THE SAVANNA VEGETATION OF NORTHERN TROPICAL AMERICA

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INTRODUCTION

Until quite recently the writer of this paper was resident in the Caribbean Islands, a part of northern tropical America, and had frequent opportunities for studying the ecology of the region. This meant mainly dealing with forests, being employed as a forest officer, but in Trinidad there are some very typical though limited areas of tropical American natural grasslands and in studying these the writer so came to the conclusion that there was great need for a new approach to the baffling problems which this type of vegetation was found to present. Natural grasslands, commonly called savannas, cover vast areas of tropical America, but as this part of the world is still very much a "dark continent" scientifically we know very little of their composition or ecological relationships. The literature on the subject is relatively scanty and is dispersed in eight languages. Various different and opposing theories about the ecological relationships of the savannas are extant based often upon inadequate field data and (with the honorable exception of Rawitscher's recent work (1948)) with a total lack of experimental evidence. The writer formed the opinion that there was a need for a review in one monograph of existing information and theories and it is this object which the present study has before it. It begins with a review of existing definitions and theories about American savannas, which are discussed briefly. After this an attempt is made to set down what is known of the facts relating to savannas, region by region, and to examine the adequacy of current hypotheses in relation to them. Initially in this section the results, hitherto unpublished, of the writer's studies of the Trinidad savannas are set down in detail followed by observations drawn from travels in the West Indies and Venezuela. Available literature is drawn upon for information about other regions.

Finally there is a discussion of the whole subject in which an attempt is made to deal with some of the major questions which these grasslands present and which do not appear to have yet been adequately answered. The study is confined to savannas north of the Equator, partly for economy of space and partly because the writer has not had an opportunity to visit those lying to the southward. Passing references to

the literature only will be made where it is of particular interest to refer to savannas of the Brazilian plateau. Warming's (1892) work at Lagoa Santa is considered to be in conformity with the conclusions on the northern savannas, and more recently Waibel's (1948).

REVIEW OF LITERATURE

On their advent to tropical America, Europeans found vast stretches of land covered with more or less open grassland. These communities still exist much as they ever did, and appear to be quite stable. Such grasslands cover the greater part of the basin of the great river Orinoco, much of the South Brazilian highlands, some of the Guiana plateau and limited areas elsewhere in the Amazon, lowland Guiana, the Antilles and Central America. To them, the term "savanna" is commonly applied, though the terminology is confused. Any grassland in tropical America, with or without trees or shrubs, natural or man-made, is called a savanna today and in British Guiana it is even applied to areas of herbaceous swamp land from which grasses may be absent just as well as trees. The word is variously spelled—*sabana, savana, zabana* or *zavana* in Latin American countries; Bennett & Allison (1928) used *savana,* but *savannah* is the general English-language spelling. In English usage there seems no justification for the "h," but pronunciation seems to call for a double "n." Many dictionaries derive the word from the Spanish *sábana,* a sheet or blanket, the inference apparently being that the ground is as flat and bare as a sheet. The derivation ignores the difference in fall of the accent, very important in Spanish, and is clearly not the correct one. In a review of this matter (1936) Lanjouw showed by a series of quotations from early writers that savanna was an Amerindian word used in Haiti and Cuba for treeless plains. The first published mention of the word seems to have been made by Oviedo in 1535: "Este nombre *savana* se dice á la tierra que está sin arboledas, pero con mucha é alta hierva, ó baxa" (This name *savanna* is applied to land which is without trees but with much grass either tall or short.) The term savanna will be used here generally to designate all tropical American natural grasslands, but its exact application will be discussed more fully in the concluding section. In Brazil the word "campo" appears to be synonymous.

Ecological treatment of savanna began with Grisebach (1872) who attributed it to the alternation of wet and dry seasons. Grisebach envisaged a series of climatic zones. An equatorial region along the Amazon characterized by well-distributed rainfall and covered with rain forest was supposed to be bordered to north and south by drier regions with marked seasonal periodicity of rainfall in which grasslands became dominant.

The great ecologist, Warming, labored early in this field and his paper "Lagoa Santa" (1892) was not only the first special study to be directed to American savannas, but remains the finest to this day. Warming ascribed the savanna vegetation to a combination of special soil conditions and a dry, seasonal climate. His deep knowledge of field conditions made it clear to him both that there are curious and peculiar features about savanna as opposed to forest soils and that the climate by itself was adequate to support forest. The theory that the savanna had originated from destruction of forest by fire he excluded as "totally inadmissible."

Schimper (1903) was still obsessed by the climatic theory and wrote always of distinct woodland and grassland climates. A good grassland climate, he considered, should have frequent, even if weak, precipitations during the vegetative period and a moderate degree of heat then. Unfavorable to woodland is a dry, cool winter or a very long rainless season. The llanos of Venezuela, he said, have a climate "hostile to woodland" with a quite rainless dry season of five months and a continuously rainy wet season. The savanna country of South Brazil, on the other hand, he admitted to be less dry than the thorn bush and cactus country to the northeast of it, but explained this on the ground of the cool winter in the savannas.

In his later work (1909) Warming came out more fully in favor of a climatic theory and we find no mention of the soil beneath the savannas. "The vegetation is *xerophytic* in many places because of the dry season that lasts for months and . . . coincides with *winter,* during which often no rain falls and dew appears to be the sole atmospheric source of water. But the xerophily is also due to the dry continental climate in general." In Warming and Graebner (1918), we find the definition: "Tree-steppes (Savannas, Campos)—under this name we include those tropical grasslands with summer rain and winter drought, which are more or less covered with small trees. . . . The reasons for lack or scarcity of trees are partly geological, partly climatic." Hayek (1926) followed a climatic approach: "The typical form of the tropical grassland is the tree steppe or bush steppe. It is widespread in the dry parts of the tropics where the bulk of the rainfall falls during the vegetative period of grasses." Bews (1929), in a study of the world's grasslands based upon the historical evolution of the grasses which penetrated very deeply into the problem, regarded "tropical high-grass savannas" as derivatives from forest destroyed by fire. "Tropical bunch-grass savannas" however he regarded as essentially occupying areas where climatic factors are not suited to the maintenance of closed forest.

Other writers since have continued to adhere to the climatic theory, of whom we may mention Bouillenne (1930) and Myers (1936), authorities on the savannas of the interior Guiana plateau. Myers stated "the savannah vegetation is thus of climatic origin," associated with alternating wet and dry seasons. Later in the same work he qualified this categorical statement with the remark that "we are justified in regarding the present vegetation as a fire climax."

Nearly all writers have regarded fire as a second-

ary factor, on the assumption that a grassland or other low open vegetation was first present due to some climatic or edaphic cause and became liable to take fire easily, the fire later modifying the vegetation somewhat. Degradation of forest to savanna by felling and repeated burnings, the savanna thus being purely a fire climax, is popular with very few. Exceptions are Christoffel (in Aguerrevere & Ors 1939) who described the process of felling and burning practiced by aboriginal Indians of the Guiana plateau, and Rawitscher (1948) who arrived at this conclusion for savannas near São Paulo in Brazil.

As early as 1906 Pulle suggested that the savannas of Dutch Guiana were of edaphic origin and caused by leaching of the soil. For the same locality Ijzerman (1931) pointed out that the soil must be the cause since the savanna climate does not differ from that of surrounding forest country. He envisaged severe leaching, the rain water soaking into the soil of the savanna plateaus and down into the creeks. In due course the soil would become impoverished and "the result is an extremely barren soil on which nothing will grow." Lanjouw (1936) accepted the leaching theory of Pulle and Ijzerman, and added a rider on burning which he considered to have entered the picture as soon as the soil deterioration had sufficiently impoverished the forest, and further changed the character of the vegetation.

This view was reiterated by Pulle in 1938 and was taken up by Hardy (1945) who associated savannas with impoverished "Bleached Earth" soils which could only support a "poor sort of forest" due to their "inherently low fertility." In regions where there is a severe dry season this poor forest would be apt to be burned off and replaced by grassland or scrub.

Waibel (1948), studying the Planalto Central of Brazil, found "within a few square miles and under the same climatic conditions . . . semi-deciduous forests, cerradões transitional in character, campos cerrados with many low trees, the more open campos sujos, and the treeless campos limpos." These differences in vegetation, he concluded, depend mainly on differences in soil and ground-water conditions and, ultimately, the parent rock material. Waibel thus coupled geology with soil moisture. Jones (1930) had sought a purely geological relationship between savanna lands and sandstones and between forests and igneous rocks.

Bennett & Allison (1928) on the other hand, in their work in Cuba, ignored the geology wholly in favor of soil moisture relationships.

These authors wrote that "in Cuba the term savana, as applied to land, carries both a vegetative and a soil meaning. . . . As a rule the savana lands have at relatively shallow depths subsoils composed of material which affects the soil moisture conditions unfavorably." Generally, the savanna soils feature a permeable horizon overlying an impermeable subsoil. Sometimes this effect is due to the presence of rock which has not decayed deeply, sometimes to the superposition of a sand upon a clay horizon, sometimes to the occurrence of layers of pebbly ironstone concretions or massive ironstone sheeting. The result of these circumstances is drainage impedance, which is accentuated by low relief.

Charter (1941), working on the soils of British Honduras, a region physically very similar to parts of nearby Cuba, found the relationship of the savanna soils to be essentially similar with drainage impedance as the dominating factor. Charter further declared that the impedance was a natural development, with maturity, of alluvial soils and traced a series of soil types with increasingly impeded drainage covered with increasingly impoverished vegetation from forest to savanna, which he claimed to stand in a development relationship one to another.

Drainage impedance was also held to be the essential factor differentiating savanna from forest vegetation by Beard (1944) in a general treatment of the vegetation types of tropical America. Conditions too severe for tree growth result, it was suggested, from alternating periods of waterlogging and desiccation on lands with perched water-tables (generally on somewhat flat areas with impermeable subsoil of rock, claypan or ironpan).

To summarize, the following are the various theories in the field in connection with American savannas:

1. Climatic. Based on moisture deficiency.
   a. The savannas are due to alternating wet and dry seasons (Grisebach; Schimper; Hayek; Bews—for bunch-grass savanna; Bouillenne).
   b. The savannas are associated with a seasonal climate and special soil conditions which decrease available moisture (Warming).
   c. Rainfall periodicity is the root cause but the vegetation has subsequently been modified by fire (Myers).
2. Biotic. Based on man's activity.
   a. Savannas have resulted from destruction and burning of the forest by man (Christoffel, Bews—for high grass savannas, Rawitscher).
3. Pedological. Based on chemical deficiency in the soil.
   a. Profound leaching of the soil produced a poor, low forest which became liable to take fire readily and so was converted into savanna (Pulle, Ijzerman, Lanjouw, Hardy).
   b. Certain geological formations develop soils which can only carry savanna (Jones, Waibel).

Based on defective subsoil drainage.

   a. Savannas occur upon more or less flat areas with impeded soil drainage generally due to the presence of an impermeable layer in the soil (Bennett & Allison, Charter, Beard).

It will thus be seen that a very wide range of theory is in the field and that no one has yet brought forward a single and convincing viewpoint which has met with universal acceptance. The idea of a climatic relationship is the oldest, and theories which take account of the nature of the soil are more modern, particularly those which stress the drainage factor.

The more modern work has not, however, as yet generally ousted the older, principally, one supposes, because it has been of a specialized nature and limited to local areas. We still find that reputable authors continue to repeat and expound the traditional theories of the past without, apparently, having any knowledge of the evidence provided by more recent, more specialized work. A very good example of this occurs in the "Phytogeographic Sketch of Latin America" (Smith & Johnston 1945). The authors, botanists of international repute, speak of the bulk of savannas as being "definitely climatic rather than edaphic in origin."

Much of the confusion about the ecological relationships of savanna has evidently resulted from the fact that some areas suggest one explanation, some another. The Venezuelan llanos suggest a climatic origin, the savannas of Cuba and Surinam each suggest a different edaphic origin, while the Gran Sabana and the São Paulo area are both suggestive of the influence of fire.

DESCRIPTIVE MATTER

The Orinoco Plains

The basin of the great river Orinoco contains a considerable area of savannas which stretch virtually unbroken from the foothills of the Andes and Coastal Cordillera in the north and west, across the river to the forested broken country descending from the Guiana shield. To the north and west of the river the savannas cover extensive flat plains formed by sediments of Quaternary age and at a very low elevation above sea level. These are the well-known "llanos." To the south and east of the river the savannas cover low, undulating country of small relief underlain by ancient rocks and representing a reduced and eroded portion of the Guiana shield. The latter region is described below in the section on lowland Guiana. The island of Trinidad, lying off the north-east Venezuelan coast, is structurally a part of Venezuela and has only become separated from the mainland in geologically recent time. At no very distant date the Orinoco entered the sea further to the eastward and the Gulf of Paria was an extensive plain of dry land uniting the flat southern portion of Trinidad with the Venezuelan plains north of the Orinoco. Savannas in Trinidad may, therefore, logically be grouped with those of the llanos for purposes of study. The writer has spent many years in the island of Trinidad and has had abundant opportunity to examine the savannas which occur there. A journey was made in February 1945 across the llanos of Venezuela along the main road from Ciudad Bolívar to Caracas via El Tigre, Pariaguan, Santa Maria de Ipire, Valle de la Pascua and El Sombrero.

THE ISLAND OF TRINIDAD

In the days of Christopher Columbus, the West Indian island of Trinidad was almost entirely covered with forest. Certain low-lying, inundated areas bore then as they do today a herbaceous vegetation of giant sedges or semi-woody plants such as *Montrichardia aborescens*. Around the coasts a few clearings had been made by scattered communities of Arawaks for planting their gardens. The overwhelmingly greater portion, however, of Trinidad must have supported various types of forest as the climax vegetation.

Settlement of Trinidad by the Spaniards did not take place on a large scale. In 1797 a British force conquered the island, which has since remained under the British Crown. After the conquest a survey of the colony was undertaken by Capt. F. Mallet of the Royal Engineers and a map published in 1802, a copy of which is still preserved at the Crown Lands Office in Port of Spain. This map, on a scale of about 1:100,000, showed the existing estates and indicated the crops they were producing: such settled lands amounted then to about 10% of the total land area and were situated around the coasts. Remaining lands, where considered suitable, were shown marked out for settlement and indications were given of the main features of the colony, such as "mountains of the north coast, inaccessible and generally covered with incorruptible woods" (*sic*). In the interior of the country in several places, buried often deep in forest, he indicated a number of "natural savannas." These still exist to this day. None has been utilized for agriculture, though in some cases cultivation has reached their borders. Several of the savannas remain surrounded by more or less undisturbed forest. At the present time some additional areas of grassland exist in the island, not shown by Mallet and differing from those he recognized in important respects. Mallet's "natural savannas" are all in the lowlands and are of closely similar floristic composition. Of the others, one is floristically similar (in part) to Mallet's but covers mountainous terrain, and the remainder lie in the lowlands but are floristically dissimilar. In summary the grasslands fall into three groups:

1. "Natural Savannas" (lowlands)
   a. Erin and St. John savannas
   b. Piarco, Mausica and O'Meara savannas
   c. Aripo savannas
2. Other savannas (mountain)
   a. St. Joseph savanna
3. Other savannas (lowlands)
   a. Cocorite savannas of the Northern Plain.

The above list does not include pastures and other grasslands deliberately created by man, but embraces only areas which have become covered with grass in response to natural conditions or to man's unintentional influence.

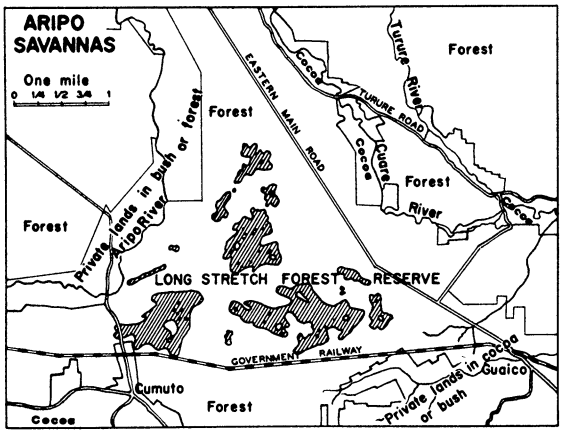
Reference to these savannas is found in Marshall (1934, p. 39-40) and in Myers (1933, pp. 344 *et seq.*). The writer has also had access to an unpublished thesis on "The grasses of Trinidad" by J. H. Hinds, 1940, at the Imperial College of Tropical Agriculture.

THE ERIN AND ST. JOHN SAVANNAS

The Erin and St. John savannas are the two savannas, or rather groups of savannas, in the south of the island and may be described together as they are very closely similar. The Erin savanna—it is generally referred to in the singular—is a group of small stretches of grassland varying in size from less than one acre to one hundred acres lying immediately east and west of Buenos Ayres village on the Erin—Cap de Ville Road. The total area of the grasslands is about 240 acres, and they are shown mapped in Figure 1. On Mallet's map the Erin savanna is not accurately placed, but is shown surrounded by forest as there was very little settlement in the vicinity at that time. One or two small parcels of savanna have since been included in alienated land near Buenos Ayres village but the bulk remains as before deep in forest. The St. John savanna occupies about 20 acres on the St. John estate near Oropouche village about eight miles south-west of San Fernando. On Mallet's map it is marked as a "natural savanna" on the estate which was then cultivated in sugar canes. The savanna today is used for rough grazing and is surrounded by degraded secondary forest.

The savannas are generally flat and occupy plateau sites, though in places the grassland covers slopes descending round the plateau edges. The Erin savanna lies along the crest of a watershed and the St. John savanna caps a Pleistocene terrace deposit. There are strong indications that these savannas occupy the remnants of an ancient land surface, a peneplain which in recent geological time has been uplifted and which is still being very actively dissected. Forest lands surrounding the savannas occupy sharply undulating topography.

The savanna soils are of a very special character. The geological parent material underlying the savannas does not differ from that beneath the surrounding forest but the soils developed on the two sites are dissimilar. In the surrounding country there are occasional outcrops of sandy beds and porcellanites which yield sandy soils, but in the main the formation is a clay-shale which yields on the forest sites an exceedingly stiff clay soil, sticky and impermeable in the wet season, hard and deeply cracked in the dry season. From the surface down to about 12 in., the clay is dark brown and crumbly with good penetration of small roots and organic matter. Below this depth it merges gradually into a greyish-brown clay with red mottlings into which roots still penetrate, and below some 6 ft. into a bluish grey clay with red and tawny mottlings and some iron concretions. Typical profiles of forest and savanna soils are pictured in Figure 2 by permission of Prof. F. Hardy from notes taken by C. Swabey and C. G. Akhurst in 1930 and the relevant laboratory data are given in Table 1. On the flatter, more definitely



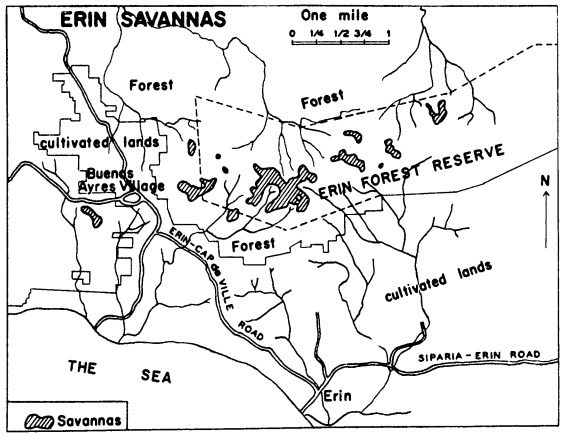


FIG. 1. Large scale maps of the Aripo savannas (top) and Erin savannas (bottom), from aerial survey.

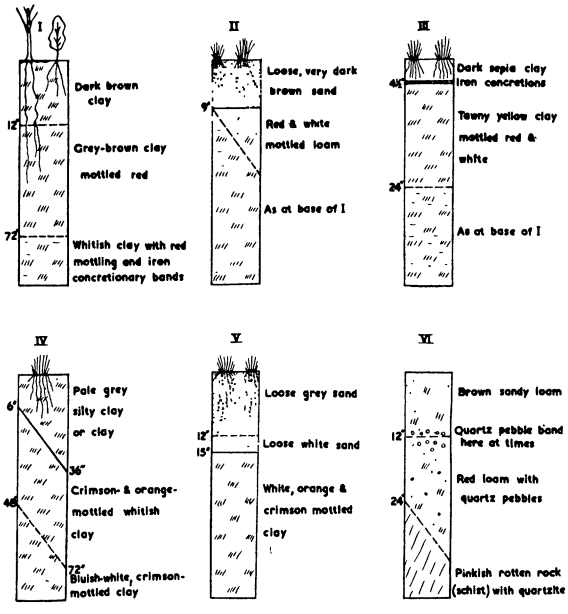


FIG. 2. Typical profiles of savanna and forest soils in Trinidad. I. Forest soil. II. Erin savanna soil (Beard). III. Savanna soil at the Erin Savanna (after Swabey & Akhurst). IV. Long stretch silty clay of Aripo savanna area. V. Piarco light sand of Piarco, Mausica and O'Meara savanna areas. VI. Maracas light sand of the Northern Range (after E. M. Chenery).

TABLE 1. Laboratory Data for Soils at the Erin Savanna.†

Depth ins.		Index of Texture	Reaction Norm. pH	Reaction Exch. pH	Org. Matter* %	N %	C/N Ratio*	Av. Nutr. mhos	Rate of Soln. x 10^{-6}	Av. P^2O^5 p.p.m.
	GRASS TYPE. (grass, with Curatella and Byrsonima)									
½	Black, humic, roots	35	4.4	3.8	6.66	0.24	15.9	98	8	13
2	Dark, sepia humic	34	4.6	3.8	6.12	0.28	12.5	38	5	19
4½	Sepia, iron concretions	34	4.6	3.9	5.56	0.21	15.2	43	5	9
8	Tawny, mottled red	34	4.5	3.9	3.12	0.16	11.3	28	12	6
14	White, tawny, red mottling	40	4.6	3.9	1.35	0.08	10.4	22	9	4
24	Grey-white, red mottling	51	4.6	3.8	0.48	0.06	4.4	19	4	5
36	Ditto	51	4.5	3.8	—	—	—	27	6	5
48	Ditto. Iron concretions	46	4.5	3.7	—	—	—	31	21	5
60	Ditto Ditto	38	4.6	3.7	—	—	—	17	6	6
84	Ditto Ditto	43	4.5	3.6	—	—	—	28	13	5
	FOREST TYPE. (Carapa, Eschweilera, Maximiliana, etc.)									
½	Dark sepia humic	36	4.6	3.8	7.31	0.26	16.3	68	11	15
2	Ditto	31	4.6	3.8	6.37	0.26	14.3	53	12	39
4	Ditto	30	4.6	3.9	5.97	0.23	15.1	52	8	19
6	Paler sepia	28	4.8	3.9	4.99	0.19	15.3	34	14	18
9	Ditto	25	4.5	3.9	3.72	0.14	15.9	27	6	14
13	Yellow sepia	27	4.5	3.9	2.09	0.10	11.9	23	6	10
20	Grey sepia	37	4.4	3.9	1.21	0.10	7.3	23	11	8
36	Grey, red splotches	36	4.5	3.9	—	—	—	20	4	6
48	Ditto	31	4.4	3.8	—	—	—	26	5	8
63	Ditto	27	4.4	3.8	—	—	—	21	2	7
72	Blue-grey, red & tawny mottling	43	4.5	3.7	—	—	—	47	1	10

*Corrected.
†Published by permission of Professor F. Hardy from records of samples taken by C. Swabey and C. G. Akhurst in 1930 and analysed at the Imperial College of Tropical Agriculture.

plateau-like portions of the savanna the clay is found to be overlain by a horizon of loose, dark sand (profile II, Fig. 2), but on sloping ground this sand capping is absent (profile III). In the former case the sand is some 9 to 12 in. deep, very dark colored and incoherent, full of grass roots. A sudden break occurs at the base of this horizon and there is a change to tawny, red and white mottled loam or whitish clay with red mottlings. Iron concretions may be present. Grass roots but not tree or shrub roots penetrate this layer which is extremely compact. The soil of sloping ground is typically at the surface an almost black clay, hard and very compact, full of grass roots. Below 4 or 5 in. scattered iron concretions appear and the upper horizon gradually merges into a tawny yellow clay mottled red and white. This in turn merges below some 2 ft. into a whitish clay with brilliant red mottlings and abundant iron concretions which often occur in bands. In many places on sloping parts of the savanna, often appearing as an outcrop just below a plateau rim, there are abundant ironstone boulders of all sizes, but there were never any ironstone boulders or slabs at depth in any soil profile examined. The clay topsoil is highly compact and impermeable and during a heavy rainstorm the water moves off the surface in a sheet. Apparently there is little absorption of water into the soil or erosion of the surface by this sheet runoff. The ground surface is regular on slopes but on plateau sites is often "hogwallowed," that is, shows a curious irregular configuration of hummock and depression (Fig. 3).

FIG. 3. Area of low bush adjoining the Piarco savanna after a fire, showing "hogwallow structure" of the ground surface, an irregular configuration of hummocks and channels.

The savannas are of "tall bunch-grass" type with scattered shrubs (Fig. 4). A photograph taken after a fire (Fig. 5) shows the arrangement of the grasses into scattered clumps with bare soil between. The grasses grow normally to a height of about 18 in. During the dry season which lasts generally from January to May and during which there is usually between ½ and 2½ in. of rain each month, the grasses dry up and die down somewhat. During this period the savanna may be swept by fire, presumably set by human agency. On the average a fire occurs probably once every 4 or 5 years. At the onset

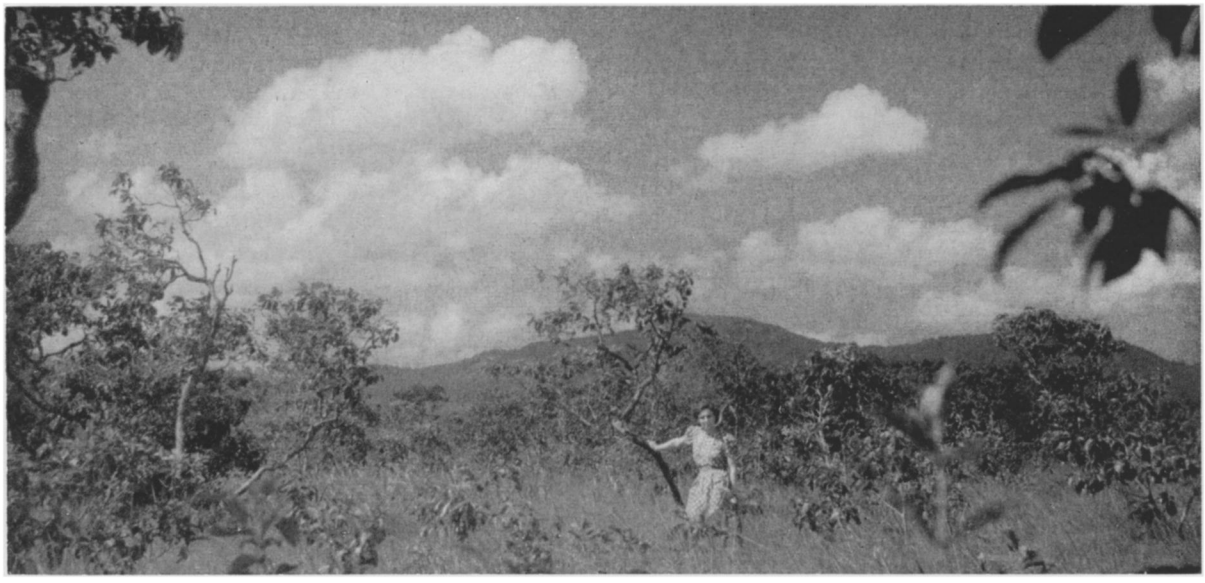


FIG. 4. Typical physiognomy of the neotropical savanna: the Mausica Savanna, Trinidad.

FIG. 5. Savanna shortly after a fire, showing the disposition of grass clumps and the actual extent of soil cover. The machete and notebook give the scale. In rear are two small Byrsonima bushes with scorched leaves. Note that the fire was not fierce enough to consume the grasses to the root.

of the rainy season in May or June the grasses, whether burnt or not, sprout vigorously and proceed to flower, the spikes reaching about 5 ft. high. After this general flowering, individual grass clumps can be found flowering sporadically for the remainder of the wet season. During the rainy period from 5 to 24 in. of rain may fall each month. Total annual precipitation amounts to about 60 in. on the average. The dominant grass is *Axonopus anceps* (Mez) Hitchc. Associates are *Setaria geniculata* (Lam.) Beauv., *Paspalum fasciculatum* Willd. *Sporobolus* sp., *Andropogon bicornis* L. and *Leptocoryphium lanatum* Nees. In sandy places *Trachypogon ligularis* Nees is common as is a small sedge with delicate feathery leaves, *Bulbostylis junciformis* (HBK.) Lindman. In many places, particularly near the borders of the savanna, "razor grass" (sedge) *Scleria bracteata* Cav. is abundant. Many herbs are found among the grasses, and one may mention *Sipanea pratensis* Aubl., *Crotalaria pterocaula* Desv. and *C. stipularia* Desv., *Elephantopus angustifolius Sw., Sida linifolia* Cav., *Rolandra fruticosa* Rottb., *Desmodium barbatum* Benth. & Oerst., *Buettneria scabra* L., *Martiusia laurifolia* (Poir.) *Britton, Curculigo scorzoneraefolia* (Lam.) Benth., *Eriosema* spp., *Hyptis* spp., and *Polygala* spp. Small gnarled trees up to 10 ft. high occur scattered freely about the savanna and with the exception of some little melastomes (conspicuously *Miconia macrophyrsa* Benth.) which do not often exceed 2 or 3 ft. in height, belong to *Byrsonima crassifolia* HBK. and *Curatella americana* L. Of these two Byrsonima is the commoner, the proportion being about four to one, but Curatella grows the larger. The peculiar gnarled form of these trees may be seen in the photographs. On the average they are scattered about 20 ft. apart. Leaves are coriaceous and large (4″ x 2″ in Byrsonima, 8″ x 5″ in Curatella) and the bark is thick, giving resistance

to grass fires. Very occasionally, usually in hollows, a palm, *Mauritia setigera* Gr. & Wendl., is found.

In sandy places small mound-nests of two species of termite are occasionally found on the ground, frequently based on an old stump or rootstock. These nests are seldom more than 12 in. high and narrow in proportion, and they are built of a brittle, blackish material exactly like the nests constructed by forest termites in trees. The late Prof. A. M. Adamson examined these mounds and their inhabitants with the writer and found two forms of Nasutitermes, one of which appeared to be morphologically indistinguishable from *N. ephratae*—a forest termite—and the other to be a new species. Prof. Adamson believed that the former will prove to be distinct from *N. ephratae* so that both these termites will belong to a distinct savanna fauna.

Very rarely do the grass fires penetrate the surrounding forest, they run up to its borders and there stop. Much of the forest in Trinidad has, however, been burnt by human carelessness in recent years during severe droughts, and the whole of the forest in the Erin district has been badly burnt out. In the vicinity of the savanna the fire may have run over from the grassland or may just as likely have originated on cultivated lands nearby. Formerly the forest surrounding the savanna was an evergreen seasonal forest of the *Carapa guianensis*—*Eschweilera subglandulosa* association, a dense "moist" forest 120 ft. high. It is today somewhat ruinate and the principal components are *Pentaclethra macroloba* (Willd.) Ktze, *Protium guianense* (Aubl.) March, *Clathrotropis brachypetala* (Tul.) Kleinh., *Cecropia peltata* L., *Inga* spp., species of *Lauraceae* and *Melastomaceae, Vismia* spp., *Guazuma ulmifolia* Lam., *Spondias mombin* L., *Byrsonima spicata* (Cav.) Rich., *Laetia procera* (Poepp. & Endl.) Eichl., *Pouteria minutiflora* (Britt.) Sandwith and the palms *Maximiliana elegans* Karst. and *Astrocaryum aureum* Gr. & Wendl.

Transition from the savanna to forest is very abrupt. The actual transition zone is only a few feet wide and is marked by an abundance of melastomes—notably *Miconia ciliata* (Rich.) DC. and *M. minutiflora* (Bonpl.) DC.—and razor grass (Scleria) and the sporadic occurrence of the grugru palm, *Acrocomia ierensis* L. H. Bailey.

Almost the whole of the savanna flora is peculiar to such grasslands and is not found in other types of vegetation. The Acromia palm has become common in Trinidad in areas subject to shifting cultivation but is unknown elsewhere in natural forest. As *A. ierensis* is endemic to Trinidad, its focus of origin must be in the fringes of the Erin Savanna. It appears probable that burning is essential to the germination of the thick-walled Acrocomia seed and hence its appearance in the much burned bush in and around peasants' gardens, and on the fringes of the savanna where soil conditions are substantially those of the forest but where the fire sometimes passes. The occurrence of this endemic palm, restricted as it is to this place, would seem to indicate that the savannas are very ancient and that in terms of human time they are practically stationary, neither expanding nor contracting.

Chemical analysis of savanna and forest soils derived from the same parent material as shown in Table 1 does not disclose any significant differences. Evidently the important differences must lie in the physical character of the soil and concern moisture relationships. This is in any case what one would expect, since it is a circumstance that has been repeatedly proved in studies of natural vegetation in the tropics.

Studies were made of the root-systems of savanna plants. The typically fine fibrous roots of the grasses were found to ramify abundantly in all directions in the upper, sandy soil horizon and there was also some penetration of the underlying red mottled clay zone. Root systems of the Byrsonima and Curatella trees were essentially similar to one another and a noticeable feature was the absolute lack of any penetration of the red mottled clay zone. In the upper sandy layer the root stock typically sent off a whorl of roots about ½ in. thick which meandered for long distances through the sand horizon without much branching and without any small lateral roots with root hairs. A typical root of this type was traced from a parent 6 ft. high Curatella tree for 27 ft. before it gave off a single branch. These root systems are feeble indeed, so much so that the trees are often blown down by the wind. The clay zone of the savanna soil is so compact that it may present a physical obstacle to the penetration of tree roots, but a physiological reason seems more probable. Clay soils of the forests are crumb-structured at the surface and are of a shrinking type so that the lower layers are to some extent opened and aerated in the dry season. Tree roots are able to penetrate and are not entirely deprived of air. On the other hand the brilliant mottling of the clay zone under the savanna indicates that it is largely sealed off from any aeration. In effect, a clay-pan is present. Water collects in the sand horizon over the clay in flat places and forms a swamp in the wet season. In the dry season the sand horizon dries out completely and the trees, having no deep roots, are subjected to severe desiccation.

THE PIARCO, MAUSICA AND O'MEARA SAVANNAS

The savannas of Piarco, Mausica and O'Meara are a group lying on the western part of the northern plain at the foot of the Northern Range. The topography of the whole area is very even and consists of a series of flat terraces deposited during Pleistocene time from erosion of the mountains to the northward. More recently the rivers have cut down their beds below the terraces, leaving these as dissected plateaus. The savannas occupy the central portions of certain of these terrace-plateaus. In Mallet's day they were more or less surrounded by forest, but since that time abortive attempts have been made at cultivation in the immediate vicinity and the savannas today are surrounded by an ex-

ceedingly poor secondary growth. Formerly this was evidently of the same Carapa-Eschweilera type as surrounded the Erin savanna, but it is now a tangle of low trees and lianes about 50 ft. high and with a very high proportion of the cocorite palm, *Maximiliana elegans* Karst. This bush merges gradually into the savannas and there is no sharp transition. Both forest and savanna here are very frequently burnt in the dry season, the fire generally escaping from a peasant's garden or a cane-field.

There is considerable similarity between forest and savanna soils on these terraces. A typical profile is shown in Fig. 3 (V). The upper layer of the soil down to some 12 in. consists of a dark to whitish-grey, loose, fine sand merging into a narrow band of loose white sand. Below this an abrupt change takes place to a stiff and compact white, orange and crimson mottled clay. The ground surface is deeply "hogwallowed" both on the savanna and in the flatter parts of the forest.

Floristically these savannas resemble the Erin savanna very closely. The tops of hummocks are occupied by *Paspalum pulchellum* HBK., co-dominant with *Leptocoryphium lanatum*. *Paspalum serpentinum* Hochst. is frequent, and *Thrasya paspaloides* HBK. and *T. robusta* Hitchc. & Chase are rarer. *Trachypogon ligularis* is present under trees. In the hogwallow channels and depressions one finds *Leersia hexandra* Sw., *Panicum stenodes* Gr. and *P. parvifolium* Lam., and *Sacciolepis myuros* Chase., *Andropogon leucostachyus* HBK., *A. selloanus* (Hack.) Hack. and *Paspalum pilosum* Roth., are sporadic throughout. Round the edges of the savanna *Arundinella confinis* Hitchc. & Chase and *Imperata brasiliensis* Trin., appear. The bladderwort and sundew, *Drosera capillaris* Poir., and *Utricularia* spp., are found in depressions.

The list of herbs present is substantially the same as for the Erin savanna and the same *Byrsonima crassifolia* and *Curatella americana* form the tree crop. Many little melastomes are also present, notably *Miconia albicans* (Sw.) Triana, *M. macrothyrsa* Benth., *M. stenostachya* DC., and *M. savannarum* Williams (an endemic). The palm Mauritia does not occur here.

In the very centre of the Piarco savanna where the ground is flattest and worst drained there are patches where shrub and tree growth ceases, the only woody plant being *Byrsonima verbascifolia* (L) Rich., which is a ground plant (Fig. 6.). Grasses here are shorter and *Paspalum densum* becomes common. The little sedge, Bulbostylis, becomes abundant. This is the only place in Trinidad where *B. verbascifolia* is found and its occurrence along with the endemic *Miconia savannarum* and several endemic herbs would indicate that at least the central portion of the Piarco savanna is of great antiquity.

Mounds of the same two termites described from the Erin Savanna are quite common on these savannas.

The former borderlines between these savannas and the forest have been destroyed by intensive burning.

FIG. 6. Centre of the Piarco Savanna. In the foreground, waterlogged area with sedge and *Byrsonima verbascifolia;* in rear, trees of *B. crassifolia* and grass.

Towards the edges Imperata and Arundinella become abundant. Maximiliana palms appear among the savanna shrubs and gradually increase in number until the poor forest is entered.

THE ARIPO SAVANNAS

The savannas of Aripo are a group of grasslands of variable size totalling some 680 acres, enclosed within the forest of the Long Stretch Reserve on the east-central portion of the northern plain. Mallet does not show these. Possibly in his day they were too remote to be noticed. There is an account of them in Charles Kingsley's "At Last" (1871). The savannas are found in the middle of a single large old alluvial terrace lying between the Aripo and Cuare rivers and forming the central watershed of the northern plain. The Aripo river joins the Caroni and flows westward, the Cuare flows east to the Oropouche. Topography is very flat across the whole terrace and some of the savannas were found to occupy slight depressions when some level traverses were run in 1941. The terrace land here is well recognized to have absolutely no agricultural value so that the forest has never been cleared away and is now a Forest Reserve. The rainfall here is much higher than further west, averaging about 110 in. annually. The dry season is shorter, only three months of the year, on the average, having under 4" of rain but over 2". As a result, neither the forest nor the savannas are known to have been burnt in recent times.

There is only a single soil type beneath the savannas and their surrounding forest Fig. 2 (V), consisting of an exceedingly stiff, very fine clay containing almost no sand. The surface horizon down to between 6 and 36 in., is a pale grey silty clay or clay and merges below into a brilliantly crimson and orange mottled whitish clay. The parent material is a bluish white, crimson-mottled clay. This clay is kaolinitic and exceedingly compact and impermeable. There seems to be almost no downward percolation and the soil remains remarkably dry at a depth of several feet even when the surface is waterlogged. In the northern part of the terrace, forest of substantially the same type as that surrounding the savanna is underlain by a soil consisting of about 36 in. of

loose grey sand overlying an iron-cemented gravel which creates an impermeable pan.

In the forest the ground surface is very markedly hogwallowed and this phenomenon is still present to a less pronounced degree on the savanna.

By strictest definition the Aripo savannas should be considered properly as herbaceous swamp since sedges predominate over grasses. On general characters of physiognomy and habitat it is preferable, however, to class them as savannas. This is a typical savanna site in point of soil and topography but the high rainfall so accentuates and prolongs waterlogging that the habitat begins to approach that of herbaceous swamp where the site is more or less deeply inundated for most of the year.

The dominant sedge is *Lagenocarpus guianensis* Nees., and associates include *Rhynchospora longibracteata* Boeckl., and *Bulbostylis junciformis* (HBK.) Lindman. Grasses are not very abundant but one finds *Paspalum pulchellum, Thrasya paspaloides,* and *Leersia hexandra.* The Lagenocarpus grows to about eighteen inches high. Most of the other sedges and grasses only reach about half this height and the general appearance is of shorter growth than the true grass savannas. *Drosera capillaris,* and *Utricularia* spp., are present and a number of small ferns. A sphagnum-like moss covers the open ground between sedge stems and grasses. Rather a prominent feature of this area are the several beautiful terrestrial orchids, of which the commonest are the white-flowered *Otostylis brachystalix* (Reichb. f.) Schltr., and the red flowered *Epistephium parviflorum* Lindl. During the dry season the soil often dries hard and cracks deeply. At the beginning of the rains the herbaceous plants sprout vigorously and flower but activity dies away at the height of rains when the ground is covered with standing water. At such times and in drought also the Aripo savannas exhibit a somewhat sere and drab-brown appearance. The savannas are dotted with small shrubs about three feet high and ten to twenty feet apart of *Chrysobalanus pellocarpus* Mey., *Miconia ciliata* and *Ilex arimensis* (Loes.) Britt. *Byrsonima crassifolia* is occasional and prefers any places where the ground is slightly raised. Curatella is absent. Occasional clumps of the endemic spiny palm *Bactris savannarum* Britton may attain 6 ft. high. Mounds of the same termite are found but are not as common as on the Piarco group of savannas.

The flora of this area is much the richest of any of the savannas and contains a greater proportion of endemic plants. These features may be attributable to the higher rainfall both directly in point of moisture and indirectly in point of the absence of burning.

Transition to forest is abrupt (Fig. 7). Along a sharply marked line one enters a dense thicket about 20 ft. high of small and rather gnarled trees with very long branches, of which the principal are *Chrysobalanus pellocarpus* Mey., *Ilex arimensis, Pouteria* sp., *Clusia nemorosa* Mey., and *C. palmicida* Rich., *Symphonia globulifera* L.f. and several Melastomaceae. Palms of *Mauritia setigera* Gr. & Wendl., stand out above the pole thicket. In the ground layer one finds *Bactris savannarum,* a Gleichenia fern, a Eupatorium and a cutting Scleria. Besides fringing the savannas this type of vegetation is found as "islands" in their midst. Away from the savanna the woody growth increases rapidly in height and at a distance of 20 yards from the edge has merged into high forest. This forest is not the same as that surrounding the savannas previously described. It is a somewhat specialized type, and belongs to the marsh forest of Beard (1944), the lower type of fringing thicket described above being his palm-marsh. The marsh forest is two-storied. Canopy is formed from 10 to 30 ft. from the ground by a lower story above which stand out occasional trees reaching about 80 ft. high in places. The bulk of the lower story is composed of the palms *Jessenia obligocarpa* Gr. & Wendl. and *Manicaria saccifera* Gaertn., with species of *Euterpe* and *Oenocarpus.* Conspicuous among large trees are *Calophyllum lucidum* Benth., *Pouteria* sp., *Parinari campestris* Aubl., and *Terminalia amazonia* (J. F. Gmel.) Exell. Tree roots seem to be confined to the upper layers of the soil but palm roots penetrate deeply into the clay pan.

FIG. 7. The Aripo Savanna and its sharp boundary fringed with Chrysobalanus and Mauritia. The savanna itself is a low growth of sedge with a few tiny shrubs.

THE ST. JOSEPH SAVANNA

The St. Joseph savanna is situated on the slopes of the Northern Range above St. Joseph and St. Augustine, between altitudes of 500 and 1500 ft. The slope is southerly and steep, the average slope being about 2 in 5. The mountains are composed of schists of lower Cretaceous age in which there is a variable proportion of quartzite. At this particular place the rock appears to be exceptionally highly quartzitic, the mineral occurring in particles of all sizes from small grains to large boulders.

In the Northern Range as a whole and in forest areas hereabout the soil developed over schist has a typical profile as shown in Figure 2. (VI). On the savanna there is, properly speaking, no soil but only bedrock and the savanna is clearly very severely eroded. The bunch grasses offer no protection against surface erosion and gullies form in between

the clumps. A little reddish earth covers the surface for the most part but the parent rock shows in many places and quartz boulders are abundant everywhere. The effect of erosion, by bringing bedrock close to the surface, is to create the effect of a pan, the rock being substantially impermeable to moisture and mechanically resistant to root penetration. External drainage of the profile is very good owing to the steepness of the slope.

The history of this savanna is obscure. It is not shown on Mallet's map but there is a vague record by an early Spaniard who was taken by Indians to an open place above St. Joseph whence he could view all of Trinidad. The present boundaries of the savanna are probably by no means stationary. Shifting cultivation has been practiced for a great many years on these mountain sides and the original forest, whose nature can no longer be decided, has been reduced to a secondary growth up to 50 ft. in height containing principally *Tabebuia serratifolia* (Vahl.) Nichols, *Machaerium robinifolium* (DC.) Vogel, *Protium guianense* (Aubl.) March and *P. insigne* Engl., *Oliganthes condensata* Schulz., *Apeiba schomburgkii Szyszyl.*, species of *Pisonia, Coccoloba* and *Croton,* and numerous Myrtaceae. Transition to grassland is gradual and usually takes place through a zone of low, burnt bush thick with vines and containing a few unhealthy looking Acrocomia palms.

There are two types of savanna here: the one, which may be called the Byrsonima-Curatella type (Fig. 8), resembling the lowland savannas of Trinidad and the other, the Myrcia-Roupala type (Fig. 9), which is *sui generis.* In only one place are the types contiguous and there the transition is abrupt and occurs along the crest of a ridge. The dominant grass *Trachypogon ligularis* is the same in both. On the Byrsonima-Curatella savanna it is associated with *Arundinella confinis* Hitchc. & Chase, *Thrasya paspaloides* HBK. and *T. robusta* Hitchc. & Chase. A Scleria "razor grass" is occasional. Shrubs of *Byrsonima crassifolia* and *Curatella americana* cause a very strong resemblance of this type to the lowland savanna, though the shrubs here are frequently more stunted and more scattered. On the Myrcia-Roupala savanna Trachypogon is less abundant and is almost co-dominant with the Scleria. Grass cover is much less dense, bare soil being rather generally visible, and the shrubs grow relatively thickly almost touching one another. The most abundant shrub is the microphyllous *Myrcia stenocarpa* Kr. & Urb., associated with *Roupala montana* Aubl. Others noted include *Rapanea guianensis* Aubl., *Curatella americana* L., *Pisonia eggersiana* Heimerl., *Inga venosa* Gr., and several melastomes, but all these are much rarer than Myrcia and Roupala. *Byrsonima crassifolia* seems to be absent or very rare in this type.

FIG. 8. Section of the St. Joseph mountain savanna with Curatella and Byrsonima trees.

FIG. 9. Section of the St. Joseph mountain savanna with almost closed scrub of Myrcia, Roupala, etc.

Very occasionally a shrub of Myrcia, Roupala, etc., can be found on the Byrsonima-Curatella savanna. The characteristic gnarled growth of the shrubs on the latter is not adopted by *Myrcia stenocarpa* and its associates, which are of low growth, never over ten feet high but of erect form.

COCORITE SAVANNAS OF THE NORTHERN PLAIN

In certain parts of the northern plain occur grasslands characterized by the presence of the cocorite palm, *Maximiliana elegans* Karst., and known to have succeeded forest within the last half-century due to repeated fires set by the shifting cultivator and cane farmer. These grasslands lie on the western part of the northern plain where the rainfall is relatively low so that the vegetation often dries up enough to burn easily in the dry season. They are in the same district as the Piarco group of savannas and occupy similar alluvial terraces, being similarly rather flat

and illdrained and having similar impeded soils. The former forest was of the same Carapa-Eschweilera type as surrounded the Piarco and other savannas, conditions on the sites of these cocorite grasslands being in fact substantially equal to those of such surrounding forests. The soil drainage is bad, but just not too bad to support forest.

The dominant grass is always *Imperata brasiliensis* Trin., associated with *Arundinella confinis* Hitchc. & Chase, *Paspalum pilosum* Roth., and sundry *Andropogon* spp.—*A. bicornis* L., *A. selloanus* (Hack.) Hack., and *A. leucostachyus* HBK. *Heliconia psittacorum* L., is generally very abundant. Woody growth consists typically of an occasional fire-blackened Maximiliana palm (Fig. 10) and scattered bushes or little trees (most of which have sprouted from an old root stock since the last fire) of *Coccoloba latifolia* Lam., *Cordia cylindrostachya* (R. & P.) R. & S., *Tabebuia serratifolia* (Vahl) Nichols., *Terminalia amazonia* (J. F. Gmel.) Exell., *Protium insigne* Engl., *Vismia* spp., and Melastomaceae. The flora is quite different from that of the savannas previously described.

FIG. 10. Fire grassland of Imperata on the northern plain of Trinidad with Maximiliana palms as relics of the original forest.

THE VENEZUELAN LLANOS

THE MESA OF GUANIPA

During the two days February 10th-11th, 1945, the writer travelled by road from Ciudad Bolívar on the Orinoco River to Caracas, a distance of 480 mi. The most part of this journey is across the great llanos, plains sloping down to the Orinoco in the south and formed of Plio-Pleistocene alluvial deposits. From Soledad on the north bank of the Orinoco opposite Ciudad Bolívar, through El Tigre and almost to Pariaguan (about 90 mi.) the road traverses various so-called "mesas," the Mesa de Guanipa and others, which are savanna country *par excellence*. From Pariaguan to El Sombrero in the foothills of the northern Cordillera (250 mi.) the road crosses the *alto llano*, a transitional zone between flat savanna country to the south and more dissected, geologically older, bush-covered country to the north. The mesas traversed lower down are so-called because they are slightly elevated sections of the plains, in the form of huge terraces, which are not subject to inundation in the rainy season. The mesas are bordered by small scarp faces fronting towards rivers and are dissected by occasional trough-shaped valleys.

The road out of Soledad runs north-eastward in a straight line for mile upon mile across broad, even, very gently inclined expanses with scarcely a sign of a ravine or river bed breaking the sweeping monotony of the landscape (Fig. 11). The whole area is covered with bunch-grass savanna dotted with occasional trees of *Curatella americana* L., *Bowdichia virgilioides* HBK., *Byrsonima crassifolia* HBK., and *Roupala complicata* HBK. Such tree-dotted savanna is commonly known in Venezuela as *chaparral* from the most abundant tree, *chaparro* (*Curatella*, a name transferred from the European Cork Oak, *Quercus suber*). Chapparal both in Spain and North America has a meaning quite different from this in Venezuela. Trees are about 30 yards apart on the average and reach a much greater size than on the Trinidad savannas, up to 20 ft. high and often with a definite trunk 1 ft. in diameter. They retain, however, their gnarled habit and have rounded crowns.

FIG. 11. View of the Mesa de Guanipa, typical of vast areas of the Orinoco *llanos*. Trees are Curatella and Byrsonima.

This region has recently been studied botanically in some detail by Pittier (1942) who listed 44 species of grasses out of 109 species of plants comprising the savanna association.

Five of the 44 grass species attain sufficient abundance in certain parts to be called dominants. *Leptocoryphium lanatum* is dominant on low ground where the soil is not sandy: it is relatively rarely en-

countered. *Trachypogon vestitus* and *Axonopus chrysodactylus* occupy depressions where sand has collected and is deepest. *Trachypogon montufari* and *T. plumosus* are found on the sloping ground with a clay or gravel topsoil. These are the dominants of the ordinary plateau surface of the Mesa. A change occurs on river flats bordering the rivers and streams which have cut trench-like valleys into the Mesa. Here Trachypogon and Axonopus disappear and give way to *Mesosetum chaseae,* 5 species of Paspalum and *Sporobolus indicus.* The bunch-grass character of the savanna is less plainly marked and the grasses are finer and more delicate.

Cyperaceae are well represented. *Dichromena ciliata* is ubiquitous and here and there one finds a peculiar little plant, *Oncostylis* (*Bulbostylis*) *paradoxa,* which has a little woody aerial rhizome sheathed with old leaf bases. Termite mounds like those of the Trinidad savannas are seen with a like frequency.

The savanna soil is a loose, yellow sand usually about a foot deep, overlying a hard and compact red clay. The surface is never "hogwallowed." Stones are are rarely seen and when they occur they are of ironstone. Here and there occasional low knolls disturb the plain and these are seen to be capped with a layer of coarse ironstone gravel up to a foot or more in thickness lying upon the red clay. These knolls are virtually treeless and their herbaceous vegetation is markedly scanty. After passing through El Tigre the road crosses country which grows progressively flatter and more open, the savanna trees becoming smaller and extremely scattered, and opening up wide views of the country. Whole stretches are absolutely bare of trees. There is the same sandy topsoil, the same occasional knolls capped with ironstone gravel or massive ferruginous conglomerate. No termite mounds were seen here.

The rainfall of the Mesa de Guanipa, as given by Pittier (1942), for the 9 years 1933-41 varied from 26.3 to 64.7 in. per annum. Average figures for the period showed an annual precipitation of 43.8 in. distributed in a wet and a dry season of which the former lasted 5 months (June-October) with 5 to 7 in. per month and the latter 7 months with under 4 in., 3 months receiving ½ in. or less. The actual figures are:

Jan.	Feb.	Mar.	Apr.	May	June	July
26	5	13	14	93	167	173
1.0	.2	.5	.6	3.6	6.7	6.9

Aug.	Sept.	Oct.	Nov.	Dec.	Total
194	152	123	92	43	1095 mm
7.7	6.0	4.9	3.6	1.7	43.8 in.

There appears to be no reason why this should not be considered a forest climate which, given favorable soil conditions, would support a deciduous seasonal forest such as is actually found a little further to the northward. Pittier did not put forward any theory to account for the presence of grassland on the Mesa, though he evidently discounted recent origin due to fire stating "these savannas have never been covered with forests" (p. 14). It would appear from general inference that he attributed the lack of tree vegetation to the infertility of the soil.

MORICHALES AND GALLERY FORESTS

The rivers which meander across the llanos in trough valleys between the mesas are bordered by *morichales,* that is, by groves of Mauritia palms. Pittier (1942) described the typical *morichal* as follows (translation):

"These ravines are marked at least by dense thickets from which arise slender *moriches,* at first more or less isolated, but which soon form on both banks of the stream a continuous belt of variable width, broken by open swamps in which grow thickly the erect stems of *Montrichardia arborescens.* The number of species which grow within the *morichales* of the Mesa of Guanipa appears very limited for the crowded palm trees form a closed canopy which hinders the passage of light. . . ."

Pittier noted only 9 plant species in the *morichal* of which three were palms (Mauritia, Euterpe, Bactris). Associated with the *morichal* proper he noted areas of herbaceous swamp dominated by grass and sedge, and along certain streams *dry morichales* which appear to be transitional between pure *morichal* and woodland. All this vegetation is clearly swamp, associated with a perennially high water-table. It duplicates exactly certain swamp vegetation in the Blanquizales Lagoon in Trinidad (Beard 1946).

Gallery forests are very little seen in the Venezuelan llanos. One commonly imagines strips of tall, evergreen forest bordering the rivers when thinking of savanna country but in this region *morichales* for the most part replace them.

THE UPPER LLANO

Shortly before reaching Pariaguan the road descends from the Mesa of Guanipa across the head of the Rio Pao—bordered by a *morichal*—and enters a tall, dense chaparral. The Curatella and other trees are up to 30 ft. in height, though retaining their curious gnarled form, and grow thickly so as almost to touch one another. Occasional Acrocomia palms join the assemblage and the grass ground cover is somewhat reduced. This community is strongly suggestive in appearance of examples the writer has seen of the African *miombo* (Isoberlinia-Brachystegia woodland). Beyond Pariaguan the country is much more undulating than on the Mesa and as the brokenness increases the high chaparral merges into a true deciduous seasonal forest which was leafless at the season of the writer's visit. This is normal, dissected, forest country and the soil appeared as a red-weathering clay at the surface. Some

distance further on the country flattens out again and the forest is joined by numbers of a small palmetto (*Copernicia tectorum*) which eventually comes to form on level stretches a palm savanna, grassland scattered with these palmettoes instead of with Curatella and its associates. This palmaceous vegetation should not be confused with the *morichal*. Mauritia grows to be a tall, slender palm in dense stands along river banks. Copernicia is a short fuzzy palmetto and occurs irregularly scattered singly and in pairs across savanna country, given certain soil conditions (Fig. 12).

FIG. 12. Palm savanna with *Copernicia tectorum* on flats of the upper *llanos*. Ground burnt clean in the foreground.

Copernicia is seldom absent from the landscape all the rest of the way across the *alto llano* to El Sombrero. The country is variable, now flat, now undulating and in sympathy the vegetation varies constantly between deciduous forest, thorn bush, chaparral and palm savanna. The sand-capped soils of the Mesa are no longer seen and the red-weathering clay shows everywhere at the surface though many of the hill crests tend to be capped still with ironstone gravel. Where this gravel capping is thick, the chaparral is seen. Otherwise the hilly and sloping land is covered by forest or by thorn bush which represents forest degraded by man's interference. The palm savanna comes in on swampy levels with the deciduous forest appearing again as a narrow gallery forest along streams. At the time of the writer's visit the clay soil of the palm savannas was dry, hard and cracked but had the appearance of being waterlogged in the rainy season. The surface is slightly hogwallowed.

MYERS' JOURNEY TO SAN FERNANDO

In his journey to San Fernando de Apure in 1930-31 Myers (1933) observed the same succession of types. He travelled by road from Caracas via San Juan de los Morros, Ortiz, El Sombrero and Calabozo and thus passed through the whole transition from the mountains to the lowest river flood plains.

"South of San Juan de los Morros," wrote Myers, "one passes through large continuous areas of a low, open type of forest. Some of this is definite thorn forest, with *Acacia macracantha* H.B., dominant, but the larger area, consisting of taller, now largely leafless trees, approaches more to a monsoon type. The rainfall, of which there are unfortunately no records, can only be about 40 in., thus falling much below that required for monsoon forest in Schimper's definition (70 in.). It agrees better with his savanna-forest, to which he actually refers it (1903, p. 352), but I consider the term very misleading, since none of the typical savannah trees or shrubs, such as *Curatella, Bowdichia* and *Byrsonima* are present. It is probably best to follow Troup (in Tansley and Chipp 1926 p. 292) and call this merely "deciduous forest" until a better classification can be drawn up."

The present writer has described this type of forest as "deciduous seasonal forest" and regards the thorn bush as a secondary stage due to the shifting cultivator. The term "savannah-forest" would certainly be very misleading, though it could perhaps be applied to the transitional bush between forest and savanna which the writer saw near Pariaguan, where the savanna trees closed up almost to form a forest. Any such broad intermediate stage is, actually, very rare in the northern tropics and the writer has never seen another example. It seems to be more common in Brazil, passing by the names Catanduva in Warming (1892) and Cerradão in Waibel (1948).

The higher llanos from El Sombrero to Calabozo, as reported by Myers, agree with those seen by the writer from Pariaguan to El Sombrero. Deciduous seasonal forest alternates with orchard savanna bearing *Curatella americana* and *Bowdichia virgilioides* or Copernicia palms, with *Cymbopogon rufus* as the dominant grass.

After leaving Calabozo, Myers crossed the true lower llanos which the writer missed in journeying up from Ciudad Bolívar since at the start on the Orinoco the road was already on one of the Mesas. "This plain," he wrote, "opens out still more and we see for the first time a view such as inspired Humboldt's classical description of the llanos—an apparently limitless expanse of grass as flat as the sea, with the hazy presence of a few scattered trees on one horizon only, barely discernible. This is evidently typical low bunch-grass savannah."

Cymbopogon rufus was still the dominant grass, giving way in places to *Andropogon condensatus*. A herb, a blue-flowered Labiate, *Hyptis suaveolens* was always conspicuous and in places assumed complete dominance for miles. This appeared to be due to the effect of heavy grazing. In places the savanna was absolutely treeless, in places with Copernicia palms and in places with Curatella and Bowdichia shrubs. Occasional belts of "low, open deciduous forest, with a most unusual abundance of strangling figs (*Ficus* sp.)" were crossed. As the road approached nearer to the Apure and Portuguesa rivers the plains showed signs of inundation in the rainy season. These flats were treeless save for a bush, *Ipomoea crassicaulis,* and the grasses were short and differed from those of the Cymbopogon savanna. *Sporobolus indicus* and *Steirachne diandra* were noted. Lower still in the llanos the route crossed the zone of the *esteros,* wide shallow depressions covered

with standing water in the rainy season and still moist enough throughout the dry season to enable growth of the grasses. The grass cover of these *esteros* is markedly distinctive, "a pure knee high stand of a much stouter grass with long trailing stems rooting at the nodes, and close, leafy, sterile culms, erect and somewhat hirsute. Although no flowers were to be found, this grass is undoubtedly *Paspalum fasciculatum* Willd."

"Apart from the fringing forest along this river (the Portuguesa) and one palmetum (*Copernicia*) near San Fernando de Apure, the route from Camaguan to the latter town, on the banks of the Apure passes through practically nothing but vast plains of *Paspalum fasciculatum,* up to waist and even breast-high. Occasional damper areas and lagoons support stands of *Ipomoea crassicaulis.* On dryish areas there are stretches of *Malachra alceifolia* Jacq. The *Paspalum* covers dried, cracking mud. Rarely, among its close-growing sterile culms, appears a flowering stem of another, more slender grass, *Eriochloa punctata* (L.) Desv. Hamilt."

Here for the first time Myers mentions the nature of the soil, "dried, cracking mud." This is evidently quite different from the sand-over-clay soil of the higher llanos and presumably consists of recent alluvium of which a fresh film is deposited every year.

Myers considered this Paspalum grassland as "true high-grass tropical savannah" according to Bews' classification (1929).

THE LLANOS IN COLOMBIA

The great savanna-covered plains of the left bank of the Orinoco extend far to the south-west into Colombia. According to Dugand (1945) and Bates (1948) the ultimate boundary is the Guaviare River, one of the tributaries of the Orinoco, beyond which the Amazonian rain forest is entered. Dugand described the predominating vegetation as "immense grassy savannas, dotted with palms and scattered shrubs." Patches of forest and groves of Mauritia palms occur in "humid bottom-lands" and there are extensive gallery forests along the rivers. Photographs by Bates demonstrate the association of these savannas with quarternary terraces.

THE NORTHERN CORDILLERA OF VENEZUELA

The highway from Ciudad Bolívar to Caracas, after crossing 600 kms. of plains country, reaches at Ortiz the foothills of the northern cordillera, a great series of mountain ranges which rises east of Barquisimeto and runs eastward bordering the Caribbean Sea for several hundred miles. This is not properly a section of the Andes, being detached therefrom and taking a totally different direction. The highest peaks exceed 9,000 ft. and in the centre the ranges include a basin of interior drainage containing the Lake of Valencia lying some 1500 ft. above sea level. This region is the most densely populated in Venezuela and has been the longest settled. Accordingly, since Venezuelans are particularly careless in their treatment of natural resources, there are abundant signs of devastation by humans. The region has a low rainfall since the coastal ridge is the highest and catches the rain from the prevailing north-east winds, setting up a rain shadow in its lee. This leads annually to a vast outbreak of fires in the dry season and the mountain slopes which are known from early accounts to have been formerly covered with forest are now largely covered with grass.

The town of San Juan de los Morros is set in the midst of mountains rising 3-4,000 ft. above it. The "Morros" from which the town is named are limestone pinnacles which have stood out in the form of "haystack hills" or "mogotes" as they are called in Cuba, after erosion has removed the surrounding schistose rocks. They are spectacular and are not the only examples in this district, which might be termed the Venezuelan Dolomites. The limestone is covered with a thin woody scrub but the neighboring schist mountains have been almost entirely denuded right to their summits and are covered with grass, with occasional shrubs. At the time of the writer's visit in February slopes were extensively fire-blackened. Around the Lake of Valencia the mountains are similarly grass-covered up to a height of 5-6,000 ft. on the northern or seaward range. Above this height a belt of cloud is usually present and with it there is an abrupt transition to evergreen forest. Since their denudation the mountains have evidently been severely eroded. Between Caracas and Los Teques the mountains are covered with poor xerophytic scrub full of cactus and agave rather than with grass, but immediately to the north of Caracas itself the steep lofty Avila range is grassed up to the cloud belt at 5,000 ft. above sea level.

The vegetation of the Caracas valley was described by Tamayo in 1943. The average annual rainfall he gives as 824 mm (34.3 in.) but precipitation is very erratic, and has varied between 459 mm (18.7 in.) and 1244 mm (51.8 in.) per annum. Soils are developed either over schist or over limestone, with grassy vegetation predominant on the former and a scrub of cacti, agaves and leguminous bushes on the latter. From all accounts and inferences the entire region was formerly covered with forest which has gradually disappeared due to cutting, fire and grazing. Various stages of degradation can still be seen: deciduous forest, thorn bush, *"crassuletum"* of *Cordia curassavica* and finally savanna or cactus scrub. Tamayo gives a long list of constituent species for two types of savanna, but it is not clear which are the dominants or the most abundant unless these should be the species appearing first on the list. On the tops of the ridges *Aristida adscencionis, Eragrostis trichocolea, Paspalum notatum, Sporobolus indicus* and *Cipella linearis* achieve first mention. Shrubby constituents include four melastomes, *Clidemia ciliata, Miconia albicans, M. rubiginosa* and *M. rufescens.* Savanna of slopes and lower parts of hills is evidently richer and features three species of *Andropogon,* five of *Aristida,* three of *Paspalum* and *Trachypogon plumosus.* Tamayo mentions elsewhere that "chaparro" is present in the savannas but his list

does not include *Curatella americana*. Pittier (1939), however, mentions this species which is certainly present, as the writer has seen for himself, together with a Roupala and *Oyedaea verbesinoides*. During the degradation process the hills, which are very steep, appear to have become severely eroded and for the most part there is now very little soil, the vegetation having little between it and the bedrock. This erosive process continues since the grasses are nearly all of the bunch-grass type and do not form a continuous turf.

These grasslands are clearly of recent origin due to human influence and seem closely comparable to the St. Joseph savanna of Trinidad.

In the Andes proper substantial areas of mountain slopes formerly covered with forest, at all elevations from the foothills up to the *páramos* at 10,000 ft., have been converted into grassland by fire and grazing since the arrival of Europeans. Such areas may be excluded from this study of natural grasslands of the lowland tropics.

The West Indies

The Lesser Antilles

The Lesser Antilles are a festoon of small oceanic islands disposed between Trinidad and Puerto Rico at the eastern end of the Caribbean Sea. For the most part they are high, volcanic and mountainous, though some of the offlying islands are low and formed of limestones. The vegetation throughout is typically forest of one type or another, developed under rainfalls varying from 40 to 400 in. per annum and on a variety of soils and sites. Grasslands other than strictly artificial pastures occur only on three islands, Dominica, Antigua and Barbuda. On the last named only is there any indication of natural savanna. Fuller details of the vegetation of these islands are available (Beard 1947).

Dominica

Dominica is an exceedingly mountainous volcanic island with an area of 304 sq. mi. within which there are five peaks over 4,000 ft. high and a great number number exceeding 3,000 ft. The rainfall in the interior is very high, over 300 in. a year having been recorded in gauges, and the greater part of the island is or was originally covered in high, dense rain forest. Only on a narrow strip down the west or leeward coast does the rainfall become too low to support rain forest, decreasing to some 60 in. annually. All the original forests in this part have been destroyed, but the widespread areas of secondary bush indicate by their composition that some kind of sclerophyll or "dry evergreen" forest was formerly present. In the centre of this coast there is a district called the Grand Savanna where a good deal of grassland is mixed with the bush in large patches.

The principal savanna area is on a promontory sloping gently up from sea level to a height of several hundred feet but the grasslands also ascend the mountain slopes and cover certain upland plateaus overlooking the coast at a height of about 600 ft The soil throughout is of the type known as shoal (Hardy 1941). The area is burnt annually.

The dominant grass throughout appears to be *Sporobolus indicus*, associated with an Andropogon and a sedge. Some woody growth is always present in the savannas and is very variable. One phase comprises low shrubs of *Byrsonima lucida* up to 5 ft. high and *Stigmaphyllon cordifolium* up to 2½ ft., the latter normally a vine but here assuming a shrubby habit. A species of *Heliotropium* associates freely with the grass here. Elsewhere, isolated trees of the introduced logwood (*Haematoxylon campechianum*) or of *Tabebuia pallida* are seen, or the savanna is plentifully dotted with *Guettarda scabra*, a forest tree here assuming a suffrutescent habit. This last is most characteristic of the upland plateaus. The savannas are mixed with patches of degraded bush containing mostly Haematoxylon and species of *Croton*.

The soil here exhibits impeded drainage and the natural conditions are in many ways not unlike those typical of savanna lands. With the exception of the *Byrsonima lucida* phase, however, we are obviously dealing with fire-degraded woodland and this is probably true for the entire area. None of the typical elements of American savannas except *Sporobolis indicus* are present here and in the writer's opinion the area was formerly all forested.

Antigua

Antigua is a more or less lowlying island in the Leeward group, of some 108 sq. mi. It includes a range of old volcanic hills up to 1,200 ft. high but the greater part is formed of sedimentary lowlands less than 300 ft. in elevation. All the island was formerly cultivated in sugar but certain areas of the less tractable soils have been abandoned and are mostly now used for grazing cattle. The general appearance of these areas, according to Charter (1937) is "course grassland scattered over with small patches of scrub. The dominant grasses on these areas are species of *Paspalum* and *Andropogon* and include *P. plicatulum*, Michx., *P. secans* Hitchc. & Chase, *P. notatum* Flügge, *A. glomeratus* (Walt.) BSP. and *A. saccharoides* Sw." Unless such pastures are given frequent attention they rapidly become covered with a dense growth of thorn trees, principally *Prosopis chilensis*, *Acacia nilotica* and several other Acacia species. The cattle themselves spread the thorn bush by browsing the seed pods and so distributing the seeds in their dung. All stages in the growth of thorn bush can be seen, from the still grazed pasture with small thorn shrubs to the dense and impenetrable thicket and finally, after the axe has been at work, to the "thorn savanna"—a fresh pasture with scattered Prosopis and Acacia as shade trees (Fig. 13). This forms a landscape strongly reminiscent of African "thorn veld," but is entirely artificial and owes its existence to man and cattle. There is no doubt that all Antigua soils were formerly forested, and when abandoned to bush directly from cultivation they come up in secondary woodland without

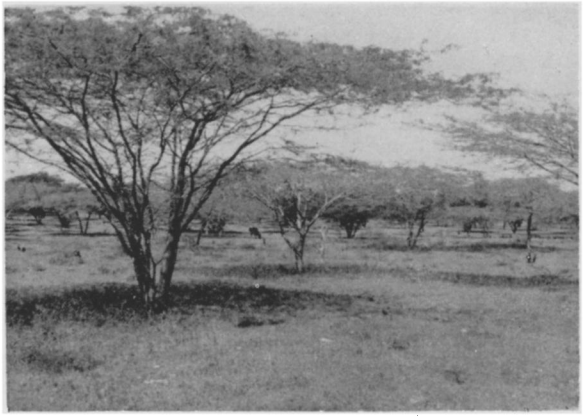


FIG. 13. Thorn bush in Antigua with *Prosopis chilensis* and *Acacia* spp., grazed pasture beneath.

FIG. 14. Barbuda: mixture of grassy glades and patches of bushland. Right to left: open patch which is a rain puddle in wet weather, grass, bushes of Eugenia, Comocladia, etc., spiky Plumeria tree and Bucida behind.

Acacias. These latter are a feature of grazed land only and all of the species concerned are introductions from outside.

BARBUDA

Barbuda is a small island with an area of only about 35 sq. mi., scantily populated and composed of a series of flat limestone terraces rising in the centre to a height of about 100 ft. Two thirds of the island consists of a flat plain less than 10 ft. above sea level. Rainfall is low and erratic, having varied (since 1920) between 26 and 61 in. per annum, with an average of 36 in. Long droughts occur and the island is severely windswept. The underlying coral limestone carries very little depth of soil. Frequently it is exposed and forms a bare pavement, with soil only in the pockets, potholes and crevices between the slabs. The soil, such as it is, is a stiff clay varying in color from black on the lowest lands to red on the highest. There are no rivers or ravines and the soils on the lower sites are waterlogged after rain.

In view of these adverse conditions it is natural to find that the most widespread type of vegetation on Barbuda is Warming's "Evergreen Bushland" (1909)—"a grey, desolate, useless and scorching bushland, between whose thorny shrubs and small trees one cannot penetrate without the aid of an axe." The bushland is from 10 to 30 ft. high, composed of gnarled little trees and bushes with small, hard, evergreen leaves. It does not seem to have been much disturbed by man except near the village.

On the marginal plain the dominant tree in the bushland is *Bucida buceras,* associated with *Tabebuia pallida, Coccoloba diversifolia, Byrsonima lucida, Guettarda scabra, Pisonia fragrans* and many others, including a Coccothrinax palm. On the southeastern part of the plain drainage seems to be at its worst, leading to the appearance of extensive pockets of savanna. Changes in site drainage, apparently quite slight, lead to abrupt alternations of bushland and grassland. The savannas are quite treeless and composed of *Paspalum bakeri,* a bunch-grass with coarse, cutting leaves growing in well developed tussocks. The savannas occur as glades varying in extent from several acres down to a few square yards. The larger ones are bordered always by Bucida trees assuming a domed form with long branches given off from the base, loaded with bromeliads (*Tillandsia utriculata*). Smaller glades pass directly into bushland (Fig. 14). The whole area is an irregular mosaic of glades of savanna, scattered, domed Bucida trees, patches of saplings (mainly Myrtaceae) and clumps of trees with cacti and palmettoes. These alternations seem to be dictated solely by very slight changes in relief and soil depth. The savannas occupy slight depressions where water collects in wet weather and the woodlands cover the slight rises. The savannas are alternately waterlogged and dried out, while the woodland sites are less prone to waterlogging, better aerated and with effectively more root room. Deeper depressions in the plain which are more or less constantly under water are filled with sedge (*Fimbristylis ferruginea*) and bushes of *Annona glabra.*

There can be no doubt that these savannas are of natural origin and their association with soil drainage conditions is clear. Fire seems to be unknown.

THE GREATER ANTILLES

The Greater Antilles comprise essentially the four major West Indian islands of Puerto Rico, Hispaniola (including Haiti and the Dominican Republic), Jamaica and Cuba. Where there are mountain ranges or other broken country on these islands, the vegetation is or was typically forest. Where there are plains of large extent with mature soils, the vegetation is typically savanna.

No natural savannas are known from Puerto Rico or Jamaica, being relatively small mountainous islands, though in the latter there are in many of the drier parts grazing areas with thorn bush similar to those of Antigua. These are similarly artificial and represent a degradation of deciduous forest. There are certain savanna areas in Hispaniola and wide extents of savanna in Cuba, situated on plains in those islands.

HISPANIOLA

This large island is divided politically by a north-

south boundary between Haiti and the Dominican Republic, but the natural features run the other way in the long axis of the island and cross the political frontier.

The island is traversed by a number of mountain chains running more or less in an east-west direction and containing the highest peaks in the Antilles with a maximum elevation of 10,000 ft. Between the ranges there are flatter lands at various elevations, comprising one rather extensive central plateau and several smaller plateaus or plains. The bulk of the island is, or was, forested, most of the forest being of a xerophytic nature due to inadequate rainfall (20 to 50 in. annually). In the mountains there are moist evergreen forests, and also pine forests whose ecology presents interesting problems. There are savannas on the plains and plateaus.

The writer has unfortunately been unable to consult the solitary modern ecological work on the vegetation of the island, Ciferri's "Studio geobotanico dell' Isola Hispaniola" (1936). Dr. J. T. Curtis, of the University of Wisconsin, has, however, been kind enough to supply information on the savannas of Haiti from his own observations, in considerable detail, and the data which follow are taken from his letters. Dr. Curtis distinguishes three types of savanna, "open," "orchard" and "dry."

Open Savanna covers an area of 80,000-100,000 acres on the Central Plain at an elevation of some 1,700 ft. above sea level. The region is unpopulated, primarily because of the severe annual fires and also because of the scarcity of water in the dry season. The rainfall varies from an average minimum of only ¼ in. in February to 8¼ in. in June, with an annual total of 48½ in. (1167 mm.). The dry season lasts from November to April, during which less than 4 in. of rain a month fall. No records of temperature are available, but there is certainly no frost at any time. Dr. Curtis estimates the extreme minimum temperature at 45°-50° F. Streams are infrequent and deeply entrenched, the surface of the plateau level to gently undulating.

The soil profile was studied in connection with attempts to grow Cryptostegia and revealed a uniform black surface horizon 28 to 36 in. deep, grading into a grey or almost white impervious hardpan layer of 6 to 10 in. thickness. This was underlain by weathered rock material. The hardpan was hard only in the dry season. In the rainy season, the overlying black layer was very wet, almost boggy, and the white layer was soft but still apparently impervious. The latter was of a gley-like appearance, in places having reduced iron spots or mottles. Test plots of Cryptostegia died out completely in the dry season, and Dr. Curtis is of the opinion that woody plants in general would have difficulty in penetrating the hardpan layer.

There is a spring-like resurgence of growth when the rainy season commences. It is marked by the appearance of many showy flowers, most coming from bulbs or fleshy roots and rootstocks. Among the forbs noted were *Zephyranthes eggersiana, Stenorrhynchus orchioides, Lobelia domingensis* (?), *Polygala* sp., *Stigmatophyllum* sp., *Euphorbia prostrata* (?), and *Crotalaria* sp. There are no trees. The dominant grass over large areas, in which it grows in a nearly pure stand, is *Themeda quadrivalvis.* Other grasses and grass-like plants collected on the savanna by Dr. Curtis and identified by Mrs. Agnes Chase were *Andropogon bicornis, Andropogon tener, Aristida refracta, Paspalum milligrana, Paspalum plicatulum, Paspalum densum, Sorghastrum parviflorum, Fimbristylis diphylla, Fimbristylis monostachya, Scleria hirtella* and *Scleria pterota.*

Orchard Savanna includes savanna with pine (*Pinus occidentalis*) as well as with the typical orchard trees (Curatella, Byrsonima, Anacardium) since Dr. Curtis says that here at any rate they mingle and cannot be separated. The orchard savanna is also seen on the central plain, on its eastern and south-eastern part where the ground is more broken. The northwestern portion is open grassland on a gently rounding, undissected plateau, as described above. The only trees are along the few ravines or draws present and hence there are great areas with no trees whatsoever. The country where the orchard savanna appears is deeply dissected, the ravine bottoms are wooded and the intervening country is under savanna with scattered trees, the open grassland still being seen on hilltops which represent relics of the dissected plateau surface. The orchard type appears to be associated with topography in process of rejuvenation, where drainage conditions have improved slightly from the flat country of the open grassland. Fully mature topography, which Dr. Curtis calls "Knob-hill country" is covered with xerophilous bush containing pines and small hard-leaved evergreen trees, with Themeda grassland or patches of shrubs (Pictetia, Brya) in the valleys between the "Knobs." The position is now reversed, with grass and not trees along the bottomlands. The bush clustered on the tops and sides of the "Knobs" is apparently somewhat open and, except for the pines, of low stature. *Pinus occidentalis* is typical, with *Coccoloba rotundifolia, Acacia scleroxyla, Pisonia domingensis, Comocladia* sp. and *Coccothrinax argentea.* Dr. Curtis states that grass is ecologically dominant. The soil is a heavy yellow clay from limestone bedrock. No details are available on the soils of the orchard savanna, other than that they do not show the surface black horizon. Dr. Curtis is of the opinion that this type is the result of fire rather than of climatic and soil conditions.

Dry Savanna is found on Miocene limestone on the low foothills near the ocean in regions of 20 to 30 in. annual rainfall with a severe dry season. Almost no soil is present, the substratum consisting of rock detritus. This is due in part to the considerable surface drainage so that at no time, even in the rainy season, is the ground wet for more than a few hours. The typical grass is *Uniola virgata,* in many places the only grass. Another grass on the more level areas is *Bouteloua heterostega. Agave antillana* is well distributed. The shrubs are *Plumeria alba,*

Maytenus buxifolia, Schaefferia ephedroides and *Jacquinia berteroi.* An unimportant but characteristic and widespread plant is the orchid *Tetramicra ekmani,* epiphytic on the Uniola clumps. Judging by old French records, says Dr. Curtis, this savanna was present in 1750; even so, it may originally have been of fire origin. In any case, it is now stable, and has little prospect of successional change, regardless of fire.

The presence of pine savanna in Hispaniola brings forward interesting ecological problems in connection with the distribution of the pine in question, *Pinus occidentalis,* in the island. This pine is found on a great variety of soils and geological formations, on a diversity of landscape and at altitudes ranging from 500 to 10,000 ft. above sea level. It tends to occur in more or less pure stands with a grassy ground cover beneath, but in by no means the majority of cases could the vegetation be termed pine savanna. As Chardón (1941) has pointed out, the real domain of the pine lies above the contour of 2,000 m. where it covers wide areas in the central cordillera and more southerly ranges, forming absolutely pure stands above a carpet of the grass *Danthonia domingensis.* This behavior is limited to mountains where the climate is seasonally dry enough to encourage forest fires, and according to Holdridge (1945) there is reason to believe that the pine has succeeded various types of mixed montane forest as a result of burning. Where fires are prevented for several years, he states, hardwood seedlings start coming up in the understory. Such pine forests, though grass carpeted, are not pine savanna, since the grass is not ecologically dominant. True pine savannas are found only in the lowlands and foothills where the pine is much less widespread and occurs in limited areas forming much more open stands. The lowland vegetation, it seems, has more resistance to fire and to the invasion of the pine which is only able to penetrate depauperate communities such as orchard savanna and dry evergreen scrub. We may regard the pine as a fairly recent colonist from North America which has sought to establish itself wherever it could find favorable conditions. Fires set in the high mountains by the aboriginal Arawaks or by lightning led to its wide extension there, and in the lowlands it became a component of preexisting orchard savannas and scrubby communities. The species is evidently extremely tolerant and also fire resistant and these two qualities enabled it to add itself to the aborescent members of the savanna community. Pine savanna should probably be regarded as only a variant of the orchard type.

In the Dominican Republic, according to Chardón, the pines where they occur at low elevations, often are mixed with considerable groups of *Byrsonima crassifolia, Chrysophyllum olivaeforme* and *Eugenia* sp. and the grass cover is provided by Andropogon. Such areas are probably closely similar to the Nipe plateau of Cuba of which we have a detailed description (Carabia 1945), reviewed in the following section.

CUBA

Cuba is the largest of the Greater Antilles, an island 720 mi. in length, and is replete with savanna lands. No satisfactory detailed ecological study of the vegetation exists but the writer has drawn upon Seifriz's (1944) "Plant Life of Cuba" (a useful work though somewhat generalized, and botanical rather than ecological) as well as on the travels of Brothers Marie-Victorin and León (1942, 1944), which yield many interesting botanical details. Carabia's "Vegetation of the Nipe Plateau" (1945) is a useful local study of a complex area. For study of savannas, the most fruitful work of all is Bennett & Allison's "Soils of Cuba" (1928) which gives very thorough data on savanna and forest soils as well as notes on the vegetation types. Thanks to this, in conjunction with Charter's soil work in British Honduras, to be discussed in the next section, we understand these savannas more thoroughly than any others in tropical America.

Cuba lies just within the tropics, between 20° and 23° north latitude. The climate is a typical moist tropical one, with the average temperatures for all months of the year lying between 70° and 80° F. Frost has never been reliably recorded. The greater part of the island receives an annual rainfall of between 40 and 60 in., a few very limited areas receiving less, and the mountain chains locally attracting more. Distribution is fairly consistent throughout the island, entailing a dry season from November to April, during which which generally from 1 to 4 in. of rain a month are received, and a wet season from May to October, with from 4 to 10 in. of rain a month. The rainy season has two maxima but the drop in between is insufficient to constitute a second dry season. The dry season is a severe one and consequently the vegetation, except in the mountains, is mainly xerophytic.

Geophysically, Cuba consists of a low, continuous plain rarely raised 200 ft. above sea level and floored with Tertiary deposits, through which rise here and there isolated hill and mountain masses of older Tertiary and Cretaceous sediments and igneous intrusions, rising to a maximum elevation of some 7,000 ft. The hills and mountains fall roughly into five groups. At the western end are the Organ Mountains, formed of cavernous limestones which stand out typically as "haystack hills" or "mogotes." Three groups of hills and low mountains, mainly igneous, occur in the centre, in Santa Clara Province, and another range of low hills in Camagüey. Finally at the eastern end of the island is the great Sierra Maestra of lofty peaks with associated ranges such as the Sierra de Nipe.

The mountains of the island, with the exception of the Sierra de Nipe, are or were covered with forest, the soil-less limestones of the Organ Mountains with a low, highly xeromorphic growth, the low mountains of the centre and the foothills of the eastern mountains with seasonal forests and the higher elevations of the eastern group with montane forests —rain forest and elfin woodland. The Sierra de

Nipe features certain pine savannas and will be discussed further.

The plains fell originally into three categories, swamps, savannas and well-drained forests. In this island, savanna is typically the vegetation of plains, though not of all plains. Bennett & Allison wrote: "Predominantly, savannas, are somewhat to very flat: there are also undulating areas but very rarely is relief stronger than this." Much of the swamp and savanna land remains in its original condition, but the bulk of the forest land has been cleared for agriculture. Relics indicate for the most part the former occurrence of deciduous seasonal forest. From the earliest times in Cuba it was appreciated that there are essential differences between forest and savanna soils, the savannas being infertile and seldom lending themselves to the production of crops.

So well recognized is this fact that Bennett & Allison could write that "in Cuba the term savanna, as applied to land, carries both a vegetative and a soil meaning. . . . As a rule the savanna lands have at relatively shallow depths subsoils composed of material which affects the soil moisture conditions unfavorably." Marie-Victorin & León expressed it: "One calls savanna, in this country, a stretch of non-mountainous terrain, with poor soil, with herbaceous or shrubby vegetation in a natural state." It is not even suggested that the savannas have a climatic relationship. Scattered as they are throughout the island mixed with forest (or potential forest) country and receiving a rainfall which though sometimes meagre is nearly everywhere adequate to support forest of some kind, the climatic explanation does not suggest itself. On the other hand the intricate relation between the savannas and special conditions of soil and landform is arrestingly obvious. Generally, the soils feature a permeable horizon overlying an impermeable subsoil. Sometimes this effect is due to the presence of rock which has not decayed deeply, sometimes to the superposition of a sand upon a clay horizon, sometimes to the occurrence of layers of pebbly ironstone concretions (perdigón) or massive ironstone sheeting (mocarrero). Drainage impedance is accentuated by the low relief. Savannas, therefore, occupy portions of the plains where these special soil conditions have developed. Bennett & Allison's soil map indicates that more than one third of the Cuban plains is savanna country. The soil pattern is repeated over and over again. The Santo Domingo savanna is on sand (with or without ironstone) over clay over chalk. The coastal savannas of the Trinidad plains show a sandy loam over mottled clay containing quartz gravel. On the Camaguey plain there is the Oriente clay, a forest soil (black clay over whitish clay over chalk) and also the Estrella fine sandy loam (a sandy loam over yellow and red mottled clay over chalk) which is a savanna soil with its alternation of texture in the horizons. Another savanna soil at Camagüey is a brown clay over serpentine rock at only 2 to 8 in. depth, or else sandy loam over clay over serpentine at 5 to 18 in. The Holguin savanna has a red shallow clay over chalk. Typical savanna soil profiles of the South Plain of western Cuba were expressed diagrammatically by Bennett & Allison, from whose illustration Figure 15 has been adapted.

The savanna soil departs somewhat from this dominant pattern in the case of the Nipe clay soil of the Sierra de Nipe, already noted as the solitary case of savanna on mountain land. The Nipe soil consists of a friable red-brown clay filled with *perdigón* and about a foot deep overlying a horizon 5 to 6 ft. deep of deep red clay with *perdigón,* over, in turn, an orange friable clay with boulders of decomposition, reaching serpentine bed rock at a depth of some 16 ft. (Marbut 1932). This is a very peculiar soil of remarkable structure and composition: the internal drainage and chemistry of the profile are not clear. Presence of *perdigón* in the top horizon seems to indicate poor drainage.

Upland forest soils and swamp soils are both of distinct character from those of the savannas. The former are red, brown, yellow or grey but one does not remark the differentiation into textural horizons, nor the prominent occurrence of *perdigón* and *mocarrero.*

These are well drained soils both externally by reason of sloping topography and internally by virtue of a more or less freely draining profile. Swamp soils are generally dark colored, often black. The subsoil may or may not be impermeable but there is a permanently high water table due to low relief. "Hog-wallow" structure is a feature of these soils and a characteristic vegetation is often the Haematoxylon thicket. This tree is a thorny, microphyllous legume of stunted and gnarled growth (about 30 ft. in height at most) which when growing in a swampy habitat develops a much thickened base to the trunk with innumerable flutings or small buttresses. This community occurs also in Honduras.

In endeavoring to arrive at a generalization for the vegetation of the savannas it would appear that the two predominant grasses are *Sporobolus indicus* and *Andropogon virginicus.* Other grasses of more localized dominance mentioned by Marie-Victorin & León are *Sorghastrum stipoides, Arundinella deppeana, Panicum tenerum* and *Imperata brasiliensis.* Sedges are represented abundantly by *Rhynchospora globosa* and *Bulbostylis paradoxa.* Greatest variety seems to be lent to the savanna associations by changes in the arborescent components rather than in the herbs. One may naturally expect to hear of *Curatella americana, Byrsonima crassifolia,* and *B. verbascifolia.* Other small trees often found are *Brya ebenus, Rondeletia correifolia, Anacardium occidentale, Xylopia grandiflora* and *Tabebuia lepidophylla.* Such a chaparral, however, is not the predominant phase. Two different, very distinctive types are exeedingly well developed: the oak-pine type and the palm type. The Curatella-Byrsonima assemblage may be replaced by or mixed with Quercus and Pinus, single or together, or else the two latter may be replaced by groves of palmettoes of the genera *Sabal, Copernicia, Acoelorraphe* and *Colpothrinax.*

Pinnate palms (Roystonea, Acrocomia) are only rarely present. Most of the species of palmetto are endemic and some of them develop curious bulbous swellings on the trunk. They may occur in dense groves or as single, scattered individuals. All kinds of variations and combinations between *chaparral,* oak, pine and palmettoes are possible.

On the Holguin savanna in the east, where the soil is a clay over chalk, the aboreal element is said by Bennett & Allison to be a dense stand of *Sabal florida.* Much of this savanna, however, is on a shallow soil over serpentine rock, and the palms in this case are given by Seifriz as *Copernicia yarey* and *Coccothrinax garciana,* two species of smaller growth than the Sabal. The grasses *Andropogon virgatus, A. gracilis, Leptocoryphium lanatum, Sporobolus indicus* and *Panicum* spp. are noted as present, but the ground cover is said to be composed principally of "a rather dense growth of small shrubs, in part thorny" (Seifriz).

The Camagüey savannas, partly serpentine, partly sandy over clay, are of the palm type. Seifriz lists three species of Corpernicia and three of Coccothrinax, while Bennett & Allison mention *Sabal maritima, Byrsonima crassifolia* and *Sporobolus indicus.* The Santo Domingo savanna features the last three species without the Copernicia and Coccothrinax.

On the South Plain (*fide* Bennett & Allison) the vegetation associated with the typical soils of the rolling, well-drained region (see Fig. 15), is a savanna of *Sporobolus indicus* with Byrsonima, Sabal, and locally Roystonea and Colpothrinax. Sometimes this changes to Andropogon savanna with Byrsonima, Anacardium and pine. The savanna of the imperfectly drained flats is composed of *Andropogon virginicus* with a Paspalum and contains Colpothrinax, Copernicia and other palmettoes, *Byrsonima crassifolia* and *Malpighia glabra.*

Seifriz has given us a more complete list of the principal elements in the flora of this area, as follows: Palms are *Sabal florida, Colpothrinax wrightii, Copernicia glabrescens, Acoelorraphe wrightii.* Shrubs or small trees: *Byrsonima crassifolia, Rondeletia correifolia, Miconia delicatula, Tabebuia lepidophylla, Curatella americana, Vaccinium ramonii, Befaria cubensis* and *Kalmiella ericoides.* Grasses: *Paspalum pulchellum* and *P. plicatulum, Aristida refracta* and *A. neglecta, Cenchrus distichophyllus, Sporobolus*

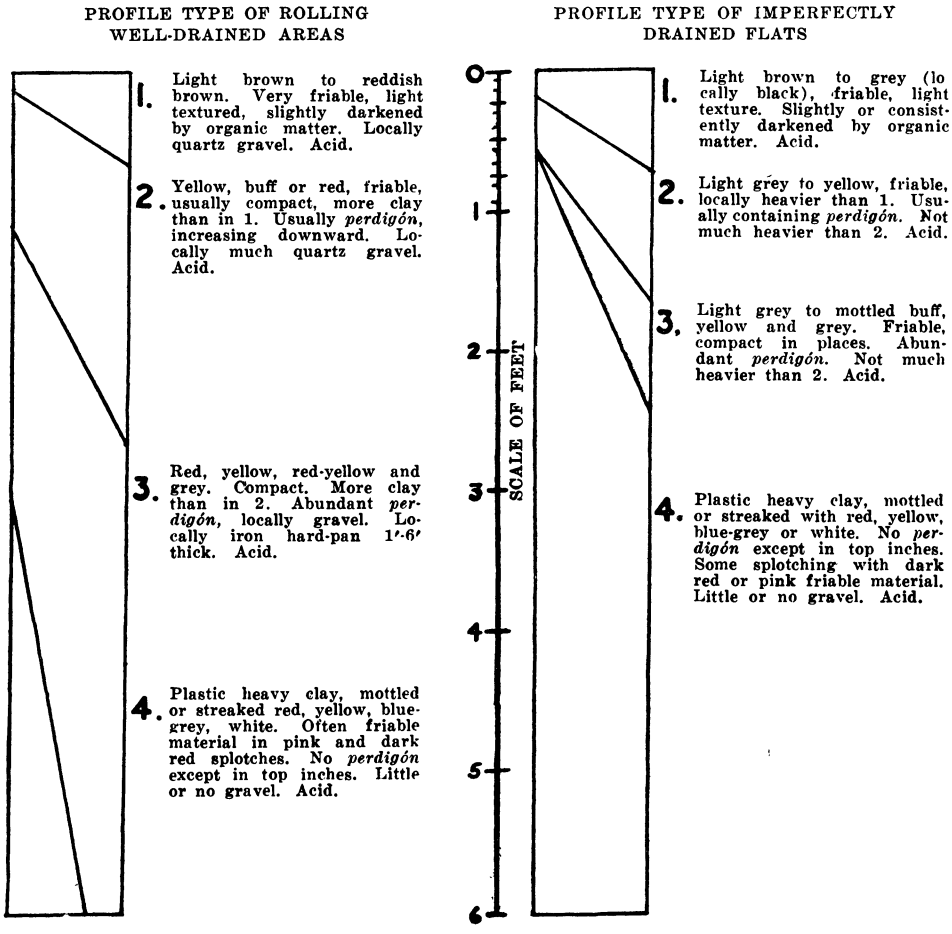


FIG. 15. Profiles of savanna soils from the south plain of Cuba, redrawn from Bennett & Allison (1928).

purpurascens, Andropogon virgatus and *A. virginicus, Panicum condensum, Trachypogon filifolius, Imperata brasiliensis.* Sedges: *Dichromena ciliata* and *Rhynchospora globosa.* Herbs are said to comprise numerous species of Xyridaceae, Eriocaulaceae, Droseraceae, Polygalaceae and Compositae.

Among the hills of the Sierra de los Organos Marie-Victorin & León encountered an association of *Quercus virginiana* and *Pinus tropicalis* in grassland of *Sorghastrum stipoides,* which they found to bear a striking resemblance to the *Quercus ilex-Pinus halepensis* association of the Mediterranean region, with this difference, that the other woody associates in the Mediterranean are microphyllous (Erica, Ulex) whereas those in Cuba have quite large leaves (Byrsonima, Rondeletia, Curatella). A variant of this association is *Quercus virginiana—Byrsonima crassifolia* over *Arundinella deppeana* with pine absent.

On the Isle of Pines the variations seem endless: "the appearance of the savannas changed unceasingly" wrote Marie-Victorin & León. Just a few of the types are:—*Sporobolus indicus* with Curatella, Tabebuia, Byrsonima, Brya and Rondeletia; *Imperata brasiliensis* and *Rhynchospora globosa* with Pinus and Colpothrinax; *Bulbostylis paradoxa* with Pinus and Tabebuia, or with Tabebuia alone or with Tabebuia and Rondeletia; *Rhynchospora globosa* with *Byrsonima verbascifolia.*

None of these variations in composition of the savannas has yet been studied in detail, and the reasons for them therefore are not yet understood. Clearly the variations are related to variations in soil moisture and drainage due to topography and soil structure.

The writer suggests that the palm savannas may be found to occupy the areas with clay or clayey topsoil and the orchard savannas the more sandy ground. Such floristic variations as occur do so, it will be observed, within rather narrow limits. There is a definite savanna flora which seldom mingles to any extent with forest elements. The Cuban savanna flora is closely related to that of other typical savannas of tropical America, but is remarkable in certain respects: it is very rich and it is very highly endemic. It seems probable that, if the plants of the Cuban savannas were completely catalogued, they would come near to equalling in number those found within any equivalent area of the Brazilian plateau, and would far outnumber the components of any other savannas north of the Amazon. The increased number of plants in Cuba is not due to the reappearance of Brazilian species of disjunct distribution which bypass Venezuela but to the many endemic species peculiar to the island. This high endemism is paralleled in the forest floras of the Greater Antilles also. Many of these endemic plants are also highly specialized, mostly with underground perennating organs which enable them to survive the fires. Among the most interesting of these are the species of the cycad genus Zamia, little plants with a bulbous underground stem.

Two further matters now remain to be considered: the vegetation of the Nipe plateau and that of the man-made grasslands.

For data on the Sierra de Nipe, we may refer to Carabia (1945). He described five vegetation types from the area, designated by their vernacular names. The *pinar* or pine savanna appears to be the most widespread, and next to it the *charrascal* or bushland. There is also *monte* or forest, mostly lower montane rain forest; *sabana,* mostly palm, savanna, and *sao,* a type of thorn scrub. The last named is associated with the dry habitat of the porous limestone *mogotes* and we need not be concerned with it. The remaining four communities occur upon soils developed to varying degrees from the same geological formation, serpentine. The *monte,* the forest, occurs on the most favorable sites "wherever the ground is not too steep and soil is deposited, enough to support a typical wet forest" (Carabia). The forest appears to occur, in fact, wherever a considerable depth of permeable, well-drained soil has developed above the serpentine rock and where the land is sloping. It occurs around the edges of the plateau, clearly where the soils are fairly young but developed to a reasonable depth. The forest appears from the description given to correspond to the formation lower montane rain forest and may be regarded as the climatic climax of the area.

The *charrascal,* on the other hand, occupies the least developed soils, shallow and rocky, where the serpentine has not decayed deeply. It varies from a rock-pavement vegetation of small, scattered shrubs to a "semi xerophytic community, formed mainly of woody shrubs and small trees 6 metres high or less, with stems 5-10 cm in diameter. The leaves are generally small and coriaceous, revolute, smooth, and lustrous on the upper part and with tomentum on the 'under surface." There seems little doubt that this corresponds essentially to the bushland of Barbuda.

The two savanna types, *sabana* proper and *pinar,* occupy in general the more highly weathered soils on the plateau, what Carabia calls "limonite soil" owing to the predominance of iron oxide. This is the Nipe clay of Marbut described above. The *sabana* is dominated by grasses and sedges, among which principally *Imperata brasiliensis* and *Leptocoryphium lanatum,* and typically it contains scattered palmettoes, *Copernicia yarey* and *Coccothrinax yuruguana.* According to Carabia, the presence of these latter in certain areas shows that they are true savannas. In other parts the *sabana* appears to have supplanted the *pinar,* the *charrascal* and the *monte* through burning.

Pinar occupies all the "limonite soils" between 400 and 600 m elevation. Grasses and sedges represent the true dominants of the *pinar* and forms a layer not much over 18 in. high. The actual dominant species are not stated but the list of components embraces seven species of *Panicum,* three each of *Andropogon* and *Laciasis,* two of *Paspalum, Imperata, Lithacne* and *Ichnanthus,* and *Leptocoryphium lanatum*: seven species of *Rhynchospora,* three of

Bulbostylis and two of *Scleria*. The list includes many typical savanna components. Several herbs and small woody subshrubs are also mentioned. The only tree is *Pinus cubensis*, reaching 50 to 80 ft. in height and 12-16 in. in diameter, the stems distributed 12 to 30 ft. apart.

Here and there in Cuba one has to deal with the effects of man's interference, and since the arrival of the European settler, many modifications have been brought about. As in Antigua, cattle-keeping has produced an entirely artificial type of grassland which has nothing in common with the natural savanna but resembles the grasslands of tropical Africa. Marie-Victorin & León observed: "In Africa the acacias are propagated by the great numbers of herbivorous animals: giraffes, antelopes, etc. There is a striking general analogy between the African savannas of the natural *Acacia-Andropogon* type and these Cuban savannas or pastures of the artificial *Samanea-Panicum* type. The same general appearance; the same complementary relation between a continuous stratum of Glumiflorae and an open formation of microphyllous leguminous trees; the same umbrella-shaped crowns of these trees, a form which seems to mark some height-ceiling. The general appearance of these two associations is the same, even if the genera and species which compose them are different."

In some other cases there is apparently a mixture of savanna with thorn bush or cactus. On the Trinidad plains, for example, Bennett & Allison describe a predominant savanna of Sporobolus with small trees of *Brya ebenus* and local thickets of *Copernicia macroglossa*, *Acacia farnesiana*, prickly pears and cacti. This intermixture seems to take the form of a mixture by patches rather than of an intimate mixture of the flora, and appears confined to the areas of lower rainfall.

CENTRAL AMERICA

BRITISH HONDURAS

Central America is a region of whose vegetation we know relatively little, ecologically. British Honduras is the only country in the region where the savannas have been studied in any detail. For the other countries we have only brief general accounts. The work of Charter (1941) in British Honduras is the only thorough study made of savanna vegetation in relation to soil and site in Central America and one of the best studies of the spbject to be made in all of the American tropics. The savannas are found on the lowlying parts of the country, principally on the northern plain, associated with soils developed on alluvial sands and clays deposited on top of the predominant limestones. Annual rainfall varies locally between 40 and 100 in. on the average, irregularly distributed, with generally four dry months in which less than 4 in. of rain falls. The limestones which underlie the bulk of the country are covered typically by a forest which appears to correspond

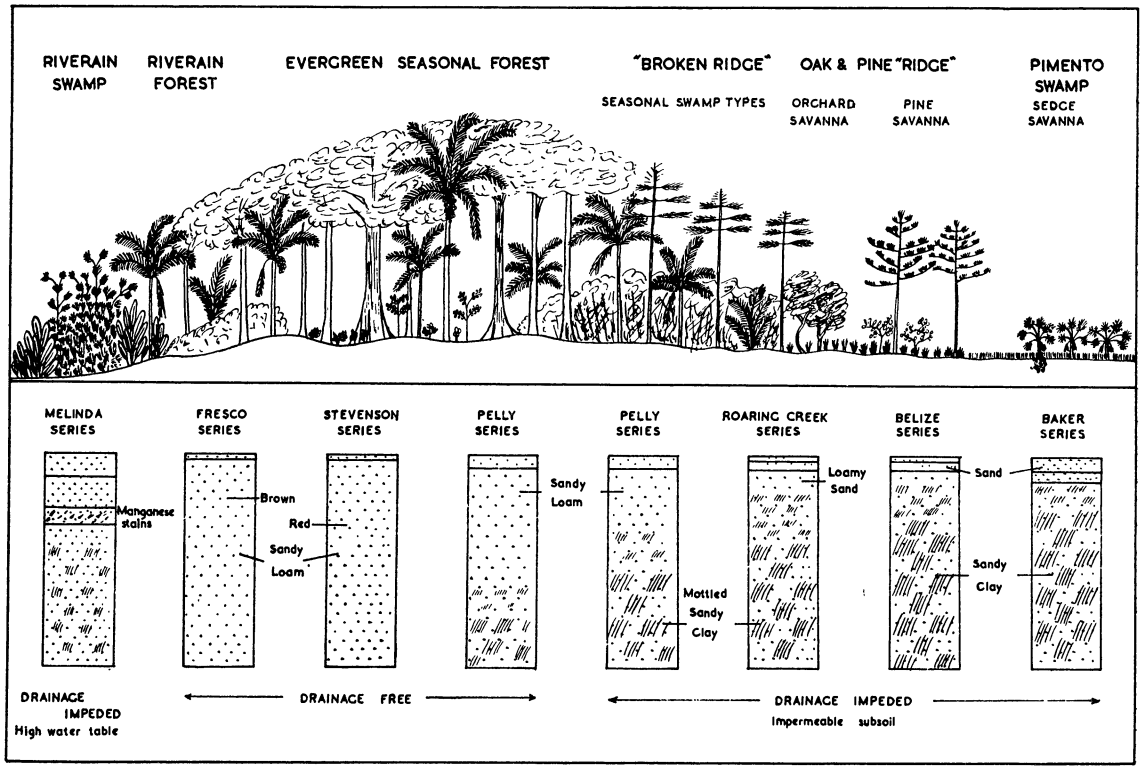


FIG. 16. Soil and Vegetation profiles from British Honduras. Redrawn from Charter (1941).

to the Semi-evergreen Seasonal Forest of Beard (1944), called "Quasi-rainforest" by Lundell (1945). Savannas do not occur on them. There is other forest on the mountains (? Lower Montane Rain Forest) and certain swamp types on flats. On the alluvial areas of the northern plain Charter described seven vegetation types, two of which are savanna. All of the seven are related to definite conditions of soil and site and were regarded by Charter as forming part of a developmental series. (See Fig. 16.) He suggested that the different soils of the area represented different stages of weathering and soil development, occurring on alluvial material of different age. The flattest areas forming terraces between the rivers would consist of the oldest material and show the most highly developed soil profiles, as indeed does appear to be the case. Nearer the rivers the parent material would be younger and the soil less developed. The following is an outline of Charter's description of this process.

Mixed alluvium derived from non-calcareous rocks is being deposited at the present day in the lower parts of the river valleys. The sites have a periodically high water-table and are subject to frequent flooding. The Melinda type of soil (Fig. 16) is developed, with a surface horizon of grey or grey-black loam overlying yellow-brown loam mottled grey and with manganese stains. The vegetation is riverain swamp with spiny bamboo (Guadua), Heliconia and palms.

With further development of the flood plain, the river cuts into the deposits it has laid down, the water table is lowered and flooding becomes less frequent. Products of drainage impedance thus disappear from the soil profile which becomes a uniformly yellow-brown loam (Fresco soil). A low riverain forest develops.

With the development of further relief and still better internal drainage, the soil undergoes more leaching and oxidation and becomes red or reddish-brown in color (Stevenson soil) carrying "high riverain rain forest." This is a more luxuriant forest than that found on the limestone areas of the Colony and probably corresponds to Beard's "Evergreen Seasonal Forest."

Later, obscure red and orange mottling develops at the base of the profile and the surface horizon assumes a greyish-brown tint. Gradually the upper humic layer becomes more pronounced, white mottling appears, and the lower part of the profile becomes an impermeable red and white mottled sandy clay (Pelly soil). Drainage impedance set up by the subsoil causes regression of the forest to a shorter, denser type, "broken ridge with cohune" (possibly Beard's Marsh Forest or Marsh Woodland).

With further aging of the soil material and with further increases in drainage impedance, the red and white mottled clay creeps higher up the profile (Roaring Creek Soil) and the woodland regresses still further to pure "broken ridge" (Marsh Woodland).

The impervious clays thus developed, apparently by illuviation of the lower layers, undergo further changes if they are of a sandy nature, due to sheet erosion. Surface water is now almost wholly removed by run-off and this carries with it clay to be deposited in depressions, leaving behind the sand. Eventually the mottled clay comes to be covered with a sandy layer a foot or more in depth. (Belize soil.) The vegetation changes over to savanna, at first with *Quercus* spp. ("oak ridge"), later with *Curatella americana* ("yaha") and *Byrsonima crassifolia* ("craboo"), when fully developed with pine (*Pinus caribaea*)—"pine ridge."

The final development of soil and site takes place with a levelling of the surface by sheet erosion. In the early stages, both internal and external drainage were good. Internal drainage gradually worsened and ceased as the subsoil became compacted. Now, on the flat expanses finally produced, external drainage ceases also and surplus water must be disposed of by evaporation. The Baker soils underlie level terraces flooded for long periods during the rainy season and completely dried out during the dry season. The vegetation is sedge savanna, expanses of sedgeland dotted over with clumps of the palm *Acoelorraphe wrightii* and isolated trees of *Crescentia cujete* and *Cameraria belizensis*.

A similar series of soil and vegetation types from mangrove swamp through high forest to pine and palm savanna was distinguished by Charter on the coastal plain.

"Mountain pine ridge" consists of areas of pine savanna in hilly areas over granodiorite intrusions. Charter showed this type to be associated with an impeded-drainage, sand-over-clay profile essentially similar in physical structure to the pine savanna soils of the plains.

OTHER CENTRAL AMERICAN COUNTRIES

Conditions typical of the low country of British Honduras are repeated in neighboring Guatemala and Yucatan. Standley & Steyermark (1945) described forests in the Petén province of Guatemala similar to those on the limestone areas of British Honduras, adding that "lakes, wooded swamps, undrained sinkhole ponds or aguadas, and stretches of grassland are scattered throughout, especially in central Petén, but in general the country is densely forested." The grasslands were further characterized as low savannas and said to consist of open stands of *Pinus caribaea, Curatella americana* and *Byrsonima crassifolia*. Evidently we have here the same mosaic of swamp, savanna and forest types as in British Honduras.

In the Republic of Honduras savannas with pine are found on hilly ground in the interior on sites probably similar to the "mountain pine ridge" of British Honduras and situated on geologically similar country. Treadwell, Hill & Bennett (1926) wrote that "much of the hill country of Honduras, in the western part at least, has a thin soil, often stony, on which there are extensive forests of pine. A considerable portion of this is covered with soil which will not average two feet in depth over bedrock (mainly

mica schist and light-colored volcanic rocks); often there is no soil covering at all." The rainfall here is said to average 30-60 in. a year, irregularly distributed with a severe dry season.

In the eastern part of Nicaragua, outside the young volcanic mountains, there appear to be savanna lands similar to the above, but we know little about them.

El Salvador contains savannas on the plains of the Pacific coast. According to Kovar (1945) "no small extent of arid and stony areas in the interior of the country are covered with *Curatella americana*, which at times grows associated with the "jícama," *Pachyrrhizus*." Other savannas on "plains with barren soil or badly drained in the rainy season" are characterized by the presence of *Crescentia alata*.

In Costa Rica and Panama savannas occur only on the drier Pacific side, the Atlantic slope being covered everywhere with heavy rain forest. On the Atlantic slope rainfall is in excess of 150 in. a year and there is no effective dry season. On the Pacific slope on the other hand precipitation is about half that of the Atlantic and is distributed with a severe dry season from January to April. Deciduous forests predominate on the Pacific side, interspersed with savanna areas. Of the latter, unfortunately, we know next to nothing.

THE GUIANA LOWLANDS

VENEZUELAN GUIANA

Guiana is, roughly, the region between the mouths of the Orinoco and Amazon rivers. Its heart consists of the Guiana shield, a highland massif of ancient rocks, and this is surrounded by lowlands which are in part reduced remnants of the same ancient core and in part land formed from the comparatively recent deposition of sediments on the continental foreland. The Venezuelan Guiana is of the former structure and it consists of the country immediately to the south of the Orinoco River and draining towards it. South of the Orinoco, therefore, the country is radically different in form from the flat plains of Pleistocene alluvium north of the river. It is developed upon a solid geology of hard metamorphic rocks and consists of gently undulating land, all less than 1,000 ft. above sea level, broken up with little hill ranges not exceeding 2,500 ft. in height. It is almost entirely savanna covered.

Between January 16th and 18th, 1945, the writer travelled by road from Ciudad Bolívar to Tumeremo via Upata, Guasipati and El Callao. Later, on February 8th, he crossed the same tract by plane at a low altitude and was enabled to get a general, bird's-eye view of conditions to add to the closer inspection made by road. From Ciudad Bolívar to Upata is 95 mi., from Upata to Guasipati 60, thence to El Callao 15 and finally from El Callao to Tumeremo 25 mi. The road leaves Ciudad Bolívar through country somewhat resembling the Mesa de Guanipa, gently undulating ground with a sandy topsoil and thickly grown with the usual gnarled savanna trees, called chaparral (Figure 17). *Curatella americana* is very abundant, other trees relatively rare. They include

FIG. 17. Typical savanna south of the Orinoco, near Upata, Venezuela. A light sandy topsoil ill-covered by the sparse grasses, and Curatella trees.

Byrsonima crassifolia, *Bowdichia virgilioides* and a thorn tree, possibly an Acacia. The small *Byrsonima verbascifolia* is occasionally seen. The ground is covered as usual with coarse bunch-grasses. On the flatter places, plateau sites rather than depressions, the tree growth thins out markedly, showing its sensitivity to drainage. The soil is sandy at the surface, littered with ironstone pebbles in varying quantity and of varying size. Some times the surface is quite thickly covered with gravel, in other places it is stoneless. All sizes of pebble are seen from that of a pea to that of a tennis ball. The sand horizon is yellowish to pale grey in color and changes abruptly at from one to two feet depth to a brilliant red, or red-white mottled, clay, extremely compact and hard. Small termite mounds like those of the Trinidad savannas are not uncommon. Rocky knolls disturb the general evenness of the savanna here and there and appear to be outcrops of some hard, igneous rock, possibly granite. These knolls consist for the most part of naked bosses of rock with a little thin chaparral in crevices. Sometimes, presumably when a reasonable depth of soil is present, the knolls bear a fair growth of deciduous seasonal forest, leafless at the time of the writer's journey. This same forest occurs in narrow strips along water courses where the principal trees are *Copaifera officinalis* L., *Bursera simaruba* (L.) Sarg. and *Cochlospermum vitifolium* Willd. Rarely, this streambank forest is replaced by thorn bush and often scattered Mauritia palms are present.

The road dips down gently to cross the Rio Caroní 78 km out of Ciudad Bolívar, with a magnificent view of range upon range of low hills beyond the river. The river itself is broad and sluggish and full of sand bars. Its level is subject to marked seasonal variation as the thickets of Annona and Pterocarpus lining its banks show, not only in the muddy marks of flood water on their trunks but in the adventitious root system which is put out at high level and left high and dry in the low season. Beyond the Caroní River to Upata the country is definitely hilly and is mainly covered with semi-evergreen seasonal forest, a slightly moister type than that seen further west. Savanna persists in a number of often rather unaccountable pockets, usually in the flatter places or where the soil is obviously shallow. Road cuttings

show the underlying rock to have decayed to very variable depths. Under forest, rock may not be encountered before 50 ft. depth, having weathered above to a red clay which turns brown in the surface horizon and is of good crumb structure. Roots penetrate deeply. Typically under savanna, rock is seen only 2 ft. below the surface and the ground is strewn besides with a layer of ironstone and quartzite pebbles. The brown clay topsoil below this merges at a foot depth into a red and white mottled zone which merges below into rotten rock. On such shallow sites there is equally poor drainage and little root-room as in the sand-over-clay soils, whereas on the very deep sites there is every opportunity for the development of forest growth. There does not, however, appear to be an invariable correlation here between the vegetation and the depth of soil. Leaving Upata on the road for Guasipati the hills are about half covered with savanna, half with forest and soil conditions could not be investigated. Savanna areas on flatter ground crossed by the road show a sand-over-clay type of soil for the most part, though outcrops of bosses of rock are frequent. The semi-evergreen forest contains *Copaifera officinalis* L., *Hymenaea courbaril* L. and *Genipa americana* L. Some miles further on, the road crosses a wide plain, very gently undulating and almost entirely covered with chaparral of Curatella, Bowdichia, Byrsonima and ?Acacia. The sand-over-clay soil is extremely quartzitic here and abundantly littered with quartz stones and boulders. Depressions and lines of drainage are occupied by dense thickets of Acacia, not the same species as occurs in the chaparral. Beyond this plain some hill ranges are crossed, their steep summits mainly clad with very open, almost treeless savanna. Deciduous seasonal forest occurs in a few haphazard patches on the slopes and at their feet together with some thorn thickets. Finally another plain, gently dissected, leads to Guasipati. Here there are actual ravines marked by occasional Mauritia palms instead of gentle depressions with thorn bush. Dense chaparral with Curatella dominant covers the lower ground while the tops of rises are almost bare and show dominance of *Byrsonima crassifolia*. These circumstances probably are due to a higher rainfall here.

El Callao nestles inside a range of low mountains which are unbrokenly covered with forest of semi-evergreen seasonal type. The savannas give place to forest midway between Guasipati and El Callao. The road from El Callao to Tumeremo is a very bad one and beginning in broken forested country is very muddy and difficult. When travelling on earth roads one appreciates an immediate difference between savanna and forest soils. The ground in savanna is compact, indurated and can be crossed even in wet weather. Forest ground is soft and loamy and readily forms into ruts and mudholes. After a mile or two, fortunately, the Tumeremo road emerges from the mountains and enters country of low relief consisting of a mass of little, gently rounded hillocks with depressions between them. This country is more settled than that previously crossed on the journey and carries more head of cattle. Consequently the vegetation has been somewhat disturbed and large areas consist of open pasture land or pasture with thorn bush. It seems that originally the little hills were covered with chaparral and the depressions with evergreen forest.

The forest grows more luxuriant and more evergreen steadily all the way from Ciudad Bolívar and one would expect a marked increase in rainfall. Actually the records show an average rainfall of only 55 in. per annum at Tumeremo which is still a low figure and cannot be more than 10 or 15 in. above that of Ciudad Bolívar. The average figures (courtesy of the Venezuelan Government) for the seven years 1938-1944 were:

Jan.	Feb.	Mar.	Apr.	May	June	July
86.1	60.4	66.5	84.4	157.1	191.7	188.5
3.6	2.5	2.7	3.5	6.5	8.0	7.9

Aug.	Sept.	Oct.	Nov.	Dec.	Total
159.9	50.7	94.1	85.9	101.3	1326.7 mm
6.7	2.1	3.9	3.5	4.2	55.2 in.

If these figures are correct one would not expect such a marked change in luxuriance of the forests seen along the route, but there are other factors at work such as the greater exposure to wind and lower humidity in predominantly grass-covered country.

From Tumeremo, making for the interior highlands, the journey was continued by plane to the southward and a month later the writer returned by plane all the way to Ciudad Bolívar. South of Tumeremo the country continues apparently somewhat flat for some little distance until the Cuyuni River is crossed, a wide, sluggish and meandering stream. Beyond the river the country rises in irregular mountain masses to the 6,000 ft. high Sierra de Lema which here marks the northern edge of the interior Guiana plateau. Immediately beyond the Sierra begins the open country of the Gran Sabana but the range itself and its foothills falling to and across the Cuyuni are covered with unbroken forest which appeared entirely evergreen from the air. This forest ceases at a definite line running in a north-east south-west direction between Tumeremo and the river. The writer did not have any opportunity to enter these forests nor to examine the nature of this forest boundary. It is possible that it marks the edge of the Cuyuni flood plain. On the Tumeremo side of the line the country takes on, from the air, a kind of checkerboard pattern: a mass of little, rounded rises (they are not worthy of the name "hills") covered with open savanna set in a matrix of evergreen for-

est which occupies the shallow depressions in between. The impression is not so much that of a dendritically arranged drainage system with forest along its channels and savanna on its watersheds as of a checkerboard system of small hillocks often almost circular in plan. From the air this is seen to remain the essential arrangement all the way to Ciudad Bolívar, a fact that is not so readily appreciated from the ground. Due apparently to gradually decreasing moisture along the line of flight the forest occupying the depressions and drainage channels is seen to change gradually from a tall evergreen type of Tumeremo to a low deciduous forest and finally to thorn scrub with a few Mauritia palms. Mountain ridges breaking out of the peneplain appear from the plane to be almost entirely forested with only occasional savanna patches on them, though exposures of absolutely bare rock are not uncommon.

Additional information on the Venezuelan Guiana is provided by Williams (1940, 1941). Along the lower Paragua savanna is the dominant formation. There are two main types, "fresh-water savannas" and "inland savannas," of which the latter is further divisible into two distinct communities. "Fresh-water savannas" correspond to the *esteros* of the llanos, depressions completely submerged in the rainy season. There are a number of small trees such as *Duroia sprucei* and *Erythrina glauca*. Herbaceous vegetation seems to be dominated by sedges, of which only *Rhynchospora globosa* is named. The "inland savannas" are situated beyond reach of seasonal floods upon a "well-drained sandy soil overlying marl beds." There are two divisions, treeless, and scattered with the usual Curatella-Byrsonima-Bowdichia shrubs. The exact composition of the grass association is not clear.

Along the Caura River, further west than the Paragua, there is a dominating distinction between savanna-covered plains and forested mountain country. The savannas appear to occupy flat terraces and conform to the usual floristic pattern with Curatella, Byrsonima, Bowdichia, etc. The soil is sandy or pebbly over a compacted sub-soil of quartz gravel.

Williams' observations reach as far as the upper Orinoco at the island of El Ratón above Puerto Ayacucho. In this region, he wrote, "it may be safely stated that the rainfall is much heavier in this territory and the dry season shorter than in the lower reaches of the Orinoco basin." At this point on the Orinoco the sedimentary llanos have been left behind and the savannas, stretching far away to the west of the river into Colombian territory, are interspersed with rounded, black (? granitic) rocks, some of them 200 or 300 ft. high.

The island of El Raton is traversed for almost its entire length north and south by a narrow savanna composed of *Bulbostylis junciformis, Scleria scabra, Trachypogon ligularis, Axonopus aureus, Panicum cervicatum* and *Clitoria simplicifolia*, as well as "a few low shrubs."

The headwaters of the Orinoco and its tributaries are said to be densely forested.

BRITISH, DUTCH AND FRENCH GUIANA

The lowland savanna country of the three European colonies in Guiana forms a definite unit and is quite a separate region from the Venezuelan Guiana savannas. The coastal region of the European colonies is low-lying and formed largely of Plio-Pleistocene alluvial deposits, mainly loose sands. The actual coastal belt is very swampy and contains large areas of mangrove, palm and herbaceous swamp vegetation. The open herbaceous swamps, filled with giant sedges and herbs such as *Cyperus giganteus* and *Montrichardia arborescens*, are referred to in British Guiana as "Savannahs," but this is not the legitimate use of the term. The true savannas occur on the slightly higher ground behind the coastal swamps, on the tops of the flat watersheds between the rivers and creeks, in the form of relatively small blocks and patches surrounded by forest, often by high rain forest. There is no broad belt of savanna country as in the Venezuelan Guiana. The region of these savannas begins in the east of British Guiana adjoining the Berbice River and continues eastward across Dutch and French Guiana to connect with similar country in Brazil about the Amazon mouths. There are no savannas between the Berbice-Demerara watershed and the Venezuelan frontier. A map showing the distribution of savanna country in British Guiana is given by Davis & Richards (1933, p. 354).

BRITISH GUIANA

Some of the savannas of the Berbice River district of British Guiana were described by Follett-Smith (1930) and Martyn (1931). The area surveyed covered some 70 sq. mi. of the Wiruni-Ituni savannas, about 60 mi. inland from the sea. The country consists of open undulating grassland 80-90 ft. above sea level, with scattered areas of forest varying in extent from several square miles to narrow belts of trees bordering creeks and streams. The savannas are covered by a thin, xerophytic vegetation which occupies no more than 60% of the surface of the soil and consists of a mixture of grasses and sedges. A feature of the open savanna country is the number of mounds raised by ants (*Atta* spp. according to Martyn, though Myers (1936) ascribed them mainly to Syntermes); "This subsoil, brought up by their activities, supports a flora apparently capable of withstanding the periodic savannah fires and resembles that found in the narrow transition zone between forest and open savannah country" (Follett-Smith). Other variations are the presence of water-holes, water-logged in the wet season, but dry during periods of drought, and the occurrence of slightly elevated and isolated areas of coarse white sand locally known as "muri" sand.

The average rainfall for the six years 1924-1929 at Ida Sabaina eleven miles from the area studied is shown in the following table. The rainfall of the savanna country is thought to be similar. Rainfall of this quantity and distribution is associated with country under high evergreen forest in Trinidad.

Jan.	Feb.	Mar.	Apr.	May	June	July
86.8	81.6	62.8	127.2	283.2	326.8	266.4
3.7	3.4	2.7	5.3	11.8	13.7	11.1

Aug.	Sept.	Oct.	Nov.	Dec.	Total
216.0	100.8	81.6	110.8	182.4	1934.4 mm
9.0	4.2	3.4	4.7	7.6	80.6 in.

Follett-Smith distinguished three main soil types —the brown sand type, the sand hill type and the muri sand type. The brown sand was found to be the most widespread. It consists of a fine brown sandy topsoil 10 in. deep over a subsoil slightly lighter in color merging at a depth of 2 ft. into a slightly heavier red brown loam. The soil is highly acidic throughout and organic matter content is low at the surface decreasing to negligible quantity below 10 in. The sand hill type of soil is a light to dark grey deep sand, occurring near to Waranama Creek. Muri sands occur on slight elevations and are usually accompanied by the presence of a waterhole. They consist of coarse white rounded grains of quartz. All of these soils are highly leached siliceous sands, permeable, acid in reaction and of low organic matter content. They are probably deficient in plant nutrients.

Martyn found that four species of grass and two of sedge were the chief constituents of the savanna vegetation which he termed the grass-sedge association. Composition was found to vary with soil type. On the sand hill soil the principal grasses were *Trachypogon plumosus* (H. & B.) Nees, *Axonopus aureus* Beauv., *Andropogon leucostachyus* HBK. and *Aristida setifolia* HBK., with *Leptocoryphium lanatum* (HBK.) Nees as a less common associate. *Trachypogon plumosus* was dominant, accounting for a quarter of the association. Sedges were represented principally by *Rhynchospora pterocarpa* R. & S., with *Stenophyllus coniferus* (Kunth.) Britton appearing as tufts in bare patches of soil. On the brown soil type the vegetation is thinner, sedges are more prevalent, and Andropogon and Aristida are less frequent.

Stunted bushes of *Byrsonima coccolobaefolia* and *Curatella americana* occur here and there, becoming a "dominant feature" in certain areas. The recumbent woody *Pavonia speciosa, Palicourea rigida* and *Byrsonima verbascifolia* are seen throughout.

Scattered across the savannas at intervals are shallow depressions called "pans" which seem analogous to the *esteros* of the llanos and *baixas* of the interior. They are under water in the rainy seeason, dry during drought.

The muri sands do not carry savanna at all, but a distinct, woody plant association, markedly xerophytic in character. This consists of thick patches of bushes and small trees, interspersed with open areas on which the vegetation is of a very sparse nature. *Clusia nemorosa* is usually the largest component of the scrub and arises in the centre of the thickets, attaining a height of fifteen to twenty feet. It is sometimes accompanied by stunted trees of *Byrsonima spicata.* A shrub, *Pagamea capitata,* normally some 6 ft. high, and the low-growing "muri bush," *Humirium floribundum* var. *guianense,* make up the remainder of the thickets.

The open areas of the muri bush are sparsely occupied by *Cassia uniflora* and clumps of "muri grass," *Axonopus attenuatus,* together with *Cryptangium uliginosum* and scattered shoots of *Trachypogon plumosus.* Small patches of the fern *Schizea incurvata* are always present and two species of Borreria.

Transition to forest at the borders of the savannas is abrupt and there is only a narrow transition zone. No details of the structure or composition of this forest are available. Martyn described, however, the plants of the transition zone, which he found repeated, in a rather interesting manner, on the ant hills in the savanna itself. A definite series of communities intermediate between savanna and "transitional bush" can be traced. In the first stage there is merely a richer herbaceous vegetation: two new sedges appear, *Rhynchospora cephalotes* and *Dichromena ciliata. Sipanea pratensis* and *Tibouchina aspera* are conspicuous. In the next stage, *R. cephalotes* attains greater prominence and several species of *Miconia* including *M. macrothyrsa* are found, with seedlings of *Byrsonima spicata* and bushes of *Siparuna guianensis* and *Eugenia benthamii.* In the third and final stage a little island of bushes is formed, surmounted by one or two trees. *Byrsonima spicata* is dominant accompanied by *Miconia rubiginosa, Solanum asperum* and *Wulffia baccata* among others. Martyn tentatively attributed this phenomenon to immunity from fire conferred by elevation upon the ant mounds. These savannas are frequently burned over but the fires never appear to penetrate the surrounding forest.

DUTCH GUIANA (SURINAM)

One of the best analyses of the savanna question that has been written in South America, together with some very clear descriptive matter on the lowland savannas of Surinam is that of Lanjouw (1936).

These savannas are found principally in the coastal region of the country, in the zone of continental alluvia adjoining the fluvio-marine deposits inland. Their surface is gently undulating and they occupy plateau sites on the watersheds between the rivers and creeks in the form of small blocks and patches surrounded by forest, very much as the savannas in Trinidad do. The exact nature of the soil was not made very clear by Lanjouw who quoted a work by Ijzerman (1931): "the sharp and coarse quartz sand found on the surface is typical of the savannahs: by the side of this sand, sandy clays occupy no insignificant part and both may occur in the same sa-

vannah." Ijzerman evidently considered both soil and subsoil to be readily permeable as he accounted for the presence of the savannas on the ground of impoverishment of the soil by leaching. One interesting fact brought out is that "it should be expressly pointed out that the profile of the subsoil in the savannahs shows no difference from that which characterizes the continental alluvia elsewhere; borings made in the savannahs and in the neighboring forest indicate this clearly."

The rainfall of the savanna region is given for three stations in the vicinity, Republiek, Sectie O, and Brownsweg, the average precipitation being 86.2, 85.7 and 92.5 in. per annum respectively. This rainfall regime shows a double seasonal fluctuation with two maxima and two minima, but the dry seasons are short and mild. The figures do not differ much from those for the Berbice savannas, the chief difference being that the second dry season is here sharper than the first. These savannas are subject to frequent fires.

Lanjouw wrote: "The general aspect of the Suriname savannahs is a slightly rolling landscape for the greater part covered with herbs, most of them with a more or less xeromorph habit or with a short and rapid vegetation period, and here and there some shrubs, or low and often deformed trees. An important part of this vegetation is occupied by the *Cyperaceae,* while in most places the *Gramineae* come on the second plan, though there are savannahs where the *Gramineae* are dominant. The dominance of the species changes often on short distances and in many places sharp lines can be drawn between the "associations." I have noticed that nearly always one can assign 1 or 2 species which are dominant." Most of the herbs and shrubs are said to flower at the end of the major rainy season, that is, in August.

Details of composition show several different types of savanna communities. There are two broad divisions, "wet" and "dry" savannas, the terms being relative only. In the former *Lagenocarpus tremulus* Nees is the dominant, with several species of *Rhynchospora,* a *Utricularia,* a *Drosera,* a *Lycopodium* and several herbs of the Xyridaceae and Eriocaulaceae. Grasses are rare to absent. Some fifteen species of shrubs and small trees are mentioned, but from the photographs these appear to be few, small and scattered. The vegetation does not cover more than 20%-40% of the soil, which several of the photographs (even one of "dry" savanna) show to be covered with standing water. Lanjouw mentions one "wet" savanna as being covered with 5 cm of water at the end of July. This is against the leaching theory of Ijzerman: evidently the soil is not at all permeable, at least in parts. Parts of the savannas are said to be inundated and to carry groves of *Mauritia flexuosa* L.f.

On the "dry" savannas Rhynchosporas may be dominant, but generally grasses, either *Trachypogon plumosus* or *Gymnopogon foliosus* Nees. The shrubs may often be taller and more abundant.

The forest surrounding these savannas is evidently often of a somewhat specialized type and is referred to by Lanjouw as "Savannah Forest," but unfortunately it is not described and it is difficult to gain an idea of the tree composition from the list of species. It is said to be less dense than the rain forest and to have a different, more or less xerophytic vegetation in the undergrowth.

Lanjouw's very interesting theory of the origin of these savannas has been outlined in the introduction to this paper.

Ijzerman (quoted by Lanjouw) wrote "Parts that seem destined later on to give rise to savannahs may also be met within the forests. The soil there has the same character as in the savannahs and the trees . . . are greatly stunted in growth. Such like forests are known in Surinam under the name of "Moeri-moeri-bosch," and, in so far as they are not caused by solid rock lying close to the surface, they are produced by the same factor as the savannahs." Stahel (1936) gave some notes on this moeri-moeri bush (translation). "Before the line reaches this creek it crosses an area which the woodsmen call 'moeri-moeri.' Here the granite rocks either come quite to the surface or are only covered with a thin layer of soil. This formation, the moeri-moeri, I very often met in the Surinam forests, generally only in small patches. These are covered with low shrubs and small trees, and only on the parts with rather more soil are there any large trees, which notably include many species with latex. The "bolletrie" (*Manilkara bidentata*) is chiefly sought for in moeri-moeri, as is well known to the balata bleeders. Wherever the rock pavements are not covered with humus, large bromeliads grow with Aroids and Orchids."

In the latter case the moeri-moeri seems to be a low evergreen scrub such as one would expect to find on rock pavements. If, as according to Ijzerman it is also found on deeper ground, then this presumably consists of reefs of white sand as in British Guiana. In neither case is it easy to understand how Ijzerman and Lanjouw can consider the soil as intermediate between that of forest and savanna.

FRENCH GUIANA

The topography of French Guiana is similar to that of all this region; a low-lying swampy coast rising gently inland, the higher interior being formed of ancient continental rocks and the coastal lands of alluvial deposits. According to Benoist (1924) the annual rainfall on the coast amounts to some 3.50 m, that is, 140 in., well distributed throughout the year with only a mild "dry season" often of no more than a few weeks duration between July and September. Humidity is high and variations in temperature slight. We may, therefore, expect to find that the bulk of the country is covered with high rain forest and in Benoist's account this is said to extend over 7/8ths of the area. Benoist distinguished two other botanical regions: a littoral zone of tidal mudflats and sea-sands, covered with mangroves and so on, and an intermediate belt some 10 to 15 mi. wide between the littoral and the rain forest which

is covered with savannas. These are described as sometimes dry, sometimes swampy, broken up by clumps of woodland or scattered over with isolated trees. As in British Guiana, the term "savane" is said to have a wide application locally and be extended even to everything which is not forest. For the most part, however, the "savanes" of French Guiana are true savannas and correspond very closely to those of Surinam in composition and habitat. Just as the Surinam savannas were divided by Lanjouw into "wet" and "dry," those of French Guiana were divided by Benoist into "wet," "intermediate" and "dry," of which the last two correspond closely to the "wet" of Surinam, Benoist's wet savannas being equivalent to the wet savannas of British Guiana and correctly herbaceous swamps, not savannas at all. They are perpetually inundated and filled with giant herbs such as Montrichardia, many tall Cyperaceae and water-loving grasses such as Leersia.

The dry savannas are described as relatively large, undulating expanses, abruptly bordered by high forest. There may or may not be shrubs and small trees present. The nature of the soil is not stated: it is only clear that these savannas occupy alluvial terraces and become very dry in the short dry season. The herbage dies down at this stage and it is generally burned off in September or October where fresh pasturage is required for cattle. Maximum vegetative activity occurs in May, followed by the flowering season in June. The herbaceous cover consists of both small sedges and bunch-grasses, the former predominant. No list of the Cyperaceae is given by Benoist but the principal grasses are said to be *Aristida tincta* Tr., *Trachypogon plumosus, Axonopus scoparius* Hitchc., and *Panicum cyanescens* Nees. There are also many dicotyledonous herbs, the recumbent shrub *Byrsonima verbascifolia* is locally abundant, and where there are taller shrubs and small trees they are *Curatella americana* L., *Byrsonima crassifolia* and *Palicourea rigida* HBK. The palm *Mauritia flexuosa* L. is found along streams.

The "intermediate" savannas lie nearer to the coast on lower ground, are wetter in the rainy season being sometimes actually under water, and less completely dry in the dry season. They are smaller and frequently consist of quite small patches set in the midst of forest, or of a maze of small glades: as Benoist puts it in one case, forming "a veritable labyrinth." Sedges here are completely dominant, numbering *Rhynchospora pterocarpa* R. & S. and several other Rhynchospora species, *Lagenocarpus tremulus* Nees, two species of *Scleria* and *Bulbostylis capillaris* Clarke. The less numerous grasses include *Echinolaena inflexa* Chase, *Panicum cyanescens* Nees, *Aristida tincta,* and *Andropogon leucostachyus.* Small flowering herbs are plentiful, including *Utriculariaceae.* Trees and shrubs are smaller, Curatella disappears, giving way to *Chrysobalanus pellocarpus* and smaller shrubs such as *Cassia uniflora* and *Tibouchina aspera.* The larger woody plants are usually loaded with epiphytic bromeliads. In the marshier places, *Mauritia flexuosa* becomes very abundant. The resemblance between these and the Aripo savannas of Trinidad is very close.

Benoist considered that the savannas of French Guiana must be due to man, who has cut down the forest in shifting cultivation, subsequently burning and pasturing the regrowth. He cited cases where pastures for stock have originated in this way from forest, though their flora was admitted to be quite different from that of the natural savannas.

THE GUIANA HIGHLANDS

LA GRAN SABANA

In the south-eastern corner of Venezuela lies the great, grass-covered plateau known as La Gran Sabana—the grand savanna. This region is some 150 miles square, in the angle formed by the Venezuela-British Guiana and Venezuela-Brazil frontiers. It is bounded on the north by the 6,000 ft. Sierra de Lema, a forest covered range forming the edge of the Guiana plateau and described in the section on the Venezuelan Guiana. On the south the Gran Sabana is bounded by the ill-defined Sierra de Pakaraima, the watershed between the Amazon and Orinoco basins, which is also the line of the Brazilian border and is partly forest covered. On the east and west the Sabana is limited by systems of huge sandstone mesas typical of which is the world-famous Mount Roraima, 9,300 ft. high (Fig. 18).

FIG. 18. Mount Roraima from the south. In the foreground are a few trees and bushes along a stream and the rest is open country.

The Gran Sabana itself is a plateau 3,000 to 4,000 ft. above sea level formed for the most part of horizontal sandstone strata of the Kaieteurean formation with basic igneous intrusions. It drains towards the south and south-west, all streams being caught in the south-west corner by the Rio Caroní which turns north to join the Orinoco. The Sabana is by no means an even, level plateau for the vertical block formation of the great mesas is continued in miniature down to the smallest features and the plateau is a disordered arrangement of flat-topped mesetas, benches and terraces bounded by scarp faces, a grand design of horizontal and vertical planes. Rounded country is only seen in the extreme south in and close to the Sierra de Pakaraima where the Kaieteurean rocks give way to the ancient igneous and metamorphic rocks of the basement complex. The streams draining the Gran Sabana flow in sluggish

stretches across great levels, swinging in prodigious meanders, until they drop suddenly in a spectacular waterfall over an escarpment and resume their slow meandering across another level stretch below until another waterfall is reached. The Gran Sabana landscape is, therefore, compounded of three features: broad and swampy river flats, wide, upland plateau levels and very steeply sloping scarp faces joining these two. Small rounded knolls are a minor feature.

The vegetation of the Gran Sabana consists for the most part of an absolutely treeless, open grassland, the chaparral of lowland Guiana being quite absent (Fig. 19). The writer did not see *Curatella americana* or *Bowdichia virgilioides* anywhere on the Sabana and *Byrsonima crassifolia* is rare. The herbaceous vegetation consists of bunch grasses and small sedges. The grasses are dominant in the sense of physical superiority as they outgrow and overshade the sedges at the time of most luxuriant growth, but the sedges are frequently present in equal numbers.

FIG. 19. General aspect of the Gran Sabana with *Uei tepui* in the background. Patches of forest are seen following streams or nestling into escarpment valleys. The savanna is treeless on the higher ground but becomes sparsely dotted with *Byrsonima crassifolia* in the hollow.

FIG. 20. Mauritia palms decking the swampy savanna of the flat Kukenan valley.

One of the commonest sedges is one which forms a short thick trunk up to 6 in. high with a rosette of leaves and inflorescences on top (Figs. 25-29). In addition to the open grassland there are lesser areas of morichal, scrub and forest. The morichales occur in the swampier parts of the river flats and consist of open stands of Mauritia palms with a sedge undergrowth (Fig. 20). Low woody scrub is found on beds of deep, white sand which occur rather rarely (Fig. 21). Forest occurs as gallery forest along the river banks and as rather odd pockets on many of the steep scarp slopes, usually nestling into a hollow. Its distribution in the latter cases is very irregular and inconsistent.

FIG. 21. "Muri bush" on a reef of deep sand, in the midst of open savanna.

The Gran Sabana has recently been thoroughly explored by the Venezuelan Government and a report published (Aguerrevere y otros, 1939), describing the geomorphology, geology, minerology and soils.

The rainfall at Santa Elena on the Sabana for the 5 years 1940-1944 (courtesy of the Venezuelan Government) showed the following averages:

Jan.	Feb.	Mar.	Apr.	May	June	July
51.7	37.0	96.6	122.0	184.8	266.5	198.7
2.2	1.5	4.0	5.1	7.7	11.1	8.3

Aug.	Sept.	Oct.	Nov.	Dec.	Total
185.2	111.5	85.5	145.8	145.9	1631.4 mm
7.7	4.6	3.5	6.1	6.1	67.9 in.

This rainfall and its distribution is closely similar to that obtaining over a large part of Trinidad where the vegetation is an evergreen seasonal forest.

In the last decade the discovery of diamond workings and the development of air transport has encouraged the much greater accessibility of this formerly very remote region and there is now a regular plane service from Ciudad Bolívar and Tumeremo to Santa Elena de Uairén on the southern edge of the Gran Sabana. The writer travelled by this route to Santa Elena on January 19th, 1945, accompanied by his wife and Mr. Alan Jones, Zoologist, and after staying a few days in Santa Elena left on foot for Mount Roraima on January 24th. The summit of Roraima was reached on January 30th travelling by the direct route up the Rio Kukenán, and the more circuitous route by Arabopó was taken for the return journey to Santa Elena, reached on February 5th. The party left Santa Elena by air for Ciudad Bolívar on February 8th. This journey was assisted by the Venezuelan Government to whom thanks are rendered. The observations which follow are being published for the first time.

Roraima lies fifty air-line miles to the north-east of Santa Elena across typical country of the Gran Sabana. The writer was unfortunately unable to collect any plants for identification but information on the grasses is taken from Myers' paper (1936). Santa Elena is a small village set in a valley among hills forming the outskirts of the Sierra de Pakaraima. The track towards Roraima follows the valley of the Rio Uairén, flowing northwards, to its junction with the Rio Kukenán which comes down from Roraima itself. The valley of the Uairén is broad and flat and the river meanders widely. It is bordered by lines of hills forming escarpments in an east-west direction, that is, at right angles to the line of the river. The rocks here are quartzites forming part of the basement complex and they dip towards the north. The steep scarp faces are rocky and covered with a sparse grass vegetation but the dip slopes are capped with loose white sand of unknown depth and bear a low open, woody scrub with very little grass. This consists of low trees, less than 10 ft. high, with small, hard leaves, evergreen and with ground plants containing a bracken fern and a number of terrestrial orchids. The general appearance is suggestive of the vegetation of coastal sand dunes, or of the "muri" scrub of lowland Guiana and this vegetation is undoubtedly related to similar scrub noted by Myers (1936) *in the midst of forest* south-east of Roraima. The Rio Uairén is bordered by tall evergreen gallery forest and the valley floor outside the forest is open grass with occasional morichales.

On reaching the Rio Kukenán one is properly on the Gran Sabana, on the Kaieteurean rocks whose horizontal strata form the steep and cliff-like walls of the valley. The valley floor is wide and flat, evidently filled with alluvial material. The river meanders very markedly and is bordered by a narrow belt of gallery forest, the remainder of the valley being about two thirds open grassland one third morichal. At the time of the writer's visit most of the valley bottom was firm and dry but it is evidently somewhat swampy in the rainy season. The morichales occupy the swampiest portions: frequently depressions which are clearly occluded meanders of the river. The ground surface is frequently hog-wallowed in and around morichales but this phenomenon is not otherwise observed on the Gran Sabana. The soil at Divina Pastora on the Kukenán flat was seen to be a blackish loam merging at 3 ft. depth into a grey loam, which merges at 6 ft. into a reddish loam and this at still greater depth leads to a red-mottled sand or clay. This is a deep soil without impedance, but presumably it has a seasonally high water-table due to low relief.

Large termite mounds are a prominent feature of these alluvial sites. They are not found on residual soils, in forest or in morichales but only on the drier alluvial savanna-covered soils where they are invariably present in large numbers. The large conical termitaria of Amitermes mentioned by Myers (1936) on the Rupununi savannas were not seen by the writer on the Gran Sabana, only the low, wide mounds of the type ascribed by Myers to a Syntermes. These mounds measure commonly from 6 to 12 ft. in diameter and from 1 to 3 ft. in height, in the shape of a gently raised dome. The largest mound seen by the writer measured 40 ft. by 27 and was 6 ft. in height, but such a size is exceptional. The mounds are often surprisingly regularly spaced, being distributed at approximately 30 ft. centres with almost mathematical regularity (Fig. 22). They carry a characteristic grass vegetation (Myers 1936, p. 179) but no woody plants.

FIG. 22. Termitaria on an alluvial flat along the Arabopó River. (Photo by Allan Jones.)

From the junction of the Uairén and Kukenán rivers, the route lies up the right bank of the Kukenán all the way to Roraima, first north-east to the Morock Falls and the junction of the Arabopó River, thence due northwards. The valley up to the Morock Falls is broad and flat with abrupt scarp-faces set well back. Tall, evergreen gallery forest borders the meandering Kukenán and there are substantial patches of forest surrounding the headwaters of most tributaries, clustering into the valley walls. In nearly every case these forests give place to morichales along the streams when these reach the valley floor and they are not, therefore, continuous with the gallery forests. The forests of the slopes nearly always give the impression of nestling into some protective cranny in the hills. The valley floor outside the gallery forest is as usual divided between dry grassland (*Sporobolus indicus*) with termite mounds and morichales. The hill-slopes, where not forested, are exceedingly bare and covered with such a thin growth of grass that the red color of the soil shows through, and is visible for miles. Even the soil-covering itself is thin and the nature and strike of the rock strata can often be readily seen. The waterfall Luei Meru is passed on the way to Morock Meru, formed by descent of a tributary stream into the valley. Some areas of white sand occur close to the fall and are covered with the usual "muri" scrub. The rocky walls of the gorge are tree covered.

Above Morock Meru the Kukenán valley is higher and narrower but the river still swings in sluggish meanders between small sudden descents at rapids and waterfalls. Morichales gradually disappear altogether. One begins, however, to encounter much larger and better developed patches of hill forest on

the sides of streams coming down from the hills. There is no difference in type between the gallery and hill forests anywhere along the writer's route and they belong to a formation not hitherto seen elsewhere. It should probably be classed as "dry evergreen." In the height of the dry season, no deciduous trees were seen and evergreens with hard leaves predominate. The forest is not tall, about 80 ft. in height at most, and composed of crowded, rather slender stems with a general maximum girth of 3 to 4 ft. There is a closed upper canopy and a small tree layer below. The palm *Jessenia oligocarpa* Gr. & Wendl. is rather abundant and reaches the canopy layer. Trees noted include:

Simaruba amara Aubl.
Didymopanax morototoni (Aubl.) Dcne & Pl.
Buchenavia capitata (Vahl.) Eichl.
Tabebuia sp.
Symphonia globulifera L.f.
Clusia sp.
Tovomita sp.
Rudgea sp.
Vismia spp.
Myrtaceae and Melastomaceae spp.
Bactris sp.

The boundary of a patch of forest is generally a ravine or a sudden break in the ground, the crest of a ridge or edge of a declivity. Boundaries are usually sharp and not marked by a transitional zone save rarely when a species of bamboo may form small thickets between the forest and the savanna.

Eight miles above Morock Meru, about 35 mi. from Santa Elena, the trail passes through the first Indian village seen on the way. It consists of two huts only. In the last generation these people, who are of the Arecuna tribe, have been brought into some contact with civilization through the visits of explorers and missionaries and are now familiar with the uses of clothing and firearms and certain other civilized equipment but their ways of life remain as yet unchanged. They live by cultivating small provision patches, chiefly for cassava, in the forest lands (they do not cultivate the savanna) and supplement this vegetable diet with such wild animal food, including insects, as they are able to catch. They have no domestic animals, and there is no native fauna of grazing animals on the grasslands of South America. Such animals as the Indians have available for hunting are forest animals—deer, wild pig, agouti, capybara, monkeys and birds—which are quite rare in this region. In this particular district the fish in the rivers are at most 6 in. in length. Meat diet for the aborigines is thus very scanty and is said to be augmented with termites and other insects. The termites and the "ant eaters" which prey upon them are in fact almost the only legitimate savanna fauna in South America.

Only two other aboriginal villages were seen on the Roraima expedition: Kunu-tá, about 8 mi. north-east of the two huts mentioned above, with about 10 houses and Arabopó, 5 mi. east of Roraima, which is only inhabited today by one family. An abandoned site was seen between Kunu-ta and Roraima which is probably the Kamaiwawong of the earlier explorers. The aboriginal population is thus extremely small, perhaps averaging one person per 10 sq. mi. None the less they manage very thoroughly to set fire to the savannas every year. Grass seems to be regularly fired as soon as it gets long enough and full of enough dead trash to burn. These savannas are swept by strong breezes and dead grass dries rapidly after rain so that a fire can be set at almost any time though of course the dry season provides best conditions. The writer's three Indian carriers, on being allowed to have matches, set fire to the grass along the trail several times a day, whenever a patch of tall grass was crossed. When questioned they were unable to give any coherent reason for their actions. It is probable that basically the desire is to keep the country open. Other wandering Indians were evidently doing likewise for columns of smoke were often seen and later, from the camp site on Roraima overlooking the Gran Sabana, many grass fires could be seen blazing at night.

Nearing the base of Roraima, many of the patches of forest are seen to have been overrun by fire and are now fringed by dead trees or even consist entirely of groves of blackened trunks (Fig. 23). The sloping base of Roraima itself between the foot of the great vertical cliff and the level of the savannas, has been forested in the recent past and the base of its neighbor Kukenán-tepui is still covered with evergreen forest. Fire passed across the slopes of Roraima, perhaps in the drought of 1926, and killed the trees for miles. They still stand there, dead, their trunks blackened by subsequent fires, over a low understory of bracken and small bushes (Fig. 24). Relics show that there was formerly a succession of montane vegetation-types on the mountain, due to increasing altitude and higher rainfall attracted by the massif. The general dry evergreen forest of the Gran Sabana gave place to lower montane and montane rain forests and finally to elfin woodland at 7,000 ft. close up under the cliff-foot. A certain amount of the latter has escaped the fire and is seen to contain characteristically an Oreopanax, Weinmannia and Hedyosmum, a large, stout, Geonoma

FIG. 23. Relationship of savanna and forest on the Gran Sabana. The two forest patches were once united but have been sundered by fire, which is steadily reducing them. Note the darker colored area between the forest patches which consists of low bush and bracken recently burnt over, and the dead trees at the forest borders.

FIG. 24. The dead forest on the slopes of Roraima.

palm and a small Euterpe. Mosses and epiphytes are much in evidence. The actual summit of Roraima supports a type of wet *páramo* vegetation growing in peat bog.

After coming down from Roraima a trail was followed eastwards to Arabopó village on the headwaters of the river of that name which unites with the Kukenán below Morock Meru. Arabopó lies between Roraima and Uei-tepui, the watershed linking these two mesas marking the line of the Brazilian frontier. Beyond Arabopó and stretching over into Brazil and beyond to British Guiana is solidly forested country, its border with the Gran Sabana marked by broad belts of dead trees killed by the same fire that exterminated the Roraima forest. One leaves the country of scarp and flat for an undulating landscape of ridge and valley in crossing over to the forest country, also the rainfall appears to be higher in that direction (the north east) judging by a comparison of cloud formations that way and over the Sabana at this particular season. To the northeast there was a thicker and more persistent cloud formation, suggesting a higher and more persistent rainfall. The same appears to be true of the Sierra de Lema on the north of the Gran Sabana. It would be natural to find that mountainous country rising up to the interior plateau on its windward side would catch a heavy rainfall and that plateau itself was somewhat drier.

The first few miles of the return journey from Arabopó follow the river downstream and pass through the tension belt between forest and savanna. The uplands to the west of the river are in pure grass, to the east in dense forest. The escarpment above the west bank has been covered with forest, which has suffered severely from fire and now consists of groves of dead trees or small bush or bracken. On the east bank there are many irregular patches of savanna set in forest mostly either in the river flat or on ridge tops and little plateau sites. There is a quantity of dead forest also. Five miles downstream from Arabopó the trail crosses the river and leads up onto the plateau between the Arabopó and Kukenán rivers, crossing over to join the trail of the up-journey above Morock Meru. This plateau is relatively even on top and entirely open, affording magnificent views in every direction, limited on the north and east by the great mesas. It is formed by a series of vast, sweeping levels, bordered by long flat ridges or by small rounded knolls and draining off at the sides into ravines which plunge suddenly to the valleys. The land is utterly treeless, stretching away for miles without so much as a shrub in sight, a monotonous carpet of grey grass broken on the flats by rows of termite heaps. A strong breeze is continually blowing and at this altitude (about 4,000 ft.) is pleasantly cool, though the sun's rays are fierce.

There are two principal types of site on the savannas which may be termed the alluvial and the residual and are repeated both in the valleys and on the uplands. The alluvial sites are flat and lie below some other feature such as a knoll or escarpment. They appear to have been formed by deposition of fine alluvial matter washed from above and laid down probably in fine sheets. The vegetation consists of coarse grass in scattered clumps (*Trachypogon plumosus* on the Uplands, *Sporobolus indicus* on the river flats), and sedges, particularly the little trunk-forming species (? *Bulbostylis paradoxa*). Termite mounds are almost invariably associated with these alluvial sites (Fig. 25). The soil is a greyish-white silty clay, stoneless and merging below a depth of 2 to 3 ft. into a pink and white mottled silty clay. It is non-cracking and quite extraordinarily hard and compact. With only a spade at one's disposal it was practically impossible to dig the ground and a couple of termitaria were only taken to pieces with the greatest labor. Admittedly this was the dry season but several rainy days occurred during the writer's journey to Roraima and the rain was quite without effect. There seemed to be no absorption by the soil. During rain, water collected in pools and began to stream off laterally in little clear rivulets. After two days of intermittent rain, moisture had not penetrated the soil for more than ¼ in. and after a day's sunshine this top layer had again dried off. With the light rainfall of this region and exposure of the soil to sun and wind it seems doubtful if there is much penetration of moisture at any time. The soil may be perpetually somewhat dry due to its own intractability, and it certainly suffers from extreme lack of aeration.

FIG. 25. "Alluvial site" of the Gran Sabana, with machete to give the scale. Treeless, sparse grass and sedge, including the trunk-forming Bulbostylis, and a termitarium at right.

The residual sites are those of upland flats, hills, knolls and scarps, with soil developed in situ or from ancient alluvia. A feature of these sites is the surface layer of stones and rocks, often so thick as seriously to impede the growth of vegetation (Fig. 26). The usual grass cover is formed by *Paspalum contractum*. The stones are generally sub-angular to rounded and of all sizes from ½ to 4 in. across, sometimes much larger up to the dimensions of irregular rocks several feet in length. Angular fragments of sandstone and rounded white quartz pebbles are seen but predominantly the litter consists of ironstone in lumps and nodules. There are never any termite mounds here and the vegetation is much reduced in stature and quantity. Small hairy sedges are often dominant. The soil below the surface stony litter is, curiously, entirely without stones and down to a depth of at least 5 ft. is a pink and white mottled clay loam, non-cracking, hard and compact, merging below into a pinkish-white clay-loam. There is no humus coloration at all in this soil and there are generally signs of active surface wash in progress in between the surface stones. The soils of steep slopes are similar except that rotten rock is often seen at shallow depth and the surface stone layer is reduced or missing.

FIG. 26. "Residual site" of the Gran Sabana, a knoll capped with stones and boulders, between which a few grasses sprout with difficulty.

Morichal soil has been described previously. Forest soils on the hills are seen to be a stiff, non-cracking yellowish-brown clay at the surface merging into a pink and white mottled clay at depth. They only differ from savanna soils of sloping ground in their surface humic coloration. Crumb structure is poor and they probably suffer from lack of aeration. The abundance of the palm Jessenia and the reduced, "dry evergreen" physiognomy of the forest are probably significant of this. These forests are in many ways reminiscent of the marsh forest at the Long Stretch in Trinidad (Beard 1944, 1946) where the soil is closely similar to that observed on the Gran Sabana. The topography of the two areas is unlike, however, the Long Stretch being flat. The forest soils of the Gran Sabana probably owe most of their superiority over savanna soils to the improved drainage conferred by slope. The possibility that many of the forest patches occur over intrusions of igneous rocks which develop a more favorable soil could not be investigated.

In "Exploración de la Gran Sabana" (Aguerrevere y otros 1939, pp. 596-631) Christoffel described a number of soil types from parts of the Gran Sabana not visited by the present writer. Some of these differ from those seen by the writer, others are similar. In a part of the valley of Kamarata the soil is derived from the disintegration of the nearby sandstone Auyán-tepui massif, and consists of three to five feet of grey or brown sand over gravel or boulder beds. The surface sand is loose and windblown. There are also stone-capped hill tops and some red clay soils derived from igneous rocks. The sandy soils are said to be well-drained.

The Luepa region of the north of the Gran Sabana has some very interesting soils. Christoffel's illustration of their profiles is reproduced in Figure 27. Profile No. 1 shows a sand-over-clay soil with iron pan. The uppermost horizon is a black sand a foot thick, over a ferruginous pan up to two inches thick, below which is a great depth of pale-colored, Kaolinitic clay. This is evidently a soil where drainage is impeded to an acute degree and it shows a typical formation of iron concretionary matter at the top of the impermeable horizon. This is the only soil-type reported from the Gran Sabana where there is actually an iron pan *in situ*. In places the pan is said to be greatly thickened and to crop out on the surface of the ground. This evidently gives a clue to the origin of the great masses of ironstone pebbles found littering the hilltops all over the Sabana. In

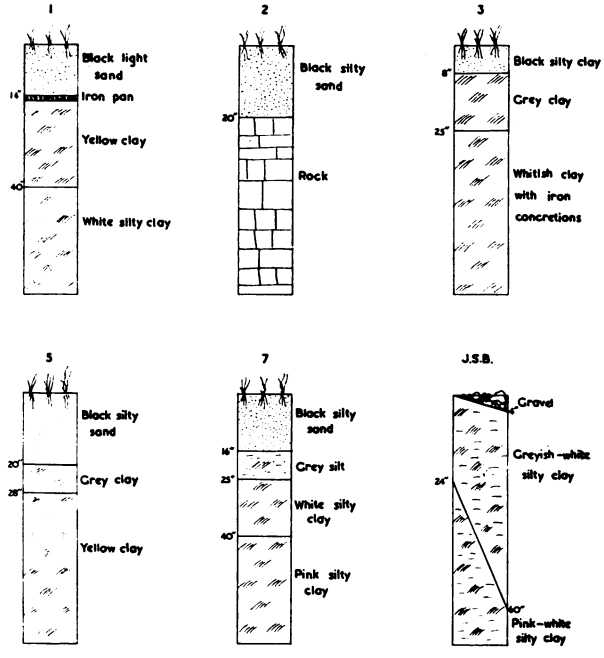


FIG. 27. Soil profiles of the Gran Sabana. Nos. 1 to 7 redrawn from Christoffel's profiles 1 to 7 of the Luepa district (in Aguerrevere and others 1939); "J.S.B. is a diagram of the soil as observed by the writer on the way to Roraima.

some past era sand-over-ironpan soils have presumably been more widespread and have disappeared by erosion leaving the remnants of the iron-pan on the surface of the clay horizon.

Profile No. 2 shows a predominantly silty, humic layer over a hard rock horizon. It is a savanna soil with drainage impeded as in No. 1.

Profile No. 3 while shown with grass tufts at the top, is actually taken in an aboriginal cultivation cut out of the forest. It is really a forest soil, and is a clay deeply colored towards the surface by humus.

Profiles 5 and 7 show a black, silty topsoil merging below a depth of two ft. into a pink and white silty clay which is stated to be impermeable. This is evidently closely similar to the "soil of alluvial sites" described by the writer, though the surface horizon may be of less compact character. Christoffel considered it suited to cultivation, whereas the soils seen by the writer certainly would not be. Even so, the soil is infertile and would need heavy manuring. The sandy soils of this region are clearly infertile, consisting largely of pure quartz, and would not lend themselves to crop-production. In the case of these loamy soils Christoffel seems to have been over-impressed by their favorable texture, and suggested cultivation of wheat and many other field crops as well as fruit trees and Cinchona. The adverse drainage factor appears not to have been considered. Attempts to cultivate the savannas in Trinidad have failed very miserably. On the Rupununi savannas of British Guiana crops are only cultivated in old cattle corrals. The aborigines studiously avoid cultivating savannas and invariably make their gardens in the forest. Christoffel's viewpoint, stated in a long preamble, is that the whole region was formerly covered with forest which has been destroyed and converted into savanna over a very long period of years by the encroachments of the Indians who fell patches of forest for cultivation and subsequently burn off the secondary vegetation repeatedly, so that grass takes possession. During this process the soil is progressively impoverished and loses its humus, and is then incapable of going back to forest "A clear proof of the infertility of these lands is the poor vegetation which covers them" (p. 600). To one taking this view it is clearly only a question of suitable treatment, working of the soil and improvement with green manures, to bring it back into good condition.

Conditions around Santa Elena and to the southward are somewhat different from the Gran Sabana proper since the Kaieteurean sandstones have given way to rocks of the basement complex. North of an east-west line through the village is a series of scarps formed by northward dipping quartzites, whose vegetation has already been described. Immediately south of the village in an east-west direction runs a range of high, rounded hills due to a basic igneous intrusion and south of this across into Brazil is a region of undulating country upon mixed igneous and metamorphic rocks. All of this area, both the hills and the undulating country, is about equally covered with forest and savanna in a highly haphazard manner and there is no apparent correlation between vegetation and topographic factors. Savanna sometimes ascends to the tops of the highest hills, but just as often these are forested. Some of the forest land in the neighborhood of Santa Elena has been cleared for agricultural purposes and is said to be fertile. The plantations appear to be doing well and are yielding good crops of sugar cane, plantains, maize, cassava and other root vegetables. A soil profile examined at the hacienda of Coronel Mendez showed a stoneless clay soil, brown, crumbly and cracking at the surface with plentiful humus and small roots, merging gradually to a dark red clay below 3 ft. depth. The distance to which the igneous rock had decayed could not be ascertained. This appeared to be a normal "red earth" soil developed over basic igneous rocks. The forest occurring on this soil is a luxuriant evergreen seasonal forest. Most of the component species were unknown to the writer but it corresponds in physiognomy closely to the evergreen seasonal forest in Trinidad. It is much taller than the forests seen out on the Gran Sabana, with stouter trees, a greater variety of strata, forms and species, and several deciduous species are present. Towards the hilltops there is some reduction and assimilation to the dry evergreen type, with abundance of Manilkara trees. This is presumably due to the shallowing soil and exposure to wind. The occurrence of evergreen seasonal forest here where the rainfall is not likely to differ substantially from other parts of the Gran Sabana tends to show that the forests on the Kaieteurean sandstones are a special type due to adverse soil conditions.

The boundaries of forest and savanna in this area are abrupt, large trees rising straight from the edge of the grass. Areas of dead and burned forest were not seen by the writer. There is likewise an abrupt change in the soil on entering the savanna. It becomes bright red instead of brown at the surface and is thickly sown superficially with pebbles, stones and rocks apparently of an ironstone conglomerate. There was no opportunity to examine the subsoil but it may be that undecomposed rock lies close to the surface. The difference between forest and savanna soils would then be similar to that observed near Upata in Venezuelan Guiana. The geology of the basement complex on the Gran Sabana is imperfectly known and it may be that different geological formations underlie the savanna and forest areas, the one weathering readily into a deep forest soil and the other being resistant and forming a perpetually shallow site. The only other possible explanation would be that forest formerly covered the whole area but was destroyed by fire in certain parts which then became severely eroded and were reduced to rocky, shallow sites. If the forest soil profile which the writer investigated is a typical one, this explanation would not account for the superficial mass of ironstone in the savannas. Further it is much easier to imagine a whole stretch of country being burned off than small patches which are not readily set fire to

repeatedly. In crossing this country the writer crossed a small patch of savanna which had evidently not been burnt for years. The grass was breast-high in parts and densely, almost impenetrably tangled, including a certain amount of unpleasant cutting sedge (Scleria). The ecological relationships of forest and savanna here are obscure at present and require further detailed study.

THE RUPUNUNI—RIO BRANCO SAVANNAS

Two detailed studies exist of the savanna region of interior British Guiana and the adjoining portion of Brazil, by Follett-Smith & Frampton (1935) and Myers (1936). Myers stated that this region was bounded on the north by the Pakaraima mountains of British Guiana (to the east of Roraima and forming the Amazon-Essequibo watershed), on the west by the "Parima mountains" (apparently the "Sierra de Pakaraima" of the Venezuelans on the Gran Sabana), and on the south by the great equatorial forest of the Amazon with the River Mocaja-i, a tributary of the Rio Branco, forming the exact boundary. To the east and south-east the boundaries are not well known and presumably the savanna country of the Surinam-Brazilian border is contiguous. The Gran Sabana is actually contiguous with this region also, the Sierra de Pakaraima (or Parima) beeing only patchily forested where it divides the two. In British Guiana the savannas are divided into two by the Kanuku mountains. A map of the region is given by Myers.

This region does not consist of a definite plateau like the Gran Sabana, the elevation varying from only 200 ft. at the junction of the Rios Branco and Mocaja-i to 4,500 ft. at the Orinoco-Amazon watershed. Most of the country is mountainous or undulating but still preserves, particularly on the highest lands, a tabular structure.

No climatic data were given by Follett-Smith & Frampton but Myers stated that "the lower savannah climate is essentially similar to that of the llanos—a restricted season of heavy rains and a long dry season, leading to the same effects on the vegetation. In the wet season large tracts are under water; in the summer the land is parched for long distances, and even drinking water is hard to procure. The savannah vegetation is thus of climatic origin" (p. 166). Myers qualified this, however, on p. 176 by stating that "we are justified in regarding the present vegetation as a fire climax."

This region is not so consistently grass-covered as the Gran Sabana. Myers noted the constant alternation of savanna and forest, plain and mountains. "Occasionally, on the Uraricuera savannahs, one sees vast level plains, very reminiscent of the llanos, without so much as a bush or a hillock to the horizon. Usually, however, on the most open, level and treeless stretches of savannah, there is always forest in sight, either in the form of fringing woods along one of the numerous rivers, or as bush islands, large or small, while mountains, either the Kanukus, the Pakaraimas or some of the isolated savannah ranges, usually close at least one horizon."

The soil analyses given by Follett-Smith & Frampton, show in all cases that, throughout the region they examined, forest soils are only slightly more fertile than savanna soils. There is little essential difference in chemical composition between them. There are, however, considerable differences in drainage since their savanna soils are mainly on flats subject to inundation in the rainy season and their forest soils mainly on mountain slopes. Their description of the main soil types agrees exactly with those seen by the writer on the Gran Sabana, viz.: "The elevated soils usually fall into two main classes (a) a highly acidic grey or buff sandy topsoil which merges into a highly acidic clay loam subsoil of pinkish color and (b) a highly acidic red clay topsoil often covered with a layer of ironstone gravel and resting on a highly acidic red clay subsoil. The soils of the swampy flats consist of pale colored sands, silts or clays often covered by a thin layer of acid organic matter." In general the Rupununi savanna soils seem to be more often sandy at the surface than those in the part of the Gran Sabana seen by the writer, though other parts of the Gran Sabana appear comparable.

Trachypogon plumosus is the dominant grass throughout the region and on Myers' estimate it forms 90% of the total population. Important subsidiary grasses are *Aristida setifolia, Axonopus aureus, Andropogon angustatus* and *Mesosetum liliiforme.* Woody elements include the recumbent *Byrsonima verbascifolia,* and the shrubs *Curatella americana, Byrsonima crassifolia, B. coccolobaefolia, Bowdichia virgilioides, Plumeria* sp., *Roupala* sp., *Psidium* spp., and *Anacardium occidentale.* Myers found these to be usually more scattered than in "orchard" formation, but they are evidently more common than on the Gran Sabana. Riverain flats, particularly at the higher elevations, are covered with *Sporobolus cubensis.*

A feature of the Rupununi-Rio Branco area is the *baixa* or swampy depression, covered with sedges and inundated for half the year. Many of these *baixas* are several miles across, with groves of Mauritia palms occupying the position of "bush islands" in them. They are evidently analogous to the *esteros* of the Orinoco llanos. According to Myers, "the determining factor between sedge flat and *Trachypogon* savannah is apparently the duration of flooding. The latter type can endure flooding for a limited time, while the former cannot stand desiccation." Areas of this nature were not seen on the Gran Sabana.

Some additional facts of significance can be obtained from Schomburgk's account of his travels (1847). This author repeatedly mentioned the stony surface of the savannas, encountered everywhere except on the swampy depressions. The ground was strewn with quartz and granite fragments or pebbles and boulders of ironstone conglomerate. In travelling

up the rivers he observed that wherever savanna came right down to the river's edge, thus permitting a section of the savanna subsoil to be seen in the river bank, it generally consisted of a ferruginous conglomerate covered only with a shallow soil, whereas the gallery forests were underlain by deep alluvial soil. Termite mounds were mentioned as a feature of rising ground in the savannas. These might be as much as 12 ft. high and were of irregular shape—"now they formed spiral pyramids, now columns with capitals, or resembled giant mushrooms with brimmed tops." These ant-heaps were said to be devoid of all vegetation. A second species was found to form low flat mounds on the lower parts of the savanna and this is presumably the same species as found on the Gran Sabana.

The Amazon Basin

The Amazon is the largest river system in South America, draining 40% of the surface of the continent. For the most part the basin is extremely low-lying. Ocean-going vessels ascend the stream as far as Iquitos which is 2,500 mi. from the ocean and less than 500 ft. above sea level. It is therefore readily understandable that enormous areas are subject to inundation in the rainy season and alluvial sediments are being deposited there. The lower course of the river flows between the Guiana and Brazilian highland masses, in which the lower tributaries originate. The upper tributaries rise in the Andes and drain a large basin floored with Mio-Pliocene sediments. Although the river now flows east to the Atlantic, until mid-Miocene times it flowed west to the Pacific. Elevation of the Andes then obstructed the drainage and caused the formation of enormous lakes in which the sediments referred to above were deposited. Eventually a new outlet was cut to the Atlantic, the lakes drained, and more recently a new cycle of sedimentation has begun along the lower course.

Active sedimentation along the courses of the rivers has caused them to become embanked by strips of relatively raised ground known as "restingas." Behind these natural bunds lie enormous depressed areas, particularly along the lower Amazon, which are either perpetually filled with stagnant water or are subject to seasonal flooding by the rise of the rivers during the rainy season. Land of the former type is known locally as "igapó" and of the latter type as "varzea." Some distance back from the watercourses is the higher ground out of reach of the floods, known as "terra firme."

The upper Amazon, defined as that portion of the river and its tributaries lying above the confluence with the Rio Negro, is distinguished by different natural conditions from the lower Amazon—the portion of the stream below the Rio Negro down to the head of the delta—and both these two regions differ again from the delta itself.

The delta is entirely a lowlying region, much of it permanently below water level, a maze of creeks and distributaries bordered either by restingas with permanently swampy igapós behind them or by varzea land which is flooded diurnally by the ebb and flow of the tides. In the centre of the larger islands there is older alluvial ground high enough to be considered terra firme. The delta has a high rainfall; for example (Bouillenne 1930), there was recorded at Para in the delta an average rainfall from 1894 to 1911 of 2486 mm annually (103 in.) distributed in 252 rainy days. There is a very wet season from January to August, followed by a pseudo-dry season, also rainy but receiving the precipitation in heavy showers instead of unrelenting downpours.

The lower Amazon region above the delta, on the other hand, has a relatively much drier, more seasonal climate. Again according to Bouillenne, Obidos in this region receives only 1592 mm of rain annually distributed in 157 days, most of which are confined to the rainy season. The alternate season is now no longer "pseudo-" but actually a dry one and its influence is reflected in the character of the vegetation on terra firme. The river courses here are mainly bordered by restingas enclosing here and there swampy igapós but more generally varzeas which become deeply covered by water poured off from the main river during flood, and completely dry during the low season. Tides are no longer felt here. Owing to the flooding of major tributaries of the Amazon at different seasons, the duration of the flood along the lower course is about 8 months. The lowest varzeas are covered for the whole of this period, the highest for some weeks only. The water level rises during flood from 6 to 9 m annually (Bouillenne 1930). Terra firme comes in many places very close to the main stream and, since this is the area through which the Amazon carved its new course to the eastward in Plio-Pleistocene time, consists of low hills and plateaus formed of ancient continental rocks. Between Prainha and Obidos, on the north bank, Bouillenne described an intermittant escarpment edging a plateau of these rocks rising some 300-400 m and set back 25 to 50 km from the river. These low hills form the connecting link between the highland masses of Guiana and south-central Brazil.

The upper Amazon is again a rainy region, receiving from 80 to 100 in. annually, the dry seasons being short and only moderately severe. There are two rainy and two dry seasons in the year, most of the rain falling between October and June. In the north of this region, granites of the continental basement come to the surface but the major portion of the geology consists of the Mio-Pliocene lacustrine sediments, forming a vast plain across which the rivers meander. As lower down, there are seasonally inundated lands, the rise of the rivers being even greater, though for a shorter period. For the most part, the land appears to be terra firme.

The whole Amazon basin is covered for the most part with forests, which have become almost legendary as the archetype of equatorial rain forest. This great jungle, dense, gloomy and impenetrable, is supposed to extend in unbroken, impressive vastness for thousands of miles. Whether such a popular

impression is justified is another matter. In the words of Bouillenne (1930), "the exuberance of the forests and the humid nature of this equatorial region are well known and commonly pass as geographical dogma. None the less, the virgin forest is broken all of a sudden by patches of the poor vegetation of numerous savannas. . . . The presence of savannas in Amazonia is a surprising fact." And it is not only the radically divergent formation of the savannas which must be separated from the equatorial rain forest. The actual forests of Amazonia are very diverse both in form and in habitat. As the writer has previously remarked (1944), it is doubtful if the bulk of the forest in Amazonia can truly be considered as rain forest except in the widest sense of the term.

It will be desirable to consider separately the vegetation of the three regions of the Amazon.

THE AMAZON DELTA

Since the bulk of this region lies below flood level, we shall naturally find that the vegetation is predominantly of swamp type. On the terra firme of alluvia which now lie above flood level there are both rain forests and savannas. A whole belt of savannas, in fact, runs along the Atlantic littoral from the border of French Guiana to the island of Marajo in the Amazon mouth. This belt is a continuation of the savannas of lowland Guiana and as Benoist has remarked for French Guiana it characterizes a zone of Pleistocene alluvia between the coastal swamps and the interior forests. According to Ducke (1938), these savannas are characterized by the presence of the tree *Hancornia speciosa,* which may be taken to indicate that the flora generally resembles that of the savannas on the South Brazilian plateau.

THE LOWER AMAZON

The restingas which border the rivers in the lower Amazon are forest covered. This is described as varzea forest, though generally inundated for only short periods. Similar varzea forest occurs on the landward margin of the flood plain, but in between there are large open expanses known as *campos de varzea,* which we may translate as "seasonally inundated savannas." Behind a thin screen of trees on the restingas lie these large open stretches, covered deeply with water in the flood season, grassy in times of low water. Describing the scene from a commanding hill top at Monte Alegre, Bouillenne (1930) wrote: "This expanse of watery, herbaceous flats is astonishing. Where are the deep forests of the Amazon? One scarcely notices the thin strip of marginal forests. Travellers who have not left the banks imagine immense forests. But behind these, there are only varzeas."

There is forest growth on the varzea here only where the inundation is not too deep. In the swamp forests of the igapós the water, though permanent, is not deep and in the palmaceous marsh forests of the delta the flood water ebbs twice daily. In these *campos de varzea* water stands for months to a depth sometimes of over thirty feet, and we find in consequence a specialized grassy vegetation. Three species of grass were mentioned by Bouillenne: *Panicum amplexicaule, P. spectabile* and *Paspalum repens.* At low water, when the ground is exposed, these grasses have the aspect of an ordinary tall grassland. As the flood begins and the water rises, the grasses rise with it and form floating mats. Frequently these mats become detached by the current and float away down stream, the grasses still living and vegetating.

Perpetually swampy places in the *campo de varzea* which never dry up are filled with Montrichardia. Trees of *Salix martiana* line creeks and thickets of *Alchornea castaneifolia* occur on the transition to varzea forest. There are no other trees. It is clear that in these campos, as in the wet savannas of British Guiana, we have correctly herbaceous swamps and not savannas at all. The physiognomy of hygrophilous grasses forming a floating mat upon deep water constitutes one of the sub-types of Herbaceous Swamp in the Beard classification.

The forests of terra firme on the lower Amazon appear to be evergreen and semi-evergreen seasonal forests, for the most part, judging from the accounts of observers. They are broken in many places by campos which in this case are true savannas, raised well above flood level. One of our best accounts of these is due to Bouillenne (1930) who visited certain savannas both on the south bank at Santarem and on the north bank at Monte Alegre. These savannas are surrounded by forest with the usual abrupt boundaries and occur over ancient continental rocks on sites which are predominantly flat or at most gently sloping. The savannas at Santarem slope gently up from the river Tapajoz rising at the back into low hills (Spruce 1908). At Monte Alegre they occupy more or less flat plateau sites or the gentle dip slopes of scarped ranges of hills (Bouillenne). The soil is a loose sand on the flat portions and a clay strewn with stones on the hilly portions. Spruce remarked that at Santarem "the soil is mostly a loose white sand, but the hills are strewed with volcanic scoriae and towards the summits appear volcanic blocks of considerable size." It was a source of wonderment to Spruce that he should find this material which he took for volcanic lava "at various points in the Amazon valley," without a sign of any volcanoes. He described it as "a honeycombed rock with a reddish vitrified surface, quite resembling masses of slag." In the light of modern knowledge it is quite clear that this material is actually concretionary ironstone, such as we very frequently find associated with savannas. Bouillenne, a more recent observer, described the stone littering the savanna at the Serra de Itauajury as a brownish, angular sandstone veined with "filons limoniteux." The soil beneath the adjoining forest in these parts is said to be tropical red earth and this presumably underlies the sandy or stony top layers of the savanna, though we are not told so. The forest occupies the more broken country such as the steep scarp-

faces of the hills and the valleys and ravines. It occurs also as gallery forests in the savannas.

According the Bouillenne there are three types of savanna to be distinguished. The flora is much the same throughout and the types are differentiated mainly by the form or disposition of tree growth. The most general type of savanna is the common "Orchard" form, known as *campo cerrado* in Brazil —the *chaparral* of Venezuela. Small gnarled trees of no great height and numerous shrubs are scattered here and there over a herbaceous stratum of the usual type of bunch grass and sedges and flowering herbs. In very stony places and the higher ground the trees thin out becoming rare and stunted, so that the savanna could almost be classed as open. Thirdly, there is what Bouillenne called Parkland, with the savanna trees up to 10 m in height, closed up into clumps of bush with shrubs collected at the foot of the trees. This appears to be an unusual aspect of the savanna and Bouillenne remarked that he had not encountered it elsewhere. "Bush islands" are a feature of the Guiana savannas, particularly in the moister parts, but they are formed of forest, not savanna, trees. The closing up of the savanna trees to a regular stand suggests the *catanduva* of south Brazil.

The trees are short, gnarled, brittle, and thick barked. Their leaves are few, large, vertically hanging, stiff and brittle, generally simple, waxy or felty. Few have scaly buds, a usual feature of xeromorphic plants, and few are thorny. Bouillenne claimed that most of the trees and shrubs are deciduous, contradicting other observers who have held that they are evergreen.

Herbs and subshrubs are tufted, with bare soil between plants, and grow to a height of 1 to 2 ft. Subshrubs are mainly formed of multiple shoots sent up each year from a woody rootstock. Herbs have underground perennating organs, which do not act as water storage tissue to any extent. Annual herbs are rare.

Bouillenne made no mention of the names of grasses, except at Santarem. Here Spruce noted "but one species of Paspalum in scattered tufts." Bouillenne named *Andropogon virginicus, Sporobolus indicus* and a sedge, *Rhynchospora* sp. The trees belong to numerous species, among which may be mentioned *Anacardium occidentale* and *A. microcarpum, Curatella americana, Bowdichia virgilioides, Aeschynomene paniculata, Salvertia convallariodora, Qualea grandiflora, Vochysia ferruginea, Byrsonima poeppighiana* and *B. coccolobifolia, Xylopia grandiflora, Sclerolobium paniculatum.* Melastomaceae are prominent among the shrubs, among which may also be mentioned *Byrsonima verbascifolia, Tecoma caraiba, Polygala spectabilis, Rhabdodendron amazonicum,* species of *Cassia, Calliandra, Crotalaria, Eugenia, Mouriri.* At Monte Alegre *Qualea grandiflora* is mentioned as extremely abundant and the commonest of the trees.

Spruce described a slightly different type of savanna near Manaos in a wetter region. The soil was said to be a stiff clay, the vegetation grasses and sedges in tufts with a Scleria conspicuous, Utricularia, Drosera, 3 orchids, a Polygala, several rubiads, the shrubs including several melastomes, Byrsonima and Curatella.

The flora of all these savannas is essentially that of the Brazilian plateau, though much poorer in species. The Amazonian savannas must be regarded as off-liers of those on the higher ground to the southward. In spite of their stronger floristic affinity with the south, the Amazonian savannas form a connecting link between the wide savanna regions of the Guiana and south Brazalian Highlands. There is no continuous connection, at any rate at the present time, but savanna patches of varying size from small to large are scattered at no great distance from one another from the edge of the Amazon floodplain in both directions towards the highlands. North of the Amazon, towards the frontiers of the several Guianas, according to Ducke (1938) the country is covered, outside the riverain forests, with expanses of low, dry forest of the type called *campina-rana,* and *campos.* These savannas are in connection with those of the Rupununi-Rio Branco on the highlands and with those of the Brazil-Surinam frontier region noted by Pulle (1938). They extend, according to Ducke, from the upper Rio Branco by way of the headwaters of the Trombetas to the upper Jari. They are said to be in part high-lying and dry, in part low and swampy. They share the *flora geral* of the South Brazilian savannas though on the Rio Branco there are found some species which have come down from Venezuela.

In a southerly direction we have less positive information. It seems that there are fairly frequent occurrences of savannas on the higher ground between the rivers, but we know little about them since the rivers themselves are bordered by forests and few travellers wander far from the streams.

Bouillenne was of the opinion that the causes for the presence of savannas on the lower Amazon are climatic. The lower Amazon has a more seasonal climate than the upper Amazon and this would be the major cause of the savannas, though not the only one, for the climate as it stands is quite able to support forest. In Bouillenne's view, the savannas are all to be found located in the lee of some topographic obstacle and thus occupy small rain-shadows, patches of "less atmospheric precipitation." Fires, he considered, have had no important effect other than to keep sharp and abrupt the boundaries of the savannas. Cattle are too few and too recent in their arrival and the effect of man is also held to be insignificant. While admitting that in general savannas are on sandy and stony soil and forest on clay, Bouillenne could not admit that the soil had anything to do with the question, because, in his view, first the bulk of the Amazonian forests are on sand, and secondly, the same sandy and stony soil carries both forest and savanna, witness the gallery forests.

THE UPPER AMAZON

The Upper Amazon basin, a relatively little known region, appears to be devoid of savannas. Ducke (1938) described it as an immense plain covered with luxuriant forest, not all of which is very tall. Even here, the rain forest is not universal, being broken by substantial areas of lower growth, *campina* and *campina-rana* ("Bastard campina"), particularly in the region of the Rio Negro.

The *campina-rana* is also known as *caa-tinga* though it is not the same as the caa-tinga of the Brazilian north-west which is thorn and cactus scrub. The name caa-tinga was said by Spruce (1908) to mean "light forest" in Lingoa Geral, referring to the lack of shade cast by the open canopy. These types are associated with deposits of white sand derived from granite and are therefore to be found where the ancient rocks come to the surface rather than on the Tertiary sediments.

DISCUSSION

NOMENCLATURE AND CLASSIFICATION

The writer proposes to confirm the use of the name "savanna" for the plant formation to which the natural grasslands of tropical America belong, because as Lanjouw showed (1936) this is historically correct, the aboriginal word from which "savanna" is derived being a local name for that formation. Whether there is sufficient affinity between the grasslands of tropical America, Africa, Asia and Australia to permit the wider use of the name for a world "formation-type" the writer is not prepared to say, having no personal knowledge beyond the Americas. If we establish the name "savanna" as the correct one on historical grounds for neotropical grasslands, however, it will be legitimate for others to apply it to those of the old world if they consider there is sufficient affinity in physiognomy and ecological relationships.

In an earlier paper (1944) the present writer advocated that the plant formation should be regarded as a physiognomic unit into which are grouped numerous floristic associations showing equivalent structure and life-forms. In keeping with this view, savanna will be discussed here as a physiognomic entity. The information collected in the earlier part of this study is sufficient for a grouping and classification of savanna types on such a basis and it will be possible to delimit certain subordinate physiognomic units or sub-formations. The available information is not yet detailed enough over sufficiently wide regions to enable floristic associations to be recognized and in this respect it will only be possible to indicate the composition of certain known communities belonging to the sub-formations.

All American savanna is sufficiently homogeneous to be regarded as a single formation, corresponding to that originally defined in the writer's paper of 1944. The more detailed study carried out here does not appear to necessitate any departure from the earlier viewpoint. It may perhaps, however, be desirable to attempt a more precise definition of the formation. In 1936 Lanjouw proposed this definition in supersession of earlier ones:

"Savannahs are plains in the West Indian Islands and Northern South America covered with more or less xeromorph herbs and small shrubs and with few trees or larger shrubs."

While this definition marked an advance on its predecessors, it is now open to several objections in detail. If we are to regard it as a physiognomic unit the savanna should not be defined by any environmental factor, and the word "plains" should be omitted. The essential unity of savannas throughout tropical America revealed in this general study makes undesirable Lanjouw's restriction as to locality, made on historical grounds. If the type of a botanical species were collected say in Mexico, we cannot for that reason exclude from the species plants collected outside that country.

Finally, Lanjouw's definition of the woody element implies that trees and shrubs must always be present, which is not the case. Bews (1929) very rightly pointed out that it is "unnecessary to separate tree savanna from pure grassland since the presence of trees does not alter the composition of the latter, and any differences in the grass flora that may exist between pure grassland and tree savanna depend on climatic and soil differences. As a matter of fact, the differences between the grasses of tree savanna and pure grassland savanna are, floristically, very slight." This observation was based upon African conditions but is equally applicable to American.

Robyns (1936) proposed this definition in preference to Lanjouw's:

"Savannas are open herbaceous communities, mainly of grasses, with or without a scattering of tropophilous trees and shrubs, localized in the tropical regions with a well marked dry season during which they dry up generally, and differing from steppes as much from the ecological point of view as from the floristic."

This is in some ways a better definition. However, if savanna is to be a physiognomic unit we must not admit habitat factors to the definition, and the localization of savannas in regions of well-marked dry season is not correct.

The writer proposes the following definition:

Savannas are communities in tropical America comprising a virtually continuous, ecologically dominant stratum of more or less xeromorphic herbaceous plants, of which grasses and sedges are the principal components, and with scattered shrubs, trees or palms sometimes present."

The essential point is that the herb stratum is ecologically dominant. This definition appears adequately to separate savanna from all forest and woodland types, from the Andine *paramo* and *puna,* and from herbaceous swamp.

Warming (1909) allocated tropical grasslands to True Savanna and temperate to Grass-Steppe, including in the latter the steppes of Russia, the prairies of North America and the pampas of Argentina.

This is a very acceptable view, and the present writer urges that the names steppe and prairie should be restricted to temperate grasslands, whose ecological relationships are quite different from the tropical. Warming set up two other categories, Thorny Savanna Vegetation and Savanna Forest. The former includes open thorny bush types with grass and in the Americas refers both to artificial grasslands of some grazing areas which are not correctly savannas and to vegetation like that of the Chaco which is really a mosaic of savanna and thorn woodland as separate formations. Savanna-forest may perhaps describe *catanduvas* or *cerradões* of Brazil and warrant consideration as a separate but related formation.

In classifying subordinate groups within the principal savanna formation, reference should be made to the work of Bews (1929) which, although based on African experience, is essentially so sound that it is directly applicable to the Americas. Bews made the following classification of tropical grassland types, based upon the morphology and evolution of the grasses, and there is no reason why we should not endeavor to apply it to our American conditions:

1. Forest margin and hygrophilous types.
2. High-grass savannas.
3. Bunch-grass savannas.
   (a) Tall bunch-grass savannas.
   (b) Short bunch-grass savannas.
4. Tropical alpine grasslands.
5. Semi-desert and desert types.

In the present study we are concerned with groups (2) and (3), which it should be possible to recognize in tropical America and to constitute as subformations of our savanna. Two major factors seem, however, to lead to important differences in American conditions—the relatively weak assault, hitherto, by man and animals upon the vegetation, and the generally higher rainfall. These interact, for under moister conditions, fire is not so frequent nor so intense and the plant cover recuperates more quickly. On the African continent areas with more than 40 in. of rain a year on the average are an exception; in South and Central America they are the rule. The only parts of tropical America where the average annual precipitation does fall below 40 in. are the Pacific coastal desert in Peru and Chile, the Andean *puna,* the Brazilian North-west, the Guajira and Paraguaná peninsulas of the Caribbean and the Paraguayan-Bolivian Chaco. For these reasons, as will be seen, it may not be possible to recognize High-Grass Savanna in the Americas. Tall Bunch-Grass Savanna is the predominant type. Short Bunch-Grass Savanna is doubtfully recognizable (being associated with rainfalls under 35 in.) and it will be desirable to define an additional subformation, Sedge Savanna, found in certain areas of very high rainfall. The Tall Bunch-Grass Savanna is capable of further subdivision into four phases (Open, Orchard, Palm and Pine) according to the type of woody growth present (or absent).

Physiognomy and Composition

We may now examine and define in detail the various types of savanna which it is possible to recognize, these being:

1. Tall Bunch-Grass Savanna: the predominant type—in fact the neotropical savanna *par excellence.*
2. Sedge Savanna: associated with high rainfalls.
3. Short Bunch-Grass Savanna: low rainfalls.
4. High-Grass Savanna: a doubtful type.

TALL BUNCH-GRASS SAVANNA

To typify the tall bunch-grass savanna we cannot do better than to take up Warming's original exposition from Lagoa Santa (1892), although strictly this lies outside the area of the present work. This was the first good and thorough description of the formation in modern ecology and may therefore claim priority as a definition. If we wish to borrow from botanical practice, we may regard this of Warming's as the first publication of the description of the type, and the type locality as being Lagoa Santa in Brazil. To qualify for classification as tall

FIG. 28. Original sketch by Eugen Warming of the neotropical savanna at Lagoa Santa, Brazil (1892).

bunch-grass savannas, other communities must correspond sufficiently closely to this type. The following is a translation from Warming's original Danish in "Lagoa Santa," p. 244:

"Lagoa Santa's campos are thus a plant formation which mainly and in all its modifications is characterized first and foremost by perennial grasses growing in slender tufts at intervals and other herbs, particularly composites, together with subshrubs whose height for the most part is ⅓-⅔ m (1-2 ft.), and over whose flower-decked expanse may rise bushes and low, crooked and gnarled trees with open crowns and in a more or less close stand (campos cerrados), but never under natural conditions in such a close stand that one cannot pass through it unhindered in all directions. The entire Flora has a xerophilous, but not strongly xerophilous character which expresses itself in the coarse, often hairy, greyish leaves of the grasses and of many other plants, in the stiff, leathery or densely pubescent leaves of the trees and bushes and of certain herbs, in the trees' gnarled form, in the frequency of essential oils and so on. Next must be emphasized the frequent appearance among both herbs and shrubs of underground, irregular but often tuberous growths and among trees of great thickness of bark, as well as the lack of lianes

and epiphytes and especially also of epiphytic mosses and lichens as well as these latter growing on the ground. Finally may be added what I shall a little later have to say in the section on the seasons, that all trees and bushes are deciduous, so that the leaves can usually live about 12 months and in many cases fall off before they have attained this age. The vegetative period may, on the whole, be said to extend over the whole year. But the campo vegetation is not a strongly xerophilous vegetation and has nothing of the most marked characteristics of the steppe or desert: thus, annual plants are very rare, bulbiferous plants and succulents are absent, thorny bushes extremely scarce and finally, there are not few plants whose organs of transpiration are reduced in that the leaves are narrow, small or divided, but this is not carried to such an extreme as in steppes and deserts.''

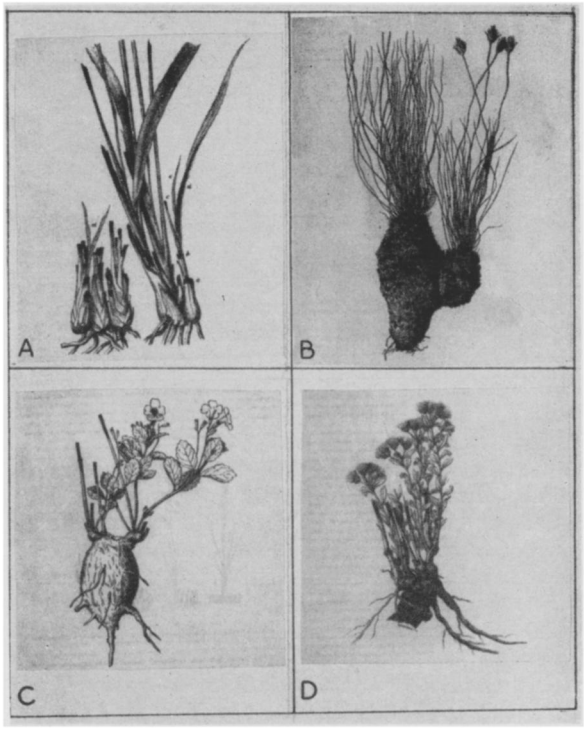


FIG. 29. Sketches by Eugen Warming (from *Lagoa Santa,* 1892) of the life forms of savanna plants.

A.—*Andropogon villosus,* a typical bunch-grass.

B.—*Bulbostylis* (*Scirpus*) *paradoxa,* the sedge with thickened aerial stem.

C.—*Casselia chamaedryfolia,* a forb with tuber.

D.—*Baccharis humilis,* a suffrutescent shrub with rootstock.

This type of savanna, according to Bews, is the most extensive in the world and certainly all the savanna in America belongs to it with the exception of the limited areas under sedge or short grass. Throughout tropical America these savannas exhibit a remarkably high degree of uniformity in flora and differ markedly in this respect from the forest formations.

The community is dominated by a moderately dense layer of herbs among which *Gramineae* generally number over 90% of the individuals. *Cyperaceae* are nearly always present and may cometimes (where conditions begin to approach those of sedge savanna) become almost co-dominant with the grasses. The remainder of this stratum is composed of dicotyledonous herbs and procumbent woody plants. The height of this herb layer is normally between 14 and 20 inches, but it will increase to about 36 in. if it remains unburnt for several years. During the flowering season, the spikes of the grasses reach 3 to 5 ft. in height. The growth of the herbs is characteristically tufted, in the form of a bunch of stems springing from an underground rhizome or rootstock, rather than of a plant with a basal rosette of leaves. It has been estimated (Martyn 1931), that these tufts occupy 60% of the soil surface (see Fig. 6). The rest is quite bare, though normally concealed by the spreading stems and leaves of the tuft-plants. Where there is a tendency to "hog-wallow structure" the soil between the tufts is excavated and upstanding tussocks are formed. During the dry period when growth dies down, the soil is visible and its color becomes apparent at a distance.

The grasses and sedges are of xeromorphic structure, coarse, tufted plants, their leaves invariably narrow and harsh, often rolled and hairy, many of them with sharp, cutting edges. Only fresh young growth is really palatable to grazing animals. The dicotyledonous herbs belong mostly to the Compositae and Leguminosae and are practically all perennial with an underground tuber or rootstock which is not usually water-storage tissue but a simple perennating organ enabling the plant to withstand repeated fires. Most of the herbaceous plants spring into activity early in the rainy season, put out new leaf growth, and flower. If the soil becomes waterlogged later in the rains, they die down into a dormant state which in any case supervenes on the arrival of the dry season and is continued until the following rains. Grass roots ramify thoroughly through the top soil and where a claypan is present they are capable of penetrating the subsoil deeply.

Scattered shrubs are generally present, so many of them being procumbent and having underground, perennating organs that is is frequently difficult to make an exact distinction between herb and shrub. There are three principal types of shrub. The first, typified by *Byrsonima verbascifolia* and *Palicourea rigida,* consists of an underground stem which protrudes above ground level sufficiently to give off a rosette of large, stiff leaves which lie upon the ground. The second type also has an underground woody stem or rootstock from which after every fire a bunch of herbaceous or woody shoots is sent up. These may reach a height of two to three feet and the whole plant may form a miniature thicket ten feet in diameter. The third type is a single-stemmed, low shrub 2-3 ft. high like a small tree. Succulents (*Cactaceae, Agave*) are very rare in savannas. There is an almost complete absence of epiphytes, lianes, mosses and ferns, but there are some woody plants of scandent habit which are found to be related to forest lianes.

The amount of tree growth present is very variable and the writer has proposed a division of the Tall Bunch-Grass Savanna into four phases according to the type of tree growth present, or its absence. *Open Savanna* is completely or virtually treeless, though shrubs of the *Byrsonima verbascifolia* type will frequently be present. Almost the whole of the Gran Sabana area of the Guiana highlands is of this type. Elsewhere it comes in as local patches usually on river flats or the flat tops of ridges. *Orchard Savanna* comprises a growth of small trees which invariably assume a characteristic, curiously gnarled, bent and twisted form. Both the height of these trees and their density are enormously variable. For the most part they are between 10 and 20 ft. in height and 20 to 30 ft. apart, but there may be almost treeless areas with an occasional specimen 4 ft. in height or dense stands 40 ft. high forming almost a forest. The form of these trees is a very characteristic feature and may be appreciated from the photographs reproduced with this monograph. There is seldom any definite trunk, numerous branches arising low down, and these are bent, twisted, crooked, leaning or otherwise distorted. A more or less domed crown is produced. The branch wood is very brittle. Bark is thick, corky, corrugated, generally sloughing off in large flakes: it is fire-resistant.

The thorny, microphyllous type of tree, such as is typified by the genus Acacia, is virtually unknown in these savannas. The typical savanna trees are unarmed, evergreen, with large, simple, stiff, brittle, coriaceous leaves. The leaves of *Curatella americana*, one of the commonest species, measure 8″ x 5″ and those of *Byrsonima crassifolia* 4″ x 2″. A felty or hairy covering on one or both faces of the leaf is a very common feature, or else they may be markedly roughened, or waxy. The leaves droop and are not directly exposed to the sun so that even when the trees grow closely together, they cast little or no shade. The buds are seldom protected by scales as in the case of more extreme xerophytes. The root systems of these trees are superficial and feebly developed, the roots being long and rambling, but few.

It is a disputable point whether the savanna trees should be considered evergreen or deciduous. Warming, followed later by Bouillenne, held that they are deciduous because individual leaves live only 12 months, and are shed annually. Other authors have held that the trees are evergreen and that general leaf fall only occurs as a result of a fire. With this view the present writer is inclined to agree. By deciduousness, as applied to tropical vegetation, we should understand a relatively prolonged period of complete or partial leaf-fall coincidental with dry weather. It is true that many trees shed all their leaves annually not necessarily in dry weather, and put out a new crop immediately or after a short period in which flowering or fruiting may take place. Such plants are generally common in forests under mildly seasonal climatic conditions. They are certainly deciduous in a sense, but not in the sense of those trees growing under severely seasonal conditions which stand bare for months. Savanna trees may belong to the former category but they certainly do not belong to the latter. In the height of a dry season one may pass from a parched, leafless forest to an adjoining savanna and, if there has not yet been a fire, find every leaf intact. Once fire passes the leaves on the smaller trees are withered and fall, but in the writer's experience the trees never stand bare in the absence of this and must be considered evergreen.

Palm Savanna comprises a scattered growth of palms. It is very rare for both palms and trees to occur together. Sometimes the palms congregate to form "witches' rings" but almost always they occur singly and evenly scattered across the savanna. As with trees their density varies, and height depends on the species. *Copernicia tectorum*, where the writer saw it in Venezuela, never exceeded 6 ft. in height. In Cuba 60 ft. is exceeded by some species, while others are dwarfs, and do not exceed 18 in. Palms forming dense groves are not to be included in savanna. *Mauritia flexuosa*, for example, where it congregates as a gallery forest in the Venezuelan llanos constitutes a swamp formation and only takes part in savanna when it occurs scattered singly over grass. Savanna palms are typically of the fan-leaved type. Pinnate palms occur very rarely indeed and then, it seems, only under marginal conditions. The leaves of *Copernicia cerifera* are very richly coated with wax. Some of the Cuban palms have curious bottle-shaped swellings on their trunk. Where there is clay-pan, palm roots seem able to penetrate it and to survive adequately the poorly aerated conditions.

Pine Savanna is perhaps only a variant of Orchard and occurs in the limited area of tropical America where *Pinus* is present. Scattered pine trees of erect form and up to 60 ft. in height occur in the grassland, often mixed with orchard species of trees.

The physiognomy of the herb stratum varies but little with the changes in the tree layer. Very many variations in the grass associations do occur but not necessarily in keeping with variations in the trees. The grass is frequently shorter and less tufted with a higher proportion of sedges in palm savanna than in orchard.

The savanna flora exhibits a number of peculiar features. Compared with forest types the flora is poor in species and is apparently at its richest on the Brazilian plateau. At Lagoa Santa Warming found over 800 species on the savanna, while for the Mesa de Guanipa, Pittier listed only 109. While Pittier's list probably does not represent so exhaustive a search, it remains true that the Orinoco-Guiana savannas are poorer in species. A rich flora is, however, again encountered in the savannas of Cuba. An extremely small number of plant species occur in both savanna and forest, the floristic boundary between the two being as sharp as the physical. Everywhere in the Americas the transition from forest to savanna is abrupt, and there is seldom more than a transitional zone two or three yards in width. For-

TABLE 2. Composition of Local Communities in Tall Bunch-Grass Savanna.

Locality	Phase	Trees	General Herbaceous dominants	Variant dominants on river flats or depressions
TRINIDAD				
Erin	Orchard	*Curatella, Byrsonima, Miconia*	*Axonopus anceps, Trachypogon ligularis*	
Piarco	do	do	*Paspalum pulchellum, Leptocoryphium lanatum*	*Leersia hexandra Paspalum densum*
St. Joseph	do	do	*Trachypogon ligularis, Arundinella, Thrasya*	
VENEZUELAN LLANOS				
Mesa de Guanipa	Orchard	*Curatella, Byrsonima, Bowdichia, Roupala*	*Trachypogon* spp. *Axonopus chrysodactylus*	*Mesosetum chaseae, Paspalum* spp. *Sporobolus indicus*
Calabozo-San Fernando	do	do	*Cymbopogon rufus Andropogon condensatus*	*Sporobolus indicus, Steirachne diandra*
	Palm	*Copérnicia tectorum*	?	
WEST INDIES				
Hispaniola	Open	None	*Themeda quadrivalvis*	
	Orchard	*Curatella, Byrsonima, Anacardium*		*Themeda*
	Pine	*Pinus occidentalis*	*Andropogon*	
Cuba	Pine Orchard	*Pinus* spp. *Quercus, Curatella, Byrsonima, Anarcardium, Tabebuia, Brya*	*Andropogon virginicus, Andropogon, Sporobolus, Panicum, Paspalum, Leptocoryphium*	*Andropogon virginicus*
	Palm	*Sabal, Copernicia, Acoelorraphe. Colpothrinax*	do (?)	
GUIANA LOWLANDS				
Venezuelan	Orchard	*Curatella, Byrsonima, Bowdichia*	?	
British	do	do	*Trachypogon plumosus, Axonopus, Andropogon, Aristida*	
Dutch	do	do	*Trachypogon plumosos, Gymnopogon foliosus.*	
French	do	do	*Trachypogon plumosus, Aristida, Axopus, Panicum*	
GUIANA HIGHLANDS				
Gran Sabana	Open	None	*Trachypogon plumosus, Paspalum contractum*	*Sporobolus indicus*
Rupununi	Orchard	*Curatella, Byrsonima, Bowdichia, Anacardium*	*Trachypogon plumosus, Aristida, Axonopus, Andropogon*	do
Amazon Basin	Orchard	*Qualea, Anacardium,*	*Paspalum, Andropogon, Sporobolus*	
BRAZILIAN PLATEAU				
Lagoa Santa	Orchard	*Bowdichia, Qualea*	*Trachypogon macroglossus Aristida tincta*	
Bolivia	Orchard	*Curatella, Tabebuia*	?	

est trees rise at the very edge of the savanna, their branches overhanging the grassland. Where forest and savanna country mingles, each type occurs as pure patches surrounded by the other, the forest as "islands" in the savanna, the savanna as "lakes" in the forest. Only in the short bunch-grass type of savannas is there anything like a mingling of forest and savanna elements. Forest trees never occur in tall bunch-grass savanna and savanna trees are never found in forest. The savanna grasses are morphologically different from forest grasses and the two do not interchange. Occasional clumps of savanna grass may be found in other low, open forest or bush communities such as the "muri-muri bush" and that is all. Such plants as are found both in high forest and savanna are mostly forbs or climbers.

The principal genera to which savanna grasses belong are: *Trachypogon, Paspalum, Panicum, Andropogon, Axonopus, Arundinella, Sporobolus, Thrasya, Leptocoryphium, Setaria, Mesosetum, Sacciolepsis, Cymbopogon, Steirachne, Aristida, Eragrotis, Sorghastrum, Cipella, Gymnopogon, Clitoria, Cenchrus, Chloris, Ctenium.* In one locality in Haiti, Themeda is dominant but this appears to be essentially a subtropical element: it is further stated to be a sod-grass rather than a bunch-grass.

Sedges belong mainly to *Rhynchospora, Scleria* and *Bulbostylis* (*Scirpus*) also *Dichromena, Stenophyllus* and *Fimbristylis.*

Forbs belong mostly to the families Compositae, Leguminosae, Convolvulaceae, Malvaceae and Polygalaceae.

Shrubs are most commonly Miconia and other genera of the Melastomaceae. Others noteworthy are *Byrsonima verbascifolia, Palicourea rigida, Pavonia speciosa,* all of which are quite widespread. Among palms, the principal genus is *Copernicia.* Others are *Acoelorraphe, Colpothrinax, Coccothrinax, Mauritia* and *Sabal.*

Trees do not belong to any particular families: some are localized and some very widespread. *Curatella americana* and *Byrsonima crassifolia* are almost invariably present throughout. *Anacardium occidentale, Bowdichia virgilioides, Roupala* spp., other *Byrsonima* spp. and *Xylopia grandiflora* are very widespread. The principal Brazilian elements are *Qualea grandiflora, Hancornia speciosa, Plathymenia reticulata, Salvertia convallariodora* and *Vochysia ferruginea.* Cuban species are *Brya ebenus, Tabebuia lepidophylla, Rondeletia correifolia, Malpighia glabra* and *Quercus virginiana.* The pines in Cuban savannas are *Pinus tropicalis, P. caribaea* and *P. cubensis.*

There is insufficient information at present to delimit plant associations, but the accompanying table shows the dominant species of the best-known areas. Dominance among the grasses seems to vary fairly rapidly from place to place and few of the known localities show exactly the same composition. *Trachypogon plumosus* is generally dominant all over Guiana, both on the highlands and lowlands.

Trachypogon ligularis occupies much the same position for Trinidad and the eastern llanos, *T. macroglossus* for the Brazilian plateau. It may in fact be possible to speak generally of a Trachypogon-Aristida association for the savannas on the South American mainland. *Sporobolus indicus* is another widespread dominant, generally on the lower-lying ground

Among the trees, Curatella and Byrsonima are widespread to an astonishing degree, from Cuba to South Brazil, a range of some 3,000 mi. Other species are localized. The whole flora embraces elements of all degrees of distribution from the most localized endemics to general species of the wide range of Curatella. Most of the savanna plants may be considered specialized in some manner.

SEDGE SAVANNA

As has been seen, sedges are always present in the Tall Bunch-Grass Savanna. In some of the wettest areas, where the rainfall is high or flooding prolonged, sedges become more abundant than grasses and a distinctive type of savanna is formed. There are, of course, many intermediate cases, but when fully developed, the Sedge Savanna is quite distinctive. It occupies only relatively limited areas, and is principally typified by the Aripo group of savannas in Trinidad and many of the coastal savannas of Surinam and French Guiana. Elsewhere it occupies the swampy depressions on the Guiana plateau. We hear of it on the Amazon (Spruce 1908) and it was described by Williams (1940) on the Paragua River in Venezuela and by Charter (1941) in British Honduras. Of all the savannas this approaches closest to swamp in type of plant growth and habitat, and has been regarded as swamp by some writers (Marshall 1934), but it is distinguished by the xeromorphic structure of the dominant plants and by the seasonal desiccation of the ground, swamp soil being by definition perpetually wet.

The dominant herbaceous stratum is shorter than in the Bunch-Grass Savanna, but the plants are not so well tufted and a greater proportion of the soil is covered. Sedges are predominant, and grasses relatively rare. There are many small herbs, including terrestrial orchids and, typically, Drosera and Utricularia; also Lycopodium and many ferns, while a spongy moss covers most of the soil between these plants. Some of the dominant sedges may attain a height of 18 in. and their infloreseences 3 ft. at flowering, but most of the plants are only 6 to 9 in. in height. The plants are either weakly or not at all tufted and raised tussocks are not formed.

Many small hygrophilous plants are present but the dominant sedges and grasses are xeromorphic in structure with narrow, harsh leaves, flat or rolled, cutting or pilose. The type of sedge with broad and flat or triangular, pith-filled leaves is not present. The herbs have most of them underground perennating organs. In Trinidad, the plants have a short vegetative period at the beginning of the rainy season

after the soil is moistened and before it becomes waterlogged. In Surinam, according to Lanjouw (1936) the vegetative period is at the end of the rains.

Scattered small shrubs or palms are generally present, the shrubs only 2-3 ft. high and generally some 20 ft. apart. They do not adopt any special gnarled form, bark is generally thin and leaves smaller than those of savanna trees such as Curatella, generally about 2″ by 1″. The shrubs are unarmed and evergreen, their leaves simple, coriaceous, entire, generally waxy, sometimes felty or hairy.

Dominant sedges belong to the genera *Lagenocarpus, Rhynchospora, Bulbostylis,* and *Scleria. Leersia hexandra* is generally present, and many other grasses typical of bunch-grass savanna occur sporadically. Shrubs vary: in Trinidad and the Guianas, Chrysobalanus, Byrsonima, Ilex, Miconia; in Venezuela (Williams 1940) *Duroia sprucei* and *Erythrina glauca;* and in British Honduras (Charter 1941) *Crescentia cujete* and *Cameraria belizensis.* In British Honduras the palm *Acoelorraphe wrightii* is present, and in Guiana, Mauritia occurs locally.

Another feature of the sedge savanna is its tendency to occupy relatively small patches alternating rapidly with forest and woodland of a specialized kind and forming a mosaic. This tendency is first remarked in the tall bunch-grass savanna of wetter areas, where "bush islands," inclusions of the local forest, may become common. In the sedge savanna the dispersion and intermixture of savanna and woodland becomes extreme and the woody communities more specialized.

SHORT BUNCH-GRASS SAVANNA

This name should only be tentatively applied at present in tropical America as we have, unfortunately, insufficient detailed information about the communities to which it may pertain. In Africa, the short bunch-grass savannas, in Bews' account (1929) occur in areas of lower rainfall than the tall bunch grass, between limits of 20 and 35 in. per annum. The grasses reach only a height of one foot, and the trees are fewer and more xeromorphic, generally of the Acacia type.

We must certainly recognize that the savannas of the drier parts of tropical America, where the annual rainfall drops below 40 in. differ considerably from the pattern predominant elsewhere. Whether these are correctly worthy of the term short bunch-grass savanna it is difficult to say. On extending our knowledge we may have to allot some other name. For the present, however, the writer proposes the use of this term.

The principal feature of this type of savanna is that it does not form the vast, sweepingly monotonous expanses of tree-dotted grass typical of the tall bunch-grass type. It is essentially a component of an intricate mosaic of rapidly alternating communities of various kinds—low thorny bush, taller evergreen forest, palm groves, grassland with or without trees. In the well-watered parts the evergreen forest is common, in the drier parts we see more of the thorn bush and even patches of cactus. Each of the components of the mosaic is a distinct plant formation and they alternate rapidly according to slight changes in site factors. The savanna itself thus occupies only a portion of the ground.

The "Dry Savanna" of Haiti should probably be classified under this head, with its dominant grass *Uniola virgata* and accompaniment of Agave, Plumeria, Maytenus, Schaefferia and Jacquinia. Here also belong the *Paspalum bakeri* savannas of Barbuda surrounded by Bucida trees, disposed as pockets in Bushland. In Cuba, on a part of the Trinidad plains near the coast, savanna of *Sporobolus indicus* dotted with small thorny trees (*Brya ebenus*) is mixed with local thickets of *Copernicia macroglossa, Acacia farnesiana,* prickly pears and tall cacti. The writer's observation of Acacia thickets in the savannas of Venezuela south of the Orinoco may be taken to indicate an approach to these similar conditions.

In the extreme south the chaco vegetation (*Parque chaqueño*) appears to include short bunch-grass savanna intermingled with thorny thickets and with low evergreen forest and cactus scrub, as well as with swamp communities such as herbaceous swamps and palm groves. On the borders of the arid zone of the Brazilian north-east in the state of Ceará, there are flat plains with a vegetation very similar to that of the Chaco, both floristically and ecologically. It seems probable also that the *campos mimosos* of the São Francisco valley which likewise border upon the arid north-east should be so classified.

HIGH-GRASS SAVANNA

Even with the aid of Bew's qualifications that the important criterion is not so much the height of the grasses as their hygrophilous character, it is difficult to find any very convincing examples of this type of savanna in America. In Africa, according to Bews, it consists of tall, coarse grasses 5 to 15 ft. in height and occurs either around forest margins or over wider areas where forests have been destroyed. The community depends on fire for its maintenance. The forest margin type of habitat is limited in area and examples are afforded by the appearance of Scleria and Imperata forming a taller growth at the borders of savannas—Trinidad and elsewhere. Schomburgk (1847) mentioned very tall thickets of grass bordering the rivers in the Rupununi savanna area in places where there was no gallery forest, and this is doubtless another example, as are the numerous patches of tall grass on river banks everywhere, although these cannot be said to depend on fire for their maintenance. Perhaps they should be placed with Bews' "forest margin and hygrophilous types."

The degraded forest type of habitat is less common in America than in Africa since man and fire have had much less effect on the primaeval vegetation. In some intensively disturbed areas there are certainly grasslands which have supplanted forests in historical times and these are of three kinds. The

first, typified by the Gran Sabana and the Venezuelan mountains, differs scarcely, if at all, from the general type of tall bunch-brass savanna. The second is typified by the "fire savannas" of the northern plain of Trinidad with Imperata, Arundinella, Andropogon and Maximiliana palms. The grasses here are only slightly taller than those of the tall bunch-grass savanna and include species of the latter. Thirdly, there are grazing lands like those of Antigua and Cuba, whose African appearance was commented on by Marie-Victorin and Léon (1942-44). These are floored with soft grasses, which grow tall if ungrazed, and covered with flat-topped leguminous trees.

In none of these cases do the grasses at all approximate to the height of the African high grasses. There is, however, one example which must be quoted where really tall grass is involved, the low floodplains of the middle Orinoco, where Myers (1933) was confident that he had found true high-grass savanna. On first reading his account, the writer was inclined to agree with him. The vast expanses of *Paspalum fasciculatum* as high as a man are suggestive, though the obviously swampy habitat of the *esteros,* under deep water for much of the year, would be difficult to reconcile. Acquaintance with the *campos de varzea* of the Amazon (Bouillenne 1930), with their *Paspalum amplexicaule* and *P. spectabile,* throws the Venezuelan community into its true perspective. Clearly both phenomena are the same and the type that Myers found is not high-grass savanna at all, but swamp grass, the same phase of Herbaceous Swamp as the *campos de varzea* represent, and a very different ecological proposition.

On the whole it cannot be said that the evidence in favor of recognizing high-grass savanna in tropical America is very strong. We could say that certain man-induced grasslands are equivalent to the African high-grass savanna, or resemble it ecologically. The influence of man in this connection will be discussed further under Habitat.

HABITAT

CLIMATE

In discussing the savanna in relation to climate, we must distinguish between the microclimate of the savanna itself and the macro- or regional climate to which both the savanna and any forests of the vicinity are subjected. A dense tree cover exerts such a profoundly modifying effect that the microclimates of adjacent savanna and forest must be radically different, but such variations are the result of differences in the plant cover and cannot be said to have any major controlling influence upon it. If we are to examine the contention, supported by so many eminent authors, that the savanna is a climatic formation, then it is the macroclimate which must receive closest scrutiny and we must be able to define the typical savanna climate in terms of rainfall, temperature and so on.

It will be clear from the outset that the savannas are found under a great variety of regional climates and are juxtaposed with a variety of forest types.

Temperatures are essentially similar throughout, averaging between 65° F and 80° F "in the shade" —of which, actually, there is none in the savanna. Temperatures of surfaces exposed to the sun are of course rather higher. For the Guiana plateau Schomburgk mentioned figures of about 120° F. There is little seasonal variation in temperature and frost is unknown. No savannas occur at altitudes where temperatures become effectively low. It therefore seems wrong to speak of a "winter" season in the savannas as some writers have done. It is perhaps difficult for a person accustomed to temperate conditions to realize that there is no winter in the lowland tropics in the sense of a season in which temperatures become effectively lowered. The tropical year is divided into one or two relatively hot *dry* seasons alternating with one or two relatively cool *rainy* seasons (actual temperature differences are slight) and in Latin America it is customary to refer to the former as *verano, verão,* "summer," and to the latter as *invierno, inverno,* "winter," by analogy from the Iberian peninsula with its hot, dry summer and cold, wet winter. However, this is not a scientifically correct practice since the "summer" and "winter" do not necessarily coincide with the solar seasons. In Venezuela, for example, the *verano* is from January to May, in the late winter and spring of the solar season! We cannot admit that the "dry, cool winters" regarded by Schimper, Warming and others as characteristic of the savanna climate represent a correct interpretation of the facts.

Rainfall is the all-important climatic factor in the tropics and the vegetation everywhere shows important responses to variations in the amount and distribution of it. Rain forests are found where drought periods are insignificant and increasing xerophytism becomes apparent with greater incidence of drought periods. Drought becomes felt whenever evaporation exceeds precipitation for long enough to begin to dry out the soil and a number of students of this question (Charter 1941, Mohr 1944, Hardy 1946, Beard 1946) have concluded that drought periods in the moist tropics can be said to occur whenever the monthly rainfall fails to attain 4 in. in a month. One or two months with less than 4 in. will not perhaps be perceptible unless quite or almost rainless, but three, five or more drought months are bound to be effective and where they occur regularly at definite seasons the vegetation shows xeromorphic characters.

The savannas are subject to a wide range of rainfall conditions, which is reflected in the accompanying distribution of the three savanna types, sedge, tall bunch-grass and short bunch-grass. Some of the wettest conditions are experienced at the Aripo savannas of Trinidad and the Guiana coastlands from British Guiana to the Amazon mouths. Here the average rainfall is everywhere over 80 in. a year and ranges locally to a recorded maximum of 140 in. (*fide*

Benoist) in French Guiana. Drought months are normally three or less each year and there are still at least 2 in. of rain during each of those months. Associated forests are rain forests for the most part. In such areas savannas are very commonly of the sedge type or, if not, of the tall bunch-grass type with a high proportion of sedges. The greater proportion of American savannas lie in rainfall zones of between 50 and 65 in. per annum with five drought months in a year. Absolutely rainless months are extremely rare anywhere and a few showers continue to fall in the driest weather. The Gran Sabana is a slightly moister area with 65-70 in. of rain and three drought months, the eastern Venezuelan llanos are a drier area with 40-45 in. and seven drought months. Within the above limits, the tall bunch-grass savanna reaches its optimum development, alongside seasonal forests. Savannas continue to be found in the limited semi-arid regions of tropical America, in the Brazilian north-east with 30-40 in. of rain and in the Chaco with its 35-50 in. which drop locally to only 20 in.: in such areas, distribution of rain is irregular and long droughts are liable to occur. Savanna here is of the short bunch-grass type, and associated woody growth is thorn bush and cactus.

What then constitutes the typical savanna climate? In what way do savanna and forest climates differ? We have seen that savannas and forests exist side by side under rainfalls varying from 20 in. a year to 140 in. and that over this range there is a variation in life-forms in both savanna and forest from short bunch-grass to sedge and from thorn bush to rain forest. It is substantially the view of most writers concerned that a long, severe dry season characterizes the savanna climate. According to Warming (1892) this is generally true, in wetter regions some unfavorable soil factor being present to depress moisture supply. In Schimper's view (1903) a dry, cool winter would be equivalent to a long rainless season and savanna would be further favored by frequent, even if weak, precipitation during the vegetative period of the grasses. Hayek (1926) stated that savanna would be widespread where the bulk of rainfall falls during the vegetative period of grasses, a curious inversion of cause and effect: for in the tropics, where there is no winter, properly speaking, the vegetative period of grasses will naturally coincide with the rainy season, whenever that is. This period is not fixed but is conditioned by the prevailing climate, moreover rain at any season favors trees as much as grasses. We fall back, essentially, on the supposition that a severe annual dry season climatically favors grassland. The great range of rainfall conditions demonstrated above under which savannas occur does not necessarily exclude the possibility of a typical savanna climate, if this is a very dry one, since some adverse edaphic factor may be present in the moister areas to depress the availability of moisture down to a level equivalent to that afforded by a drier climate. We have merely to enquire whether there is any climate which will cause the appearance of savanna in the absence of fire or any adverse edaphic conditions.

We are bound to conclude that there is not. Meteorological data available to us today show that former inferences of the long, rainless dry seasons in the Venezuelan llanos and elsewhere were not factually correct. The average savanna climate is not as dry as used to be believed and in the really dry and semi-arid regions, savannas become less and not more conspicuous. Where there are less than 40 in. of rain a year savannas become restricted to relatively small patches mixed with xeromorphic bush and with under 20 in. grassland disappears altogether. The typical vegetation of the arid regions of tropical America is thorn woodland and cactus scrub, formations of which grasses are insignificant components. Even if we suppose that a forest type growing under a rainfall of say 60 in. is occupying a moister site, due to some soil factor, than the savanna alongside it, we should also expect to find the savanna occurring on optimum sites under lower rainfall elsewhere but we do not: we still find woody growth, only of a more highly xeromorphic character than before. There is no climate on record under which there is savanna on optimum sites. In a previous work (1944) the writer described a series of "seasonal" plant formations showing progressive reduction in stature and forms from rain forest to desert and corresponding to progressive increase in the incidence of the drought factor. Savanna has no place in this series and all the formations are woody. Evergreen, semi-evergreen and deciduous seasonal forest lead on in descending series to thorn woodland, cactus scrub and so to desert. These are all essentially climatic formations and the only way in which we could envisage savanna as a climatic formation would be to insert it in the series between deciduous seasonal forest and thorn woodland, which is theoretically inadmissible because thorn woodland is a less reduced type than the savanna and because savanna life forms show xeromorphy of a different order from that of seasonal forests and thorn woodland. The writer concluded (1944) that "the tropical grassland climate simply does not exist" and wishes to reaffirm that conclusion here.

Due to the difference in microclimate, the savanna is of much drier appearance than forest at any time of the year and this probably led early observers, who had few or no meteorological records for study and who saw the broad regions of savanna rather than the localities where savanna and forest mingle, to the conclusion that the savanna must represent a drier regional climate. Later this became a fixed idea so that a modern observer like Bouillenne (1930) was constrained to advance a quite fantastic theory in support of it. Meteorological observations made in Trinidad (Brooks 1936) in the forest and in the open showed very great differences in temperature ranges and humidity. Sun and wind get to the soil and a savanna dries out after rains more quickly than forest. It must be appreciated, however, that this drier microclimate is not a cause but an effect, due to preexisting vegetative cover. If all

factors other than the microclimate favored the growth of forest, succession would take place and the microclimate become ameliorated. This is what happens when forest is cut down and the soil bared.

Savanna vegetation is of xeromorphic order partly in response to the microclimate—excessive insolation and drying winds—but principally because, as will be shown later, the habitat is physiologically dry. The life forms of savanna trees and herbs, it may be noted, differ radically from those typical of seasonally dry forests and woodlands—deciduousness, microphylly, spinescence, stem and leaf succulence and water storage tissue. The savanna grasses were shown by Bews (1929) to be highly developed and specialized and they represent a life form closely adapted to the savanna habitat but rarely seen in seasonal forests and woodlands.

In summary:

(a) Savannas occur under a variety of climatic conditions, from an annual rainfall of 20 in. with over 7 drought months up to over 100 in. with negligible drought periods.

(b) Under rainfalls between 20 and 40 in. short bunch-grass savanna is found, tall bunch-grass between 40 and 80 in., while sedge savannas become very common with more than 80 in.

(c) All the climates, given suitable soil conditions, can and do support forest or woody vegetation of some kind.

(d) The driest climates in tropical America support thorn woodland, cactus scrub or desert, never savanna.

(e) Savanna life forms indicate a response to edaphic conditions rather than to climate.

(f) There is no such thing as a tropical grassland climate, and it therefore follows that the savanna is an edaphic or biotic formation.

TOPOGRAPHY

There is a relation between the savanna and its landscape, so compelling that Lanjouw (1936) began his definition of the plant formation: "Savannas are plains. . . ." This is generally, if not always strictly literally, correct. Savannas occur at any altitude from sea level up to 4,000 ft. above it, their highest point being on the Gran Sabana. They are absent from the Andine mountain chains. Geologically, they overlie a great variety of rock types, and the nature of the parent rock is not significant. Certain rocks, notably serpentine, seem predisposed to an association with savanna but no absolute correlations can be made. A study of geomorphology, however, gives us interesting evidence. In the majority of cases, savannas are seen to occupy very gently undulating country. Very frequently the land is level or almost so: rarely, it is sharply undulating and in a very few cases mountainous. Often, where there are savannas in broken country, they are patchy and cling to flat surfaces at the top or foot of the steeper slopes. Savannas are predominantly associated with plains, terraces or plateaus.

All this is capable of a geomorphological interpretation. As far as the writer is aware, the study of land forms has not hitherto been invoked to any important extent in the elucidation of plant ecological problems in tropical America. It is worthy that it should be, and in this particular case it is indispensable. Land form has an important influence on the plant habitat, not only as the present and actual configuration of the ground surface which determines external soil drainage, rate of water run-off, predisposition to flooding and so on. Past history and the evolution of the present landscape are also important because of the soil-forming processes which may have taken place. Soil development owes much to topography; in fact in its more advanced stages it may be said to owe everything to this. In studying plant formations, therefore, which are associated with special soil conditions the land form must be taken into consideration as a soil-forming factor. (Ref. Milne's work in East Africa: 1937, 1941.)

Land form is the product of a series of constructive and destructive cycles, of a continual building up and tearing down. A constructive phase will occur when land is built up from the sea floor by the emission of ashes and lava from volcanoes, or alternatively, by the deposition of sedimentary strata beneath the sea, followed by their uplift and exposure. Such newly formed, young landscapes are flat and featureless, undissected and without regular drainage channels. Their soils also are young and undeveloped. As soon as a new land surface is exposed to the atmosphere, however, a destructive phase sets in, and after a shorter or longer period the surface becomes deeply dissected by drainage channels, broken up into ridges and valleys whose depth will depend upon the degree of uplift to which the young surface was subjected, and to the amount of the rainfall. Generally, the higher the rainfall the steeper the erosion slopes. On such mature, diversified topography soils develope to some, but not to their greatest, extent. Finally, the land is reduced to lower and lower outline and in extreme old age is once again flat and featureless, undissected and without regular drainage channels. The soils in this case are very highly developed because there has been a long period without either erosion or aggradation at the surface, and the fullest extent of weathering and translocation of materials takes place, usually under the influence of ground water due to the flatness of the site.

It will be found that in almost all cases savannas cover senile topography, either old alluvial plains or ancient highlands on which an old-age topography has developed. North of the Orinoco and the West Indies and Central America the savannas occur for the most part upon plains of Quaternary alluvia whose formation has been long since completed but which are not yet beeing subjected to destructive erosion. In a sense, these are still young landforms, not having passed through a destructive cycle since their formation. This has been due solely to lack of uplift and they have in effect passed directly from

youth to old age. As will be seen, highly mature soils have developed upon them. This type of landform is seen also in lowland Guiana and in Bolivia and Paraguay, but on the Guiana and Brazilian highlands the savannas occupy peneplaned stretches of the uplands, plateaus where a temporary base level of erosion has been reached and where, again, highly mature soils have developed. In a few cases, as on Barbuda Island, savannas are found on very young sites, and here the lack of soil and landscape development is found to lead to similar effects on soil moisture and drainage as the well-matured development of senile landscapes.

In summary:

(a) Savannas occur upon ill-drained country of little relief.

(b) Most generally this is the product of a senile landscape where there is no longer much aggradation or erosion, where surface drainage is slow due to lack of slope and of organized drainage channels, and where highly mature soils have had time to develop.

(c) Less commonly, the necessary conditions occur on country which is geomorphologically young.

(d) Savannas are never associated with young alluvia nor with uplands in a juvenile or mature stage which have steep erosion slopes and rapid drainage.

SOILS

Detailed soil investigations in savannas have been few and only cover areas in Cuba, British Honduras, Trinidad, British Guiana and the Gran Sabana in Venezuela. For other parts one cannot, unfortunately, place too much reliance upon the casual observations of passing explorers and botanists since they are not trained observers where the soil is concerned and may stress insignificant or unimportant characters, overlooking the essential. Thus, the observation that "the soil is sandy" tells us little, for it only means that the surface soil is sandy. It may be sandy to considerable depth or change to clay below, and radically different soil types may be present. For an analysis of soil information it will be desirable to rely only on the specialized work.

It will be as well to inquire, to start with, what are the important characteristics of tropical soils as affecting the natural vegetation that grows upon them. In a study of the distribution of soil and forest types in south-central Trinidad in 1936, Hardy, Duthie & Rodrigues arrived at the conclusion that soil-moisture is the essential factor determining changes in vegetation and this is a function of climate, topography and the physical character of the soil. Within a single climatic area, for example, certain combinations of soil and topography may make for a moist habitat favoring an evergreen forest and other combinations for a dry habitat favoring a semi-evergreen or deciduous forest. The moisture-supplying ability of the soil is determined by its physical structure, that is, by its permeability, aeration, conductivity and retentivity of moisture. Soils that are too freely drained, too porous and permeable, will be physically dry. Soils that are too poorly drained internally, too compact, impermeable and badly aerated, will be physiologically dry. The chemical constitution of the soil was found by Hardy, Duthie & Rodrigues to have little or no influence upon natural vegetation types. A similar view was expressed by Charter (1941) for British Honduras and by Beard (1946) for Trinidad as a whole. A classification of the soil types of Trinidad based on their natural drainage was drawn up by Hardy (1940) and applied by Beard (1946) to the ecology of local vegetation types.

The present writer finds it very hard to subscribe to the view of what may be termed the "Dutch school" (Pulle, Ijzerman, and Lanjouw) that the savannas, being associated with excessively leached soil, have originated as a result of the leaching process. This view implies that soils deficient in mineral nutrients are unable to support a luxuriant forest growth, a proposition which does not appear to the writer to be in accord with the facts. A very fine rain forest at least 120 ft. tall is found in British Guiana on expanses of deep, white, quartz sand whose inherent fertility is extremely low and must be just as low as that of savanna soils. In view of his earlier work it is curious that Hardy (1945) went over to the Dutch school and supported their view that soils of inherently low fertility are only able to support "a poor sort of forest." As an example of this he cited the white sand rain-forests of British Guiana, but it is difficult to see on what ground these can be described as a "poor sort of forest." Physiognomically they are essentially the same as rain forests on any other kind of soil, differing only in composition and in minor structural features. Chemical analysis has certainly demonstrated the extremely low nutrient status of savanna soils and of their natural herbage as a stock-feed but a low nutrient status is typical of all mature soils of high rainfall areas in the tropics. Reference may be made to the analyses of forest and savanna soils at the Erin Savanna in Trinidad and in the Rupununi district of British Guiana, cited earlier in this work, which failed to disclose any effective chemical differences between the two. In Hardy's paper of 1936 with Duthie and Rodrigues he detected no differences in composition between forest growing on fertile marl and unfertile sand.

The writer cannot admit that under the climatic conditions affecting forest and savanna in tropical America the chemical constitution of the soil can have any influence upon their distribution, and maintains that the physical constitution of the soil, particularly as regards internal drainage, is the essential factor to be considered.

Bennett & Allison (1928) found in Cuba that savanna soils have special features of physical structure which distinguish them from forest soils, in fact, "the term savanna . . . carries both a vegetative and a soil meaning." As a general rule, the savanna soils in Cuba exhibit a permeable horizon overlying an

impermeable subsoil due to the presence of rock at a shallow depth or of a clay pan or iron pan. The majority of savanna soils elsewhere, of which we have accurate descriptions, are of this character and others are similar in their drainage relationships. On the basis of the data we have, it is possible to describe a number of typical savanna soil types to which all the known soils approximate more or less closely.

The first of these may be called the "sand-over-pan" soil, divisible into "sand-over-clay," "sand-over-rock" and "sand-over-ironstone" types. The profile takes the form of a black to grey, leached, light sand generally 9 to 12 in. in thickness overlying either a highly compact and impermeable red and white mottled clay, or a dense stratum of unweathered rock, or an accumulation of concretionary ironstone in the form of small pebbles and lumps, called *perdigón* in Cuba, or of massive conglomerate called *mocarrero*. Subsoil drainage is obstructed by a clay-pan or an iron-pan or by solid rock. The upper horizon is of variable thickness, sometimes two ft. thick or more, sometimes disappearing altogether so that the clay or ironstone appears at the surface. On low ground the sand is generally very dark in color, but on rolling ground where it may be subject to blowing by the wind it is generally lighter, grey or even pale yellow. The dark color appears to be due to the incorporation of fine charcoal, the residue of fires, rather than to humus, of which there is little. If dark at the surface it may often show bleached white at the base of the horizon. This upper horizon varies in texture from sand to silt or loam but is always typically light. Ironstone concretions may be present. Transition to the underlying impermeable horizon is generally fairly abrupt. This may consist of unweathered rock of various types—chalk, sandstone, serpentine, gabbro—or of that red clay which is the typical end-product of rock weathering in the humid tropics.

The clay may be stoneless or nearly so, or may contain gravel or rotten rock or bands or lumps of ironstone. It is predominantly red in color but on closer inspection will be found to contain brilliant mottlings of red, yellow and white. It becomes a whitish clay with red mottlings at greater depth. The mottling indicates seasonal waterlogging. Where iron-pan is present it may be composed of lumps and pebbles of ironstone or of a solid band up to several inches thick. It generally caps a red-mottled whitish clay similar to the subsoil of the clay-pan type. The essential feature of these "sand-over-pan" soils is the superposition of a light-textured horizon upon a heavy, impermeable one. Such soils underlie almost all the savannas of Cuba, British Honduras and Trinidad.

On the eastern Venezuelan llanos and much of the Guiana plateau these same soils occupy the low ground, while knolls and rises feature the second general soil type which we may describe and name the "clay with ironstone" soil. This soil has evidently been derived by erosion from the "sand-over-pan" type, for it is based upon the same red clay which appears in the rising ground, either naked or capped with a superficial layer of ironstone. The sand horizon has been removed, leaving bare clay, or a layer of gravel upon the surface, or even, locally, a bed of ironstone conglomerate. Bare clay is dark and almost black at the surface, hard and impermeable. At a depth of a few inches iron concretions may be present, and it merges quickly into the usual red and white mottled clay. The stone layer, where present, varies greatly in thickness from the occasional pebble to beds a foot thick. It is composed mainly of ironstone nodules, but quartz and granite fragments are also seen locally. Little herbage grows where the stones are thick. Warming mentions this soil in the south Brazilian savannas.

A third and much less common type of savanna soil we may name the "clay flat" soil. This was typical of the part of the Gran Sabana visited by the writer and also occurs at the Aripo savannas in Trinidad and in some parts of Cuba. Here the soil consists of a pale-grey clay or silty clay at the surface, merging below into a pink or red and white mottled clay which may contain ironstone concretions. The surface clay is very hard and compact and impermeable, and seems not to be of the type which shrinks markedly or cracks when dry. In some cases such a clay soil is found overlying rock at shallow depth, as in the case of the Barbuda savannas and of the Holguin and Camagüey soils in Cuba. Soils of this type commonly occupy very flat ground or even depressions.

Finally, and rarely, there are "deep sand" soils, typified by the Norfolk fine sand of Cuba and the soils of some lowland Guiana savannas. These are deep, loose, grey or brown sands merging downwards into grey, yellow or red-brown sand or sandy loam. There is little difference in texture between the horizons and there seem to be no obstacles to downward percolation. These soils occur on areas of low relief, however, presumably with a high water table at certain seasons when stagnant ground water will be present.

"Hogwallow structure" is characteristic of the soils which are sandy at the surface when they occur on level ground. Undulating areas do not exhibit this phenomenon, nor flats where the surface sand is loose and windblown. Heavy topsoils exhibit it to only a limited extent. It takes the form of a marked unevenness of the surface which is broken up into steep-sided hummocks and depressions, generally about 12 to 18 in. across and 9 to 12 in. deep, sometimes more. Some of the depressions are more or less connected and resemble meandering drainage channels, others are not. They become pools of standing water in rainy weather. Hog-wallow structure is not a feature solely of savannas but occurs also under forests where these are growing on senile flat topography. The writer has never seen a satisfactory explanation advanced to account for the formation of these odd hummocks and depressions, and is unable to suggest one.

The lack of pronounced relief which is characteristic of savanna lands accentuates any tendency to imperfect drainage within the soil. For a soil to remain well-drained and aerated, surplus water must be fairly rapidly disposed of by either downward percolation or surface run-off or both. Otherwise, there will be an accumulation of water, particularly under heavy rainfall conditions, leading to waterlogging or even inundation. Impervious soils can occur on broken ground without becoming waterlogged, and porous soils on flats if percolation is sufficiently rapid and the water-table sufficiently deep. Where, however, there is a combination of heavy rains, flat country without a regular system of drainage channels and impermeable subsoils, then the tendency to waterlog will be strongly accentuated. Even porous, sandy soils on flats may be equally prone to this if the water table is high and the rain heavy and prolonged, and one suspects that this occurs in the case of the "deep sand" savanna soils. In accounts of savannas everywhere in the Americas we read over and over again that they are under water for long periods during the rainy season. The flood water is seldom deep, or seldom remains deep for long. Generally, water stands in shallow pools, or fills the hogwallow channels or soaks the surface soil to a boggy consistency. Where deep water collects for long the typical savanna disappears in favor of swamp vegetation.

A water-table in the correct sense can only exist in the "deep sand" type of savanna soils. Strongly impermeable subsoils, whether clay, rock or ironstone, do not permit the existence of a watertable, properly speaking. To those familiar with conditions in the temperate zone, some of the properties of tropical clays may appear astonishing and it may be hard to realize that many of them, particularly those which are most highly weathered, consist of over 90% of clay particles with a very minute proportion of pore spaces and can be almost as impermeable as a solid sheet of rock. Even when the surface has been waterlogged for a long time such soils may be relatively dry at a depth of several feet. The only type of water-table which one can associate with such a soil is a "perched" one, and that will only exist during the rainy season, disappearing altogether during drought.

Forest soils are distinguished from savanna soils in important respects of their natural drainage. Upland (as distinct from swamp) forests occur always on soils which are relatively well-drained either internally or externally or both. Such forests typically cover broken country with well-drained slopes and juvenile soils. Soils of the "sand-over-pan" type can sometimes be found under forests, but the ground will be sufficiently sloping and well supplied with drainage channels to preserve a well-aerated top soil.

The "clay with ironstone" type is never found under forests, in the writer's experience. Pure clays and deep sands are of course common as forest soils and the former may be based upon the same red and white mottled clay as savanna soils, but will show important differences at the surface. Forest clays are dark brown at the surface and of good crumb structure, both features showing the incorporation of humus. Tree roots penetrate deeply. In dry weather the clay shrinks and cracks deeply, permitting aeration of the deeper layers. Some forest soils are very shallow, with sand or clay over rock. Sometimes there is virtually no soil at all, forest of magnificent aspect continuing to grow upon a mass of stones. Such country will be steeply sloping or otherwise well drained. Specialized swamp forests occur on soils, generally young alluvia, which are ill-drained due to low relief but where the ground water does not become stagnant and deficient in oxygen. Such, for example, are the *igapo* and *varzea* forests of the Amazon, flooded for all or part of the year. True water tables exist in these soils, oscillating with the seasons.

In summary:

(a) Natural drainage is the most important characteristic of tropical soils which affects the distribution of vegetation types such as forest and savanna.

(b) The chemical composition of the soil has little or no influence upon such distribution, and it is not true that infertile soils can only support an impoverished vegetation.

(c) Savanna soils differ from forest soils in possessing features which, in interaction with topography and rainfall, affect their natural drainage unfavorably.

(d) These savanna soils in the majority of cases exhibit the superposition of a permeable horizon upon an impermeable. They may consist also of heavy, impermeable clays or porous sands, in areas of low relief.

(e) The savanna soils have, typically, no true water table. A perched water table exists intermittently during wet weather.

(f) The surface in savannas is waterlogged or flooded for periods during the rainy seasons and alternately dried out. Ground water may become stagnant.

(g) The soils of upland forests are well-drained by virtue either of their porosity or of sloping ground.

(h) Specialized swamp forests occur on ground subject to perpetual or periodic inundation but the water does not become stagnant.

BIOTIC FACTORS

One of the most arresting differences between the grasslands of the American and African tropics is the total lack on the former of a natural population of grazing animals, such as is so abundant in Africa. The great herds of ruminants and the carnivores which prey upon them, roaming the open grassy country by the hundreds and thousands, are an African phenomenon. All the mammals and marsupials of lowland tropical America are forest animals. South American forests are reasonably well populated with animals, for example the tapir and

peccary, deer, armadillo and rodents such as the capybara and agouti, together with some carnivores, notably the jaguar and puma. Where savannas exist side by side with large areas of forest these animals often move onto the savannas and may be hunted there, but their home is the forest and large areas of savanna like the Venezuelan llanos and the Gran Sabana harbor insignificant numbers of them. Savannas are plentifully populated with insects, particularly termites, and with small creatures such as snakes, lizards and mice, but the only large animal whose home is the savanna is the ant-eater which preys upon the termites. Even the deer of South America is a forest creature.

Since the arrival of Europeans, cattle have been introduced and have become more or less wild in some places, while cattle ranching is now carried on in most of the savanna areas. This activity has, however, to face certain obstacles which limit the number of stock on the range to a very low figure. In British Guiana, for example, it is not possible to run successfully more than one head to every 35 acres of savanna. Reasons are given by Follett-Smith (1930), Martyn (1931) and Follett-Smith & Frampton (1935). The principal factors are that the predominant grasses are coarse and unpalatable, and are deficient in essential minerals, notably phosphorus. Whether or not this is the cause for the absence of large numbers of wild grazing animals from the savannas, it is impossible to say. It is a curious fact that fossil evidence shows the existence of such a population during Pleistocene time. Today, the only true savanna fauna consists of the termites and the ant eaters predatory upon them. It will be seen, therefore, that since the arrival of the European, grazing has become a factor in the savanna habitat to a limited extent, but under primitive conditions it was entirely absent.

Large mounds erected by termites are a constant feature of the savannas upon the ancient highlands of Guiana and South Brazil. They are absent from the savannas of quaternary alluvial plains. Similar mounds present on the lowland alluvial savannas of British Guiana were attributed by Myers (1936) to termites (Syntermes) but by Martyn (1931) to parasol ants (*Atta*). The latter is probably correct. On the Guiana plateau, probably two species of termite are concerned, the one erecting low, flat mounds up to 3 ft. high generally and 6 ft. in diameter, the other building tall, irregular piles up to 12 ft. in height. The latter occurs on rising ground with the "clay with ironstone" type of soil, the former on flatter areas with the same soil or the "clay flat" type. Both kinds avoid inundated areas. Martyn (1931) found a special vegetation similar to that of the narrow savanna-forest transition to grow on the Atta mounds of lowland British Guiana, but on the Guiana plateau there does not appear to be a special vegetation on the termite mounds. The low type seen by the writer were covered with the usual savanna grass and the tall type are said to be bare of vegetation. Terrestrial termite mounds are only found in savannas, never in forests.

It may be conjectured that the termites find the ferruginous clay of the savanna soil a suitable material in which to nest, since it will solidify to some extent on being excavated and exposed to the air and is also so impermeable that the underground chambers and fungus gardens are kept from becoming flooded.

The influence of man and fire upon savannas is a very disputable matter. Many students have come to the conclusion that all or most savannas have been derived from forest as a result of constant fires set by man. Since the arrival of man in the Americas must be set between 10,000 and 25,000 years ago, this must all have come about comparatively recently and the process would presumably be still going on. It is true that all the major savannas are swept, nowadays, by regular fires, if not annually, at least every 2 or 3 years, the fires being set to improve the pasturage for cattle, to drive out game, or simply to keep the country open. Setting fire to grass has become traditional with Amerindians and they have evidently practiced it from time immemorial. Fire will take readily at any time in the dry season, and during short dry spells in the wet season, since sun and wind very rapidly dry out the savanna if there is an accumulation of old, dead grass. The occurrence of a regular climatic dry season is not a necessity for burning. Bunch grass savanna vegetation, as we know it, is strongly fire-resistant, the trees having a thick, corky, fire-proof bark and the herbs and shrubs underground perennating organs, which are not designed for water-storage, but, apparently, solely for regeneration after fire. Many such plants are highly specialized. An examination of the vegetation supports the view that it is a fire-climax.

On the other hand, fire does not occur readily in the forests, under the prevailing rainfall regimes in South America. It will be found that the boundaries of savanna and forest are almost invariably sharp, indicating that fire runs up to the forest border and stops there. Only in years of exceptional drought will it transgress. Where there are moist evergreen forests in tropical America the dry seasons are rarely long or severe enough to permit a destructive fire to take place. When this does happen, it will be years before a second burn is possible as in the meantime the bush recovers rapidly. In deciduous forests there is so little herbaceous ground vegetation that only a light ground fire can run through, which is seldom severe enough to harm the larger trees. It is not easy to destroy forest by this means, under South American conditions, unless soil conditions are adverse to forest growth and impede its vigorous regeneration.

Doubt may therefore well be expressed as to whether the sparse aboriginal population could have been capable of so much intensive destruction in the time available as to convert into savanna by means of fire without also grazing the vast areas we now see under grass. The Orinoco llanos alone cover about 100,000 sq. mi. It seems fairly well established that

fire can arise from natural causes in savannas, but it would scarcely do so in forest. Thus the retrogression to savanna could only have started after man's arrival. Secondly, if burning were the sole cause for savannas we should expect to find huge intermediate belts of burned and degraded bush in process of retrogression. In fact, such areas are limited. Fire could never be responsible for the alternation, seen in many places, of small patches of savanna and undamaged forest. In such localities fires are very rare and when they occur seldom penetrate the forests. The Aripo savannas in Trinidad have never been known to burn, nor are they grazed, yet never change. The shrubby elements in such sedge savannas are not even fire resistant. Bews (1939) stated that the tropical bunch-grass savanna does not depend upon fire for its maintenance and the writer is of like opinion.

The problem resolves itself into this: which came first, the fire or the savanna? Does the savanna burn frequently because it is a grassland. or is it a grassland because it frequently burns? The vegetation is, certainly, adapted to withstand fire, but it is equally well adapted to the adverse edaphic conditions of certain types of badly drained site. It has been shown that there are edaphic conditions typical of savanna and distinct from those of forest, and such habitats must have existed far back into history, long before man appeared upon the scene. If the savanna as we now see it is a fire-climax, we might expect to find some unmolested corner where some other original vegetation of the ill-drained site has persisted, but the writer knows of no such case. In the writer's opinion, the association of savanna vegetation and certain types of site is so strongly marked as to warrant the belief that grassland is and has always been the natural vegetation of such sites. Large stretches of grass, once developed, would become liable to catch fire occasionally from natural causes and burning would become more frequent after man's arrival. The vegetation would thus become secondarily adapted to withstand fire, but fire would not be a necessity to its maintenance, this depending upon drainage conditions. Intensive burning by man coupled with the fellings of the shifting cultivator, in later years and especially since the arrival of Europeans, has undoubtedly forced the forests back in some places and extended the savannas. It can, however, be argued that successful extension of the savanna has only taken place on habitats already marginal for tree growth.

It has already been observed that on the Gran Sabana, in parts of the Venezuelan mountains and of Trinidad, grassland has replaced forest in recent years as a result of fire, the grassland so produced differing scarcely if at all from the ordinary bunch grass savanna. When these areas are considered in detail in the next section it will be shown that the soil conditions were a predisposing factor. In drier regions an African-looking type of tree savanna has replaced forest, which is here more susceptible to burn and has less recuperative power. The type of vegetation produced, however, has nothing in common with "natural" or primitive neo-tropical bunch grass savannas; it is a strongly atypical, foreign element and depends directly upon man and his cattle and goats for its maintenance.

The absence under primitive conditions of anything which resembles the high-grass savanna of Africa is presumably due both to the generally higher rainfall in the Americas and the much less intensive and less prolonged assault by man and animals upon the plant cover. Forests which do not burn readily and regenerate vigorously when damaged, a small aboriginal population and absence of grazing animals, are factors insuring that grasslands which depend upon fire for their maintenance are of relatively rare occurrence.

In summary:

(a) The savannas of America were devoid of grazing animals until the arrival of Europeans and even now cattle are few.

(b) Large terrestrial termitaria are a feature of the savannas on ancient highlands.

(c) Savannas may be swept by regular fires and the vegetation is so adapted as to be fire-resistant.

(d) The savannas do not however depend on fire for their maintenance and are an edaphic climax.

ECOLOGICAL RELATIONSHIPS

In the preceding sections a theory of a typical savanna habitat was elaborated, which may be briefly expressed as follows:

Savanna is the natural vegetation of the highly mature soils of senile land-forms (or, in some cases, of very young soils on juvenile sites) which are subject to unfavorable drainage conditions and have intermittent perched watertables, with alternating periods of waterlogging (with stagnant water) and desiccation. Frequent fires occur but are not a necessity for the maintenance of the savanna, which is an edaphic climax.

In the writer's view, it is essentially the alternation of waterlogging and desiccation which is too severe for forest growth. A great many species of trees are well adapted to withstand long drought periods, as the deciduous forests and thorn woodlands testify, but such trees must have favorable moisture conditions, which implies good site drainage, during the rains when their vegetative period occurs. Similarly, the swamp forests show us that there are tree species adapted to growth in more or less permanently waterlogged soil, or on periodically inundated sites. In the latter case, however, one of two conditions must be fulfilled: either the inundation must be of very short duration so that unspecialized forest trees are enabled to grow there, or else the effective portion of the soil profile supporting plant growth must never become absolutely dry, thus enabling swamp species to persist. A true watertable must be present. It seems that there are two classes of trees adapted to severe habitats at low elevations in the tropics: those adapted to withstand desiccation

of the soil, which cannot tolerate flooding, and those adapted to flooding, which cannot tolerate disiccation. The impermeable subsoils of savanna lands create perched watertables which come and go with the rains. The layers of the soil which are above this obstruction and to which tree roots are confined are waterlogged in wet weather and dried out completely at other times, so that a constant alternation of the two extremes is set up. The only trees which seem able to tolerate such conditions are the few oddly gnarled species found in savannas, whereas the xeromorphic herbs, particularly the bunch grasses, seem to be well adapted to the site. Grasses seem to have the faculty of growing vigorously whenever conditions are favorable, and going into a resting phase when they are not. Grasses, also, appear readily able to grow successfully under waterlogged conditions and to root in badly aerated soil. The entire savanna flora is xeromorphic in life form because of the almost perpetual state of drought, alternately physical and physiological, which it is adapted to endure. It is a different order of xeromorphy from that exhibited by "dry" forests or woodlands and is again a different type of specialization from that of the swamp formations.

We still have insufficient data to be able to suggest a completely satisfactory explanation for the variations in type within the savanna itself. The three main divisions, sedge, tall and short bunch-grass savanna, have been shown to be related to the relative lengths of the dry and waterlogged seasons, which is mainly an expression of climate. Within the tall bunch-grass savanna the four subdivisions—open, orchard, palm, and pine—seem to be related to soil conditions. Pine savanna is limited to the Antilles and Central America and is probably only a floristic variant of orchard savanna to whose flora pines are added in the region where they occur. Entirely treeless open savanna seems limited to soils which are clayey at the surface ("clay flat" type) or consist of clay overlain by stones ("clay with ironstone"). Such sites are commonly either flat bottomlands or the summits of knolls and ridges. Orchard savanna appears to be typical of savanna soils that are sandy at the surface ("sand over pan" soils) the sand horizon providing a suitable rooting medium for the savanna trees. Palm savanna is again associated with clay topsoils, but the manner in which they differ from those of open savanna has not been worked out by the writer. In general, it would appear that palm savanna soils are wetter than those of open savanna, probably to the extent of having a deep source of underground water below the clay pan. It is probably fire that prevents these palms from forming up to dense groves.

The application of these general theories to particular cases will now be discussed in detail.

TRINIDAD

The savannas of Trinidad occur only as scattered tiny patches which used to be or still are surrounded by evergreen forest. They cannot, therefore, be of climatic origin. Marshall (1934) regarded the Aripo savannas as a type of swamp vegetation and attributed the others to the influence of fire. The St. Joseph savanna, certainly, has at least been profoundly modified by fire and grass now covers certain areas in the plains formerly under forest, but fire does not seem to be the correct explanation for the lowland savannas in general. Their occurrence as small patches in forest with sharp boundaries is against it, also the presence of endemic plants and the development in the centre of the Piarco savanna of the special type of sedge savanna with *Byrsonima verbascifolia*. Besides, the savannas are so obviously associated with peculiar conditions of soil and site involving adverse drainage. All the savannas of the plains occur on terraces, that is, on remnants of an ancient landsurface. Beard (1946) traced the geological history of Trinidad during Tertiary times, leading to the evolution of the present topography. During most of the Tertiary period the Northern Range existed as land but there were shallow-sea conditions to the south of it, with perhaps occasional islands formed by what are now the hill ranges of the centre and south. During Pleistocene times a great alluvial plain was built up, coextensive with and similar to the present llanos in Venezuela north of the Orinoco. As this plain matured and a senile topography developed with special soil types, savannas would gradually have occupied its surface and the forests have shrunk to the stream vegas and the hills. In more recent times earth-movement led to the formation of the island of Trinidad which became slightly raised while the Gulf of Paria was depressed and inundated. A new erosion cycle was initiated on the island, the rivers were rejuvenated and dissected the great plain little by little. As its surface was removed, an undulating topography was substituted for flat and drainage conditions again became good, so that forests could reoccupy the land. Only a few small isolated remnants of the ancient landsurface still exist and have remained covered with savanna. This explains the patchy occurrence of the Trinidad savannas. They are the vanishing survivors of a bygone age, the dwindling relics of a past geological period.

The diagrams in Figure 30 show in profile the association of soil, vegetation and landform at the Erin, Piarco and Aripo savannas. The Erin savannas are small plateaus along the summit of a watershed, flat expanses with the typical savanna soil types, sand over clay or clay with ironstone. At the margins of the plateaus or slightly below them, an abrupt transition to forest occurs, the forest occupying highly dissected topography with soils of favorable drainage. The savannas evidently occupy remnants of an earlier extensive plateau which is being eroded away, and the forests will be very gradually closing in. That the grass still persists in some cases on the upper part of the erosion-slope bordering the plateau is probably due to fire.

The Piarco, Mausica and O'Meara savannas are also on similar plateau sites with similar soils but

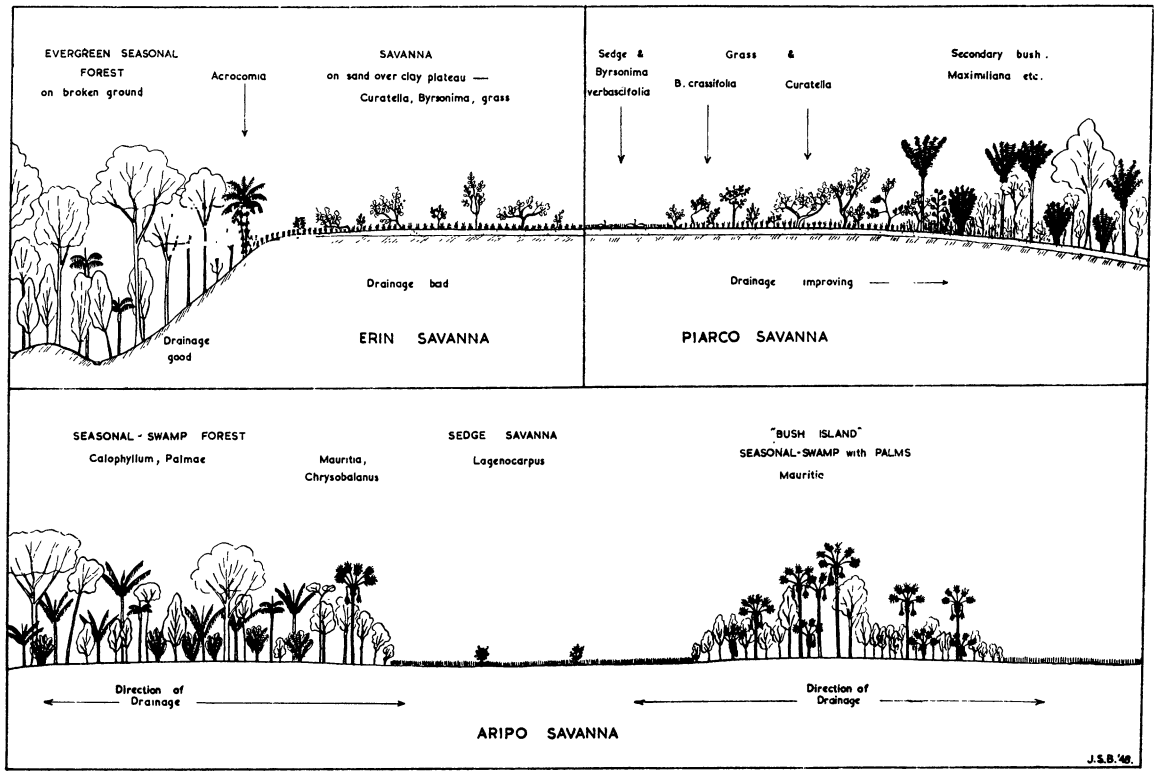


FIG. 30. Sketches of vegetation and site profiles for the various savannas in Trinidad.

there is not the sharp drop to dissected country at the edges, the plateaus sloping down gradually to the rivers. In the circumstances there are no substantial physical differences here between savanna and forest soils, and no abrupt transition to forest is to be seen. It may have existed formerly but has been obscured by burning of the forest. There is, however, a difference in drainage between savanna and forest sites. Subsoil drainage being impeded, virtually all drainage must travel across the surface. The savannas are situated in the centre of the terrace-plateaus where drainage is at its worst and where most waterlogging occurs. This is particularly clear at the heart of the Piarco savanna where there is even a special and reduced plant community, with sedge and *Byrsonima verbascifolia,* clearly associated with drainage conditions. Forest growth occupies the outer parts of the terraces where the land is sloping slightly towards the rivers. The rainfall here is substantially the same as at the Erin savanna and is not very high, about 60 inches annually, so that waterlogging even of soils with claypan only becomes severe where the ground is very flat. There is nowhere any sharp change in site conditions here such as occurs round the Erin savanna where the ground falls suddenly away from the savanna plateau and since man began intensive burning there is no doubt that these savannas have expanded onto marginal sites.

Other grasslands described by the writer as "cocorite savannas" occur on the northern plain and are known to have replaced forest in recent years as a result of repeated fires. They occur only on flat terrace sites where drainage is somewhat impeded and where habitat conditions are already close to those of the savanna.

It is interesting to observe that in other parts of Trinidad where burning is equally intense, at the western end of the Northern Range for example, the land has not gone to grass in the same way. It is true that "savannas" of the bracken fern *Pteridium aquilinum* (L.) Kuhn have appeared and that after a burn, grass may cover the ground for a short while. Grassland has only become established on these mountains where erosion has removed the soil, e.g. the St. Joseph savanna. There are no instances on hilly lands in the lowlands where burning has by itself established grassland. Fire-grasslands have only appeared in this island on flat, ill-drained lands where conditions were already not far removed from those of existing savannas.

It has been noted in the description of the Piarco, O'Meara and Mausica savannas that these can be seen to have expanded of recent years as a result of fire. The expansion areas show a combination of the true savanna flora with that of the cocorite grasslands described above. It may well be that in the course of time if burning is continued the true sa-

vanna flora may colonize all of the cocorite grasslands. Already, fringing the Piarco group of savannas, fire has brought in grassland where forest was before. Given protection from fire, forest would return unless some permanent alteration in the soil had taken place in the meantime. In these lowlands there is no evidence of this. In all cases in Trinidad where savanna has extended it has done so onto lands where soil and drainage conditions were already marginal for forest and where the incidence of a new factor, fire, hostile to forest, was able to tip the balance in favor of the grassland.

The Aripo savannas are of the sedge type and differ from the other savannas of Trinidad owing to the high rainfall which makes waterlogging more prolonged and shortens the drought period. This may be a convenient point at which to inquire how the habitat of sedge savanna differs from that of the bunch-grass. Sedge savanna is clearly, in a general way, more hygrophilous than the bunch-grass, but not in the sense in which Bews considers the high-grass savanna as more hygrophilous. It might be preferable to describe the sedge savanna as more hydromorphic, for it embodies many of the characters of swamp. As the dominant plants are still more or less xeromorphic, however, and as the site conditions are still closely similar to those of bunch-grass savanna, it must rank as a savanna and not as a swamp community. It is a type of savanna which shows affinity to swamp formations. Sedge savanna is found where inundation is prolonged and desiccation of short duration. It occurs in areas of very high rainfall or in depressions where water collects in the rainy season.

The soil beneath the Aripo savannas is exactly the same as that under the adjoining forest, nothing but surface drainage conditions differentiating the two communities. It has been shown that some of the patches of savanna occupy very slight depressions in the flat alluvial terrace, possibly sites of the occluded bends of some meandering river of the late Pleistocene. Other patches are dead-level stretches on the terrace. These sites, since the subsoil is impermeable, fill with water and can support only an herbaceous vegetation. In the forest areas surface drainage meandering through the hogwallow channels is sufficiently good to permit of tree growth, as is the case in the vicinity of the Piarco and related savannas. At Aripo both savanna and forests are different from those further west owing to the higher rainfall, and a series of highly specialized forest types are present intermediate between the savanna and the normal evergreen seasonal forest. It would appear that the high rainfall here permits the establishment of specialized forests on sites which under drier conditions would carry only savanna, and the savanna is restricted to relatively small patches which alternate in a kind of mosaic with the woody communities. This phenomenon is reported elsewhere, from French Guiana for example, where sedge savanna occurs in forest. It forms an interesting parallel to the tendency of short bunch-grass savanna to occur in a mosaic arrangement with bush and forest under very dry conditions, at the other end of the scale, so to speak.

The St. Joseph savanna consists of two separate communities, the Curatella-Byrsonima type and the Myrcia-Roupala type. The writer suggests that the latter is the primitive form of this mountain savanna and that intensive burning due to man's interference within the last two centuries has converted former areas of Myrcia-Roupala savanna and of forest (where intense erosion has followed) into a more fire-resistant type of grassland. The herbaceous growth has not greatly changed but *Myrcia stenocarpa* and other shrubs which have a low resistance to fire have given way to the fire-resistant Byrsonima and Curatella. The Myrcia-Roupala areas today occupy sites which are not so readily exposed to fire and appear to be but seldom burnt whereas the Byrsonima-Curatella areas are thoroughly burnt over almost every year. The latter are conspicuous from the plains whereas the former are not and blend into the surrounding high woods.

In both cases the occurrence of savanna may be attributed to the virtual absence of soil. Such little soil as there is on the surface (and in crannies to afford a meagre root-room) lies in contact with an impermeable, impenetrable "pan" of bedrock and the same effect of alternating waterlogging and desiccation remarked in the lowland claypan soils is present here also. Since man burned off the vegetation and exposed the soil, erosion has certainly bared the bedrock and expanded the savanna. Occurrence of a primitive savanna in prehistoric times must be explained from the exceptionally hard and quartzitic nature of the rock in this locality. Formation of soil on a mountain side can only occur if weathering proceeds at least as fast as erosion removes the surface. Where the rock is very resistant to weathering, soil formation may be indefinitely postponed.

THE ORINOCO LLANOS

The eastern part of the llanos, particularly the various extensive mesas which are not flooded in wet weather, is an area such as inspired the ideas of Schimper and others about the climatic origins of savanna. The rainfall is low for American savannas, averaging only 40-45 in. a year, and the vegetation gives the impression of even greater dryness. Schimper considered the climate "hostile to woodland" because of a long rainless dry season of five months and a continuously rainy wet season, but now that we have meteorological records we know that this characterization of the climate is not the correct one. Similar climate elsewhere can and does support deciduous forest.

Conditions on these llanos are only a magnification to very much greater scale of those in the Trinidad savannas, for we have here, still intact, the great plains of which they formerly were a part. The savannas both of Trinidad and the Orinoco llanos occupy flat alluvial terraces of Pleistocene age which are little dissected and feature soils with impeded

subsoil drainage. The nature of the soil on the llanos appears to be essentially the same as the predominant type on the lowland savannas of Trinidad, in that it is a sand over clay, and the land form is essentially similar. Diagram A in Figure 31 shows a profile arrangement for the Mesa de Guanipa. Most of the area consists of high terraces which un-

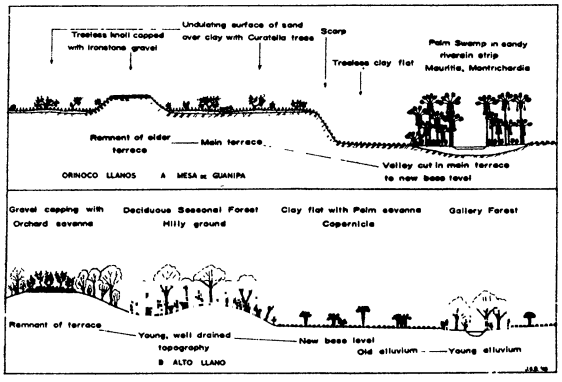


FIG. 31. Sketches to show the association of vegetation and site on parts of the Orinoco llanos.

dulate very gently and are broken by occasional knolls capped with ironstone. The rivers meander in flat valleys cut down below the high terraces, the valley floors being covered with savanna except immediately along the stream, where Mauritia groves occur.

The ironstone knolls are a feature not present in Trinidad and seem to be relics of a surface on which ironpan soils were well developed. Such soils have not been reported in situ in the area today and evidently represent a phase in the early history of the landscape. These knolls are probably very persistent as the stone capping must be a protection against erosion. On the high terraces generally, the upper sandy horizon of the soil is rather looser than in Trinidad and according to Pittier is subject to windblowing. This might account for the absence of hogwallow structure and for the lighter color which implies lack of organic remains. The low rainfall probably accounts for the preponderance and fine growth of Curatella, which flourishes under drier conditions than Byrsonima. Pittier observed that the savanna trees prefer high ground, except for the stone capped knolls, and avoid the river flats, accounting for this on the ground that a high water table in such depressions would be an obstacle to the proper development of a tree's root system. The present writer's observations of the root system of these species show that it is markedly superficial, not deep such as Pittier supposed, but it is sensitive to lack of aeration. The more prolonged waterlogging of the low flood plains would certainly discourage growth of these trees.

The Mauritia groves bordering the rivers are a swamp type of vegetation and are evidently associated with perennially swampy conditions. In the rainy season the *morichales* are inundated and in the dry season the soil is still wet. Water relations differ from those of the savanna where there is an intermittently high perched water table in the rainy season, and no water table at all during the dry period.

The distribution of vegetation on the *alto llano* is shown in B of Figure 31. This area to the north of the llanos proper is somewhat dissected and the high terraces represented on the Mesa de Guanipa have here been cut up into undulating country with the old surface persisting here and there on a ridge top capped with ironstone gravel. This again parallels conditions in Trinidad, and as in Trinidad the undulating country is forest covered, here by a deciduous forest owing to the lower rainfall, with patches of savanna on the residual surfaces. Savanna trees occur on the ironstone gravels here although they do not on the llanos proper. The greater dissection of this area has greatly extended the river flood plains, relatively narrow on the Mesa, here broad expanses covered with palm savanna. A new peneplain is being formed at a lower level than the old and its clayey topsoil encourages the palm type of savanna.

THE VENEZUELAN CORDILLERA

In these mountains the bunch-grass savanna has taken possession of slopes which have been cleared, cultivated, eroded, abandoned and subjected to frequent fires. The change has occurred within the period of European settlement, that is, the last 400 years. It would appear that the savanna has been enabled to establish itself in this way not solely owing to the fires but owing also to the severe erosion of the mountain slopes. Present vegetation has but little between it and the bedrock. The situation is comparable to the St. Joseph savanna in Trinidad and is another example of the establishment of savanna through burning on a marginal site. Fire alone would not degrade the forest to grass, and secondary bush of some kind would always spring up. A secondary factor in the form of adverse soil conditions of the type favoring savanna must always be present to enable bunch-grass savanna to supersede a forest community.

THE LESSER ANTILLES

Similar remarks apply to the Grand Savanna of Dominica where the soil suffers from impeded drainage and the natural conditions are in many ways not unlike those typical of savanna lands. Most of the "savanna" however is rather clearly just burnt-out bush. None of the typical elements of American savannas, save only *Sporobolus indicus,* are present here and in the writer's opinion the area was formerly all forested.

Grasslands in Antigua are pastures with thorn bush, created by man, and merit no discussion. The small savannas of Barbuda, on the other hand, appear to be natural. The whole island is formed of flat limestone terraces bearing very little soil and

as a result carries only a low evergreen bush which is to be regarded as rock-pavement vegetation. The savannas occupy slight depressions where water collects after rain. The soil is a reddish clay overlying limestone sheet rock and is thus of the "clay flat" type. The savanna alternates rapidly with the bushland according to very slight variations in level and soil-depth, forming a mosaic of grass and bush types reminiscent of the Chaco parkland and certain very dry areas in Cuba. Such a mosaic arrangement seems to be typical of areas of low rainfall where the waterlogging factor is at a minimum. The writer found the grass here to be about 18 in. high at the end of the rainy season and it may perhaps be regarded as a short bunch-grass savanna.

HISPANIOLA

The open savanna on the central plain of Haiti is a typical example of the association of savanna with an old peneplain, where the soil has developed impedance to drainage. The hardpan in this case is of a calcareous nature and lies somewhat deeper than is usually the case in these savanna soils, but the effect of the seasonal perched water table is there none the less. The silty-clay topsoil is no doubt responsible for the treelessness of this savanna. Both topsoil and pan reflect the influence of the parent limestone on the soil morphology. Other rock-types on the same site would have resulted in a "sand over pan" soil, with the pan formed of ironstone, instead of this, which should be referred to as the "clay flat" type.

The ecological relationships of the orchard savanna are more difficult to assess, since data are insufficient. Dr. Curtis believed the orchard savanna, in the area studied by him, to be due to fire and this may well be the case. If so, it will be another example of the ability of savanna to advance and colonize marginal sites when the forest cover is destroyed by frequent fires. On the other hand, the orchard savanna may equally well be natural. It occupies sites marginal to those of open savanna though not to such an extent as to permit the growth of forest. The latter is seen only along the bottomlands where the soil will be a deep, young and well drained alluvium. Dr. Curtis' "knob-hill country" is in a more advanced geomorphological phase and the rising ground in this case should have been rejuvenated to the extent of being able to support forest of some kind. The soil of the intervening bottomlands has now matured, presumably, and developed a profile like that of the savanna plateau, so that the vegetation has retired to savanna. On the knob-hills we should rather expect to find closed forest or bush but instead we find open pine savanna, where the grass is said to be ecologically dominant. None of the trees listed, besides Pinus, occur normally in savannas and this is probably a fire climax. A community where pine is present is not necessarily pine savanna, the tree being a component of several very different formations. As has been shown, the principal role of Pinus in Haiti is to form pine forests in the high mountains which are thought to have followed destruction of mixed montane forests by fire. These pine forests are grassed beneath, but the pine and not the grass is dominant. Pine savanna is only found here and there in the lowlands where the pine has added itself to pre-existing savanna communities.

The Themeda savanna of the central plain is not in every way typical of tropical savannas, perhaps due to its situation at an altitude of 1700 ft. and near the borders of the tropical zone, which may render the climate of a subtropical character. The genus *Themeda* is not recorded elsewhere for neotropical savannas and is said to be a sod-forming grass rather than a bunch grass. The soil has the typical drainage relationships of savanna soils but differs in structural characters from the usual pattern. There appears to be some resemblance here to the South African "High Veld," a treeless grassland of high plains with *Themeda triandra* dominant and growing upon what van der Merwe (1941) described as gley-like podsolic soils.

The "dry savanna" of Haiti should probably be classed as short bunch grass. The dominant grass, Uniola, reaches a height of 36 in. when in fruit but the general height of the leaves is much less and the growth is very open with wide spaces between the tussocks. Soil throughout is virtually absent, the surface being formed of a mass of small limestone fragments. While this savanna could have been of fire origin in pre-Columbian times, there are factors which make this doubtful—its great uniformity, the localization of *Tetramicra ekmani* which is not found elsewhere, and the evident symbiotic relations of the latter with Uniola, implying a long-term association. We have here one of the rock-pavement types of savanna.

CUBA

Cuba was the country where the association of savannas with a special type of soil and site was first suggested and worked out in detail (Bennett & Allison 1928) and it is therefore unnecessary further to labor this point, save for a few supplementary notes. The savannas occur predominantly on flat or gently undulating land, and where they do not, impervious rock will be found close to the surface. Predominantly, the soils have intermittent perched water tables due to impermeable subsoils. Only two of the savanna soil types depart from this pattern, the Nipe clay and the Norfolk fine sand. The former is a very peculiar soil derived from serpentine, highly weathered and regarded as a true laterite by Marbut (1932). It is very probable that impeded drainage is actually present. The Norfolk fine sand is a very deep soil without any impervious horizon: it occurs on areas of low relief with a high water table in the rainy season, when the savannas are probably flooded. If the dry season is so severe that the loose sand dries out very deeply and the water table vanishes, this would create the conditions necessary for savanna.

In some of the dry parts of Cuba, there is an

alternation of savanna with thorn and cactus bush forming a mosaic, rather as on Barbuda. It would appear that under low rainfall conditions patches of xerophilous bush are enabled to occupy small areas of very slightly higher relief which in a wetter district would be part of the savanna. The savanna habitat has to feature an alternation of waterlogging and desiccation, and where rainfall is low the latter will predominate, severe waterlogging only occurring on low spots. Raised patches would tend to be free from waterlogging and would resemble ordinary well-drained soils of the vicinity, carrying the climatic vegetation. A parallel phenomenon at the opposite extreme has already been suggested for very high rainfall areas, when discussing the Aripo savannas of Trinidad. Where rainfall is high and the dry season mild, waterlogging of the impeded soils will predominate for most of the year and a specialized, swamp-like forest may occupy sites which under a drier climate would carry savanna.

Marie-Victorin & Léon commented on the physiognomic resemblance between artificial grasslands with trees on which cattle ranching is practiced in Cuba and "African savannas of the natural *Acacia-Andropogon* type"—that is, the High-Grass Savanna of Bews (1929) or the High-Grass Low-Tree Savanna of Shantz (1923). These Cuban savannas should evidently be regarded as the equivalent of the African high-grass savanna and are an indication of the artificial nature of the latter.

CENTRAL AMERICA

Charter's work on the ecological relationships of forest and savanna in British Honduras (1941) is monumental and the writer is glad to acknowledge that it provided the incentive for this wider study. His theory of the aging of the soil and site on alluvial plains is a hypothesis which we may see fit to accept or not; to the writer it is convincing. The facts about the savannas and their habitats may be summarized as follows. A generalized profile diagram appears in Figure 16.

Several types of savanna are present: sedge with palms, bunch-grass with pine, or "orchard." There can be no possibility of a climatic explanation for them, situated as they are in a moist region surrounded by forests. Their occurrence is patchy and fire is clearly only a subsidiary factor. All the types of savanna are associated with impeded drainage soils. Variations in drainage differentiate them from one another and from forest types. Very much as at the Aripo savannas in Trinidad, the savannas are associated with several forest types, all differentiated by drainage factors and disposed in a mosaic arrangement about areas of pessimum drainage.

Conditions in British Honduras are repeated in Guatemala and Yucatan. Pine savannas occur in the interior of the Honduras Republic on hilly ground. We know little about them and have to presume they are equivalent to the "mountain pine ridge" of British Honduras. Of savanna lands elsewhere in Central America we know nothing significant other than that they occur on coastal plains and are of the usual bunch-grass formation with *Curatella americana*.

VENEZUELAN GUIANA

In this gently undulating region based upon ancient rocks, with soils of the sand over clay or clay with ironstone types, the savannas are clearly associated with adverse soil drainage conditions due to the gentle slopes and impermeable subsoils. Across the area from Ciudad Bolívar in the north-west to Tumeremo in the south-east, the rainfall gradually increases from 40 to 60 in. a year, but the savanna does not change. On the other hand, the forests which occupy the mountains and depressions show a marked response to the change in climate, grading from evergreen or semi-evergreen forest in the south-east down to deciduous forest and thorn bush. These forest types are climatic formations, growing on favorable soils. Mountains and hills are forest covered wherever there is adequate depth of soil, owing to the sloping, well drained land and young, immature soil profile, and even carry poor forest where there is naked rock if it has deep crevices to root in. Shallow impervious rock favors savanna, as is sometimes seen on the mountain slopes. Forests of depressions and river flats are essentially "gallery forests" and are found on deep, pervious young alluvia.

Diagrams A and B of Figure 32 show the arrangement in profile of site and vegetation, A being typical of the north-western part near Ciudad Bolívar, and B of the area near Tumeremo. Conditions at A are very like those on the Venezuelan llanos, the same gently undulating ground with light, pale, sandy topsoil and heavy red clay subsoil, and occasional knolls capped with ironstone. A new feature here is the granitic outcrop clad with thin deciduous forest, and the streams are bordered with this same formation instead of by dense *morichales*. The Mauritia palm is only present as odd specimens along the stream banks. Deciduous seasonal forest is replaced along the depressions and drainage channels by thorny thickets in some places, for which the explanation probably is that soil conditions are intermediate between those of the savanna and the riverain forest;

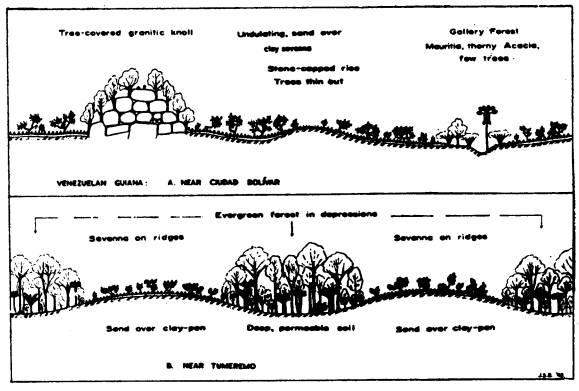


FIG. 32. Sketches to show the association of vegetation and site in the Venezuelan Guiana.

alluvial soil present but probably to no great thickness.

Diagram B shows the alternation of low, rounded hillocks covered with savanna and shallow depressions filled with evergreen forest which is characteristic of the region around Tumeremo. In plan, the savannas are seen to be more or less round patches set very regularly in the forest like a huge checkerboard. The perpetual alternation of hillock and depression is like a hogwallow surface enormously magnified. There are sand over clay soils on the hillocks under the savanna and deep brown loamy alluvia under the forest. This appears to be a senescent landscape. Mature soils with impeded drainage have developed already on the tops of the rises, the first place where they would do so. Alluvium is still being gradually deposited in the depressions which in time will be levelled up with the hillocks into a more or less even plain, by which time savanna will have developed on the flats also. The hillocks eventually will come to form, in all probability, ironstone-capped knolls in an extensive savanna. We have here savanna country in the making.

Llewellyn Williams' travels further to the westward in the Venezuelan Guiana show us sometimes undulating savannas like those seen by the writer and sometimes low-lying flood-plains of the lower river courses where conditions are like those of the llanos north of the Orinoco. There is always a general division of the landscape into savanna plains and forested mountains, an arrangement broken only by the *rebalse* swamp forests on the flood plain of the lower Caura, which correspond to the *varzeas* of the Amazon. All Williams' savannas are of the sedge or bunch-grass types and occupy typical soils—sand over marl, sand over compacted quartz gravel, and so on.

BRITISH GUIANA

The so-called "wet savannahs" of British Guiana are incorrectly termed, according to our definition, and should be regarded as herbaceous swamps. There are true bunch-grass savannas in the east near the Berbice River. Follett-Smith's description (1930) of two soil types in these savannas show both of them to be deep sands, apparently without the impervious subsoil which we are accustomed to expect. The most widespread of the two soils, the "brown sand" type, changes from a fine brown sandy topsoil at a depth of two feet to a slightly heavier red-brown loam, and it seems unlikely, from the description, that drainage impedance can be very severe. Nothing is said by Follett-Smith, however, about such things as drainage and water-tables and so we are left guessing. Conditions may be similar to those inferred for the Norfolk fine sand of Cuba, that is to say, a high water table in the rainy season which vanishes altogether in the dry. This is unlikely owing to the high rainfall of this area, but due to the latter and the flat ground, there may be effective drainage impedance in spite of the small amount of textural variation in the profile, percolation being unable to dispose of rainwater quickly enough. One way or another, the behavior of the shallow "pans" which are lakes in the wet season, parched in the dry, indicates an intermittent water table.

A very interesting point is the growth of bush upon the ant mounds in the savanna, which is "capable of withstanding the periodic savannah fires and resembles that found in the narrow transition zone between forest and open savannah country" (Follett-Smith). This seems to prove, for one thing, that it is the soil and not fires which is responsible for the maintenance of savanna, and secondly that adverse drainage is present in this savanna, the raised ground of the antheaps providing a site clear of waterlogging on which bush can develop. That the antheap vegetation resembles that of the forest margin is also significant since this is a zone where drainage begins to be improved.

Raised reefs of coarse white sand are covered not with savanna but with a low evergreen scrub called *muri bush*. It would be very interesting to have more data on the ecological relationships of this community. Evidently the raised land-surface confers immunity from waterlogging, but one may suspect, from the fact that these sand reefs have at their margins springs or waterholes, that there is an impermeable layer somewhere fairly deep in the soil profile. In some way, at least, soil drainage conditions must be superior to those of savanna but inferior to those of forest.

DUTCH GUIANA (SURINAM)

Climatic and soil conditions in the Surinam savannas are similar to those in British Guiana. From the rainfall figures one would expect normally to find rain forests in this region and they are in fact present surrounding the relatively small savanna patches. There can be no question here of climatic savanna. Both sedge and bunch-grass types are present, called by Lanjouw (1936) "wet" and "dry" savannas respectively, which is eloquent of their relative habitat. The flora of the sedge savannas is very closely similar to that of the Aripo savanna in Trinidad, so that similar soil conditions may be inferred. Both Lanjouw and Ijzerman (1931) appeared to regard the soil as readily permeable, but the writer doubts very much if this is really so. From their descriptions, the savannas are under water or waterlogged in the rainy season. Perhaps the flat sites and heavy rainfall are between them too much for the soil porosity. It does not seem to have struck the Dutch investigators as significant that the savannas occur on flat plateaus forming the watersheds between the rivers, which are either portions of an ancient peneplain like those of Trinidad or the most mature parts of an alluvial plain in formation, as in British Honduras.

Drainage is bad because of the flat and undissected landscape and we might expect that the special savanna soils would have developed. If the soil is very sandy to start with, however, no very marked differentiation into textual horizons would occur.

We have here the usual association of savannas with a senile landscape and defective drainage, and the writer does not believe in the theory of the Dutch that leaching of the soil is responsible for savanna formation.

Here and there in the Surinam forests there are found patches of low evergreen forest and scrub named locally *moeri-moeri bush* and described by Lanjouw as savanna-forest. These are considered by the Dutch to be areas of forest in process of regression to savanna as the soil becomes impoverished. The *moeri-moeri* appears to occur on two types of site: rock pavements and deep sandy soils. In the former instance, with sheets of granite rock beneath and very little soil, we are clearly not dealing with a degraded forest soil. Rather the opposite is true, for more soil can be expected to form on the rock in time, permitting a finer forest to develop. In the second site, details of the soil are less clear, but presumably the *moeri-moeri* is to be found on reefs of quartz sand like the *muri* of British Guiana. The two names taken from the aboriginal are evidently the same. Under these circumstances, the *muri* (or *moeri*) sand is certainly highly leached, but its drainage relationships differ from those of the savanna and drainage provides a more acceptable basis for an understanding of these communities.

FRENCH GUIANA

The savannas of French Guiana are only a continuation of those of Surinam and the same remarks apply to them. Both sedge and bunch-grass savanna are present, the latter corresponding to the general type for the Guianas and the former very closely to the Aripo savannas of Trinidad.

No soil data of any kind were given by Benoist (1924) who considered that the appearance of these savannas in an area where we should normally expect to find rain forests must be due "to the intervention of man." It was unfortunate that the man-made pasture lands he cited had a totally different flora from the true savannas, although they had been created by clearing, burning and grazing without the deliberate introduction of extraneous pasture grasses. Besides, how could this theory account for the frequent rapid alternations of small patches of forest and savanna across sharp boundaries? The similarity of the sedge savannas to those of Trinidad is so close that similar ecological relationships must be inferred and drainage taken to be the vital factor.

If Benoist's rainfall data are correct, it is interesting to note that the savannas here occur under the highest annual rainfall of any in the Americas—140 in.

THE GUIANA HIGHLANDS

At Santa Elena on the Gran Sabana, the annual rainfall is approximately 70 in., with a weak dry season of 3 months. The rainfall regime is the same as that of Trinidad and the same evergreen seasonal forests are found on the Gran Sabana on favorable soils. In the British Guiana interior the rainfall is less and the dry season more severe, but the savannas throughout are composed of the same dominant plants. Open savanna predominates on the Gran Sabana and orchard on the Rupununi, but the grasses are the same. Trees drop out on the Gran Sabana probably because of the clay topsoil. Unlike the Venezuelan llanos, there are seldom here any vast stretches of unbroken savanna.

A diversified landscape is the rule, savanna covering the flat ground and forest the hills and mountains with exceptions in both cases, so that some forests are found on flats and some savanna patches on mountains. This diversity of landscape is strongly against a climatic origin of the savanna, for unless the forests are on any particularly high mountain they must enjoy the same climate as the savannas. Jones (1930) sought a geological explanation, with the savanna lands on sandstones and the forests on igneous rocks, a theory that is based on soil fertility. It is not, however, in accord with the facts, as there is no such correlation of geology and vegetation here. Predominantly, there is a correlation of site and vegetation, which strikes one from all the accounts as well as on the spot. There are exceptions, but they can be satisfactorily explained. In general, as everywhere else in South America, savanna covers flat lands with impervious subsoils and forest occupies sloping or other well-drained land.

Follett-Smith & Frampton (1935) showed that in the Rupununi savannas of British Guiana there is little essential difference in chemical composition between savanna and forest soils. The savanna soils correspond, however, to the usual types in physical structure. On the Rupununi, sand over clay is predominant with many ironstone-capped knolls, as on the *mesas* of the Orinoco llanos. Both these types appear on the Gran Sabana, together with sand over ironpan, a silty soil over rock and "clay flat" soil, the last being the predominant type found by the writer between Santa Elena and Roraima. The flat bottoms of the valleys in this region were found to consist of a very compact clay soil bearing savanna, with termite mounds scattered on the drier places and Mauritia palms on the wetter. Gallery forest borders the watercourses. The high ground takes the form of a series of very flat plateaus bounded by scarps, the whole landscape being arranged as shown in Figure 33. The uplands are again mostly composed of clay flats, the soil here being even more compact and lighter colored at the surface than in the river flats, strewn with occasional stones and with few termite mounds. Ironstone-capped rounded knolls are frequent. Forest is sometimes found on the scarp faces and on other localized areas of broken or sloping ground on the Sabana where we might expect to find it owing to the improved drainage, but not invariably. The majority of such sites are covered with grass and forest is usually found nestling into deep valleys and folds of the ground. In many places, particularly on the boundary of the forest area to the north-east, the writer found clear

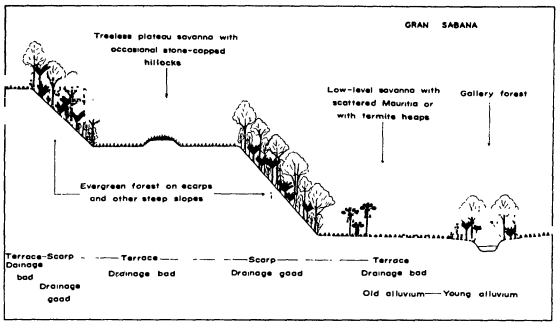


FIG. 33. Sketch to show the association of savanna and site as believed formerly to have existed on the Gran Sabana. The forests of the scarps have now mostly been destroyed by fire.

signs of regression of the forest due to fire. A fire theory, as proposed by Christoffel can, however, only be accepted with reservations.

The writer believes that the flat areas on the Gran Sabana are original grassland, associated with intermittent perched water tables, and that all the scarps, broken country and streambanks were covered with forest before man's arrival. The original pattern, in fact, would have been as shown in Figure 33. Since man began regular firing of the savanna the forests have been very gradually eaten away and now mainly nestle behind the protection of a topographical obstacle. It is surprising how often a grass fire will stop at a sharp ridge or declivity. One is compelled to believe in the natural occurrence of savanna on the flats, independently of fire, owing to the very typical senile landscape with its typical soils and also owing to the termite mounds which are unknown in forest.

The forests between Santa Elena and Roraima were observed by the writer, both gallery forests and those on the hills, to belong to a somewhat specialized type indicative of adverse soil conditions, so that their replacement by savanna after fire is only another example of the extension of savanna onto marginal sites under the influence of burning.

To the south of Santa Elena on rocks of the basement complex a very patchy alternation of forest and savanna is seen on both hill and flat. The forest is no longer a specialized type, and there is no clear evidence of recession due to fire. Forest and savanna soils were clearly quite different, the forest soil a deep and permeable clay, stoneless, dark brown at the surface, the savanna soil a bright red clay thickly strewn with ironstone. The writer was unable to study these soils and the question must be left open for the present.

Near Santa Elena to the North there are some uplands of deep white sand overlying rock which carry a low and very open scrub, evidently "muri bush." South of the Rupununi, the type of muri on granite rock pavement appears, in a very patchy landscape of forest, muri and savanna. Soil depth and drainage are evidently the controlling factors.

THE AMAZON BASIN

The majority of savannas on *terra firme* in the Amazon basin are located in the drier region of the lower course, but there are some in the high rainfall region of the Atlantic littoral and in the delta. Even if they were confined to the drier region, it would not be readily possible to ascribe their cause to the climate since they are but small patches set in predominantly forested country. The forest of the area does reflect the climatic regime. It is not rain forest but seasonal, relatively short and with many deciduous species. Bouillenne's theory of the climatic origins of the savannas is a marvel of plausible ingenuity, but scarcely credible. Had he also visited the Atlantic littoral, one wonders how he would have explained the savannas in that entirely flat and featureless region. It will be recollected that Bouillenne discounted the influence of the soil on the grounds that (a) the bulk of the Amazonian forests are on sand, and (b) the same sandy and stony soil carries both forest and savanna. The first observation is true, but to say that since savannas as well as forest are on sand, it is the same soil in both cases, is a *non-sequitur*. It matters not the surface soil is sandy; what is important is what happens underneath. Sandy soils of forests are deep and well drained with adequate root-room. Sandy soils of savannas are shallow and obstructed by clay or iron pan.

In support of this contention we cite Marbut (1932): "throughout the Amazon valley the soil consists of (1) topsoil, (2) iron oxide layer, porous and slag-like, (3) mottled layer, (4) grey layer, (5) unconsolidated clay and sand. The mottled zone, with or without the induration of its upper part to an iron oxide crust, is found invariably beneath the surfaces of broad plains with flat or nearly flat surfaces or where the relief shows that dissection is very recent. It is not found on mountain slopes or in thoroughly dissected regions where the dissection is old."

This gives us the key to the whole problem. On mountain slopes and in highly dissected country, soils are immature, usually deep and always well drained. These are essentially forest soils. On flatter ground, unless the soil-forming material consists of nothing but pure quartz sand as in the caa-tingas, ground-water soils develop, first with an impeded, mottled horizon, later with an iron pan also. Drainage conditions worsen to the point where forest must give way to savanna. Later the flat, ill-drained savanna site may be dissected by a new erosion cycle and if not totally destroyed may come to form a new, more or less flat or gently sloping surface with the topsoil gone and remnants of the broken iron oxide horizon left strewn as fragments on top of the mottled clay horizon. Thus the savannas we see are of two types, the one "sandy," on flat expanses with sand-over-clay or sand-over-ironstone soil, the other "stony" on relatively elevated ground with clay-with-ironstone soil. The forest lands are on recent alluvia where soil formation has as yet scarcely begun, on

mountain or hill slopes, or on young plains where soil drainage has not yet developed too unfavorably. Gallery forests, be it noted, although they occur in savannas, must be classed as young sites, situated on the steep slope of a ravine or a strip of recent alluvium. It is quite wrong to assume, as Bouillenne did, that the same soil underlies both the gallery forest and the savanna. It cannot possibly do so.

The occurrence of savannas on the lower Amazon and in the delta, not on the upper Amazon, is fortuitous and is not to be related to climatic factors. The savannas in the delta lie in a very wet region. The fortuitous circumstance is just that the lower Amazon and delta happen to contain the necessary sites of sufficient topographic maturity. In the upper Amazon basin the terra firme is presumably a very highly dissected peneplain of very small relief like the south of Trinidad with only immature soils on the short steep slopes.

The caa-tingas and campinas are associated with deep, white quartz sand deposits derived, not necessarily *in situ,* from granite. Consisting of little but inert quartz, this material is unable to form a ground-water laterite and remains freely permeable. It constitutes a medium excessively freely drained and of very high acidity, so that moisture is consistently of low availability. The vegetation is thus of the "dry evergreen" or sclerophyll type. There is presumably a better moisture supply in the caa-tinga than in the campina, due largely to greater depth of the sand.

SUMMARY

1. The savanna is a plant-formation of tropical America comprising a virtually continuous, ecologically dominant stratum of more or less xeromorphic herbs, of which grasses and sedges are the principal components, with scattered shrubs, trees or palms sometimes present.

2. Three sub-formations can be recognized: Tall bunch-grass savanna, short bunch-grass savanna and sedge savanna. The tall bunch-grass savanna can be further subdivided into four phases—open, orchard, palm and pine savannas.

3. Tall bunch-grass savanna is composed of perennial, xeromorphic grasses up to 3 ft. in height, disposed in clumps and associated with many sedges and other herbs. Open savanna is treeless; orchard savanna includes scattered gnarled trees and shrubs; palm savanna, palms; and pine savanna, pine trees.

4. Short bunch-grass savanna is composed of xeromorphic grasses up to only 1 ft. in height, disposed in clumps. Thorny trees may be present.

5. Sedge savanna is composed of relatively xeromorphic sedges up to 18 in. in height, not tufted, and associated with many small moisture loving ground plants such as bladder-worts, ferns and mosses. Small evergreen trees and shrubs may be present.

6. Savannas occur under a great variety of climatic conditions from annual rainfall of 20 in. with seven or more drought months up to over 100 in. with negligible drought periods. Short bunch-grass savanna tends to predominate where there are less than 35 in. annually and sedge savanna with over 80 in.

7. All types of climate in lowland tropical America, given favorable site conditions, are adequate to support woody growth of some kind. A tropical grassland climate does not exist.

8. Savannas occur upon ill-drained country of little relief, most generally a senile landscape such as an old alluvial plain or a reduced upland.

9. All types of savanna may be swept by regular fires and the vegetation is so adapted as to be fire resistant. The herbaceous vegetation does not, however, depend upon fire for its maintenance and the savanna is an edaphic climax, i.e., it is determined by soil and site conditions.

10. Natural drainage is the most important characteristic of tropical soils affecting distribution of vegetation and chemical status is of little account.

11. The natural drainage of savanna soils is affected unfavorably by the lack of relief and the internal physical structure. Usually savanna soils exhibit the superposition of a permeable horizon upon an impermeable, or are extremely compact and impermeable throughout the profile, so that no true water table exists.

12. Savanna may be characterized as the vegetation of the highly mature soils of senile land-forms (or, in some cases, of very juvenile sites) which are subject to unfavorable drainage conditions in the form of intermittent perched water tables, with alternating severe periods of waterlogging and desiccation.

13. The soils of upland forests are well-drained, by virtue either of porosity or relief or both.

14. Specialized swamp forests occur on ground subject to flooding, but the site differs from savanna in that a normal water table must be present.

15. Temperate grasslands, for which the term "steppe" should be used, also represent a habitat almost perpetually adverse to growth, but the causes are climatic.

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