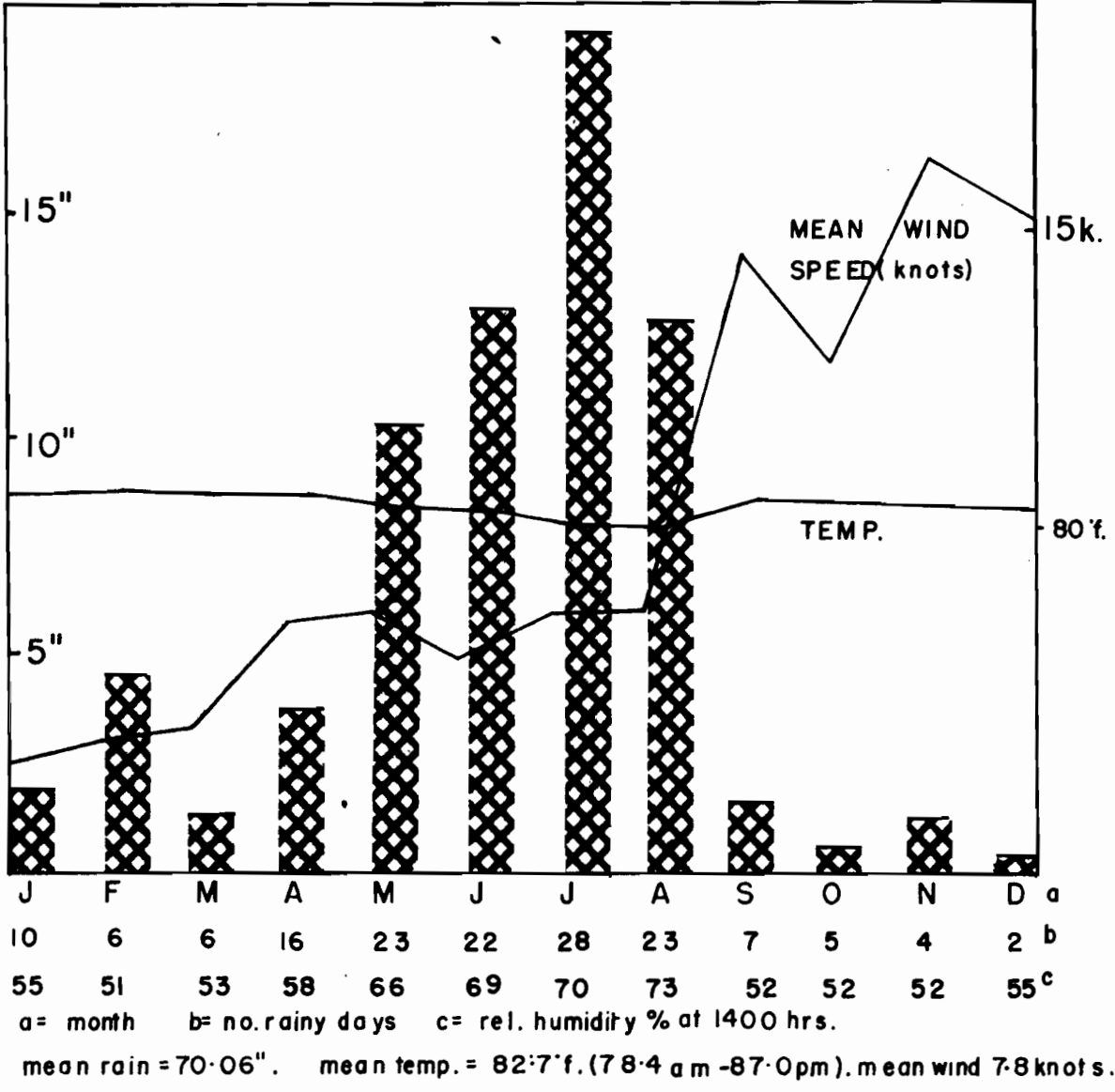
The Northern Rupununi savanna is in a state of "hydrological imbalance" (Loxton et al, 1958). Many of the rivers are dry in the dry season but may rise 40 feet to flood vast areas every wet season. The savanna is only about 350 feet above sea level but most of the water travels over 2,000 miles to the sea.

Climate:

The weather in the Rupununi savannas is pleasant in the dry season and tolerable in the wet season. As is usual for the tropics the diurnal temperature variation (10° F.) is greater than the annual variation (7° F.). The mean value in the Rupununi area is 83° F. The Relative Humidity remains fairly constant nocturnally at 80%, falling to 70% in the wet season day and 55% in the dry season day.

During the short but marked wet season from May to August about 13 in. of rain falls each month and this total is 80% of the

CLIMATE AT LETHEN, RUPUNUNI.



annual precipitation. In the long dry season from September to April only 1 in. or 2 in. of rain falls each month.

The wind speed increases gradually in the New Year from 2 knots to 6 knots in the wet season (May-August), to the strong winds of 15 knots after the rains.

This climate is not ideal for plant growth. The rain is unevenly distributed, and floods alternate with drought. The effective rainfall is much less than the actual rainfall of 70 in. The sandy nature of the soils, their poor water retention and the high winds afford very dry ecological conditions. The alternating of the wet and dry seasons has been postulated as a cause of savannas, vide Troll (1956).

Soils:

The soils of the Rupununi savannas have been studied many times (Follett Smith and Frampton, 1935, Duthie, 1939). The most recent workers using samples, surveys and air photographs produced large scale, tentative soil maps of most of the area. (Loxton, et al, 1958, Stark et al, 1959).

It has been suggested that the Rupununi soils were weathered under humid conditions, were covered deeply by white sand which was subsequently lost, and are now re-exposed. (Loxton et al, 1958).

The Rupununi soils have been classified on the basis of sample profiles and areas into many different types. (Loxton et al, 1958, Stark et al, 1959). However, the soils may be classified into three main intergrading groups:

1. Gravelly soils: these occur on upland sites and are composed of secondary laterite or peridolon (Bennett and Allison, 1928)

ranging from 3 in. diameter pebbles to pisoliths with varying amounts of red earth becoming paler below.

2. Grey soils: occur mainly on upland sites and are composed of grey sand with silt of silty clays. Massive or primary laterite occasionally outcrops in both these soils.
3. Soils of the flats: these are pale colored sandy silts and clays occasionally with a thin organic crust. They may become yellowish below and may contain red iron or black manganese nodules. These soils are often flooded. The fluctuating water table promotes lateritization.

In general the soils are highly acidic and very low in all nutrients. The chemical weathering of tropical soils is thrice as fast as temperate weathering and leads to very deep senile soils. If the surface of the soil is penetrable, as on lateritic ridges where the drainage is rapid, then the high rainfall and acidity lead to deep chemical weathering. The excessive elluviation of organic matter and clay reduces the water retaining capacity of the surface soil. The resulting deep desiccation further increases loss of soil constituents and aggravates the cycle. If the surface becomes compacted by the intensity of the rain, high insolation and the removal of the vegetation by fire, sheet wash, gullying and serious erosion usually follows. Humus is rapidly decomposed in the tropics due to the activity of the soil microflora.

Vegetation:

The Northern Rupununi savanna is bounded on three sides by

forest and to the west by the Rio Branco savanna. The Pakaraimas¹⁹⁵² to the north support Dry Evergreen forest (Fanshawe) and Deciduous Monsoon forest¹⁹³⁶ (Myers). The Kanukus to the south support some disturbed Semi-Deciduous (Myers, 1936), Montane (Fanshawe, 1952) forest. There is more interdigitating savanna in the Pakaraimas than in the Kanukus.

The vegetation of the area is not uniform. The following were distinguished:

1. Riparian Forest
2. Ité swamps
3. Bush Islands
4. Marshes
5. Aquatic vegetation
6. Muri scrub
7. Savanna

Only the savanna was studied in detail.

1. Riparian Forest:

Riparian Forest extends from the mountains along creeks. It is composed of tall forest trees resembling monsoon forest (Myers, 1936) with Palms and Bamboo while the forest floor bears a dry litter.

2. Swamps:

The Ité palm (Mauritia minor) borders some smaller creeks and may indicate areas of continuous groundwater movement or clay substrate (Jenman, 1888). Rank grasses and shrubs especially melostomes occur between the palms. These palms are much used for

thatch, ropes, and fodder and are becoming less frequent. Mauritia setigera occurs in the Aripo savanna and M. vinifera in the Amazonian savannas.

3. Bush Islands:

A few isolated patches of dry forest called Bush Islands occur in the area. They range from 50 yards to 3 miles in diameter and are composed of tall forest trees particularly of the Myrtaceae and Leguminosae (Myers, 1936). Their occurrence has been variously attributed to:

- (a) Rain path from Kanukus (Rutherford personal communication)
- (b) Fossil laterite as an aquifer (Sinha personal communication)
- (c) unimpeded drainage (Stark, 1959)
- (d) Abandoned dwelling leaving fruit trees in a dung rich plot (Waddell, 1963)
- (e) Birds that drop fruit seeds while perched in a tree (Myers, 1936)

4. Marshes:

These are low areas that remain flooded for a longer seasonal period than sedge meadows and support a mixed flora of aquatics, some suffruticose herbs and shrubs. The marshes become desiccated in the dry season.

5. Aquatic Vegetation:

Deep pools have woody species only around their edges. Rooted or floating hydrophytes and aquatics occur although most pools dry up seasonally.

6. Muri Scrub:

A peculiar and interesting type of vegetation called Muri scrub from the vernacular name for the dominant shrub Humiria spp., was observed in two small separate areas (Tiwiwid and Ebini) which becomes extensive in Suriname and other parts of British Guiana. It occurs exclusively on white sand and consists of circular clumps of bushes and small trees separated by bare "paths" of white sand about 8 ft. wide. In the clumps there are a few forbs, grasses and sedges. The flora is extremely characteristic and apparently very similar in Suriname. Muri Scrub was not quantitatively sampled but a presence list was compiled:

PLANTS OF MURI SCRUBWoody Plants

Byrsonima spp.
 Clusia nemorosa
 Humiria balsamifera
 Humiria floribunda
 Licania incana
 Myrsinaceae
 Ochnaceae spp.
 Ormosia costulata
 Pagamea capitata
 Retiniphyllum schomburgkii

Non-Woody Plants

Axonopus kaitukensis
 Cassia tetraphylla
 Catasetum
 Comolia villosa
 Epidendrum
 Lagenocarpus weigeltii
 Schizaea spp.
 Syngonanthus umbellatus
 Tillandsia flexuosa
 Xyris paraensis

7. Savanna:

These savannas are dominated by grasses and have open grown trees in them. Savannas vary from sites where sedges are co-dominant with grasses with extremely scattered trees, to those where the trees formed a canopy of almost 50%. Shrubs and forbs are usually present.

The dominant grasses are Trachypogon plumosus and Andropogon angustatus occurring with subsidiary grasses such as Axonopus chrysites

Aristida setifolia, and Mesosetum loliiforme. More than a dozen species of Paspalum have been reported from the savannas. The grasses may grow over 1 meter tall and in bunches 15 - 30 cms. apart.

Often almost half hidden by the tufts of grasses are small but brightly colored forbs such as Polygala spp., Borreria spp., Cassia spp., Merremia spp., Evolvulus spp., Stylosanthes spp. and Ruellia sp. etc.

Sedges are always present and may become co-dominant. They are Bulbostylis spp. and Fimbristylis spp. on the dryer sites with Rhynchospora spp., Stenophyllus sp., Dichromena and Scleria spp. on the moister sites. Depressions and flats may support a sedge meadow with some grasses and herbs, and an occasional suffrutescent herb. The flats are inundated for a shorter time than the marshes and also become desiccated in the dry season.

The most frequent tree is Curatella americana, with Byrsonima crassifolia, Bowdichia virgilioides and Myrtaceae sp. While the tallest tree was Plumeria inodora, up to 10 mt., most trees were less than 4 mt. high.

The shrubs and woody herbs are small but neither bushy nor dense. They include Psidium spp., Palicourea, Casahuate, Randia, and Erythroxylum spp.

The trees never form a complete canopy. However some plant species were found restricted to the shade of an individual tree or two or three trees together, often associated with a termite mound, the whole often comprising a small clump. Such species are Amasonia, Sida, Dichromena, and Heliconia sp.

Most trees had certain special features which are designated as characteristics of savanna trees. Many plants had very large

leaves. Such macrophyllous species include Curatella with leaves up to 8 inches long, and Palicourea with rather longer leaves. Further, the leaves were often sclerophyllous. Where the low nutrient level limits growth, the accumulated carbohydrate is converted to cellulose as sclerenchyma. This has been called Oligotrophic scleromorphism (Arens, 1958).

Some savanna species exhibit xeromorphic features such as a waxy cuticle (Plumeria), hairy leaves (Byrsonima verbascifolia), thick corky bark (Bowdichia sp.), low stature and xylopody (Rawitscher, 1948) (Connarus incompus). The tree species are precocious in that they flower while less than a meter tall. They are able to sprout from ground level after being cut or burned. Most savanna species are heliophytes and some produce serotinous seeds.

The nature of the forest-savanna boundary has been the subject of a recent UNESCO colloquium, but was not included in the present study. In the Rupununi savanna the boundary was often on a topographical feature such as a river. The abrupt nature of the boundary may be due to fire. The savanna near the boundary is usually of the orchard type. Although gradations from savanna to forest may exist, they were not observed in the Rupununi. Floristically, the savanna bears almost no relation to the forest.

As would be expected, the aspects of the vegetation are changed by seasonality. In the wet season there are many ephemerals especially hydrophytes. Perhaps most of the savanna species come into flower soon after the wet season especially the forbs. Some of the trees may blossom in any Christmas rain. Few if any of the trees are deciduous, but many shed their leaves after the passage of

fire. Fire causes the grasses to produce succulent green shoots among the charred stubble, and some plants flower only after fire (Stenophyllus (= Bulbostylis) paradoxa).

ILLUSTRATIONS

- TOP: Foreground is a gentle slope of orchard savanna with part of a "Bush Island" to the right. Middle ground shows a sedge meadow vegetation with scattered shrubs (Camp sujo) merging into an Ité swamp along a water course. Beyond the swamp lie the Northern Savanna Flats running to the Pakaraima Mountains.
- SECOND: Cerrado vegetation on pisolithic upland. Antonia ovata to the left, Curatella americana bush to the right.
- THIRD: An area of dense but rather small termitaria, with scattered shrubs and trees.
- BOTTOM: Muri scrub on white sand. The main plant in the sand "path" is Lagenocarpus weigeltii. The shrubs are Humiria spp. etc.

ILLUSTRATIONS

- TOP: Campo Limpo in front of a mature Ité swamp (Mauritia minor) with shrubs. Light can be seen penetrating right through the swamp from the other side.
- SECOND: Savanna edge, Campo Sujo on the flat foreground running up the slope to the left. Other slopes bear forest.
- THIRD: One of the uncommon "Bush Islands". Note the abrupt ecotone between Campo Limpo and forest. Note the Palms in the Bush Island.
- FOURTH: An area of dense Cacti (Cereus sp.?) with Randia (white flowers) and other shrubs. The Northern Savanna Flats lie in the distance.
- BOTTOM: Orchard savanna just after fire. The bare ground is showing although the ash has not yet been washed or blown away. The tree leaves are dead and will fall but the trees are probably still alive.

2. EBINI

Ebini is about 60 miles from the coast up the Berbice River and 70 feet above sea level. The soils are derived from the deep coastal sediments and are brown and white, acidic sands. The climate is similar to the Rupununi but with a less severe dry season and only parts are flooded. Ebini is surrounded by seasonal forest (Fanshawe, 1952), and supports a similar vegetation to the Rupununi. The soils have been studied by Follett-Smith (1930), and Stark (1958). The flora has been described by Martyn (1931), and Harrison (1958).

3. TRINIDAD

Three small savannas were studied in Trinidad. Aripo, (locally designated number two) on the Cumuto Road at Waller field is a flat 100 acres of fine grey sand enclosed by seasonal swamp forest. Apart from a small bush island, trees occur only on the edges. It is flooded in the wet season and desiccated in the dry season. (Richardson, 1963).

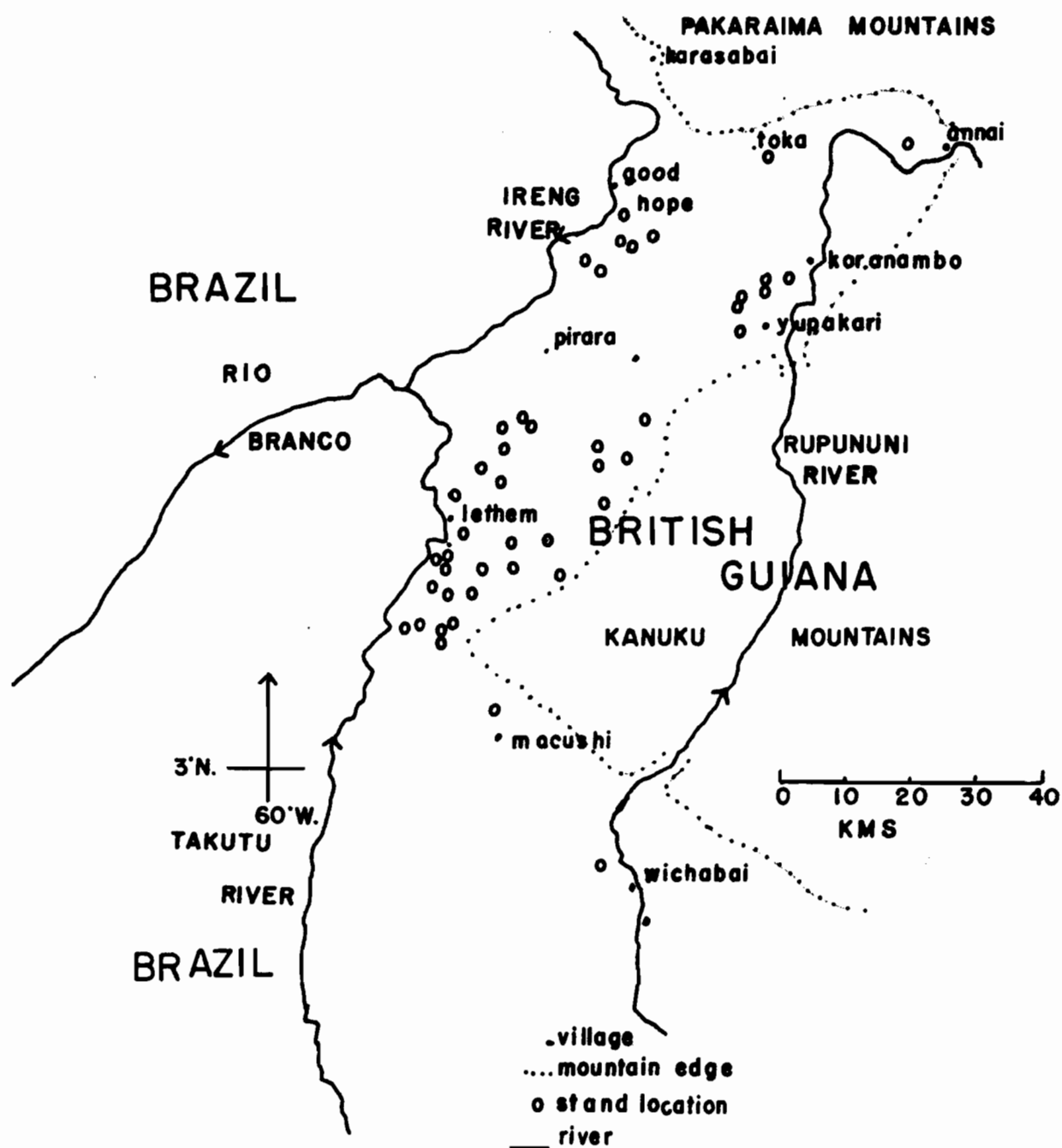
Piarco savanna lies on the edge of the International Aerodrome and is much disturbed. The part studied was well treed and had deep hogwallowing. The soil was an acidic brown sand.

O'Meara savanna is on the Churchill-Roosevelt Highway within an industrial development scheme. This savanna is similar to Piarco but not as wet nor as hogwallowed. The soil is a fine brown sand.

The climate of these savannas is similar to the Rupununi

although the rainfall is slightly less at 10 in. per month in the wet season, slightly more in the dry season (3-4 in.) with a higher annual mean (100 in.). The temperature is slightly higher, while the humidity is similar. These savannas are about 100 feet above sea level.

STAND LOCATION MAP



TERMINOLOGY

There is confusion and misunderstanding concerning the terminology of the savannas. This is not surprising for very little work has been done on them, and although savannas may vary greatly in all aspects from place to place, the conclusions drawn from one area may be glibly extrapolated to account for other savannas.

This confusion is mainly due to the use of different criteria, their inconsistency or lack of criteria. This situation is aggravated by the use of local terminology and the difficulties of language. It is not the aim of this paper to present a classification or terminology for savannas, but merely to clarify the terms used. Nomenclatural hierarchies have been presented by Burt-Davy (1938) and Cole (1963). However, before any system is accepted, more detailed work is needed to find the range of variation of savannas.

The term savanna is used in the sense of Siefritz (1943), Keay (1947), Curtis (1959), and Bray (1960). Savannas are plant communities dominated by grasses in which there are open grown, scattered trees. The grasses are termed dominant because they are the highest, more or less closed stratum. Sedges and forbs are almost always present, but usually less important ^{than} grasses. Curtis (1959) proposes the arbitrary limits of more than one tree per acre, but less than 50% canopy. Beard (1953) follows Bews (1929) in allowing that savannas may be treeless. This author agrees with Eiten (1963) in that: "If its (savannas) meaning is so extended that it includes everything from pure grassland. . . to tall closed

woodlands, then it loses all meaning." Eiten (1963) would use the term savanna woodland for the 25 to 50% canopy class. This seems more realistic as even a 25% canopy was rarely encountered in the Rupununi savannas.

Cerrado is a Portuguese word meaning dense or closed, and includes everything from woodlands (cerradao) to grasslands (campo limpo). It was used with the word Campo (Portuguese for field) as Campo cerrado, to distinguish areas with scattered woody vegetation from areas without any woody vegetation (Campo limpo or clean field). The term Campo sujo (literally: dirty field) is used for an intermediate type with a very few scattered, low shrubs. Cerrado alone is used less in a physiognomic sense and more to refer to the distinctive flora in general, while the term Cerradao refers to a rare type of tall closed woodland, possibly with some cerrado trees but with different shrub and herb layers (Rizzini & Heringer, 1962). Occasionally the word savanna may be qualified by orchard to distinguish between areas with more trees than others. Also studied in the Rupununi were areas with no trees. These may be called sedge meadows, the herbaceous swamp of Beard (1953), Patano herbaceo in Spanish, Campo de Varzea in Portuguese, or grassland (Campo limpo, or campo sujo if shrubs were present).

There are savannas in South America where the trees present may be Palms (Copernicia, Sabal, Mauritia) such areas being called Palm Savannas (Bennett & Allison, 1928), other in which pine trees (Pinus caribaea and P. oocarpa) occur are called Pine savannas (Parsons, 1955, Denevan, 1961, and Johannessen, 1963).

Most of the Rupununi savanna would be classified by Trochain,

(1954), as savane arbustive, garrigue, and by Cole (1963) as savanna parkland but the grasses need not be over 80 cms. nor Mesophytic. They are classified by Myers (1933) as low bunch grass savanna, though the grasses may be tall, (over 80 cms.) and not particularly bunched. Parts of the Rupununi are like the "Oak-ridge" vegetation in Honduras (Charter, 1941) and the Chapparal of the Llanos. (Ramia, 1959a, Blydenstein, 1962). Chapparal is a useful Spanish term meaning savanna where the most frequent tree is the Chapparro. (Curatella americana).

At Ebini, British Guiana, there were few trees, and most ^{savanna} was of the grassland and sedge meadow type. These are like the savannas described from Suriname by Heyligers (1963) and Donselaar (1964), from Cayenne ^{by} (Lanjouw, 1936) and from Puerto Rico by Gleason and Cook (1926). Aripo, Trinidad, is classified by Richardson (1963) as having a grass sedge vegetation, by Marshall (1934) as a low grass herbaceous swamp, and by Beard (1946) as marsh savanna subsequently renamed seasonal swamp (1955). O'Meara and Piarco, Trinidad, savannas are Orchard savannas (Marshall, 1934).

FIRE

From observations, interviews and the literature it seems that most of the savanna studied is burned nearly every year.

Controlled use of fire by early man may have started one million years ago (Stewart, 1956) and there is evidence that he used fire drives 10,000 years ago (Sauer, 1944). Hanno reports in "Periplus" the firing of African bush in 500 B.C. (Stewart, 1956). Sauer (1944) thinks that man may have found savannas when he arrived in South America. The low incidence of animal endemism may indicate that the savannas are most recent (Bates, 1948).

Kuhnholz-Lordat (1939) reports on the world wide occurrence of purposeful burning and Stewart (1956) documents incendiarism from Alaska to Tierra del Fuego. Myers (1936) supported by Rawitscher (1948) found evidence of more or less frequent burning on all the savannas he visited in South America. Although Myers (1933) had seen the Aripo savannas, Trinidad, Beard (1953) found no evidence of burning. These savannas have subsequently been burned (Richardson, 1963), in common with other Trinidad savannas (Marshall, 1934).

There are many non-human agencies blamed for causing fire, volcanoes for example (Hough, 1926), but well documented cases of spontaneous fires are rare (Viosca, 1931, Lindemann, 1953). Lightning as a cause has been blamed by Weaver (1954) and Budowski (1956, 1958), and exonerated by Plummer (1912), Braun-Blanquet (1932), Gleason (1913) and Stewart (1956).

There is no doubt that nowadays man is the chief cause of fire. The Amerindians were starting grass fires when the Spaniards arrived

(Schneider 1927, Bates 1948). This may have been to chase game (Sauer, 1944) including turtles (Budowski, 1958) (Heyligers, 1963) or the enemy (Herodotus 447 B.C. in Stewart, 1956) or even to clear felled trees during shifting agriculture (Bartlett, 1956). Most of the fires lit by the Amerindians are for fun (Myers, 1936), some are accidental (Stewart, 1956) while some are for communication (Bartlett, 1956).

Today fires are used to herd cattle (Kuhnholtz-Lordat, 1939) and even bees (Budowski, 1958), and to provide the fresh grazing which sprouts after fire. (Myers, 1933, 1936). Fires lit before the grasses become tall, fibrous and matted are likely to be less dangerous to property than accidental, infrequent fires (Myers, 1936, McCorkle, 1952). Fires may reduce ticks (Boophilus microplus) and other pests. Grass around dwellings is burned to reduce the snake hazard.

The incidence of fires has increased in the Rupununi due to the increase in population, and availability of matches, and the change from hunting to pastoralism and agriculture.

That fire has a profound effect on the vegetation has long been appreciated by pastoralists (Kuhnholtz-Lordat, 1939, Beard, 1949). The behavior of fire has not been studied in detail, although the gross effects are well known. Fires start in the quickly drying grassland and may penetrate the forest, but rarely the converse. However though fires are rare in tropical forests they are not unknown. The forests north of the Rupununi savanna have burned twice within living memory (McTurk, 1963, personal communication). The high water table in Gallery and Bush Island forest is supposed to prevent fire (Budowski, 1958) but both burn and disappear. The

Kanuku mountains may burn to the summit every 10 years (Gilliard, 1962).

Grassland burns in an irregular strip pattern. Usually only the aerial parts burn, leaving underground parts alive. Such surface fires are not fierce although there are very few studies of fire temperatures (Hayward, 1938, Beadle, 1940). The uninterrupted topography of the savanna and the long dry season facilitate the spread of such fires. The effect of fire on savanna biomass has been studied by Roland and Heydacker (1963).

Generally fire changes forest to grassland or savanna, as may be seen in shifting agriculture, but the grassland may require burning for its perpetuation. The reversion of grassland to forest when burning and sometimes grazing, is stopped, has been well documented. (Gleason, 1932, Aubreville, 1947, 1953, Schnell, 1945, Richards, 1952). The increase of forest into annually burned grassland is rare (Eggeling, 1947, Jackson, 1956). Fire increases grass and herbs at the expense of woody species (Weaver, 1954), and some plants have been used as indicators of burning (Aristeguieta, 1959). Frequent burning increases the bare ground (Curtis and Partch, 1948) until the vegetation is so poor that fire cannot travel. Some savanna trees may owe their survival to the absence of combustible material in their vicinity (Budowski, 1958). Fires early in the dry season are less serious than late fires (Hensel, 1923 and Jackson, 1956).

Fire may not alter the physical properties of soil (Beadle, 1940) but erosion and loss of productivity occurs (Shantz, 1947, Chevalier, 1929, Budowski, 1958, Schnell, 1945) and surface run-off increases (Anderson, 1949). Fire favors some grazing animals in Africa (Budowski, 1958) but harms others. Nearly every tree near

the line of fire is occupied by a hawk waiting for a lizard, snake or rodent to break cover. Although fire may not kill a tree, any wounds afford an entrance for insects and disease. Most of the ash is washed too deep to be recycled.

Savanna vegetation is well adapted to fire. Kuhnholz-Lordat (1939) coined the term Pyrophyte to mean a plant that is frequently burned away and may have more wood below ground than above. Pyrophytes have other characteristics. Many pyrophytes are insulated by a thick corky bark (Curatella, Bowdichia) and may be impregnated by a fire resistant substance (Byrsonima) like the silica in the leaves of Curatella. (Rachid-Edwards, 1956). Woody monocotyledons have no vascular cambium and are not killed to such a great extent by fire. Many savanna plants have seeds that are resistant to fire, and are often serotinous. Many are precocious and can flower and fruit while less than one meter tall.

The underground parts of many savanna plants are similar and are common to cormophytes and phreatophytes having xylopodia, grubs, lignotubers and burls.

These peculiar underground parts may be related to different functions. The term grub refers to the brushy growth of the aerial parts due to repeated burning but their root systems continue to increase in size. (Curtis, 1959). Where the root is long and reaches the phreatic water or water-table, the plant is called a phreatophyte (Meinzer, 1927) where the root has a swelling near its origin called a xylopodium (Rawitscher, 1948) or Lignotuber (Carter, 1929), or where the underground parts are larger than the aerial parts, such plants are called cormophytes. Phreatophytes were the subject of a symposium (Robinson, 1952) reporting a vain attempt at

their eradication by means of flame throwers, to maintain the water tables.

Lignotubers are common in the Myrtaceae and Proteaceae and act as a regenerative organ after the tops are burned (Beadle, 1940). Xylopodia are nearly synonymous with Lignotubers. They may provide a store of starch or water (Walter, 1939, Killian and Lemée, 1956) which is used during the dry season. The term burl is synonymous with grub and is used by Metcalfe and Chalk (1950) in reference to the Ericaceae. The roots of savanna plants have been studied by Rachid (1947), Rawitscher et al (1943), Rawitscher and Rachid (1946), Rizzini and Heringer (1961, 1962) and Donselaar (196-).

ANIMALS

The fauna of the savanna is strongly influenced by seasonal change. In the dry season the scarcity of water and the intense radiation exchange at ground level (as much as 45° c. in 24 hours) have produced either erosion or heliophilism. In spite of the presence of an endemic flora there are but few endemic animals in the savanna (Bates, 1948). Many dry season animals live in deep burrows, e.g. Lizards and Iguana (Vanzolini, 1963). Most birds nest at the end of the wet season. Fish-eating birds (Mycteria, etc.) and Seiving birds (Cairina, Dendrocygna, Nettion) find abundant food in the shrinking lakes and creeks. Fruit and seed eating birds (Conurus, Eupsychortyx) find most food at the beginning of the dry season. The predators (Falco, Tachytriochis, Milvago) are most easily seen near savanna fires either perched on nearby trees or struggling with a writhing snake on the ground. Vezey-Fitzgerald (1934) lists over 100 birds from the Rupununi.

Fish are most easily caught during the dry season when the water volume is small. The world's largest freshwater fish, the Arapaima, occurs near Karanambo. The more conspicuous fishes are Pirai (Piranha), Electric eel, Sting Ray, Leukananni (McConnell, 1958).

There are many insects and Blackflies and mosquitos which may distress in the wet season. Malaria occurs in the Rupununi savanna. The firefly, Ignes fatuus is common in wet places.

Some mammals are associated with termitaria. The anteater (Myrmecophagus) eats termites, the Armadillo gives birth to her quadruplets in a burrow beneath the termitaria, foxes (Dubicyon),

Lizards and snakes also shelter there.

Earthworms are not common in the Rupununi although they have been blamed for hogwallows at Ebini (Stark, 1963 personal communication), Aripo (Richardson, 1963) and in Suriname (Voorde, 1957). Apparently the worm builds a hummock to keep itself above water. These hummocks are the start of micro-relief formation and are called "Kawfoetoes" in Suriname.

Unintelligent hunting has reduced the deer (Carricus savanarum) population. Brock, (1963) presents acute personal observation on the mammalian fauna. Some of the small (3 feet high) deer have taken to the forest so there is very little grazing in the Rupununi other than that by cattle. Loxton (1958) reports a stock carrying ratio at about 70 acres per head of cattle at present. This is probably less than the carrying capacity, consequently overgrazing is not common. Legg and Hewson (1962) report on beef production at Ebini and Rupununi. Soil fertilization is being successfully tried at Ebini. The cost of transport renders this impractical for the Rupununi. The relation of man and the savanna has been studied in detail by Waddell (1963).

TERMITES

A curious feature of the savanna is the sporadic occurrence of termites. The insects themselves are inconspicuous but their termitaria are obtrusive. These termitaria vary in size from a few inches high and wide to spires as tall as 15 feet with a diameter at the ground of 12 feet. In parts of Africa the termitaria cover up to 30% of the ground (Kellogg and Daval, 1949). They are so important in places that the savanna is eponymously named Termiten-savannen. (Troll, 1936, 1950). They are found mainly in savanna (Beard, 1953), but Harris (1961) says that the Rupununi species only build on the ground due to the absence of trees.

The termites occurring in the Rupununi and Ebini savannas are Nasutitermes ephratae (Sands, 1964 personal communication). They drown their enemies in spittle. These termites eat wood but only digest a proportion of the cellulose (Harris, 1961). Their termitaria are built with a thick outer layer of earthy matter, probably digested, and cemented with excreted lignin. The inner part has more excreted lignin and cellulose and less soil. Myers (1936) reports Amitermes excellens and Syntermes snyderi from the Rupununi, both of which are in the same family as Nasutitermes. Adamson (1940) has reported Nasutitermes ephratae from the Trinidad savannas of Aripo, Mausica and Piarco. Ramia (1959a) found N. corniger in the Llanos. Martyn (1931) reports the mounds at Ebini as nests of the Coushi ant (Atta sp), which is disputed by Myers (1936a). Abandoned termitaria may be recolonised by other termites or ants.

Termites have a profound effect on the soil. Grassé (1950) reports that termites may collect clay from 5 meters deep and 300 meters around. While Nye (1955) reports clay extraction up to 12 meters in Africa. Hesse (1955) found that termitaria were formed solely of sub-soil, the chemical properties of which remain unaltered. Holdaway (1933) found about 30% Carbon and 0.5% Nitrogen in the mounds but does not indicate the composition of the surrounding soil for comparison. The composition of termitaria and soils has been compared also by Joachim and Kandiah (1940) and Murrows (1938). Where the sub-soil is better than the top-soil, then the termitaria are richer than the top-soil and conversely. The same applies to the accumulation of lime-rich water (Hesse, 1955). The use of broken up termitaria for fertilizer (Taylor, 1942) will only be beneficial where the top-soil is poorer than the sub-soil. Burnett (1948) reports the custom of piling wood on termitaria to obtain manure in the Sudan. Troll (1936) and Harris (1961) report cultivation of crops, restricted to mounds.

Erhart (1951) attributes the occurrence of a primary laterite horizon to the quaternary fossilization of termitaria and calls the latter "Cuirasses termitiques". This has been refuted by Griffith (in Harris, 1961) and Sillans (1959).

The activities of termites are reflected in the vegetation. Drummond (1886) draws the analogy between the preservation of the soil fertility by termites in the tropics with the earthworms in temperate countries. Nye (1955) estimates that half a ton of earth is deposited on the soil annually in parts of Africa. In the Rupununi, active mounds are bare; abandoned and eroded mounds support a distinct vegetation (Myers, 1936a). Many termitaria have a tree

growing through them but the mound was probably built around the tree, not the converse. This is the opposite of Oinonen's (1961) observations on Anthills. Troll (1936) explains the occurrence of non-savanna vegetation on termitaria as being relict vegetation remaining before the savanna extended into the forest. Martyn (1931) reports a complete succession from savanna to forest on termitaria at Ebiní. Troll's termite bush islands are more related to Gallery forest than savanna species. However in the Rupununi no non-savanna plants were observed on termitaria.

Little ecological work has been done on termites. The vegetation of termitaria has been studied by Murrows (1938) and Wild (1952). Sands (1961) has started quantitative work on the spatial distribution of termitaria and has found some relation to habitat. Knoppe's ecological study in Suriname is eagerly awaited.

The significance of termites is that they partially negate three of the causal factors of savannas. The termites, by their burrowing, improve drainage and aeration, thus reducing waterlogging. Termites may increase the nutrient level of the soil, and may reduce fires. Termite burrows may provide a passage through a hard pan for the roots of phreatophytes.

METHODS

PREPARATION:

Because the Rupuni savanna is so remote and relatively inaccessible, a preliminary survey to obtain an impression of the nature of the savanna, was impossible. In spite of the possible benefit of lengthy and detailed preparations these were impractical owing to the imminence of the dry season.

A card index of plant species was compiled from the limited literature available. To this was added the names of the families of the genera noted. The few descriptions available, even if only of the gross physiognomy, and any ecological information were added to the card index. There is no Manual or Flora of the region. However, some relevant papers were obtained, namely Graham (1933), Hitchcock (1922, 1936), Hitchcock and Chase (1917) and Fanshawe (1952). With the aid of these and Willis (1960), most specimens were identified to family. A surprising number of these specimens were assigned to their correct genera by elimination from the species list.

A species list form for recording data was compiled and mimeographed from the card index. Stand Record and Tree Data forms were drawn up. The species list was enlarged from the University of the West Indies herbarium in Trinidad and some of the species were learned from the herbarium.

FIELD METHODS:

Upon arrival in the savanna it was decided to deal only with

savanna and to omit from the present study the collecting of quantitative information ^{from} Ité Swamps, Bush Islands, Riparian Forest and permanent Marshes. The study of these areas was unfeasible, being floristically and physically too difficult for the time available. Further, it was considered that time spent on these possibly extreme types would be most usefully spent on other types, covering appreciable areas. The methods used had to have an accuracy reconcilable with speed, had to be suitable for use by a single worker; neither need nor assume any prior knowledge of the vegetation and finally must be quantitative, repeatable and comparable.

SELECTION OF STANDS:

A number of criteria were established to reduce any subjective selection of stands although the vegetation was so unfamiliar that there was no opportunity through lengthy observation or experience, to develop preconceived ideas about it. The stand had to be of sufficient size (about 10 acres) to eliminate from the area sampled any edge effects. Further, the stand had to be of uniform and homogenous physiognomy with respect to topography, cover, tree and herb distribution, disturbance (fire, grazing etc.) and apparent moisture conditions.

Stands were selected to attempt to include all aspects of the vegetational community. It was hoped that the force of any objections raised by the method of stand selection would be muted by the large number of stands used. In practice, the vegetation was found to be so uniform in large areas that homogeneity was not a problem.

COLLECTION OF DATA:

Data were obtained both on the characteristics of the environment and on the composition of the vegetation. Firstly, putative stands were surveyed to determine their validity. During this initial survey all plant species were recorded on a presence data form. This presence list was maintained by using a serially numbered field name for, and by the collection of any unknown or vegetative material as vouchers. The plants were named at the Smithsonian Institution. In addition, the topography, slope (direction and degree), nature and extent of any disturbance, moisture conditions, physiognomy and other environmental factors were noted on a Stand Data sheet. These observations were continued during the rest of the study for each stand.

Sampling: Sampling methods were used to save time with the hope that the sample would represent the whole. To this end a series of Points were established independently of the vegetation, along a straight line (by sighting on a distant object). A point was established on the ground every 50 paces. Points were thus randomly distributed throughout the stand. When the edge of the stand was approached, another compass direction was chosen; 20 points were sampled. This was considered to be a more practical method of establishing points than the use of random tables or an actual string grid. At each point a presence list of species occurring in a meter square quadrat was made. Frequency was subsequently derived from the data so recorded in the 20 quadrats per stand.

POINT-QUARTER METHOD:

The tree and sapling composition data were obtained by the

Point-Quarter method of Cottam and Curtis (1956), Curtis and Cottam (1962), Curtis (1959). Because of the depauperate nature of the woody vegetation a tree was defined as any woody stem of 12 sq. in. basal area. Basal area was used in preference to breast height due to the low, deliquescent branching of the trees. A sapling was taken to include all woody stems over 1 in. diameter at base but less than 12 in. basal area (1-4 in. diameter). At each point the distance to the nearest sapling and tree, their species and the basal area of the tree was noted in each of the four quadrants.

At points 10 and 20, the pH of the soil was measured with a Trueg Field pH kit. The soil to about 12 inches depth was described briefly and a sample collected.

SOIL:

The water retaining capacities of the soil samples were determined in the laboratory. A sample of each soil was lightly ground, sieved to 2 mm. and put in a pre-weighed clean Hilgard cup with filter paper and left for 8 hours dipping in a tray^{of}/distilled water to become wetted. Each sample was blotted free of excess water, weighed, heated at 105°C. for 72 hours and reweighed.

$$\text{W.R.C.} = \frac{\text{wet wt.} - \text{dry wt.}}{\text{dry wt.} - \text{empty wt.}} \times 100$$

The soils were analysed for acidity, Calcium, Potassium Magnesium and Phosphorus (as P_2O_5) and organic matter by standard procedures at the Quebec Provincial Soils Laboratory, Ste. Anne de la Pocatiere.

Two samples of termitaria were taken (Rupununi and Ebini) and analysed in the same way as the soil samples.

TREATMENT OF DATA:

A total of 50 stands were sampled, 45 in the Rupununi, 2 at Ebini and 3 in Trinidad. Field data were tabulated and ordered onto stand summary sheets. The following were calculated:

Frequency = % quadrats occupied by a given herb or shrub. (1 value per species per stand).

$$\text{Actual Frequency (A.F.)} = \frac{\text{no. of points of occurrence}}{\text{Total points sampled}} \times 100$$

$$\text{Relative Frequency (R.F.)} = \frac{\text{no. occurrences of a sp.}}{\text{Total no. occurrences all spp.}} \times 100$$

$$\text{Relative Density (R.De.)} = \frac{\text{no. individuals of 1 sp.}}{\text{Total no. individuals of all spp.}} \times 100$$

$$\text{R.F.} = \frac{\text{Frequency of 1 species}}{\text{Total Frequency of all spp.}} \times 100$$

$$\text{Relative Dominance (R.Do)} = \frac{\text{Total basal area of 1 sp.}}{\text{Total basal areas of all spp.}} \times 100$$

$$\text{Importance Value (I.V.I.)} = \text{R.F.} + \text{R.De.} + \text{R.Do.}$$

$$\text{Absolute Density: a) } \frac{\text{Sum of the distances from point to tree}}{\text{Total no. trees taken}} = \text{Average Distance}$$

$$\text{b) } \frac{43560}{(\text{Average Distance})^2} = \text{Total Density (no. trees per acre)}$$

$$\text{c) no. trees per acre} \times \text{R.De.} = \text{Absolute Density for each sp. per acre.}$$

$$\text{Dominance: a) } \frac{\text{sum of basal areas}}{\text{no. trees}} = \text{Average basal area per tree}$$

$$\begin{aligned} \text{b) Average basal area per tree} \times \text{no. trees per acre} \\ = \text{Basal area per acre} \\ = \text{Dominance.} \end{aligned}$$

Frequency was calculated for herbs and shrubs, the other values were calculated for trees; Dominance was calculated for termitaria.

TERMITES:

Termitaria were found to be physiognomically and numerically as important as trees and so it was decided to treat them in the same way as were the trees. The longest basal diameter and the distance to the nearest mound in each quadrant was measured. The assumption that the termitaria were circular at base was considered sufficiently accurate for the present study. Sands (1961) measured the longest and shortest basal diameters. Further the height was assumed to be proportional to the basal diameter and the termites were considered to be of the same species in each termitarium. The termitaria were not examined to ascertain if they were active or inactive as it was assumed that long inactive termitaria are eroded away. Two samples of the termites were collected and were identified at the Termite Research Unit of the British Museum.

MATRIX:

Finally the Matrix method on the phytosociological characteristics of species, Bray and Curtis (1957), Maycock (1957), Maycock and Curtis (1960), Curtis (1959), was applied.

This ordination technique can be performed using any quantitative values where a large number of stands is involved. In this case only herbs were considered. A list of herbs was compiled using only the taxonomic entities which at the time were known to be valid. At the time this method was first applied the specimens had not been identified, so it was necessary to use "field names". If there was any doubt as to

the validity of an entity, and surely many collections were the same, the entity was not used in the ordination. This reduced the herb list to 80 species which were prepared on a mimeographed matrix data sheet, to facilitate the comparisons required.

The quantitative values used in this study were frequency and presence. Presence only for a species in a stand was scored as one. These "Actual Frequency" values were entered into the Matrix Data sheet, one sheet for each of the 50 stands used. To take into account the fact that some species are more common than others, each frequency value was expressed as a percentage of the maximum frequency value for that species which occurred in all 50 stands. This produced a "modified frequency" value. Because the total number of species in a stand could vary greatly this "modified frequency" was expressed as a percentage of the sum of the "modified frequencies" in each stand. This produced the "score value" which totalled 100 for each stand.

The score values for each stand were compared with the score values for every other stand in the following way. Two stands were compared at a time, and wherever there were species in common, the lower score values of the comparisons were summed. This procedure was repeated comparing each stand with every other stand. This produced a number, called "Matrix value" that was entered into the matrix square of 50 stands compared with 50 stands. The matrix values may range from zero which would indicate that there are no species in common between two stands, to 100 which would indicate that the stands are identical in herb composition. This range of numbers is a quantitative expression of the vegetational similarity between stands.

1° Axis: The matrix values in each row of the matrix added to produce a matrix sum for each stand. Different axes, that is, different stand orders, can be obtained from this table. One end of the first axis is the stand with the lowest matrix sum value - stand 'a'. The other end of this axis, stand 'b', is the stand having the lowest matrix value with stand 'a', i.e. the stand most unlike it. The other 48 stands may then be arranged in order between these two ends by the following procedure based on their quantitative similarities to the end stands. All of the matrix values for stand 'b' were subtracted from the highest matrix value occurring in one of the two stands. The resulting values were added to the matrix values for the same stands in 'a' and the sum halved to give an average value for each stand. The stands were then arranged according to this order. Stands 'a' and 'b' will be at opposite ends. This is the first or primary axis.

2° Axis: The lowest value in the 1° axis was subtracted from the highest, and the result halved. This is the mid-point of the 1° axis. From an examination of the 10 to 15 stands which lie ± 5 from the mid point the one with the lowest matrix value (2° b) with that stand (2° a) was selected. These two stands are the most different of the stands near the mid point of the 1° axis and are the ends of the 2° axis. The 2° axis is then completed in the same way as the 1°.

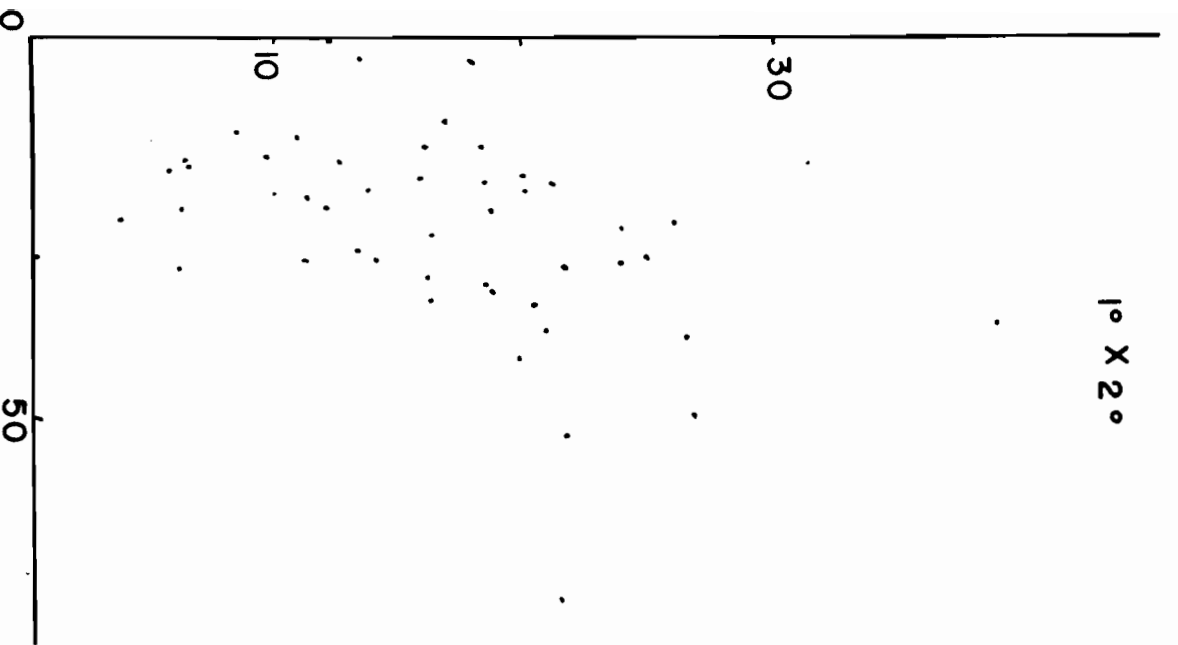
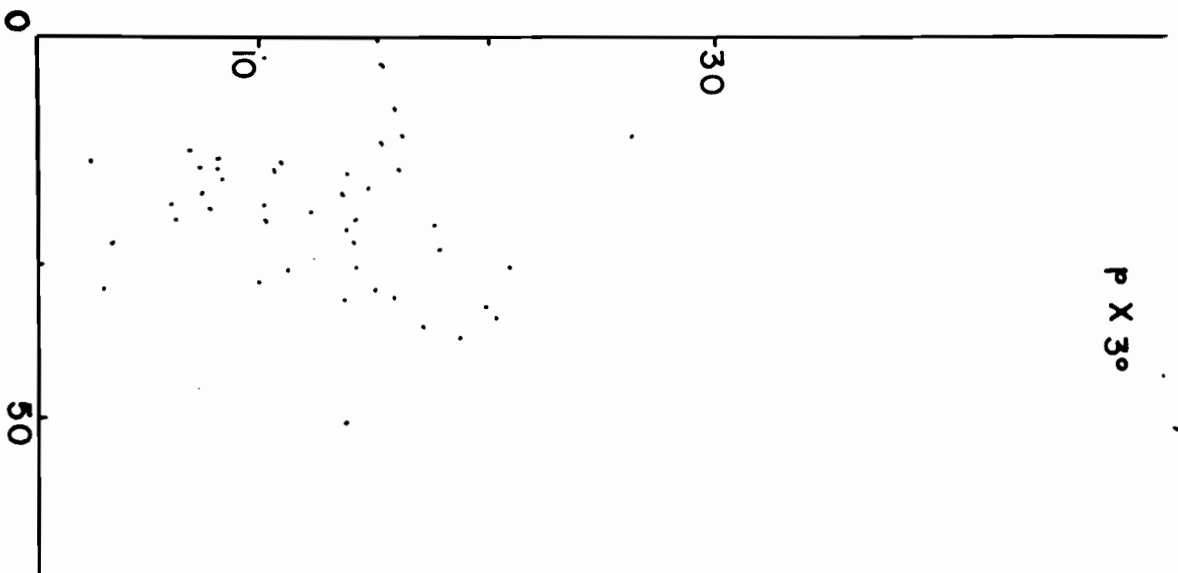
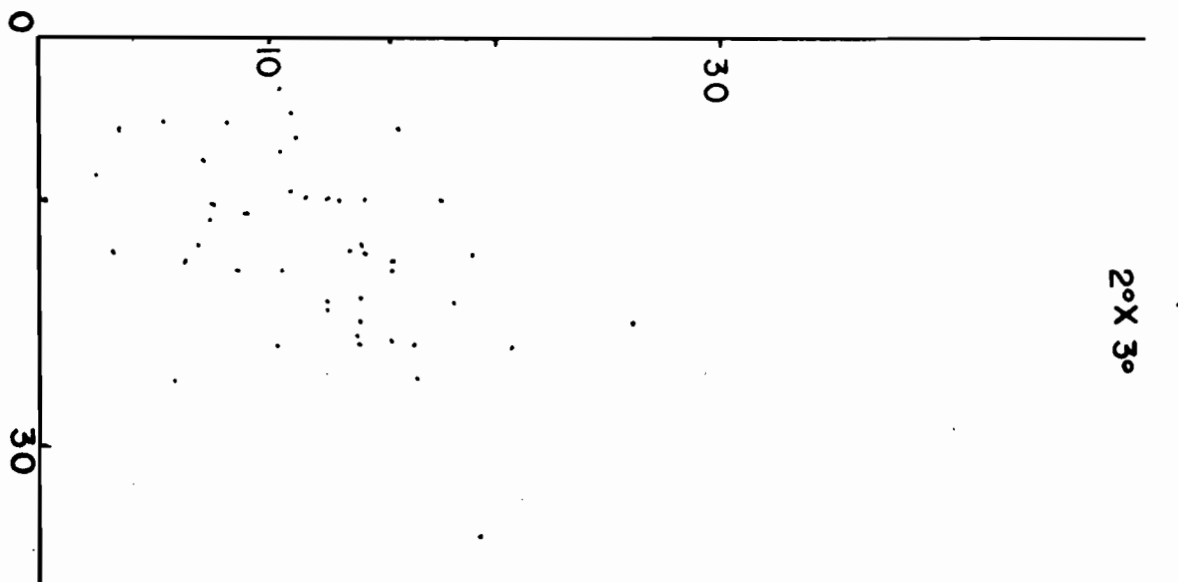
From the 1° and 2° axes, the stands may be arranged spatially in 2 dimensions. This distance between stands is proportional to their ⁵disimilarity. The pattern of stands was plotted on graph paper. x

This spatial distribution of stands is used as a base upon which may be plotted any of the quantitative data collected.

3^o Axis: Theoretically, there is no limit to the number of axes which may be used. However, in practice three axes are the most that can be easily visualised and comprehended. The third axis was obtained in a similar way to the 2^o axis. The mid point was obtained from a central group of stands on the intersection of the mid points of the 1^o and 2^o axes combined.

The three axes were plotted on graph paper in 3 dimensions (p.55) (1^o x 2^o, 2^o x 3^o, and 1^o x 3^o). A 3-dimensional model was also constructed. A base board represented 1^o x 2^o, into which were nailed 50 wires (1 per stand), and the length of wire represented the 3^o axis for each stand. It was easier and less laborious to understand relationships on the model than on the 3 graphs necessary for the plotting of a given quantitative character. Data were plotted on the model by means of colored plastic beads plugged on each wire, the colors representing different values, e.g. Red for high, Pink for medium, etc. Alternatively the colored beads could be used for mere presence or absence, or different colors could represent different entities and ecological factor magnitudes of particular stands.

DISTRIBUTION OF STANDS, three dimensions.

 $1^{\circ} \times 2^{\circ}$  $1^{\circ} \times 3^{\circ}$  $2^{\circ} \times 3^{\circ}$ 

M A T R I XSUMMARY OF PROCEDURE1. SCORE VALUE

- a) Frequencies (F) of 80 spp. in 50 stands
- b) Modified Frequency (% max. F. for each spp.)
- c) Score value (S.V.) (% per spp. of Sum of Mod. F.)

2. MATRIX

- a) Compare S.V. of 2 stands
- b) Sum the lowest of co-incident S.V.
- c) Repeat for all species
- d) Obtain one Matrix value for each stand

Comparison (50 x 50 = 2500 - unity comparisons (=50) 2500
 2500-50 = 2450)

- e) Sum the Matrix values (M.V.) for each stand = Matrix Sum
 (M.S.) (one per stand)

3. 1^o AXIS

- a) Lowest M.V. stand = stand 'a'
- b) Stand b = stand with lowest M.V. in stand 'a'
- c) Subtract all M.V. of 'b' from the highest M.V. from 'a' or 'b'
- d) Add these to M.V. of 'a'
- e) Divide by 2
- f) Arrange stands between 'a' and 'b'

4. 2⁰ AXIS

- a) Subtract lowest value in 1⁰ axis from highest
- b) Divide by 2 Midpoint of 1⁰ axis
- c) Stand 2⁰ a stand with lowest M.S. in central group
- d) Stand 2⁰ b stand with lowest M.V. in stand 2⁰ a
- e) Repeat from 3 b above.

R E S U L T S

INTRODUCTION

Each species of plant can tolerate certain conditions only, and the extent of growth within the range of these conditions is called the amplitude of tolerance or just amplitude. Each species has its own discrete and characteristic amplitude in the almost infinite range of the environment, and no two taxa have exactly the same amplitudes of tolerance. The "environment" is the resultant of all the conditions which may affect a plant and may be divided purely for convenience into mutually interacting "factors" such as water conditions, competition, and grazing etc. Although no factor acts independently it is clear that species differ in sensitivity of behaviour to the various factors. It is not easy to ascertain which factor or group of factors is the most influential in restricting an amplitude, for apparent correlation with a factor may in fact be correlation with an interacting factor. As some factors are more easily measured than others, these tend to be cited as the most important factors. Thus, when drainage is cited as being important in this study it may well be that frequency or intensity of burning which is related to drainage is actually more important although less amenable to measurement and resolution.

TREATMENT OF DATA

Quantitative data were thus obtained for the environmental and the vegetational features of each of the 50 stands. A prime aim in phytosociological analysis is to relate the two. This may be tried by arranging the samples (stands) where the data were collected, into an order, which provides an opportunity to relate vegetation and environment. There are many methods of arranging stands; all have their merits and their supporters. The method used may be basically environmental, such as by moisture conditions; by floristics such as used in plant geographical studies of range and affinity; by indicator species, by using the physiognomic dominants or life forms in the vegetation, or any other criterion or measure which can be applied to all the stands. The ecology, that is, the relations of the various aspects of the environment, of the vegetation, of the fauna and their mutual interactions, may then be elucidated by comparing and interpreting data plotted on such ordinates.

A brief account of the various attempts at ordination is included to indicate what was done, in chronological order. The first method used to obtain an order of stands was moisture condition. (Bray, 1960, Maycock and Curtis, 1960, Curtis, 1959. et al.). In such a method each stand must be assigned to a moisture class; however, lack of experience in the present study rendered this impossible.

The second attempt at stand ordering was environmental and floristic. Of the 50 stands, 3 were unequivocally wet, and 4 were unequivocally dry. From these 7 stands was compiled a list of what was hoped to be 12 wet indicator herbs and 12 dry indicator herbs. A weighting procedure, (Bray and Curtis, 1957) was then applied on

the presence in each stand of the indicator species, scoring 1 for each species indicating wet conditions and 0 for those indicative of dry sites. The stands were then ordered according to the D (dry)/W (wet) fraction or ratio. Once again this order was not conclusive.

This D/W fraction was then modified to acknowledge that some stands had more species in the list than others. In general wet had more than dry. The formula $(D/W)^2(D+W)$, (Patil, 1964) was used. This was a slight improvement over previous attempts and led to some fairly interesting graphs, but was also not particularly conclusive.

This formula could probably be improved by the incorporation of more data, as long as the trends of the data are known. Also, it is difficult to assign a weight to the factors used. In the formula $(D/W)^2(D+W)$, the number of species in the list is arbitrarily made half as influential as the D/W ratio.

The logical conclusion of this method would be the derivation of cumbersome formulae taking into account all factors measured. An easier way of achieving a similar goal is to expand the original list of 24 species to as many species as possible, and to use all of the samples, not just 7. This becomes similar to Motyka's coefficient, (vide Curtis, 1959) $2W/a \cdot b$. (where W = sum of lower frequencies in common, a = frequency in stand a of the common species, and b = same in stand b.) This is, in fact, the basis of the Matrix.

P R E V A L E N T S P E C I E S (vide Curtis 1959)

SPECIES	% PRES.	AV. % FREQ.	MAX. % FREQ.
Trachypogon	93	40	100
Andropogon spp	93	31	100
Fimbristylis	93	40	90
Aristida setifolia	87	24	65
Galactia schomburgkiana	84	24	90
Paspalum spp	75	11	100
Axonopus chrysites	73	24	95
Borreria verticillata	73	18	60
(Cassia)	--	-	-
Evolvulus becasanus	67	16	80
Byrsonima verbascifolia	67	13	95
Dichromena cilia a	64	15	90
Polygala longicaulis	64	13	75
Rhynchospora spp	62	20	100
Mesosetum loliiforme	60	22	90
Polygala angustifolia	58	7	50
Casearea sylvestris	58	5	30
Phaseolus	56	8	75
Buchnera elongata	56	2	20
Bulbostylis conifera	53	27	85
Stenopayllus paradoxus	53	22	95
Myrtaceae	53	2	15
Ruellia geminiflora	49	12	95

P R E V A L E N T S P E C I E S (Continued)

SPECIES	% PRES.	AV. % FREQ.	MAX. % FREQ.
<i>Phyllanthus niruri</i>	49	11	60
<i>Scleria</i> ("large")	49	8	55
("lax")	49	11	55
<i>Erythroxylon</i>	47	1	10
<i>Crotalaria</i> sp.	44	5	46
<i>Palicourea rigida</i>	44	1	25
<i>Loranthus</i> sp.	44	11	80
<i>Oxalis schomburgkii</i>	42	4	40
<i>Zornia diphylla</i>	42	6	40
<i>Cissampelos ovalifolia</i>	42	1	10
<i>Cassytha americana</i>	42	6	50
<i>Amasonia</i> sp.	38	2	25
<i>Lippia schomburgkiana</i>	38	3	30
<i>Paepalanthus</i> sp.	38	15	100
<i>Stylosanthes</i> sp.	38	6	100
<i>Tibouchina aspera</i>	38	9	53
<i>Richardia scabra</i>	33	5	40
<i>Panicum</i> sp.	33	10	85
<i>Eriosema violaceum</i>	31	3	40
<i>Randia formosa</i>	31	$\frac{1}{2}$	5
<i>Eragrostis glomerata</i>	29	7	100
<i>Sida</i> sp.	29	2	50
<i>Buchnera palustris</i>	27	5	100

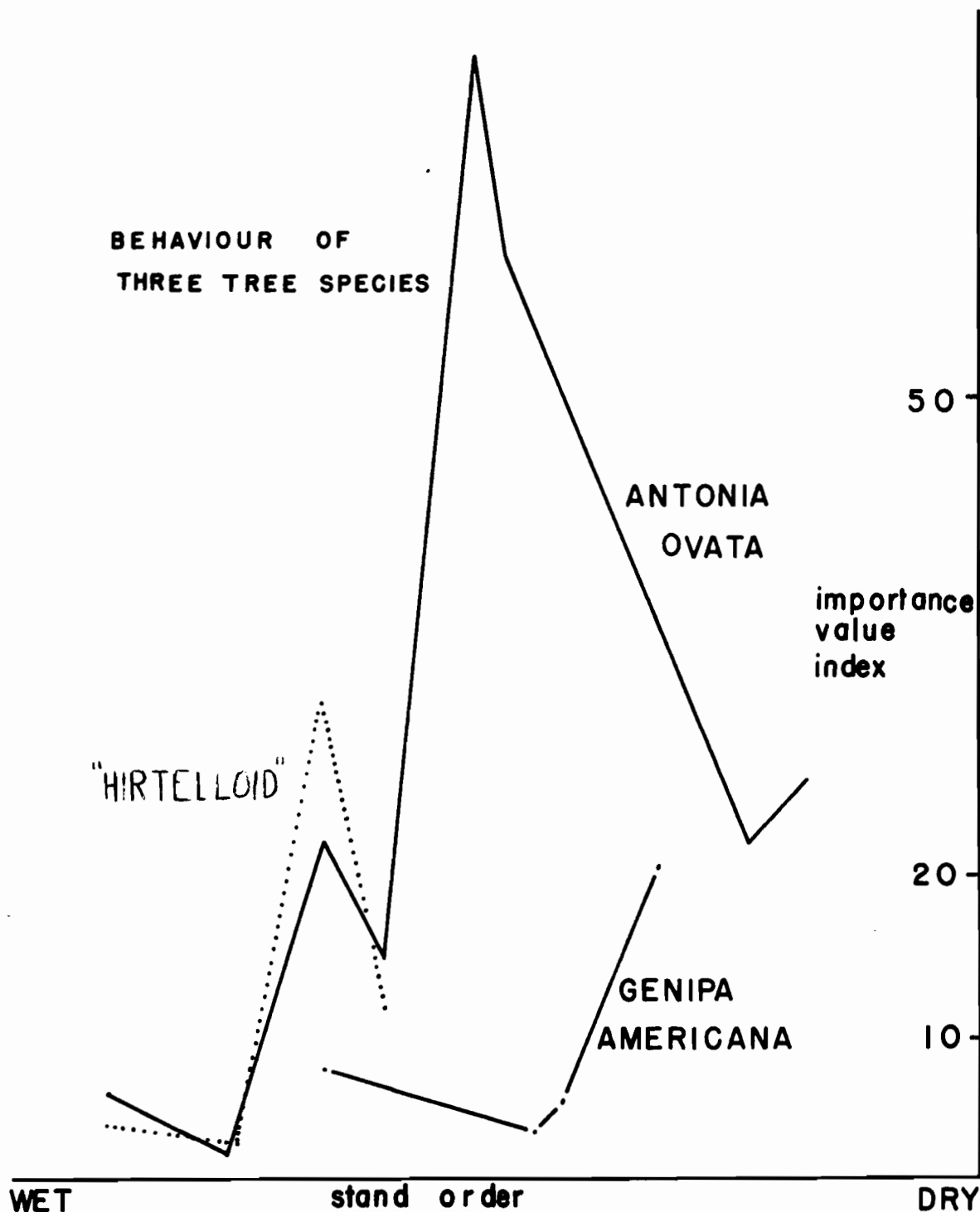
P R E V A L E N T S P E C I E S (Continued)

SPECIES	% PRES.	AV. % FREQ.	MAX. % FREQ.
Cyperus sp.	27	2	40
Setaria sp.	27	1	35
Waltheria sp.	27	5	65

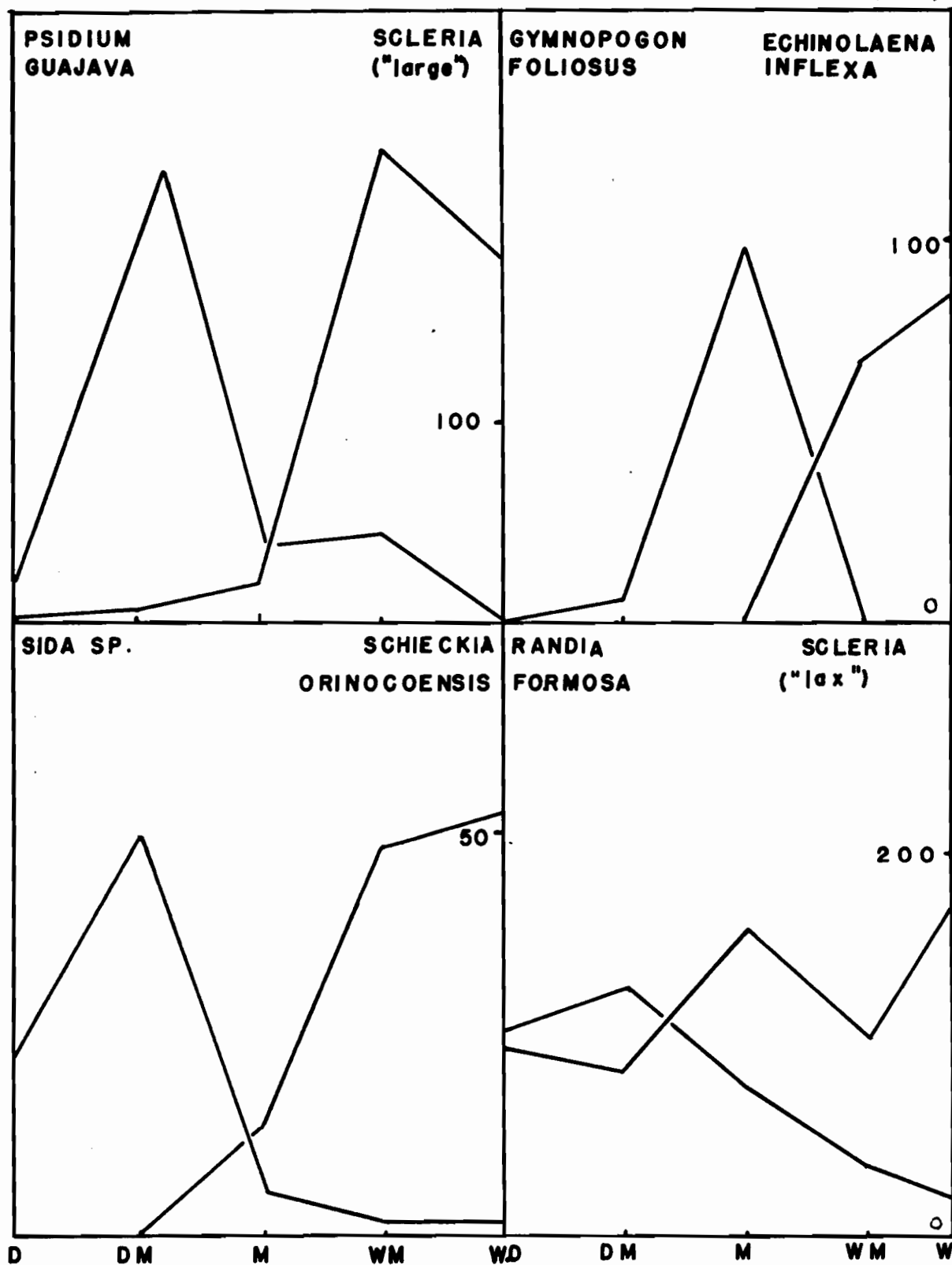
MAIN TREE SPECIES DATA

Tree	% PRES.	AV. I.V.I.	MAX. I.V.I.	No. Times Leading tree
<i>Curatella americana</i>	100	51.1	300.0	29
Myrtaceae ("pilosa")	83	13.3	139.4	2
<i>Plumeria inodora</i>	75	10.5	103.2	2
<i>Byrsonima crassifolia</i>	70	8.8	80.0	4
<i>Bowdichia virgilioides</i>	70	6.3	68.1	-
<i>Erthroxylon</i> ("flaky")	50	2.2	62.3	-
<i>Roupala</i> sp	30	3.1	104.3	1
<i>Antonia ovata</i>	22	1.7	72.5	-
<i>Genipa americana</i>	17	0.5	13.1	-
Rosaceae ("Hirtelloid")	11	0.5	33.1	-
<i>Tabebuia</i> sp	11	0.4	22.1	-
<i>Anacardium occidentale</i>	6	0.5	42.0	-
<i>Cereus</i> sp	3	0.1	10.5	-
<i>Hirtella racemosa</i>	3	0.05	3.5	-

Although the initial grouping of stands was subsequently discarded, some of the results are presented. The frequencies of the species under consideration were plotted graphically with the horizontal axis representing the 5 moisture segments: dry, dry-mesic, mesic, wet-mesic, & wet. As is usual with this method, the % frequency curve is more sensitive but less wide ranging than the presence curve. Examples are taken from trees, shrubs, forbs, grasses and sedges.



FREQUENCY - MOISTURE GRAPHS, selected species (Max. 900)



MATRIX

THE NATURE OF THE AXES:

The axes of the matrix are based on the phytosociological characteristics of herbs alone. Hence the closeness of stands indicates their degree of phytosociological similarity. The phytosociological characteristics of herbs are influenced by all the factors of the environment, including the vegetation. Their occurrence indicates a specific range of tolerance for a particular combination of factors. The axes actually are phytosociological similarities and differences not environmental factors. If an environmental factor does correlate this means that this factor influences the phytosociological relationships of the plants; that is all. Hence the axes do not represent single factors, indeed it would be surprising if they did, but probably a combination of several or many factors. Most of the factors of the environment, if the environment can be resolved into factors, are inter-dependant. Where two or more factors are in direct proportion, then they will be components of the same axis. The axes are not thought to be linear.

By plotting data for all the factors measured, certain recurring patterns become apparent. In the interpretation of these patterns it is assumed that the axis on which the gradient of the factor occurs, is the axis of that factor. That is, if a factor is very low near the origin and ranges to very high in the lower right hand corner, then this factor is a component of the first axis. By this method the nature of the parameters was analysed. The nature of the second axis was easily discernible as representing soil nutrients. The % Nitrogen, Potassium, Calcium, Magnesium and H. were all low near the primary axis and became

higher along the secondary axis.(Page 78).

The primary axis was related to the moisture and drainage conditions of the stands. However this is not the sole factor as the range of moisture conditions is from very dry near the origin to very wet at 30° from the origin. If a line is drawn through the main range of the factor gradient from the low values to the high values then the angle between that line and the primary axis is a measure of the degree to which that factor is a component of the primary axis. An angle of 45° would indicate that the factor considered was an equal component of the primary and secondary axes. It was deduced that the primary axis is controlled to a minor extent by soil nutrients.

The tertiary axis was also a combination of factors. The greatest correlation was with water retaining capacity and the pH of the soil. Thus the extremely acidic sands were low on the 3' axis, rising slightly to the less acidic, very dry sites and ending with the least acidic, rich, wet sites. There is also slight correlation with soil nutrients and moisture. Many ecologists disagree concerning the nature of the structure of vegetation. Not only is the concept in dispute but the means by which it can be explained, or what information constitutes an explanation of vegetational structure, varies widely from several extremes. McMillan's analogy (1959) is most appropriate, particularly if the environment is considered to be composed of so many interrelated factors that the oversimplified three parameter tetrahedron becomes a multi-polyhedron or sphere. However several relationships are demonstrated by this method, including the mutual relations of species and their ecological amplitude; the relation of vegetation and its components to factors of the environment and

the continuous nature of the vegetation. Maycock (1957) explains in detail the interpretation of matrix data. Whenever the matrix has been used previously, the stands have been assigned to a moisture segment before the calculation of the matrix. Here this situation has not been possible due to the complex nature of moisture relationships in the savannas, at least during the period of observation. The stands have been grouped from the model into various moisture categories. As usual water is an important influence on the vegetation. In the Rupununi savanna however, the water conditions are complex in that dry can mean either absence of water or excessive drainage. Some stands are inundated in the wet season and support a "wet" vegetation, but these stands dry out so fast and so thoroughly that they are ecologically dry. The dry season may be the period when these groupings would prove meaningful.

One feature of savanna vegetation which may be elucidated is the varying occurrence of trees. If tree density (No. trees/acre) is plotted on the model, a partial explanation is evident. The line joining stands with the greatest density of trees is nearly parallel to the 2' axis. This indicates that there is a very restricted optimum for trees on the 1' axis, and that factors on the 2' axis do not influence the trees so strongly. The optimum development potential for trees is a discrete amount of moisture here designated wet-mesic. There are trees on the pisolitic sites, presumably due to the absence of inundation, good drainage and better root aeration (vide Ramia, 1959b). It is perhaps here that the trees need and use the phreatic water more than in the wetter sites. Trees are excluded from sites where inundation occurs for long in spite of the presence of water.

This is indicated from the line joining stands without trees. The stands without trees or with a very low tree density are those which are very dry or where inundation is due to poor drainage leading to malaeeration in the soil, occurs.

The preceding paragraphs refer to trees in general. However not all tree species react to the environment in the same way.

Curatella has its optimum in wet and the wet-mesic stands, whereas Bowdichia is low in the wet-mesic but high in the mesic and pisolithic sites. Plumeria also has its optimum in dryer sites than Curatella. Byrsonima crassifolia has its optimum in the mesic and the dry-mesic sites but is low in the wet. Of the trees of lesser importance, Genipa occurs in wet stands, Tabebuia in mesic and Antonia in the dry-mesic stands. A similar restricted pattern is evident for the shrubs.

These patterns are most meaningful. The positions of the stands ^{in the ordination} are controlled solely by the characteristics of herb composition. That the trees show patterns when not used in the matrix indicates the close relation between the ground flora and the trees. This relationship probably is not causal, indeed the trees are too scarce to have an influence on the herbs. The trees and the herbs probably react to the environment nearly independently of each other, but they both react to the same or similar aspects of the environment.

Most of the herbs show correlations on the model as may be expected because the matrix was based on their phytosociological characteristics. Those few species which do not show correlations are probably invalid taxonomic entities. This is the case for the genera Paspalum and Andropogon and some other grasses and sedges.

The two species of the sedge Bulbostylis are well segregated, B.

(Stenophyllus) paradoxa is restricted to the dry and dry-mesic sites while B. conifera occurs higher on the primary axis. The woody herb Galactia jussieana is found in vegetation which segregates high on the 1^o axis also. Evolvulus sericeus, Mesosetum loliiforme, Zornia diphylla and Aristida spp. all have their optimum expression in the dry-mesic stand⁷, while Dichromena ciliata, occurs in the wet stands.

Nearly all species plotted on the model produced a closed polygonal pattern, in general with the higher values towards the center and the lower values towards the periphery. This atmospheric distribution is a three dimensional extension of the two dimensional contour patterns and the one dimensional/^(plane)Gaussian curves. (vide Bray and Curtis, 1957). Imperfections in this basic pattern were probably due to an insufficient number and distribution of stands being used. All of the patterns were intersecting yet discrete. Even the soil characteristics are clearly shown to overlap. Thus these patterns represent the amplitudes of the species on the three axes used. There were no apparent discontinuities in these patterns. This indicates that the vegetation sampled formed a continuously varying series or continuum, and vindicates the method of ordinating the stands of this continuum. This should caution workers against basing all their work on a few areas considered to be "typical". "core" or "characteristic".

Vegetation is composed of many interacting plants of the same and different species with different ranges, amplitudes of tolerance and abundance. As the components differ, then the vegetation differs. In this study the differences and similarities in the vegetation itself are used to arrange the different components of the vegetation into an orderly

spatial pattern. When the pattern emerges it is obvious that physical factors of the environment affect the vegetation to a great extent. The resulting matrix is entirely objective as it is based on quantitative data from many sites for many components species, which are "the sole determiners of the resulting patterns obtained". (Maycock, 1957). That similarly meaningful patterns were obtained from species (mainly the trees) that were not used in the construction of the matrix, is further evidence of its usefulness and validity.

M A T R I X

MATRIX
SUM
VALUE

73

STAND

1 2 3 4 5 6 7 8 9 10 48 49 50

1

2

3

4

(MATRIX VALUES)

5

6

7

8

9

10

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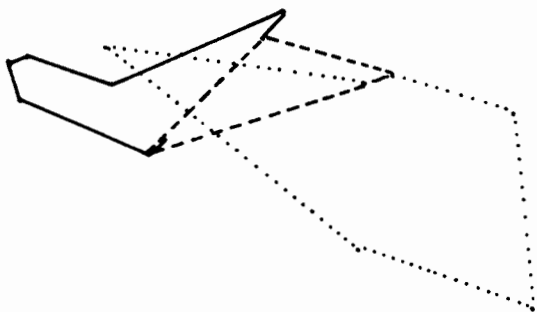
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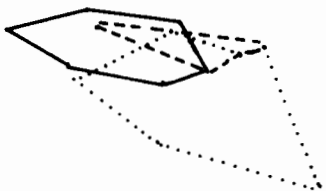
50

3 MINOR TREES, Importance values, 3 dimensions.

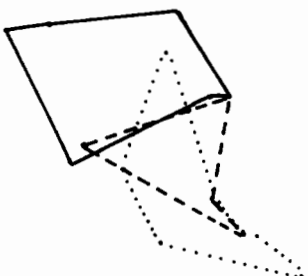
1° X 2°

Genipa americana

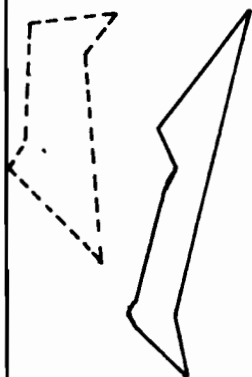
1° X 3°

Tabebeuia sp. ----

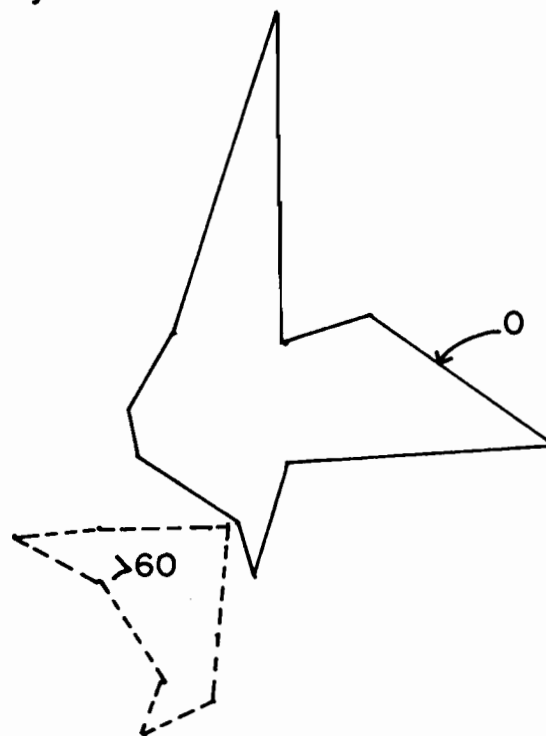
2° X 3°

Antonia ovata —

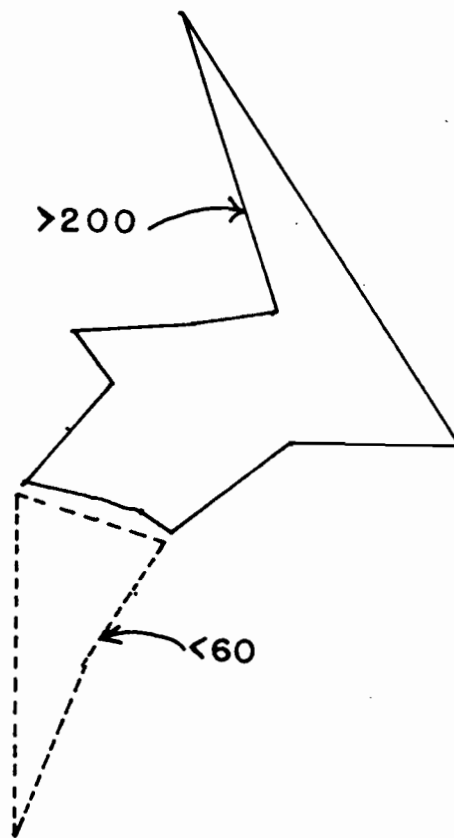
1° X 2°

Bulbostylis conifera >75f ———*Stenophyllus* (*Bulbostylis*) *paradoxa* >80f ----

1° X 2°

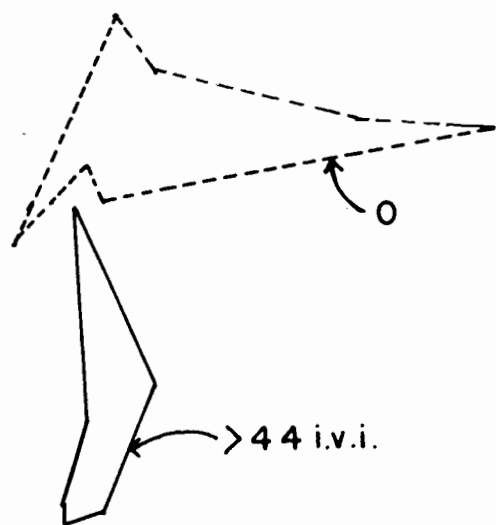
Byrsonima crassifolia i.v.i.

1° X 2°

Curatella americana i.v.i.

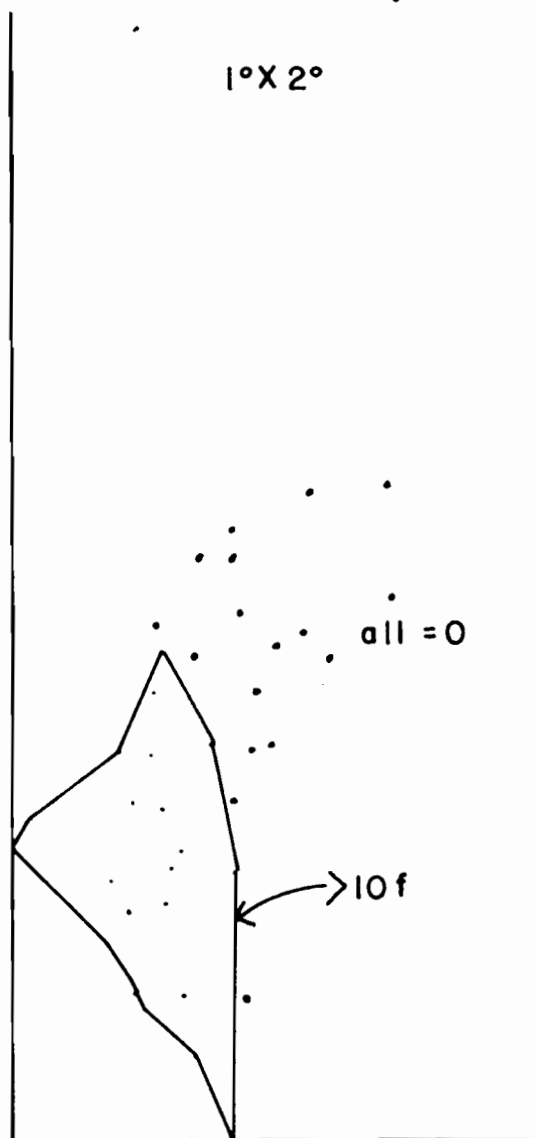
BOWDICHIA VIRGILIOIDES

1°X 2°



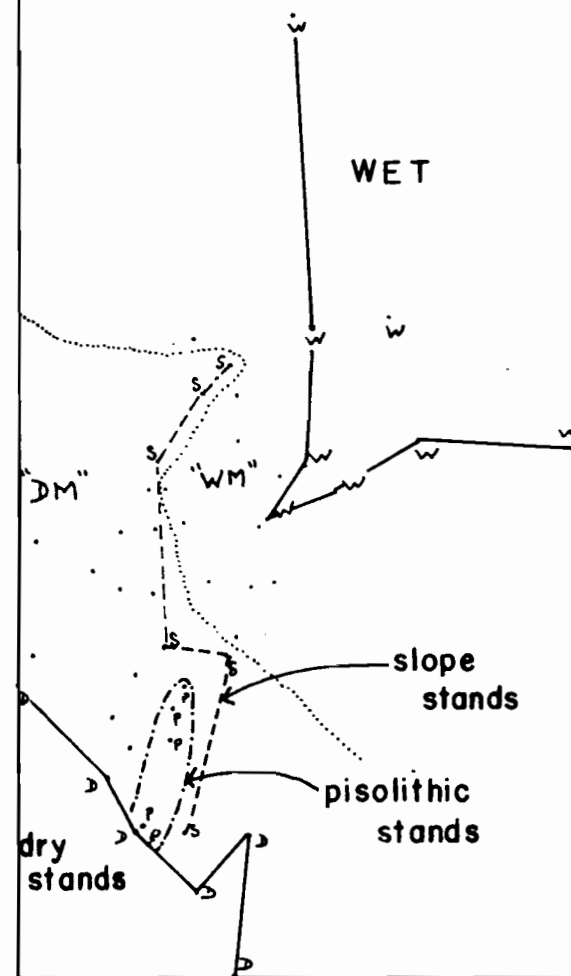
MESOSETUM LOLIIFORME

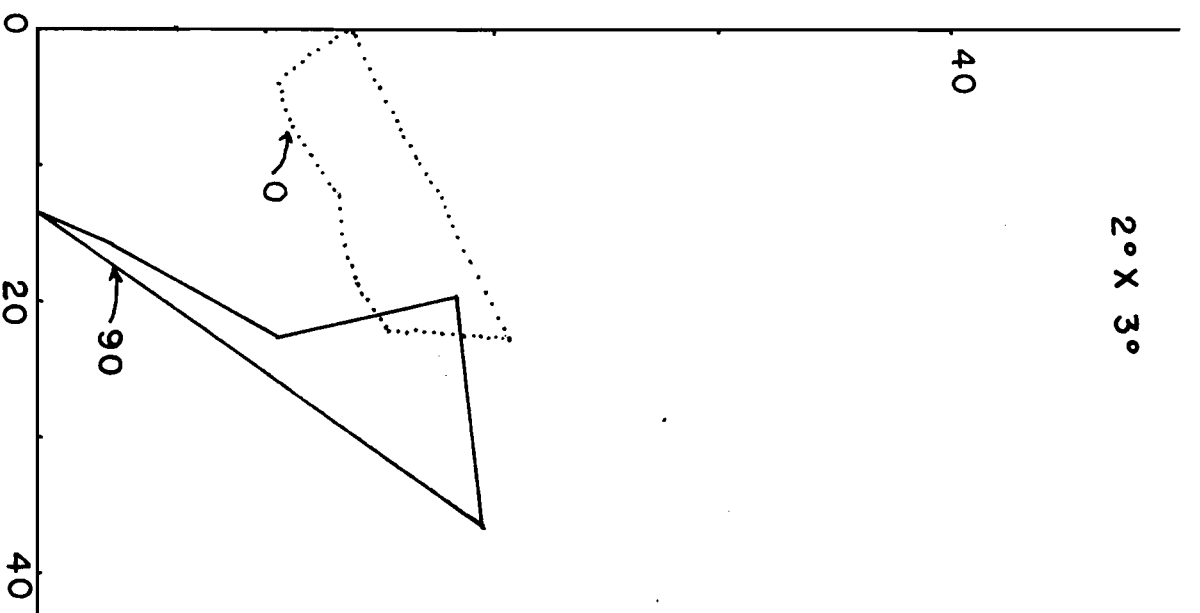
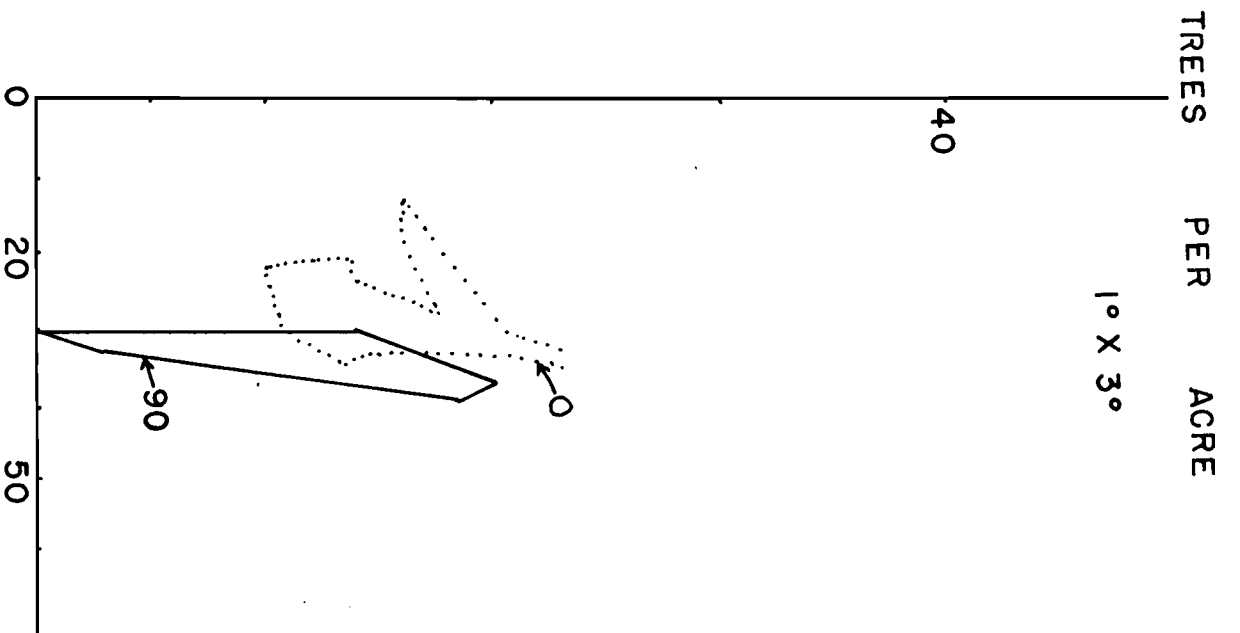
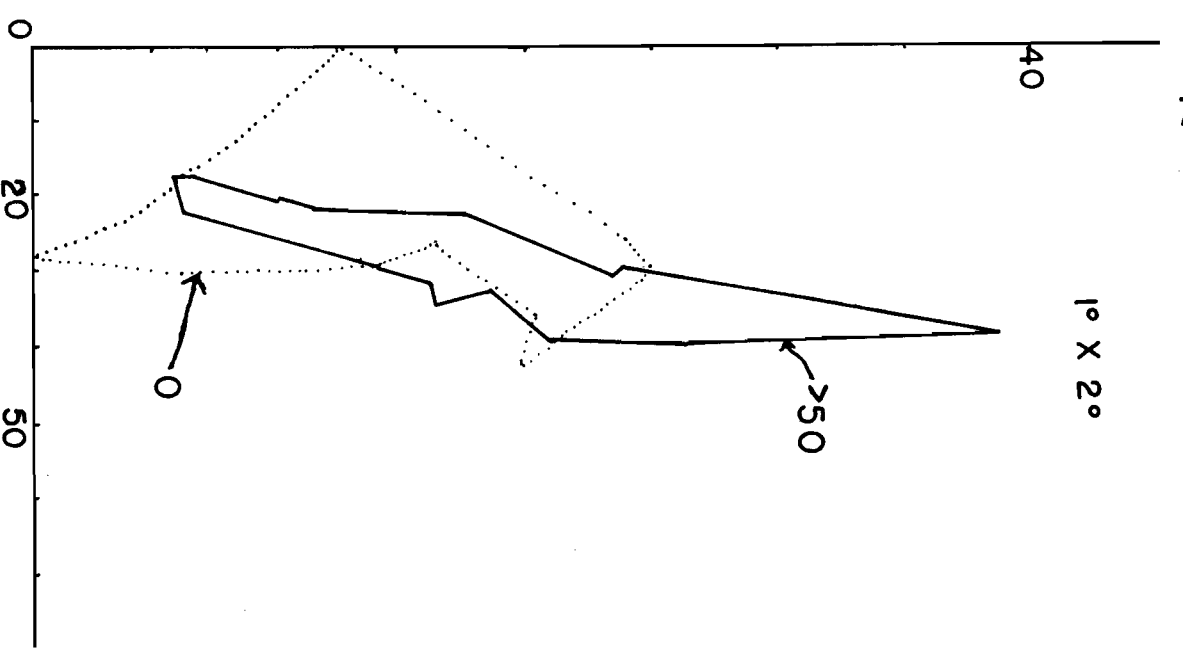
1°X 2°



STAND DESCRIPTION

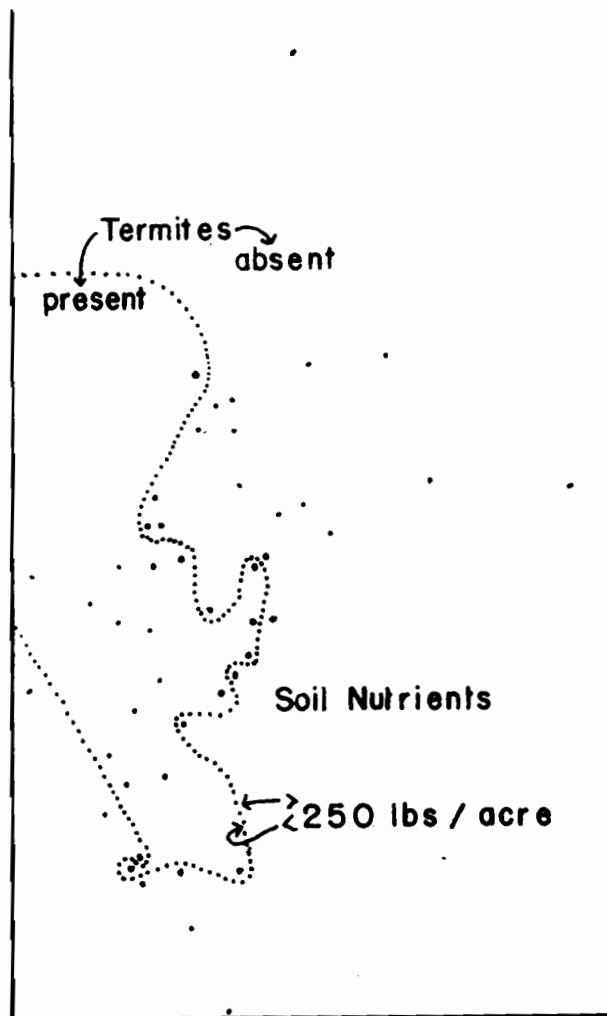
1°X 2°





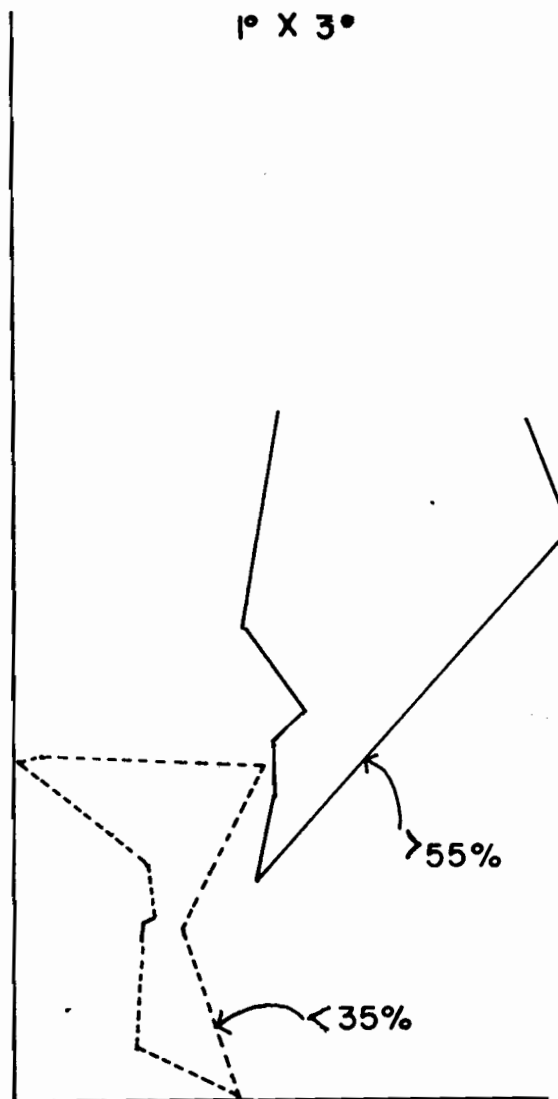
TERMITES and SOIL NUTRIENTS (K + Ca + Mg)

1° X 2°

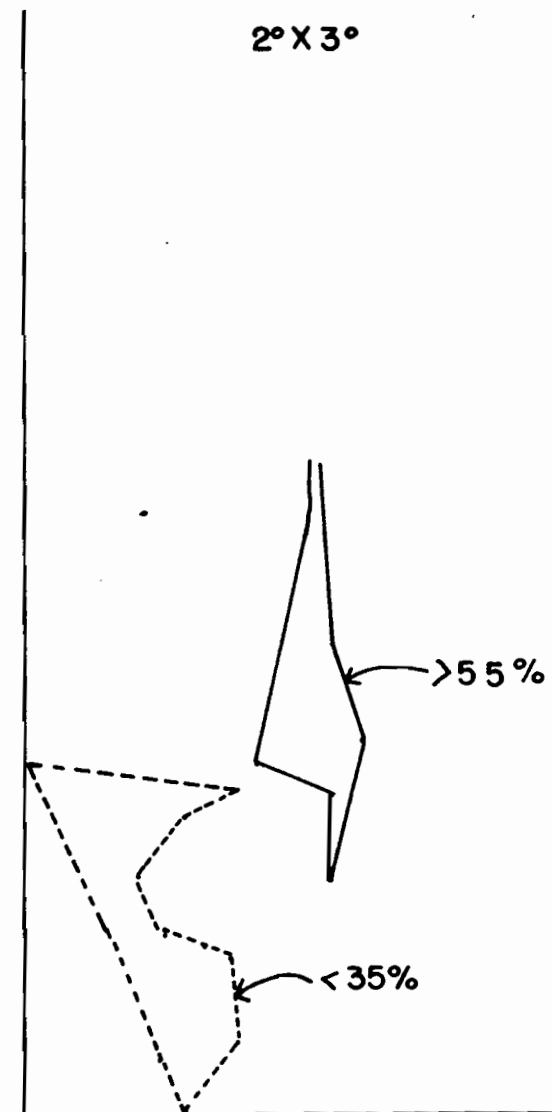


WATER RETAINING CAPACITY

1° X 3°



2° X 3°



TERMITES

The presence and absence of termitaria were plotted on the model and were found to be sufficiently sensitive although density and dominance had also been calculated. There was a striking correlation between termitaria and the stand categories. All of the stands designated dry-mesic had termitaria except one stand. This indicates that termites have a marked preference for these sites. Though not restricted to these sites a few termitaria were found in closely contiguous categories.

All three axes seem to be related^{to} the occurrence of termitaria, as they occurred near the origin of all the axes. To ascertain what factors had the most influence on termites, their occurrence was plotted against soil nutrients. There was an exact and inverse relation between soil nutrients and termites. Where the level of soil nutrients was over 250 pounds/acre, there were no termites whatever.

It is interesting to speculate whether or not the termites remove soil nutrients and concentrate it in the mounds or simply avoid high nutrient areas or the factors which produce high nutrient levels. Some factor may reduce termite populations on these rich sites.

These results were considered to be a most illuminating glimpse at the structure of the ecosystem. This is thought to be the first time that a quantitative relationship has been demonstrated by this method between the vegetation, the soil, and the fauna.

PICTURES OF THE THREE DIMENSIONAL MODEL

(Black Dot Marks Direction of Origin)

1. **SOIL NUTRIENTS:** (K + Ca + Mg) Low soil nutrients, less than 75 lbs/acre (single black bead) are to the left; high soil nutrients, over 200 lbs/acre are clustered to the right (double light beads).
2. **ORGANIC MATTER %:** Low values (black beads less than 1.5%) are low on the third axis and separated from the high values (double light beads over 2%).
3. **WATER RETAINING CAPACITY:** Low values (single black beads less than 35%) are well separated from high values (double light beads over 55%). Left photograph shows the separation on the second and the first axes from above; the right photograph shows the distribution relative to the third axis.
4. **AVERAGE COVER %:** Double light beads represent stands of over 60% cover, while black denotes under 40%. Note the similarity in the patterns of these four factors. The stands towards the origin are low in Nutrients, Organic Matter, Water Retaining Capacity and Cover. Away from the origin the situation is reversed.
5. **Ruellia geminiflora:** Beads mark the presence of this species; this itself is fairly restricted. Furthermore this presence is separated into low frequency (single black bead under 50%) and high frequency (double light bead over 50%).

6. Dichromena ciliata: Single black beads indicate stands where the frequency is less than 35%; the double light beads indicate frequencies of over 35%.
7. Mesosetum loliiiforme: The double light beads are on stands where the frequency is over 10%. The empty stands are of presence only. The single black beads mark the absence of this grass. Note how restricted is the amplitude of tolerance.
8. Byrsonima verbascifolia: The black beads mark stands of over 30% frequency and in general are towards the lower right corner. The unfilled rods indicate frequencies less than 30%, and the grey beads indicate absence. This species is therefore very wide ranging, possibly due to its habit but its optimum expression occurs in dry sites.
9. TREES PER ACRE: Black beads represent over 50 trees per acre. This has a narrow optimum on the second axis (bottom edge of photo) as the beads are in a close line parallel to the first axis. The grey beads mark treeless stands and the unmarked rods are stands with fewer than 50 trees per acre. Many of the tree-less stands are low on the first axis.
10. Byrsonima crassifolia: Black beads over 60 I.V.I., seven centrally clustered stands. Cylindrical beads mark treed stands without B. crassifolia; grey beads mark treeless stands.
11. Plumeria incidera: Black beads over 60 I.V.I., others as no. 10. This species is low on the third axis and fairly narrowly restricted.

12. Bowdichia virgilioides: Black beads over 45 I.V.I., others as no. 10. This species is even more restricted than Plumeria.

13. Curatella americana: Black beads over 200 I.V.I., grey cylinders less than 200 I.V.I. This shows a close correlation on the first and third axes. All the high values are grouped away from the lower values.

14. Genipa americana: small dark grey cylinders (5)
Tabebuia sp. large grey cylinders (4)
Antonia ovata: black beads (6)
 The beads here mark the presence alone of these minor tree species, all of which show discrete, unique yet overlapping amplitudes.

15. Nasutitermes ephratae: Black beads indicate the presence of termites. Grey cylinders soil nutrients over 250 lbs/acre. The termites are all clustered together without any non-termite stands intervening at all. In addition they are restricted around the dry mesic area. There is also a nice separation from the high soil-nutrient stands; the dividing line between the two is very distinct.

16. (as no. 15, from above.)

SOILS

From an analysis of the soils and their reactions with the vegetation, three main categories were apparent. The reddish, excessively drained soils called Rubrozem by Hardy (1962) were mainly dry-mesic. These soils are very deep and very porous. Hardy (1962) designates most of the Cerrado soils as belonging to this red-brown latosol group, although this term has been criticised. (vide Mohr and van Baren, 1954). The other well drained soils were the sands. When excessively drained on upland sites they were very light in color; if lower down the drainage catena they may become brown and darker. The sandy soils were ecologically dry although the low sand areas were seasonally inundated. The third main type of soil was dark colored and hydromorphic. Such soils occur in low moist sites and were, generally richer. These hydromorphic soils were not well drained but true planosols were rare in the Rupununi. In the Aripo savanna in Trinidad very distinct pans are present both of the clayey mottled orange type with concretions and of the fragipan type. The drainage in these areas was severely impeded but the pan was so shallow that the soils become desiccated in the dry season.

In general, the soils are very deep and water is not in short supply. In the Rupununi the phreatic level was usually above 10 meters at its lowest point. Schubart and Rawitscher (1950) and Schubart (1959) found that the phreatic level was highest in the dry season and lowest in the wet season due to a time lag of about six months for infiltration to 20 meters. Rawitscher, Ferri and Rachid (1943) claim that the Cerrado soils carry three years rainfall in some places.

The foregoing indicates a basic difference in savanna observations. The Brazilian school finds phreatophytes and no impedance (Ferri, 1943, 1944, 1955, 1960, 1961, and Coutinho, 1958, and Labouriau, 1952, and Lamberti, 1960, etc.) while in the Llanos a similar vegetation occurs on planosols where the pan offers resistance to the roots of species which elsewhere are phreatophytic. (Vareschi, 1960, Foldats, 1964, Beard, 1953, and Sauer, 1950). The main cause of poor tree growth is lack of root aeration due to flooding (Kramer, 1956, Michelmores, 1939). This appears to be a partial explanation for the denser growth of trees in the Cerrado than in the Llanos.

The various soil factors represent easily measurable components of the plant environment, and in consequence the soil was analysed in some detail. The vegetation is, of course, in intimate contact with the soil and interaction between the two can be expected. Correlations can be demonstrated but it is more difficult to cite cause and effect relationships, due to complex ecological integration, the inherent nature of Ecology. The Ecologist measures naturally occurring aspects of the ecosystem such as the phytosociology which is a statement of what exists and an interpretation of this state as far as possible. There are no control experiments and no factors can be kept constant or eliminated for the course of the experiment. So adequate analysis of the Ecosystem is both complicated and exceedingly difficult.

Without exception, every factor of the soil that was measured in this study was found to correlate to some extent with the three dimensional vegetation model. These correlations indicate relationships between the vegetation and its environment. In spite of the unusually low levels for soil nutrients, even the small differences that existed were found to

have very significant relationships with phytosociological characteristics as seen in the stand distribution in the model.

The moist, poorly drained sites were relatively high in nutrients, pH, and organic matter. The excessively drained sands and red earths sites were lowest in these factors. Even when soil color is plotted on the model the reds are clustered together apart from the group of dark colored soils. The water retaining Capacity was especially significant on the third axis, and correlated well with the occurrence and density of trees.

These observations support the theories of Alvim (1954) and Arens (1963) that mineral deficiency in the soil is important in savannas. In this respect the situation in the Rupununi savanna seems to be more like that occurring in the Cerrados than the Llanos. The soils of the Rupununi (Loxton et al, 1958, Stark et al, 1959) are similar to those of the Cerrado. (Ranzani, 1963, Hardy, 1962, Viana and Araujo, 1946, Alvim, 1954, and Araujo, 1952). Arens' Theory of Oligotrophic Scleromorphism (Arens, 1963) has been questioned by Labouriau (1963). Alvim and Araujo (1952) maintain that deep roots are more a response to the low mineral level than to obtain more water. Denevan (1964) indicates that tree roots cannot reach the fresh deep soil so that a closed cycle of nutrients occurs, further impoverishing the surface soil.

ENVIRONMENTAL CHARACTERISTICS

	SOILS			TERMITARIA		
	Min.	Max.	Av. (of 50)	Av. (of 2)	Min.	Max.
pH	4.4	6.2	4.9	4.8	4.7	5.0
pH tampon	6.1	6.9	-	-	6.65	6.7
Difference (from 7.0)	0.1	0.9	-	-	0.3	0.35
% Carbon	0.11	9.49	1.47	2.75	1.67	2.48
% Organic matter	0.2	12.4	2.5	3.6	2.9	4.3
% N ₂	0.02	0.75	0.09	0.27	0.60	0.14
P ₂ O ₅ lbs/acre	26.0	60.0	35.4	49.5	30.0	69.0
K "	3.0	148.0	41.6	155.0	90.0	220.0
Ca "	0	572.0	90.9	697.0	214.0	1180.0
Mg "	0	136.0	42.1	293.5	87.0	500.0
Total nutrients (K + Ca + Mg)	3.0	689.0	172.7	1145.5	391.0	1900.0
H. milli-equivs.	1.0	16.0	3.7	3.2	3.0	3.5
Water Retaining Capacity	28.3	186.2	50.7	40.7	37.2	44.2
%Cover	20.0	95.0	47.7	-	-	-

FLORISTICS

This list of species probably contains most of the species occurring in the Northern Rupununi Savanna, and was compiled mainly from the author's collection, determined by the Smithsonian Institution in Washington; for these the appropriate authorities are given in the list. The other species are from Myers (1934, 1936a, 1936b), McCorkle (1952), Rutherford (1958), Harrison (1963) and Graham (1964). The Ebini plants have been assiduously collected by Harrison (1958). The Aripo Savannas in Trinidad have been recently botanised by Richardson (1963).

The limitations of the list are:

1. Some habitats were not collected thoroughly, e.g. Ité Swamp.
2. Bush Island flora is not included.
3. The whole of the savanna area was not covered with equal detail.
4. Some of the flora at the end of the dry season was not collected.
5. The determinations were not complete at the time of writing.

For these reasons a statistical floristic analysis is not presented, but a general account of the flora is included. The flora may well prove to be the best criterion for savannas as it is the resultant of all previous classifications.

About 100 families of flowering plants are represented, or a third of the total number of plant families in the world. About a quarter of these families are monocotyledonous, the largest family being the Gramineae, followed by the Leguminosae, Cyperaceae and Rubiaceae, all with more than 25 species. These four families represent

40% of the flora. Thirty seven families are represented by a single species. Most of the families are tropical and many are widespread. The Martyniaceae and Bixaceae are the only strictly South American families, while the Cactaceae and Limnanthaceae are New World families. The Pedaliaceae is naturally restricted to the Old World and has probably been introduced to South America only recently.

The floristic affinities of the Rupununi Savanna are difficult to determine owing to the lack of adequate species lists from other savannas. Available lists vary more in degree of completeness than in flora. As may be expected the contiguous Rio Branco savanna is very similar to the Northern Rupununi and even more so to the Southern Rupununi savanna. Most species in Takeuchi's lists (1960a and b) occur in the Rupununi. Harrison's detailed list from Ebiní (1958) reveals a strong affinity to the Rupununi but the intermediate savannas are more similar to the Suriname savannas (Heyligers, 1963, Donselaar, 1964, Lanjouw, 1936, 1954) and the Cayenne savannas. (Bouillene, 1925, 1926, Rue, 1958 and Hooek, 1960). These Intermediate savannas are floristically related to a lesser extent to the Amazonian pockets of savanna. (Huber, 1900, Ihering, 1907, Luetzelburg, 1939, Ducke and Black, 1953, Rue, 1958, and Egler, 1960).

Parts of the Llanos are very similar to the Rupununi savanna. The comparative list of Lasser (1955) is by far the most complete. The shorter lists of Blydenstein (1962) at Calabozo, Ramia (1959a) at Apure and Hueck (1961) show strong similarities.

The Brazilian Cerrados, although thousands of feet higher than the Rupununi, show a marked similarity to it. The Cerrado flora (Rawitscher, 1948, Rawitscher and Ferri, 1942, Rawitscher and Rachid,

1946, Rizzini and Heringer, 1961, 1962, and Ferri, 1955) has many of the Rupunini species but is floristically richer in general. These important Cerrado plants have not yet been reported from the Rupunini savannas: Dimorphandra sp., Stryphnodendron sp., Andira sp., Kielmeyera, Caryocar sp., Qualea sp., and Salvertia sp. The savannas in Southern Brazil show rather less floristic similarity to the Rupunini. (Eiten, 1963, Alvim, 1952).

The savannas in Africa have some species and genera in common with the Rupunini. The affinities are limited to cosmopolitan and pantropical plants. There is a close physiognomic and ecological similarity however. (Cole, 1963). Adjahoun (1962) gives a full list for the Lower Ivory Coast, and Acocks (1953) and Bews (1917) for the Veldt. Chevalier (1931, 1933) and Schnell (1961) compare the floras of South America and Africa in detail. Good (1953) presents useful floristic analyses, and Vester (1940) maps the range of each family.

Chevalier (1931) lists 300 species as common to the American and African tropics and which are not weeds. About 7% of these species occur in the Rupunini savanna. So far only about 20 Pantropical weeds have been reported from the Rupunini, and about 8 American weeds. The genera Helicteres, Ichnanthus, and Symplocos are common to the Rupunini and Asia, while Cochlospermum sp., Symphonia sp., and Passiflora sp. are discontinuous in the tropics. The genera Cassia, Erythroxylon, Hyptis, and Turnera are mainly American.

Many savanna plants have deep and swollen roots. Ravitscher (1948) mentions ten plants which occur in the Rupunini and have roots tapping the water table, and calls them phreatophytes. There are

probably many more phreatophytes but roots are not easy to study so little work has been done on them. It would not be surprising if all the Rupununi shrubs were eventually found to be phreatophytes to varying degrees.

Xylopodia are underground swellings of root or stem, which act as a food or water store and which enable the plant to withstand fire and drought. Most of the low woody shrubs have xylopodia. Ten plants from the Rupununi are listed as good examples of xylopodia.

Ephemerals are here distinguished from aquatics in that the former live in flood water and the latter in ponds which may, however, be temporary. Some of the types are facultative. Ten ephemerals are listed as examples of which only Lophotocarpus sp. and Bacopa spp. are at all common.

The flora consists mainly of perennials, but may be divided into 6 groups according to their habit. The trees and most of the shrubs are phreatophytes. Most of the woody herbs and small shrubs have xylopodia. (Hoehne, 1939). Aquatic plants are not really part of the savanna. Ephemerals complete their short life cycle in flood water. Most of the grasses are perennials. The roots of the Rupununi grasses penetrate to a depth of 1.5 to 2.5 meters and are in contact with such a large volume of soil that the plant lasts well in to the dry season before the tops become brown and sere. Fire may sometimes stimulate the production of succulent sprouts before the rains, indicating that some stored food and water is present late in the dry season.

The final group of plants composed of annuals is very small indeed. Further study may reduce this group by demonstrating

xylopodia in some members. These plants use water in the top layer of the soil and produce seed rapidly and abundantly.

The Flora in general is very poorly known. Two new species were collected in the course of the study: Schizaea and Sacciolepis and others may be new. The flora is interesting as it is so varied and contains some beautiful and unusual plants. There are many species of the insectivorous genus Utricularia and at least two of Drosera. The tree used to stun fish, Antonia ovata is common. The uncommon Haemodoraceous plant Schieckia occurs in the wet lowland sites.

It is often said that the savanna vegetation is xerophytic. Although the vegetation has some xeromorphic features (Morretes and Ferri, 1959) in general savanna environment is not truly xeric. Most of the supposedly xeromorphic features appear to some extent adaptations to fire. Xylopodia, for example, probably are more pyrophytic in function than xerophytic. Many xylopodic plants have very deep roots supplying the plant with adequate water until the fire. Then the xylopodium provides nutrients for sprouting. In addition the trees are not truly xeromorphic. Ferri (1944, 1955, 1960, 1961a, 1961b) has shown that cuticular transpiration is very high, and that the transpiration curve in general follows that of evaporation. Tree leaves are generally large. The grasses are no more xerophytic in the savannas than in any other natural grassland. However, the space in the root cortex reported by Rawitscher (1948) may be a xerophytic feature, and Cacti are certainly xeromorphic although uncommon. Their roots were not studied.

FLORISTIC ANALYSIS

<u>LARGEST FAMILIES</u>		<u>LARGEST GENERA</u>	
FAMILY:	NO. OF SPECIES	GENUS:	NO. OF SPECIES
Gramineae	98	Paspalum	16
Leguminosae	55	Panicum	14
(Caesalpinioideae 12)		Andropogon	13
(Mimosoideae 6)		Polygala	10
(Papilionatae 37)		Cassia	9
Cyperaceae	39	Cyperus	9
Rubiaceae	26	Eriocaulon	8
Compositae	19	Axonopus	8
Melastomaceae	15	Rhynchospora	7
Euphorbiaceae	15	Byrsonima	6
Polygalaceae	12	Phyllanthus	6
		Aeschynomene	6

PANTROPICAL WEEDS

Abrus precatorius	Crotalaria
Alternanthera sessilis	Desmodium
Amaranthus spinosus	Emilia sonchifolia
Andropogon leucostachyus	Elytis atrorubens
Aeschynomene	Leersia hexandra
Bidens pilosa	Mimosa pudica
Borreria	Paspalum conjugatum
Cassia	Polycarpaea corymbosa
Cenchrus echinatus	Sida cordifolia
Clitoria	Sporobolus indicus
	Urena lobata

AMERICAN TROPICAL WEEDS

Boerhaavia coccinea
Clidemia hirta
Cynodon dactylon
Dactyloctenium aegyptium
Eleusine indica
Jussiaea peruviana
Maranta arundinacea
Phyllanthus carolinensis

RUPUNUNI TREES

Anacardium occidentale	Curatella americana	Myrsinaceae
Annonaceae	Erythroxylon (round leaves)	Ochnaceae
Antonia ovata	Erythroxylon (red flaky)	Palicourea rigida
Bowdichia virgilioides	Genipa americana	Paullinia
Byrsonima coccolobaefolia	Guettarda spruceana	Plumeria inodora
Byrsonima coriacea	Cuttiferae	Roupala
Byrsonima crassifolia	Hirtella racemosa	Rutaceae
Byrsonima stipulacea	Homalium	Rosaceae
Cactaceae	Humiria balsamifera	Sapindaceae
Coccoloba spp.	Humiria floribunda	Tabebuia
Connarus incompus	Leguminosae spp.	Turneraceae
Combretum	Myrtaceae (privet)	Verbenaceae
Copaifera	Myrtaceae (pilosa)	

COMMON TREES

Curatella americana
Myrtaceae (pilosa)
Plumeria inodora
Byrsonima crassifolia
Bowdichia virgilioides
Erythroxylon (flaky)
Roupala
Antonia
Genipa
Tabebuia

RUPUNUNI SHRUBS

Allophyllus
Byrsonima verbascifolia
Casearea
Coccoloba
Clibadium surinamense
Davilla aspera
Erythroxylon
Galactia jussieana
Guazuma
Lippia schomburgkiana
Mackaerium'
Mimosa
Ouratea
Psidium spp.
Randia formosa
Rutaceae (?Xantoxylum)
Tibouchina aspera
Tocoyena

PHREATOPHYTES

Aegiphila
Annonaceae
Byrsonima coccolobaefolia
Byrsonima verbascifolia
Connarus
Copaifera
Erythroxylon
Mackaerium
Ouratea
Palicourea
Tocoyena

XYLOPODIA

Centrosema
Cissampelos
Cochlospermum
Galactia jussieana
Helicteres
Hyptis
Lippia
Merremia
Polygala monticola
Ruellia
Waltheria

EPHEMERALS

Anacharis
Bacopa
Butumaceae
Cabomba
Callitriche
Hydrocotyle
Lophotocarpus
Mayaca
Nitella
Reussia

THE OCCURENCE OF THE MAIN RUPUNUNI TREES AND SHRUBS

	ESINI	SURINAME	RIO BRANCO	LLANOS	CIUDAD BOLIVAR	CALABOZO	APURE	CHAPPARALES	AMAZONIAN	CAMPO CERRADO I	CAMPO CERRADO II	S. BRAZIL	TRINIDAD	HONDURAS
<i>Anacardium occidentale</i>	o	o		o					'	o	o	'		
<i>Antonia ovata</i>		o							o	o				
<i>Bowdichia virgilioides</i>				o	o	o	o	o	o	o	o			
<i>Byrsonima crassifolia</i>	o	o	o	o	o	o	o	o	o	o	o	'	o	o
<i>coccolobaefolia</i>	o	o		o	o			o	"	o	o			
<i>Chrysobalanus pellocharpa</i>	o			o									o	
<i>Connarus</i> sp.				o	o	o				o	o	o		
<i>Curatella americana</i>	o	o	o	o	o	o	o	o	o	o	o		o	o
<i>Erythroxylon</i> spp.		o		o	o	o		o	o	o	o	o		o
<i>Genipa americana</i>			o		o		o		o				o	'
<i>Hirtella racemosa</i>	o	'	'	'					"	o			o	
<i>Humiria floribunda</i>	o	o							o	'				
<i>Palicourea rigida</i>	o	'	o	o	o	o		o	'	o	o	o		
<i>Plumeria inodora</i>									'					
<i>Randia</i> sp.			o	"	o	o	o							o
<i>Roupala</i> sp.		o		o	o				o	o	o	o		
<i>Tabebuia</i> sp.		o		o				o		o	o	o	o	o

THE OCCURRENCE OF SOME RUPUNUNI PLANTS

	EBINI	SURINAME	RIO BRANCO	LLANOS	CIUDAD BOLIVAR	CALABOZO	APURE	AMAZONIAN	CAMPO CERRADO II	S. BRAZIL	TRINIDAD	HONDURAS
<i>Andropogon leucostachyus</i>	o	o	"	o			o	"			o	-
<i>selloanus</i>	o	o	o	o	o	o	o	'			o	
<i>Aristida tinctoria</i>	o	o	'	o	o	"	o	o		"		"
<i>Axonopus compressus</i>	"	"	"	o	o	"	o	o		"		o
<i>Bulbostylis conifera</i>	o	o	o	"	o	o		o		'		
<i>Byrsonoma verbascifolia</i>		o	o	o	o	o		o	o	o	o	
<i>Casearea</i> sp.	o	o	o	o	o	o				o		o
<i>Cissampelos</i> sp.	o		o	o		o		o				
<i>Echinolaena inflexa</i>	o	o		o					o	o		
<i>Eugenia</i> sp.	o	o	o	o						o		
<i>Galactia</i> sp.	o	o	o	o	o	o	o			'		
<i>Gymnopogon foliosus</i>	o			o	'		'			o		
<i>Lippia</i> sp.										o		o
<i>Paepalanthus capillaceus</i>	'	'	'					"		"		
<i>Panicum laxum</i>	o	o	'	o	o		o	o				
<i>Paspalum carinatum</i>		o	o	o	o	o	o	o		o		"
<i>pulchellum</i>		o	o	o	o	o	"	"			o	
<i>Psidium</i> sp.	o	o	o	o	o	o						o
<i>Rhynchospora barbata</i>	o	o	o	"	o	o		"		"	o	
<i>Stenophyllus paradoxus</i>		o	o		o					'		
<i>Trachypogon plumosus</i>	o	o	'	o	o	"	o	'		'	o	

KEY

EBINI, British Guiana, Harrison, 1958 and Author's collection
SURINAME, Donselaar, 1964.

LLANOS, Lasser, 1955

CALABOZO, Llanos, Blydenstein, 1962.

APURE, Llanos, Ramia, 1959.

CHAPPARALES, Hueck, 1961.

AMAZONIAN Savannas, Egler, 1960.

CERRADO I, Rizzini, 1963.

CERRADO II, Ferri and Coutinho, 1958.

S. BRAZIL, Eiten, 1963.

TRINIDAD, Richardson, 1963, and Author's collection

HONDURAS, Johannesson, 1963.

RIO BRANCO, Takeuchi, 1960.

CIUDAD BOLIVAR and vicinity, Corp. Venez. de Guayana, 1961.

o Present

' Genus present

" More than one other species present.

DISCUSSION

A distinctive feature of the literature of the savannas is the search for a grand theory to explain their existence and nature. However, it seems unreasonable that one cause could be responsible for all of the many different types of savanna, which today are the result of a combination of many factors. It would seem more appropriate to study the problems of each savanna separately. A generalization may then be sought when it is based on a sufficient number of studies of different savannas.

At present, such generalizations frequently confuse different aspects of the problem. A clear distinction should be made between Predisposing Factors, Causal Factors, Resulting Factors, and Maintaining Factors. Each type of factor is susceptible to different types of study. This study is mainly concerned with maintaining factors, that is, the factors operating in a particular savanna at present.

The main theories concerning savannas fall into three categories: Climatic, Biotic and Edaphic.

Climatic:

Formerly there was thought to be a 'savanna climate'. This is no longer considered to be so (Beard, 1949) as savannas have been found to occur in many different climates. In general, a dryer climate may be a Predisposing Factor for savanna formation in some areas. Dryer microclimates may be a Resulting and Maintaining factor due to the removal of forest. Gross change in climate is considered with the Edaphic theories. Water deficiency is not thought to occur in the savannas studied by Rawitscher (1942, 1948, 1950a), Rawitscher and

Ferri, 1942, Rawitscher, Ferri and Rachid, 1943, and Vareschi, 1960, etc.). Certainly excess or paucity of water does not limit the savanna ground layer as much as low light intensity limits the forest ground layer. The effect of the alternation of wet and dry seasons has been amplified in savannas and so may be a Maintaining and Resulting effect. This does not apply to the savannas of the Amazon basin. Wind is a resulting factor as it dries the topsoil after the rains, increases in treeless areas and increases the effect of fire.

Biotic:

Man is an important Causal Factor in savanna formation due to his cutting and burning of forest. Fire is probably more of a Resulting Factor than a Causal Factor of savanna, but it is definitely an important Maintaining Factor for many such areas of savanna. One distinctive effect of fire is the abrupt nature of the savanna-forest boundary. It may also contract any intermediate areas between the two. Grazing and trampling may be a Maintaining Factor in some savannas. Occasional overgrazing was observed near gates in the Rio Branco Savanna, with a very depauperate vegetation of weedy plants especially Sida spp.

Edaphic:

Impeded drainage has been cited as a cause of savanna. It was not observed in the Rupununi and probably is not extensive there. Where it does occur it may be a Resulting and a Maintaining Factor. A shallow pan indicates a high water table and tree roots can often pierce a pisolithic laterite layer and possibly a fragipan. The drainage in

the Cerrados seems to be good. The soils in general are very deficient in minerals. This may be a Predisposing Factor or a Resulting Factor. Nutritional deficiency is an important factor in many savannas. It is not the sole cause as poorer soils are known to support forests. (The white sands which are purer than powdered window glass support Wallaba (*Eperua* spp.) forest in parts of British Guiana.) In the Rupununi savanna there is no closed nutrient cycle because of fire, leaching, and excessive drainage. Credence is given to Arens' theory of Oligotrophic Scleromorphism. (1958a, b, c.).

Studies of the causal factors of savannas are rare and difficult. Van der Hammen (1961a) has deduced from the pollen record that the savannas of Northern South America were larger in the last glacial than at present but there are signs that they may have started expanding again within the last 3,000 years. He discusses the climatic changes involved in the Quaternary, (1961b). Sauer (1944) arrived at a similar conclusion on savanna area using an anthropological approach. Hueck (1961) suggests from Plant Geographical studies that present savannas are relicts of larger formations of the last glacial, and is supported by Aubreville (1962).

There still seems to be some controversy over the Age and Area Theory. There is no doubt that "endemism" will be reduced by better collection. Bates (1948) suggests that the low endemism of the savanna fauna indicates the novelty of the savannas. This is supported by Vanzolini (1963) from studies of disjunct distributions. The converse is suggested by Sick (1959) and Warming (1899) and by the observations of Ducke and Black (1953) on the disjunct distributions of Rattlesnakes in the savannas. The distribution of plants should

prove to be a fruitful avenue of research but at present the knowledge of the flora is too limited to permit very detailed studies.

A geomorphological theory of savannas has been postulated by Veloso (1946) and by Cole (1958, 1959, 1960). Cole suggests that the Cerrado occurs mainly on flat senile landforms, where the soils are not being renewed, and that the slopes support forests. This does not strictly apply in the Rupununi as the Pakarima and Kanuku Mountains have extensive areas of savannas on their slopes.

Donselaar (1964) claims that the similarity between the mountain savannas and the white sand savannas of Suriname indicate their former geological connection. This would have been during the Mesozoic when the Guiana Shield started to rise leaving the Roraima sandstone plateau as isolated mountains. This follows the work of Fanshawe (1952) on the origins of the Guiana flora.

APPRAISAL OF METHODS

Whenever a three dimensional model has been constructed from a matrix, there have been conspicuous empty spaces. The model is a theoretical representation of the vegetation and probably has space for improbable combinations, (e.g. Wet gravel ridges), thus accounting for some of the gaps. However, in this case, it is likely that some of the gaps would be occupied by other types of vegetation. Ité swamp may be the true wet end of the continuum, Hillside savannas may be at the rich nutrient - good drainage part of the continuum. Muri Scrub may be an extreme low nutrient - sand type. These sites should be sampled as they become more important in other areas, e.g. Palm savannas in the Llanos and Muri Scrub in Suriname. An increase in the number of stands used would also reduce the gaps.

These quantitative phytosociological methods were devised for analysing well known vegetation in North America where gradient differences were so gradual that sophisticated statistical procedures had to be employed. The savannas are so little known that cruder methods would serve to accumulate information on the main types. Subsequently, sophisticated methods would be applicable. Presence lists for stands would be useful for Constancy; and Frequency would initially be adequate for trees. The Point-quarter method was derived for use in forests and where the trees become scarce this method becomes laborious. Long distance telescopic Range-finders would be useful. Air photograph interpretation of crown characteristics coupled with ground control is becoming increasingly valuable as an aid in such ecological research.

The sapling data are not presented here. The vegetative

specimens have not yet been related to the named specimens. It is probable that the "saplings" are not so much indicative of regeneration in the savanna but of a younger age class. It would still be interesting to see how the composition of the savanna is changing if the sapling data should prove different from the tree data. Coutinho and Ferri (1960) and Ferri (1960) show that germination is more common on the better soils of new savannas before impoverishment. From this study it follows that savannas may tend to the Campo Sujo type if given sufficient time.

FURTHER RESEARCH

Further avenues of research into savannas are suggested by this study. Savannas should be mapped with greater accuracy. This could be partly achieved from air photographs and by collating existing maps. At the same time, a quantitative expression of tree density even without regard to the species, could be made from the air photographs. These figures may be related to gross climatic studies such as water deficit.

Very useful information could be calculated from species Presence lists of the savannas mapped. Even a list of the Prevalent or Dominant species from each savanna would be of considerable value. Phytosociological studies, if they are based on quantitative methods so that savannas may be statistically comparable, may yet yield much of the explanation. They should be tried on the effects of fire and grazing.

On a smaller scale, root studies related to hydrology and transpiration have provided the most significant work to date. These studies would be most interesting if made in other comparable areas. If burning could be controlled or quantified it would provide useful information and help clear up much controversy. However, research studies not immediately related to commercial gain are hampered more by lack of funds than by lack of ideas.

POST SCRIPT

The people of the Rupununi savannas appear neither to need nor want advice on how to run their own affairs. The Amerindians can obtain schooling and employment. The Ranchers have a standard of living in direct proportion to their efforts, while most Governmental employees work only temporarily in the Rupununi.

The Rupununi is a very poor area in which to make a living. No amount of expertise, of which there is no lack, will produce a panacea. At present ranching appears to be the most suitable use for the Rupununi savanna. Economic considerations preclude importation of fertilisers. From an ecological point of view, there are three items which may ameliorate the harsh environmental conditions. Firstly, tree planting, starting on a small scale in the better sites. The trees should be Phreatophytes if possible. These may reduce wind and fire, increase surface soil, nutrients and litter and improve water conditions. If a crop can be gathered from the trees so much the better. The Cashew (Anacardium occidentale) thrives there already. The Cashew pears can be preserved and the nuts used for oil or air-exported as a light weight-high cost commodity. Other fruit trees may be as successful. Secondly, the rotation of Range Grazing would reduce the surface compaction by trampling and by rain, aggravated by fire and high insolation. Thirdly, small scale water control by ditches and barrages would reduce flooding and provide water for the early part of the dry season.

Agricultural information concerning the Rupununi and similar areas may be obtained from McCorkle (1952), McClung et al. (1957),

Goode (1958), Loxton et al. (1958), Stark et al. (1959), Hueck (1961), Hardy (1962), Coimbra (1963), Filho (1963) and Freitas et al. (1963).

SUMMARY

The vegetation of the Northern Rupununi savanna was studied quantitatively for the composition of the trees, shrubs, herbs, and termitaria using the phytosociological approach of the Wisconsin School. A total of 50 stands, including 2 from Ebini savanna in British Guiana and 3 from Trinidad savannas, were selected at random and sampled.

Importance Value ($\frac{\text{relative}}{\% \text{ Frequency}} + \frac{\text{relative}}{\% \text{ Density}} + \frac{\text{relative}}{\% \text{ Dominance}}$) was calculated from the data derived by the Quarter-Method for trees, saplings and termitaria. $\frac{\% \text{ Frequency}}{\text{square}}$ for shrubs and herbs was calculated from occurrence in meter/square. These data were used to determine the relationships of stands based on the phytosociological similarities of the herbs alone, by means of the Matrix Method. Three axes were derived; each axis having at its ends the most dissimilar stands, with the intermediate stands ordinated between them. From the three axes, a three dimensional model was constructed showing an abstract spatial relationship of stands.

Quantitative values of the vegetation and of the environment were then plotted on this model. Obvious patterns were taken to indicate relationships, which were observed for all trees, herbs, shrubs and environmental factors that had been measured and that were plotted. The patterns of individual species all overlapped one another, but each was unique and discrete. There were strong correlations between aspects of the vegetation and environmental factors. (e.g. water retaining capacity of the soil with tree density and $\% \text{ Cover}$; and between the occurrence of termitaria and level of soil nutrients.) From the

results it appeared that the various types of vegetation formed a continuously varying series which vindicated the ordination of the stands as a continuum.

The vegetation of the area was dominated by grasses (Trachypogon, Andropogon, Paspalum, Aristida, Axonopus, Mesocetum, Eragrostis, Panicum) with sedges (Fimbristylis, Dichromena, Bulbostylis, Rhynchospora, Stenophyllus, Cyperus, Scleria) subdominant in places. Interspersed among the grasses were many herbs (Galactia, Borreria, Polygala, Cassia, Merremia, Evolvulus). Trees (Curatella, Myrtaceae, Byrsonima, Plumeria, Bowdichia, Erythroxylon) were never dense and were restricted to well drained gravel sites and rich moist sites. Shrubs (Palicourea, Randia, Connarus, Erythroxylon, Casipourea, Myrtaceae) were usually present. The soils were deep, senile, impoverished and acidic sands and gravels along with clay and silt.

The vegetation is characterised by the frequent occurrence of Xylopodia storing food and water, by the large and sclerophyllous leaves and thick bark of the trees, by the occurrence of Phreatophytes with roots tapping the water table, and by perennials and ephemerals and infrequent annuals.

The main features of the ecosystem are: Intense, periodic rainfall of the short wet season, with leaching, sheet-wash, erosion, surface compaction and increased run-off causing extensive floods alternating with the long drought with frequent fires, removal of humus and cover, and the increase in wind, insolation and evaporation.

The terminology of the savanna has been discussed; the terms used being defined. A literature review, including the important but little known Brazilian work, has been documented with copious references.

A description of the physical features of the area studied is given together with brief sections on the Geology, Soils, Geomorphology, Climate and Geography. The fauna, especially the termites is described with a section on the importance of fire as a factor.

As complete a list of species as possible is presented for the area; over 400 species belonging to 100 families are noted. A partial floristic analysis is presented comparing the Flora of the Rupununi with the Llanos, Campos Cerrados and other tropical savannas. Lists of plants are presented for physiognomic, geographical and habit groups.

Concluding sections are presented on the savanna ecosystem, a critique of the methods used, ecological observations and possible avenues of further research.

STAND RECORD

Plant Ecology Research
British Guiana Savannas

Stand No: 109

Name

Locality:

Map Sheet:

Air Photo:

Date:

Observers:

Size of Stand:

Size of Area Sampled:

Vegetation Type

Soil Type:

Topography:

Slope:

Directions

Condition of Stand:

Open Grown Trees:

% cover:

Stumps:

1.	4.	7.	10.
2.	5.	8.	11.
3.	6.	9.	12.

Soil Data:

	pH	N	P	K	Ca	Mg	Org. Mat.	Colloids	W.H.C.
A ₀									
A ₁									
A ₂									
B									

DEPTH

Characteristics (Color, Texture, Structure, etc.)

A₀
A₁
A₂
B

Parent Material:

Map:

Termitaria:

P R E S E N C E A N D F R E Q U E N C Y F O R M

Acisanthera	Cyperus cuspidatus
Aeschynomene	flavus
Amasonia	haspan
Anacardium	luzulae
Andropogon angustatus	unioloides
bicornis	Cyrtopodium
leucostachyus	Davilla
selloanus	Desmodium
tener	Dichromena
Antonia	Diodia
Appunia	Drosera
Aristida setifolia	Echinolaena
tinctoria	Eleocharis
Axonopus anceps	Eragrostis amabilis
chrysites	guianensis
compressus	maypurenses
Bacopa	Eriocaulon
Bauhinia	Eriosema
Borreria	Erythroxylon
Bowdichia	Eupatorium
Buchnera elongata	Euphorbia
palustris	Evolvulus
Bulbostylis conifera	Fimbristylis ferruginea
Byrsonima coccolobaefolia	mileacea
crassifolia	monostachya
stipulacea	
verbascifolia	Galactia
Casearea	Gymnopogon
Cassia cultrifolia	Genipa
flexuosa	Habenaria
glandulosa	Heliconia
hispidula	Hibiscus
patellaria	Hirtella
tetraphylla	Humiria balsamifera
viscosa	floribunda
Cassytha	Hyptis
Cereus	Indigofera
Cipura	Ipomoea
Cissampelos	Jacquemontia
Clidemia	Jussieuia lithospermifolia
Clitoria	sedoides
Coccoloba	suffructicosa
Connarus	Lagenocarpus
Cordia	Leptocoryphium
Coutouba	Lippia
Crotalaria maypurensis	Lisianthus
retusa	Loranthus
stipularia	Mandevilla
Curatella	Melochia
Curtia	Merremia
	Mesosetum

P R E S E N C E A N D F R E Q U E N C Y F O R M (Continued)

Myrtaceae ("Berberis")
("pilosa")

Neptunia

Oxalis

Paepalanthus

Palicourea

Panicum cyanescens

laxum

parvifolium

pilosum

stenodes

Paspalum gardnerianum

lachneum

millegrana

pulchellum

stellatum

Phaseolus gracilis

lasiocarpus

Phyllanthus caroliniana

niruri

Plumeria

Polygala adenophora

angustifolia

langicaulis

monticola

Psidium

Randia

Rhynchospora barbata

cephalotes

cyperioides

tenuis

Richardia

Rosaceae

Roupala

Ruellia

Sauvegesia

Schieckia

Schultesia

Scleria bracteata

hirtella

tenella

Sebastiania

Setaria

Sida

Sipanea

Sphenostigma

Sporobolus

Stachytarpheta

Stenophyllus

Stylosanthes angustifolia

Stylosanthes guayanensis
hispidula

Syngonanthus

Tabebuia

Tibouchina

Tonina

Trachypogon

Turnera

Utricularia

Waltheria

Xyris

Zornia

ADDITIONAL SPECIES:

[illegible]

Plant Ecology Research
 TREE DATA SUMMARY SHEET
 British Guiana Savannas

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Stand Number:

TREE	# PTS	# TRS	TOT DOM	# SAP	D.% SAP	F.% SOL	F.% TRS	% F.TR	SUM D.% TRS	DOM% TRS	DFD INDEX
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AVE.DIST.BTW'N TREES:

AVE B.A.:

TREES/ACRE

DOM./ACRE:

M A T R I X F O R M

SPECIES	ACTUAL FREQUENCY	MODIFIED FREQUENCY	SCORE VALUE
Adiantum			
Amasonia			
Andropogon angustatus			
Aristida radiata			
Aristida setifolia			
Axonopus chrysites			
Bauhinia			
Buchnera elongata			
Buchnera palustris			
Bulbostylis conifera			
Bulbostylis paradoxa			
Byrsonima verbascifolia			
Cactus			
Casearea			
Cassytha			
Cipura			
Cissampelos			
Citrus			
Clitoria			
Coccoloba			
Connarus			
Coutouba			
Cyperus			
Davilla			
Desmodium			
Dichromena			
Diodia			
Drosera			
Echinolaena			
Eleocharis			
Eragrostis glomerata			
Erythroxylon			
Eupatorium			
Evolvulus			
Fern climber			
Galactia			
Gymnopogon			
Habenaria			
Heliconia			
Jacquemontia			
Jussieua			
Legenocarpus			
Leptocoryphium			
Lippia			
Lisianthus			
Loranthus			

M A T R I X F O R M (Continued)

SPECIES	ACTUAL FREQUENCY	MODIFIED FREQUENCY	SCORE VALUE
Mandevilla			
Mesosetum			
Milky climber			
Mimosa			
Myrtaceae (Berberis)			
Neptunia			
Orchid (Green bog)			
Oxalis			
Palicourea			
Phyllanthus caroliniana			
niruri			
Polygala angustifolia			
longicaulis			
Psidium			
Utricularia			
Randia			
Ruellia			
Sauvegesia			
Schieckia			
Schultesia			
Scleria (Large)			
(lax)			
Sebastiana			
Setaria			
Sida			
Sipanea			
Sphenostigma			
Sporobolus			
Stachytarpheta			
Stylosanthes			
Tibouchina			
Trachypogon			
Waltheria			
Zornia			

PLANTS OF THE RUPUNUNI SAVANNAS

ACANTHACEAE

- Dipteracanthus angustifolius DOH
 Ruellia geminiflora HBK
 v. angustifolia (Nees) Griseba DOS

AIZOACEAE

ALISMATACEAE

- Echinodorus N
 Lophotocarpus guayanensis (HBK) J.G.Sm. WEH

AMARANTACEAE

- Alternanthera dentata WRH
 sessilis WRH
 Amaranthus gracilus WRH
 Iresine elatior WR

AMARYLLIDACEAE

- Curculigo scorzoneraefolia WRH
 Hippeastrum solandrifolium WRH
 Hypoxis decumbens WRH

ANARCARDIACEAE

- Anarcadium occidentale L. MFT

ANNONACEAE MOT

APOCYNACEAE

- Mandevilla scabra DFS
 Plumeria inodora DFT

ASCLEPIADACEAE

- Oxypetalum N

BIGNONIACEAE

- Pyrostegia venusta (Ker-Gawl) Miers. N
 Tabebuia MOT

BIXACEAE

- Bixa orellana N

BORAGINACEAE

- Cordia WRS
 Heliotropium fruticosum DRS
 indicum DRS

BURSERACEAE DRT

BROMELIACEAE

- Ananas comosus MRS
 Bromelia karatas L. MRS
 Tillandsia flexuosa Sw. MRH

BURMANNIACEAE

Burmannia WRH
Gymnesiphon WRS

BUTOMACEAE N

CALLITRICHACEAE

Callitriche N

CARYOPHYLLACEAE

Polycarpaea corymbosa DOH

CACTACEAE

Cereus DOS
Melocactus neglyi DRS

CAPPARRIDACEAE

CHARACEAE

Nitella N

COCHLOSPERMACEAE

Cochlospermum DRT

COMBRETACEAE

Combretum MRT

COMMELINACEAE

Commelina elegans Burm. F. WRH
erecta L. WRH
Dichorisandra hexandra (Aubl) Standl. WRH

COMPOSITAE

Acanthospermum australe (L) Kuntze MOH
brasilum MOH
Alomia DRH
Baccharis DRH
Bidens pilosus L. MRH
Centratherum muticum (HBK) Less N
Clibadium surinamense L. WRH
Elephantopus angustifolius MRH
Emilia sonchifolia N
Erechtites hieracifolia (L) Raf. N
Eupatorium amygdalinum Lam. N
Ichthyothere terminalis (Spreng) Blake DOH
Orthopappus angustifolius (Sw) Gleason N
Pectis elongata HBK MOH
Riencourtia N
Wedelia DRH
Wulffia baccata (L.f) Kuntze DRH
rubens Aubl. DRH

CONNARACEAE

Connarus incomptus WOT

CONVOLVULACEAE

- Aniseia DFH
 Evolvulus beccanus DFH
 sericeus DFH
 v. holosericeus DFH
 Jacquemontia evolvuloides DFH
 tannifolia
 Merremia aturensis (HBK) Hall f. DFH
 cissoides (Lam.) Hall f. DFH
 juncea DFH
 Quamoclit coccinea N

CRASSULACEAE

- Tillaea N

CUCURBITACEAE

CYPERACEAE

- Bulbostylis conifera (Reichb.) Clarke C.B. DF
 lanata (HBK) C.B. Clarke WR
 Cyperus articulata WO
 cuspidatus HBK. WR
 flavus (Vahl.) Nees WO
 haspan L. WF
 luzulae (L.) Retz WO
 platyphyllus WO
 simplex HBK. WO
 surinamensis WF
 uniloides R.Br.
 Dichromena ciliata MF
 Eleocharis caribaea WO
 geniculata WO
 punctata WO
 Fimbristylis annua DF
 ferruginea
 mileacea
 monostachya (L.) Hassk.
 spadica
 Fuirena umbellata Rottb. WO
 Kyllinga odorata
 Lagenocarpus guianensis WF
 tremulus
 weigeltii
 Mariscus (Cyperus) flavus WF
 Rhynchospora armerioides Presl. MF
 barbata (Vahl) Kunth MF
 cephalotes (L.) Vahl WO
 cyperoides
 longibracteata
 subplumosa
 tenuis Link. MF
 Scleria bracteata MF
 hirtella Sw.
 melaleuca
 pterota
 tenella
 Stenophyllus paradoxus (Spreng.) Standl. DF

DILLENIACEAE

Curatella americana L. WFT
 Davilla aspera WFS
 Tetracera N

DROSERACEAE

Drosera capillaris N
 kaitukensis N

ERIOCAULACEAE

Eriocaulon humboldtii Kunth WOH
 tenuifolium Kl. WOH
 Paepalanthus capillaceus
 lamarckii Kunth WOH
 subtilis Miq. WOH
 Philodice hoffmanseggii Mart. WRH
 Syngonanthus umbellatus (Lam.) Ruhl. WOH
 Tonina fluviatile Aubl. WRH

EUPHORBIACEAE

Caperonia palustris (L) St. Hil N
 Croton trinitalis Millsp. N
 Dalechampia affinis Muell Arg. N
 Jatropha urens L. N
 Mabea N
 Manihot N
 Euphorbia hypericifolia L. N
 Phyllanthus amarus WOH
 hyssopifolius WHO
 carolinensis Walt. WOH
 niruri L. WRH
 stipularia WRH
 urinaria WOH
 Sebastiana corniculata WRH
 linearifolia Lamj. WRH

FLACOURTIACEAE

Casearea silvestris DFS
 Homalium racemosum MRT
 Rynia N

GENTIANACEAE

Chelonanthus WRH
 Coutouba spicata Aubl. DFH
 Curtia tenuifolia (Aubl) Knobl. WOH
 Lisianthus WRH
 Nymphoides humboldtianum (HBK) Kuntze N
 Schultesia benthamiana DC. WOH
 brachyptera WOH
 subcrenata WOH

GRAMINEAE

Andropogon angustatus (Presl.) Steud. D
 bicornis L. W.
 brevifolius Sw.

GRAMINEAE (Continued)

- Andropogon condensatus* HBK.
 ssp. *elongatus* Hack.
 glomeratus
 hirtiflorus (Nees) Kunth.
 leucostachyus HBK.
 v. *subvillosus* Hack.
 selloanus (Hack) Hack. D
 semiberbis (Nees) Kunth
 tener (Nees) Kunth
 virgatum
Aristida capillacea Lam. D
 longifolia Trin.
 radiata
 setifolia HBK. D.
 tincta T & R.
Axonopus anceps (Mez) Hitchc. D
 astragalus
 aureus
 chrysites (Steud.) Kuhlman
 compressus (Sw.) Beauv.
 kaletukensis Swallen
 leptostachyus (Flügge) Hitchc.
 surinamensis (Hochst.) Hemr.
Brachyaria emini (Mez) Robyns N
Cenchrus echinatus N
 brownii DR
Chloris polydactyla (L.) Sw. N
Dactyloctenium aegyptium (L.) Richt. N
Diectomis fastigiata (Sw.) HBK MO
Digitaria longiflora (Retz.) Pers.
Echinochloa colonum (L.) Link.
Echinolaena inflexa (Poir.) Chase WF
Eleusine indica N
Elyonurus adustus (Trin.) Ekman N
Eragrostis amabilis (L.) Wight. & Arn. DF
 glomerata
 guianensis Hitchc.
 hypnoides
 maypurensis (HBK.) Steud.
Gymnopogon foliosus (Willd.) Nees MO
Hackelochloa granularis (L.) Kuntze
Hymenachne amplexicaulis (Rudge) Nees
Ichmanthus acuminatus Swallen N
 axillaris (Nees) Hitchc. & Chase N
Isachne polygonoides (Lam.) Doell
Ischaemum
Leersia hexandra Sw. W
Leptocoryphium lanatum
Leptochloa domingensis (Jacq.) Trin.
Mesosetum elongatum Mez D
 loliiforme (Hochst.) Chase
 tenuifolium

GRAMINEAE (Continued)

Panicum chloroticum Nees
 cyanescens Nees W
 aff. cyanescens Nees W
 elephantipos
 hirtum Lam.
 laxum Sw.
 maximum Jacq. W
 parvifolium Lam. W
 pilosum Sw. W
 rudgei
 stenodes Griseb. W
 trichoides Sw.
 versicolor Doell
 zizanioides HBK.

Paspalum anceps
 arundinaceum
 carinatum
 densum
 dilatatum
 gardnerianum Nees
 lachneum
 millegrana Schrad.
 orbiculatum
 aff. plicatulum
 aff. pictum
 poychaetum Mez
 polychaetum Mez
 pullchellum
 stellatum
 urvillei

Ryttillix granularis
Sacciolepis myuros (Lam.) Chase
 strumosa (Presl.) Chase
 sp. nov.

Setaria tenax (L. Rich.) Desv.

Sporobolus cubensis Hitchc.

Thrasya paspaloides
 petrosa (Trin.) Chase
 trinitensis Mez

Trichachne insularis (L.) Nees

Tridens flaccida (Doell) Parodi

Themeda arguens

Trachypogon plumosus DF

GUTTIFERAE

Clusia N

Symphonia N

Vismia N

HAEMODORACEAE

Schiekia orinocoensis WOH

HIPPOCRATACEAE DRS

HUMIRIACEAE

Humiria balsamifera (Aubl) St. Hil. MRT
v. guianensis (Benth) Cuatr. MRT
floribunda

HYDROCHARITACEAE

Anacharis WRH

HYDROPHYLLACEAE

Hydrolea spinosa L. WRS

IRIDACEAE

Cipura paludosa Aubl. WRH
Sisyrinchium alatum WRH
marchios WRH
Sphenostigma gracile WRH

LABIATAE

Hyptis americana MOS
atrorubens MOS
Marsiphanthes chamaedris WRH

LAURACEAE

Cassytha americana MFH
filiformis MFH

LEGUMINOSAE

CAESALPINIOIDEAE

Bauhinia benthaminiana WRT
Cassia cultrifolia DFH
flexuosa DFH
glandulosa DFH
hispidula DFH
patellaria MFH
tetraphylla N
viscosa MFH
swartzii N
uniflora MFH
Krameria uniflora R
Inga MRT

MIMOSOIDEAE

Copaifera pubiflora Benth. WRT
Mimosa asperata WOS
pudica WOS
schranksioides WOS

Neptunia WOS

Swartzia R

PAPILIONATAE

Abrus precatorius N
Aeschynomene filosa Mart. ex Benth. WOS
histris v. incana (Vog.) Benth.
paniculata Willd. ex Vog.
pratensis v. caribaea Rudd
laxa
sensitiva

LEGUMINOSAE (Continued)

- Alysicarpus vaginalis DOS
 Bowdichia virgiloides HBK. WFT
 Centrosema R
 Clitoria guianensis DOH
 rubiginosa
 Crotalaria goreensis DOH
 maypurensis
 retusa
 stipularia
 Desmodium barbatum Benth (E. Oerst.) MOH
 cf. canum
 incanum
 supinum
 v. angustifolium
 Diocloea R
 Eriosema violacium MOH
 Galactia jussieuana DES
 Indigofera hirsuta MFH
 pascuorum
 Machaerium DOS
 Phaseolus gracilis DOH
 lasiocarpus
 Rhynchosia phaseoloides DOS
 schomburgkii
 Soemmeringa semperflorens Mart. WRH
 Stylosanthes angustifolia DFH
 guayanensis
 gracilis
 hispidula
 Zornia diphylla DFH

LENTIBULARIACEAE

- Utricularia benjaminiana N
 cornuta Michx.
 cucullata St. Hil. et Gerard
 foliosa L.
 hydrocarpa
 longeciliata DC.
 myriocista St H et G
 pusilla Vahl.

LILIACEAE

- Smilax N

LOGANIACEAE

- Antonia ovata v. pilosa WFT

LORANTHACEAE

- Phoradendron MFS
 Struthanthus N

LYTHRA CEAE

- Cuphea micrantha MFH

MALPIGHIACEAE

- Banisteria* N
Byrsonima coccolobiaeifolia WFT
 coriacea MRT
 crassifolia MFT
 stipulacea N
 verbascifolia WFS
 v. villosa WFS
Tetrapteris fimbripetala N

MALVACEAE

- Hibiscus* WRS
Pavonia speciosa WRS
Sida ciliaris DFH
 cordifolia
 glomerata
 jamaicensis
 linifolia
Urena lobata N

MARANTACEAE

- Maranta arundinacea* L. N
Calathea N
Thalia geniculata L. N

MARTYNIACEAE

- Craniolaria annua* N

MAYACACEAE

- Mayaca longipes* Mart. ex Seub. N

MELASTOMACEAE

- Acisanthera bivalvis* (Aubl.) Cogn. WRH
 crassipes (Naud.) Wurdack WRH
 nana Ule
 uniflora (Vahl.) Gleason WRH
 cf. uniflora WRH
Clidemia rubra (Aubl.) Mart. MRS
Comolia lythrarioides (Steud) Naud. WOH
 villosa (Aubl.) Tr. sensu Gleason WOH
Miconia albicans (Sw.) Tr. MOS
 ciliata MOS
 fallax DC. WRS
 ibaguensis (Bonpl.) Tr. WRH
Pterogastra divaricata MRS
Rhyncanthera grandiflora WOS
Tibouchina aspera Aubl. WOS

MENISPERMACEAE

- Cissampelos ovalifolia* DFS

MONIMIACEAE

MUSACEAE

- Heliconia humilis* (Aubl.) Jacq. WRS
 (= *H. psittacorum*)

MYRSINACEAE N

MYRTACEAE

Eugenia WRS

Psidium WFS

NYCTAGINACEAE

Boerhaavia coccinea N

NYMPHAEACEAE

Cabomba N

Nymphaea WRH

OCHNACEAE

Sauvegesia erecta WOH

Ouratea superba MRS

ONAGRACEAE

Jussieua angustifolia WOS

lithospermifolia

nervosa

peruviana

potamogeton

sedoides

suffructicosa

ORCHIDACEAE

Cyrtopodium andersonii WOH

Habenaria MOH

Epidendrum

Catasetum MOH

Spiranthes

OXALIDACEAE

Oxalis schomburgkiana DOH

PALMAE

Bactris N

Astrocaryum jauri N

Mauritia minor N

Maximiliana regia N

PASSIFLORACEAE

Passiflora foetida N

PEDALIACEAE

Sesamum indicum N

radiatum N

PHYTOLACCACEAE N

PIPERACEAE N

POLYGALACEAE

- Bredmeyeria MFH
 Polygala adenophora DC. MOH
 angustifolia R
 galioides Poir. MFH
 hygrophila HBK. R
 leptocaulis T et G
 longicaulis HBK. DFH
 monticola HBK. WOS
 timoutou HBK. R
 sedoides Benn. R
 subtilis HBK. R
 Securidaca marginata Benth. WRS.

POLYGONACEAE

- Coccoloba MOT
 Polygonum

PONTEDERIACEAE

- Eichornia crassipes N
 Heteranthera reniformis R et P. N
 Reussia subovata R
 rotundifolia (L.f.) Castellanos WOH

PORTULACACEAE

- Portulaca oleracea N

PROTEACEAE

- Roupala complicata MOT

RHAMNACEAE

- Gouania velutina R

ROSACEAE

- Chrysobalanus pellocharpa R
 v. icaco.
 Hirtella racemosa MFT
 Licania R

RUBIACEAE

- Appunia tenuiflora (Benth.) Hook. f. DRS
 Borreria capitata DFH
 ferruginea
 ocymoides (Burm.) DC.
 suaveolens
 verticillata (L.) G.F.W. Meyer
 Coutaria hexandra (Jacq.) K. Schum. MRT
 Declieuxia fruticosa (Willd. ex R & S) Kuntze WOH
 Diodia hyssopifolia MOH
 ocimifolia (Willd.) Brem
 (D.rigida C et S)
 Erythalis fruticosa R
 Genipa americana L. WOT
 Guettarda spruceana Muell. Arg. MRT
 Mitracarpus frigidus (Willd.) K. Schum. MOH
 scabrellus R

Oldenlandia lancifolia R
Pagamea capitata Benth. MOT
Palicourea rigida HBK. MFS
Perama hirsuta Aubl. MRS
Randia formosa (Jacq.) K. Schum. MFS
Retiniphyllum schomburgkii (Benth.) Muell. Arg. WRS
Richardia scabra L. MOS
Sipanea pratensis Aubl. WOR
Spermococce tenior R
Tocoyena DRS
Uncaria guianensis Aubl. R

RUTACEAE

Fagara pterota DRS

SAPINDACEAE

Allophyllus occidentalis MRS
Cupania NRT
Paullinia MRT

SCROPHULARIACEAE

Angelonia salicariifolia N et B. R
Bacopa flexilis WOH
 gratioloides (Benth.) Edwall
 reflexa (Benth.) Edwall
 salzmamii (Benth.) Edwall
 sessiliflora (Benth.) Edwall
Buchnera elongata DPH
 palustris (Aubl.) Spreng. WPH
 rosea
Conobea aquatica Aubl. WRH
Lindernia crustacea (L) F.v.Muell WRH
Scoparia dulcis L. WRH
Vandellia diffusa L. WRH

SOLANACEAE

Solanum americanum Mill N

STERCULIACEAE

Buettneria involucrata DOH
 scabra
Guazuma WRS
Melochia hirsuta WOH
 villosa L.
 parvifolia HBK.
Helicteres MRS
Waltheria americana MOS
 indica
 involucrata

SYMPLOCACEAE

Symplocos R

THEACEAE

Ternstroemia R

TURNERACEAE

- Piriqueta cistoides WOH
 viscosa
 Turnera guianensis DOH
 ulmifolia DOH
 sp.

UMBELLIFERAE

- Hydrocotyle verticillata N

VERBENACEAE

- Aegiphila MOS
 Amasonia campestris MFH
 erecta MFH
 Lantana camara N
 Lippia schomburgkiana DFS
 Stachytarpheta cayennensis WOH
 elatior v. jenmani
 indica
 paradoxus (Spreng.) Standl.

VIOLACEAE

- Hybanthus ipecachuana R

VITACEAE

- Cissus erosa R

XYRIDACEAE

- Abolboda pulchella H et B. WRH
 Xyris carolineana Walt. WRH
 jupical
 malmeana L.B. Smith
 paraensis Poepp. et Kunth

LOWER PLANTS

LYCOPODIINAE

- Lycopodium carolinianum v. meridionale (Underw. & Lloyd) Nessel
 cernuum L.

ISOETINAE

- Isoetes ovata Pfeiff.

FILICINAE

- Adiantopsis radiata (L.) Fee
 Adiantum pulverulentum L.
 terminatum Kunze
 Anemia villosa H. & B. ex Willd.
 Asplenium serro-dentatum Willd.
 Doryopteris collina (Raddi) J. Smith
 Dryopteris (Cyclosorus) gongyloides (Schkuhr) Kuntze
 (Meniscum) permollis Maxon & Morton
 Lygodium micans Sturm
 venustum Swartz

FILICINAE (Continued)

Poypodium consimile Eaton
 decumanum Willd.
 (*Goniophlebium triseriale* Swartz)
Schizaea incurvata Schkuhr
 pennula Swartz
 sp. nov.
Trichomanes hostmannianum (Klotzsch) Kunze
Blechnum cetarrucinum
Pteridium aquilinum v. *arachnoidium* (Kaulf) Herter

MUSCI

Cryptangium schomburgkiana
Fissideus kegelianus
Octoblepharum albidum Hedw.

HEPATICAE

Frullana exilis
Lejeunia repens
Plagiochila subplana
Radula recubans

KEY

W - Wet M - Mesic D - Dry N - Non-Savanna

(N.-e.g. Aquatics, Swamp Plants, Weeds, Cultivated Plants, Forest Plants.)

R - Rare O - Occasional F - Frequent

H - Herb S - Shrub or woody herb T - Trees and Bushes

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