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Sarmiento, G. 1983. The savannas of tropical America. En: F. Bourliere, F. (Ed): Ecosystems of the World XIII. Tropical Savannas, Elsevier, Amsterdam, pp. 245-288.

# THE SAVANNAS OF TROPICAL AMERICA

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## THE MAIN ECOLOGICAL AND PHYSIOGNOMIC TYPES OF SAVANNAS IN TROPICAL AMERICA

Savanna formations constitute a substantial part of the vegetation cover of tropical America. The total area occupied by Neotropical savannas, considering natural communities alone, exceeds 2 million km$^2$. In some regions, such as the Brazilian *cerrado* or the Colombian and Venezuelan *llanos*, only narrow fringes of gallery forests bordering the streams interrupt the monotonous continuity of the savanna landscape. In other areas, such as Amazonia or Central America, the reverse situation occurs: savannas appear as more or less isolated patches of open vegetation amid a continuous cover of rain forests.

Neotropical savannas show a remarkable floristic similarity throughout their geographic range. In fact, though they may vary widely in composition from one community to another, a floristic list, if it belongs to a Neotropical savanna, may be easily recognized wherever it may come from. A common floristic stock unifies the savannas of tropical America from their northernmost areas in Cuba and southern Mexico to their austral limits in Paraguay and southeastern Brazil (Figs. 10.1, 10.25 and 10.26).

Present-day ecological and phytogeographic knowledge of American savannas is still uneven. In more thoroughly studied areas, such as the Venezuelan llanos, they begin to be understood at least in their more essential aspects, while in other regions they remain scarcely known beyond preliminary accounts of their environmental and structural features. The treatment here will therefore appear as geographically unbalanced, since it will rely heavily on the best known ecosystems.

Savanna types will be considered from a double viewpoint, one ecological, the other purely physiognomic or structural. From an ecological point of view, tropical savannas will be divided into four major categories according to the seasonality of the ecosystem (Sarmiento and Monasterio, 1975; Sarmiento, 1978). Seasonality represents one of the most essential features of a savanna ecosystem (see Ch. 1), whether the cyclic changes in the environmental impulses and constraints during the year are considered, or the biological rhythms of plant species and of the whole vegetation that accompany those external fluctuations.

The first ecological type is the semi-seasonal savanna. It occurs under weak seasonal alter-


Fig. 10.1. Major tropical savanna regions in South America.

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nations exerted by a constantly or mostly wet climate. In this case one or two short dry seasons may represent the main rhythmic environmental strain. Under these circumstances, fires become natural events of much less frequent occurrence. Semi-seasonal savannas therefore change very little during the year. For instance, the semi-dormant phenophase of perennial grasses and sedges (see Ch. 5) is much less pronounced than in the other types. As a general rule, semi-seasonal savannas occur as scattered patches in regions with a continuous rain-forest cover.

A second type, and the most widespread in tropical America, is the seasonal savanna. Here, an extended rainless season increases the probabilities of dry season fires, and both factors, drought and burning, provide a neat rhythmicity in the functioning of the ecosystem. A good proportion of the savannas in the two major savanna regions of South America, the cerrado and the llanos, belongs to this seasonal type.

A third class of savanna is characterized by the alternation of two contrasting stresses during each annual cycle, one induced by drought and fire, the other by soil saturation. These hyperseasonal savannas experience a period of water shortage during the rainless season, and an extended period of water excess during all or part of the rainy season, when soils become waterlogged and asphyxiating. Changes in vegetation follow these environmental constraints. Hyperseasonal savannas may occur on poorly drained bottomlands in any climatic region, but they are particularly common on large, depressed regions with slow and ill-defined drainage, as the Gran Pantanal of Mato Grosso, the Bolivian llanos, and some areas of the Orinoco llanos.

In a fourth type of savanna ecosystem, the water excess period may last most of the year, while a period of acute water shortage either does not exist or is very brief. This is really a kind of seasonal swamp, and it is considered as a savanna only when grasses and sedges are the dominant plants. This type is called *estero*, using a common Spanish term widely applied to these ecosystems in several Latin American countries.

Another useful criterion in differentiating savanna types is based on the structural features of the vegetation. Various characteristics may be taken into account, referring either to the woody or to the herb component. A physiognomic system is followed here, which is simple enough to be useful, while permitting the differentiation of significant landscape types. Table 10.1 summarizes this physiognomic system of savanna classification. Four types are distinguished according to the importance attained by woody species. In the

TABLE 10.1

Main physiognomic types of tropical American savannas, with the corresponding Brazilian and Spanish-American names

| Savanna type | Total cover of woody layers (%) | Average tree density (trees $ha^{-1}$) | Brazilian name | Spanish-American name |
|---|---|---|---|---|
| *Savannas* | | | | |
| Savanna grassland | – | – | *campo limpo* | *sabana pastizal* |
| Tree and/or shrub savanna | <2 | 500 | *campo sujo* | *sabana abierta* |
| Wooded savanna | 2–15 | 1000 | *campo cerrado* | *sabana cerrada* |
| Savanna woodland | 15–40 | 3000 | *cerrado* | *sabana boscosa* |
| *Woodlands or open forests* | | | | |
| Sclerophyllous woodland | >40 | 4000 | *cerradão* | – |
| *Savannas dotted with groves* | | | | |
| Savanna parkland | <40 | | – | *sabana parqueada* |

**savanna grassland**, trees and shrubs, if they exist at all, have a dwarf form which does not exceed the height of the herb layer. A **tree** and/or **shrub savanna** has woody species scattered within a mostly continuous herb layer. Total cover of trees and shrubs is less than 2%. A **wooded savanna** has an open tree cover ranging between 2% and 15%, which corresponds to a total density of about 1000 trees ha.$^{-1}$ A **savanna woodland** has a tree cover above 15%, reaching cover values of 20% to 30% on the average, corresponding to a maximum density of about 3000 to 4000 trees ha$^{-1}$.

These four structural categories agree with the savanna formations differentiated by popular usage, corresponding for instance to the four types known as *campo limpo*, *campo sujo*, *campo cerrado*, and *cerrado*, recognized in the Brazilian literature which will be discussed later. A last type of woodland, where tree crowns touch each other but the herb layer persists, is known in Brazil as *cerradão*, and though it constitutes a useful reference to which the more open formations can be compared, I shall follow the usage of most authors who consider it more as a type of forest than of savanna.

As a last structural form, typical of some areas where savannas and tropical forests form intricate vegetation mosaics, a savanna of any one of the previous four types, may be dotted with small clumps or groves of trees and shrubs. This physiognomic unit will be called a **savanna parkland**. In fact it generally intergrades with true vegetation mosaics of savannas and rain forests.

With this two-dimensional system of savanna typification, the occurrence, habitat and composition of the main savanna types in tropical America will be discussed. The major savanna landscapes will be considered first, and subsequently the remaining regions where savannas only occur as minor components of the regional vegetation.

## THE BRAZILIAN CERRADOS

The portuguese name of *cerrado*, or its plural *cerrados*, designates a natural region, a phytogeographic province and a series of plant formations with varying proportions of woody and herbaceous species. Though these floristically related plant formations prevail within the natural region, it seems convenient, in order to prevent misunderstandings, to review the three different meanings of the cerrado concept.

The natural region occupies an area of more than 1.8 million km$^2$ in the Brazilian Shield. Ab'Saber (1971) when considering the major morphoclimatic domains of that country, characterized the core area of cerrados in central Brazil as the realm of plateaux and high tablelands covered by savannas. The higher levels correspond to an old planation surface of Middle Tertiary age. The formerly continuous surface of these extensive tablelands has been deeply dissected and fragmented, now appearing as isolated high plains or *serras*, separated by wide interfluves. Gallery forests penetrate through these wide valleys, while the uplands are completely covered by savannas (Fig. 10.2).

The flat or gently rolling tablelands range in altitude from 1000 m to about 300 m above sea level. They descend southwards to the lowlands of the Mato Grosso Gran Pantanal, and northwards to the Amazon lowlands with their almost uninterrupted rain forests. To the east and south, the transition with the humid forest landscapes of the Atlantic region is gradual, while to the northeast a rather steep climatic gradient leads to the large depressions of the dry *caatinga* region (Fig. 10.3). The whole cerrado region has a tropical wet and dry climate (**Aw** type of Köppen, 1931) with intermediate rainfall between the wetter regions to the northwest and southeast and the drier northeastern areas. Annual rainfall is of the order of 1500 mm, with extreme values of 750 mm at the caatinga border and somewhat more than 2000 mm at the Amazonian border. The dry season lasts from three to five consecutive months, during the winter of the Southern Hemisphere.

The Cerrado Phytogeographic Province (Eiten, 1978) is characterized by its rich and special flora that neatly distinguishes these areas both from the neighboring forested Amazonian and Atlantic Brazilian Provinces and from the subtropical Chaco Province. This flora has, however, a quite close affinity to that of other Neotropical savannas that have not been considered by phytogeographers as parts of this Cerrado Province. Floristically, the Province extends not only through the main continuous core area of the cerrado in Central Brazil, but also to various cerrado outliers in the southeast (São Paulo) and the northeast (Rio Grande do Norte, Pernambuco).

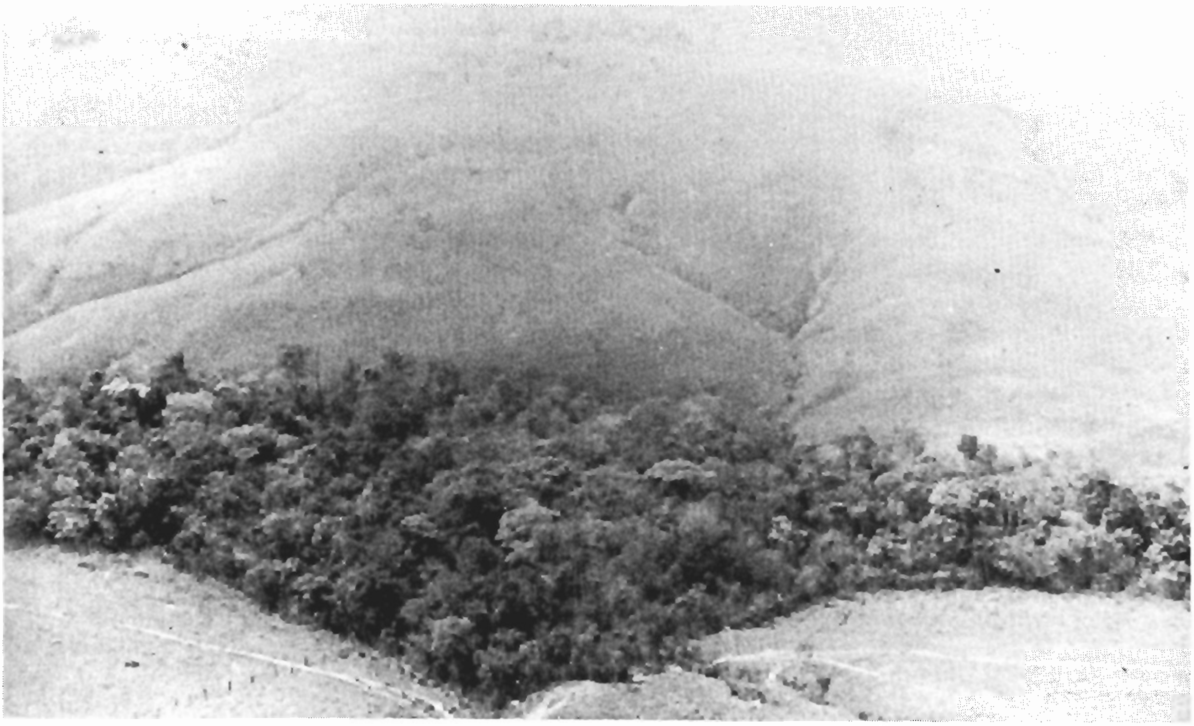

Fig. 10.2. Landscape and vegetation patterns in the cerrado region. Seasonal savannas cover the extensive tablelands and their steep borders, while gallery forests occupy the deeply incised valleys.

The cerrado vegetation has been reviewed by Eiten (1972), and four symposia have been devoted to different aspects of its floristics, ecology, environmental conditions, etc. (Ferri, 1964, 1971, 1977; Labouriau, 1966). A comprehensive bibliography has also been published (EMBRAPA, 1976). In its wider sense, cerrado refers to several structural types of open vegetation, from dense woodlands to grasslands, most of which fit the definition of tropical savannas. Ecologically, the cerrados belong to the seasonal type of savanna; the hyperseasonal savannas and the esteros are rather restricted within this area, besides having a fairly different floristic composition. Brazilian literature refers to these two types of ecosystems as *campos*, not including them among the cerrado formations because of the floristic differences. Since the word campos has too broad a meaning, encompassing quite different vegetation types, the terms "hyperseasonal savannas" and "esteros" will be retained for these ecosystems of the cerrado region. The seasonal savannas, by far the more extensive, will be considered first, and then the other types,


Fig. 10.3. The core area of the cerrados in central Brazil and its neighbouring formations (after Ab'Saber, 1971).

restricted to small areas of particular habitat conditions.

Four structural types of cerrado vegetation have been recognized and designated by popular names (Eiten, 1972). They roughly correspond to the four previously defined physiognomic types. Cerradão refers to a woodland or open low forest, with a fairly continuous tree canopy. Crown cover averages 50%, and the ground layer of grasses, forbs and halfshrubs is inversely correlated with total crown cover of woody species. Cerrado, in its restricted structural sense, refers to a savanna woodland where the total woody cover is about 20%. Campo cerrado is a wooded savanna, where the scattered low trees have a total crown cover of about 3%, but the woody species still appear as a conspicuous part of the landscape (Fig. 10.4). Campo sujo ("dirty field") is applied to a tree and shrub savanna, with widely scattered woody species (Fig. 10.5). Finally, a pure or almost pure grassland is designated as campo limpo ("clean field"). These four physiognomic types appear more or less intermingled in almost every area of cerrado vegetation. They are useful for a preliminary, overall characterization of the plant cover. One may note also that neither dense woodlands nor pure grasslands are separated from the mixed savanna communities, since all types intergrade with one another and constitute complex vegetation mosaics everywhere.

A quantitative analysis of cerrado vegetation reveals a continuous variation in physiognomy and species composition. Goodland (1971) analyzed 110 stands of cerrado vegetation, ranging from campo sujo to cerradão, in a region of Minas Gerais in central Brazil. His results show a continuous variation in all the sampled attributes along this physiognomic gradient. Thus, total basal area of trees varies continuously from 0.9 $m^2$ $ha^{-1}$ in the most treeless grassland to 51.3 $m^2$ $ha^{-1}$ in the cerradão; canopy cover ranges from 0 to 85%; ground cover from 30% in campo sujo to 2% in cerradão; tree density varies from 266 to 4925 trees $ha^{-1}$; number of tree species from 19 to 72; number of herb species from 79 to 21. The importance of most species, either trees, shrubs or grasses, also shows continuous variation along the physiognomic gradient. In a later paper (Goodland and

Fig. 10.4. A wooded savanna (campo cerrado) in the central region of the cerrado, near Brasilia.

Fig. 10.5. A tree and shrub savanna (campo sujo) in the cerrado near Brasilia.

Pollard, 1973), a significant correlation was established between the vegetation structural gradient and levels of phosphorus, nitrogen and potassium in the surface soil horizon.

The existence of a peculiar cerrado flora has already been noted. A few species occur over the whole area, but the most common situation is that of slight and gradual changes from one region to another. Widely separated areas may have only one-fourth of the species in common, but gradients of floristic similarity connect the two extremes. The precise phytosociology of cerrado communities still needs to be studied; it may be a difficult task since even now its flora and phytogeography are imperfectly known. Tables 10.2 and 10.3 give lists of the most common species of woody and herbaceous plants.

Every small area within the cerrado shows a rich and diversified flora. Heringer (1971) recorded more than 300 species in one hectare of protected cerrado near Brasilia. Sampling the area through twenty-five 20×20 m plots, he found that the number of species per plot varied from 52 to 117; these are high numbers even for tropical plant communities.

TABLE 10.2

Some of the most widespread trees in the cerrados

| | |
|---|---|
| *Agonandra brasiliensis* | *Machaerium angustifolium* |
| *Annona coriacea* | *Magonia pubescens* |
| *Antonia ovata* | *Miconia argentea* |
| *Aspidosperma dasycarpon* | *Myrcia tomentosa* |
| *Aspidosperma tomentosum* | *Piptadenia peregrina* |
| *Bombax gracilipes* | *Piptocarpha rotundifolia* |
| *Bowdichia virgilioides* | *Platypodium elegans* |
| *Byrsonima coccolobaefolia* | *Pterodon pubescens* |
| *Byrsonima crassifolia* | *Qualea grandiflora* |
| *Caryocar brasiliense* | *Qualea multiflora* |
| *Casearia sylvestris* | *Roupala heterophylla* |
| *Connarus suberosus* | *Salvertia convallariodora* |
| *Copaifera langdorffii* | *Sclerolobium paniculatum* |
| *Curatella americana* | *Solanum lycocarpum* |
| *Dalbergia violacea* | *Strychnos pseudoquina* |
| *Dimorphandra mollis* | *Stryphnodendron barbadetimam* |
| *Diospyros hispida* | *Symplocos lanceolata* |
| *Erythroxylon suberosum* | *Tabebuia caraiba* |
| *Eugenia dysenterica* | *Terminalia argentea* |
| *Hancornia speciosa* | *Vernonia ferruginea* |
| *Hirtella glandulosa* | *Vochysia elliptica* |
| *Hymenaea stigonocarpa* | *Xylopia aromatica* |
| *Jacaranda brasiliana* | *Zeyheria digitalis* |
| *Kielmeyera coriacea* | |

TABLE 10.3

Some of the commonest species in the ground layer of the cerrado savannas

| | |
|---|---|
| **SHRUBS** | |
| *Anacardium humile* | *Jacaranda ulei* |
| *Andira humilis* | *Kielmeyera rosea* |
| *Byrsonima verbascifolia* | *Mimosa polycarpa* |
| *Cochlospermum regium* | *Palicourea rigida* |
| *Davilla eliptica* | *Peschiera affinis* |
| *Erythroxylon campestre* | *Vernonia thyrsoidea* |
| **HALF-SHRUBS OR HALF-WOODY SPECIES** | |
| *Anemopaegma arvense* | *Jacaranda decurrens* |
| *Annona pygmaea* | *Kielmeyera neriifolia* |
| *Baccharis humilis* | *Lippia martiana* |
| *Borreria capitata* | *Mimosa gracilis* |
| *Clitoria guianensis* | *Parinari obtusifolia* |
| *Craniolaria integrifolia* | *Pfaffia jubata* |
| *Esenbeckia pumila* | *Stryphnodendron confertum* |
| *Evolvulus sericeus* | *Tibouchina gracilis* |
| *Gomphrena postrata* | *Vernonia elegans* |
| *Ichthyothere rufa* | *Viguiera robusta* |
| **GRASSES** | |
| *Andropogon bicornis* | *Mesosetum loliiforme* |
| *Andropogon hirtiflorus* | *Panicum cayenense* |
| *Andropogon leucostachys* | *Panicum olyroides* |
| *Andropogon selloanus* | *Paspalum carinatum* |
| *Aristida capillacea* | *Paspalum gardnerianum* |
| *Aristida pallens* | *Paspalum pectinatum* |
| *Aristida tincta* | *Paspalum plicatulum* |
| *Axonopus aureus* | *Paspalum pulchellum* |
| *Axonopus capillaris* | *Sporobolus cubensis* |
| *Ctenium chapadense* | *Thrasya paspaloides* |
| *Diectomis fastigiata* | *Trachypogon canescens* |
| *Echinolaena inflexa* | *Trachypogon montufari* |
| *Elyonurus latiflorus* | *Trachypogon plumosus* |
| *Eragrostis maypurensis* | *Trachypogon vestitus* |
| *Leptocoryphium lanatum* | *Tristachya leiostachya* |
| **PALMS** | |
| *Acanthococos emensis* | *Butia leiospatha* |
| *Acanthococos sericeus* | *Syagrus acaulis* |
| *Astrocaryum campestre* | *Syagrus campestris* |
| *Attalea exigua* | |
| **SEDGES** | |
| *Bulbostylis paradoxa* | *Fimbristylis diphylla* |
| *Bulbostylis capillaris* | *Rhynchospora barbata* |
| *Cyperus flavus* | *Rhynchospora velutina* |
| *Dichronema ciliata* | |

To give a further picture of a cerrado community, the description given by Eiten (1975) of an undisturbed cerrado on the crest of the Serra do Roncador in Mato Grosso will be examined. Eiten refers to this vegetation as "a tree and shrub woodland" where woody plants, counting those of all heights, form an open cover of about 50%. There are a few scattered tall trees (from less than 7 to 12 or even 15 m). Lower trees and shrubs of all sizes fill in the rest of the space, but woody plants do not form definite layers. Among the most common trees, Eiten lists *Aspidosperma* spp., *Curatella americana*, *Davilla eliptica*, *Kielmeyera coriacea*, *Palicourea rigida*, *Qualea grandiflora*, *Salvertia convallariodora*, and various others. Besides these trees and shrubs, some low palms, 2 to 5 m tall, and a few species of acaulescent palms are usually present, giving a characteristic appearance to the vegetation. The ground layer appears slightly open; grasses are dominant, with intermixed sedges, perennial herbs, semi-shrubs, dwarf shrubs and vines. Species of *Andropogon*, *Axonopus*, *Ichnanthus* and *Paspalum* are the most common grasses. They reach 0.5 to 1.25 m tall when in flower. Open colonies of a low terrestrial *Bromelia* occur in a few areas. As may be gathered from this description, a typical cerrado (in this case a savanna woodland) is quite a rich formation, considering either life forms or number of species. The structural variation in respect of arrangements and importance of the different growth-forms is striking.

In the same area of the Serra do Roncador, Ratter et al. (1973) described two different communities of cerradão. The *Hirtella glandulosa* cerradão is a "low savanna woodland in which the taller trees vary from 5 to 12 m in height; there is no continuous canopy and the ground vegetation is very dense and difficult to walk through". Characteristic trees of this community, besides *Hirtella glandulosa*, are *Aspidosperma macrocarpon*, *Bowdichia virgilioides*, *Sclerolobium paniculatum*, *Xylopia sericea*, and others. Fig. 10.6 shows the structural profile of this community. The ground layer contains numerous cerrado species, among which are found many grasses, acaulescent palms and ground bromeliads. Another community in the same area is the *Magonia pubescens–Callisthene fasciculata* cerradão, in which the largest trees attain 15 m high and the ground layer is quite dense. As may be realized from these descriptions,

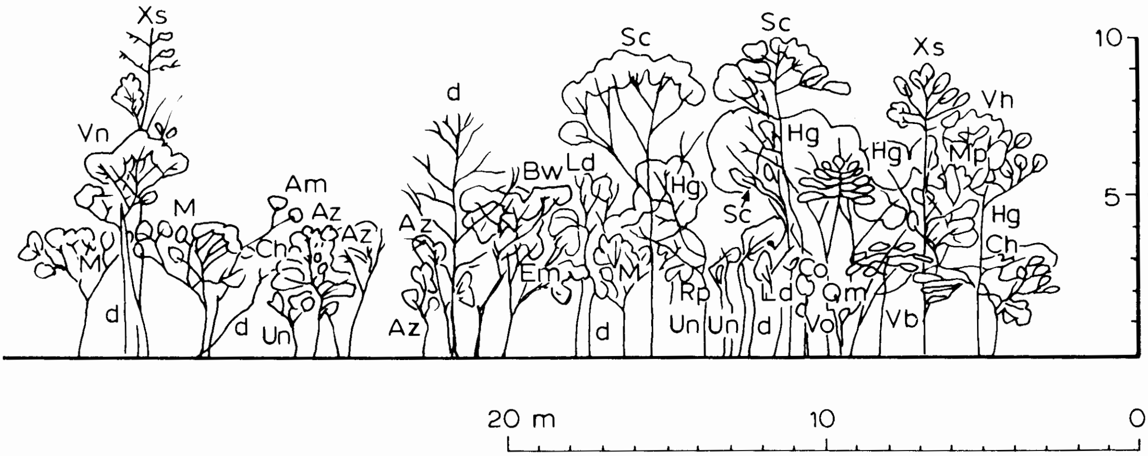


Fig. 10.6. A profile diagram (30 × 3m) of a *Hirtella glandulosa* cerradão in the Serra do Roncador, Mato Grosso (after Ratter et al., 1973). Key to the species: *Am* = *Aspidosperma macrocarpon*; (unknown) *Az* = *azeidinho*; *Bw* = *Bowdichia virgilioides*; *Ch* = *Chaetocarpus echinocarpus*; *Co* = *Connarus fulvus*; *Em* = *Emmotum nitens*; *Hg* = *Hirtella glandulosa*; *Ld* = *Lafoensia pacari*; *M* = *Miconia* sp.; *Mp* = *Maprounea guianensis*; *Rp* = *Roupala montana*; *Sc* = *Sclerolobium paniculatum*; *Qm* = *Qualea multiflora*; *Vb* = *Virola sebifera*; *Vh* = *Vochysia haenkeana*; *Xy* = *Xylopia amazonica*; *Xs* = *Xylopia sericea*; *Un* = unknown; *d* = dead.

even the densest types of woodlands have structural and floristic characteristics that relate them to the other savannas. Several authors, like Rizzini and Heringer (1962) and Rizzini (1963b), have considered the cerradão as the original forest type in the whole cerrado area, the other structural types being derived from it by burning and man's other activities. Though this is probably the case in some restricted, formerly forested areas, it seems difficult to accept this generalization as valid for the entire region.

Quite numerous cerrado outliers appear in the State of São Paulo as small islands within a landscape that was formerly forested. Borgonovi and Chiarini (1968) presented a map showing these southernmost intrusions of cerrado. They reach the border between the States of São Paulo and Parana, at about 24 S. Silberbauer-Gottsberger et al. (1977) analyzed the effects of the exceptional 1975 frost on these cerrados, concluding that frost seems to be one of the selective factors influencing the floristic composition of the cerrado at its southern limit, as many woody species were substantially damaged.

In northeastern Brazil, there also occur several small areas of disjunct cerrados among the prevailing caatinga vegetation (Valverde et al., 1962; Eiten, 1972). They occupy sandstone plateaux and tablelands. Their floristic and physiognomy are similar to those of typical cerrado in its central core area. *Byrsonima cydoniaefolia*, *Curatella americana*, *Hancornia speciosa*, *Hirtella ciliata* and *Ouratea fieldingiana* are the commonest trees (Tavares, 1964).

**The hyperseasonal savannas and esteros of the cerrado region**

A belt of natural grassy campo occurs on the valley sides or plateau edges, in almost all areas of cerrados (Eiten, 1978). Generally, it is a narrow belt separating the upland cerrado from the gallery forest. In these areas the water table is near the surface for some or all of the year. Askew et al. (1970) noticed the existence of these grassy formations, either treeless or with occasional trees or palms, in northeastern Mato Grosso. Ratter (1971) and Ratter et al. (1973) considered two types of grasslands in that area: dry or hill grasslands, and moist valley campos. In fact, the dry grasslands that occur on shallow soils or on lateritic outcrops represent a type of cerrado: the campo limpo or savanna grassland. Their herbaceous and shrubby flora is quite similar to the ground flora of the other savanna formations already discussed. The valley-side campos may be considered either as hyperseasonal savannas or as esteros, depending upon both the amount of time they remain waterlogged during the rainy season and the degree of soil desiccation during the dry months.

Eiten (1975) described the valley-side campos in Serra do Roncador (Mato Grosso) as a pure grassland with a dominant grassy layer 0.5 to 1.25 m tall, intermixed with sedges, rushes, species of *Xyris* and a great number of herbs. Scattered *buriti* palms (*Mauritia vinifera*) appear in a few cases. Eiten noticed that the dominant grass species, as well as the rest of the flora, vary from one campo to another, though a few species are present in almost all campos. These formations are subjected to frequent fires, though less frequent than other types of savannas in the cerrado area.

Goldsmith (1974) presented a quantitative analysis of vegetation in one transect from cerrado to a gallery forest traversing the wet campo, in the Rio das Mortes area of Mato Grosso. Campos soils are hydromorphic, grey or black colored, with a high organic matter content and low base status. The mean water table depth is between 1 and 2 m. Grasses form the bulk of vegetation, with 29 species from 14 genera. There are also a large number of other monocotyledons, with nine genera of sedges and representatives from the Commelinaceae, Costaceae, Eriocaulaceae, Heliconiae, Iridaceae, Rapataceae and Xyridaceae. The total campo flora reaches about 200 species.

Other common types of hyperseasonal savanna and seasonal swamp form a well-defined mosaic with seasonal cerrados. Eiten (1975, 1978) described a vegetation pattern in Mato Grosso where cerrado trees and shrubs are clumped in round groves, 3 to 7 m in diameter, raised on earth mounds, 1 to 2 m high, which always contain one or two termite mounds. The groves form a regular pattern in a continuous matrix of hydromorphic grasslands, that occupy a perfectly flat area, flooded in the wet season, either treeless or dotted with buriti palms. The raised platforms seem to be artifacts built up by termites to keep their nests above the saturated soil. As will be discussed later, this same type of landscape occurs in the neighboring Pantanal region.

In summary, floristically rich seasonal savannas prevail in the cerrado region and its outliers. They form a continuum of structural types from grasslands to woodlands, probably correlated with site conditions. In any area, different structural types coexist side by side, giving rise to vegetation mosaics at different scales and of various complexity. Hyperseasonal savannas and esteros generally occur as treeless grasslands or sometimes as palm savannas with *Mauritia vinifera*. They occupy wet sites on valley sides or tableland margins throughout the area, though they become more important in Mato Grosso, towards its boundary with the Gran Pantanal.

## THE COLOMBIAN–VENEZUELAN LLANOS AND RELATED SAVANNAS OF NORTHERN SOUTH AMERICA

The large sedimentary basin known as the llanos is a huge plain lying between the Andes and the Caribbean Cordilleras (to the west and north) and the broken landscapes bordering the Guiana Shield (to the east and south). In the popular sense, llanos means both a plain and an open landscape where savannas provide the most significant part of the plant cover. Though within this region there are several large areas covered by various types of tropical forests, and almost every watercourse is bordered by a fringe of gallery forest, most of the area is occupied by natural savannas. The llanos indeed constitute the major savanna region of northern South America.

The Guaviare River in central Colombia (Fig. 10.7) marks the limit between the nearly continuous Amazonian rain forest to the south and the savanna lands to the north. The Orinoco Delta constitutes a natural limit to the east, while the savanna landscape intermixes with rain forests on the hills limiting the plains a few kilometers south and east of the Orinoco. This big river is the major collector for the whole area, and its main right-hand tributaries, such as the Meta, Arauca and Apure, dissect and drain a large part of the llanos.

The regional climate is a typical tropical wet and dry climate, where annual rainfall increases from about 1000 mm in the eastern border to a maximum of 2200 mm at the Guaviare River on the south-western margin. Correspondingly, the number of dry months decreases from five to six in the east to one or two in the southwest. Quaternary alluvial and aeolian sediments extend throughout the major part of the llanos. In the eastern portion, a tongue of Tertiary clays and shales extends southwards from the Cordillera de la Costa and approaches the Orinoco. This is the major area of tropical deciduous forest within the llanos.

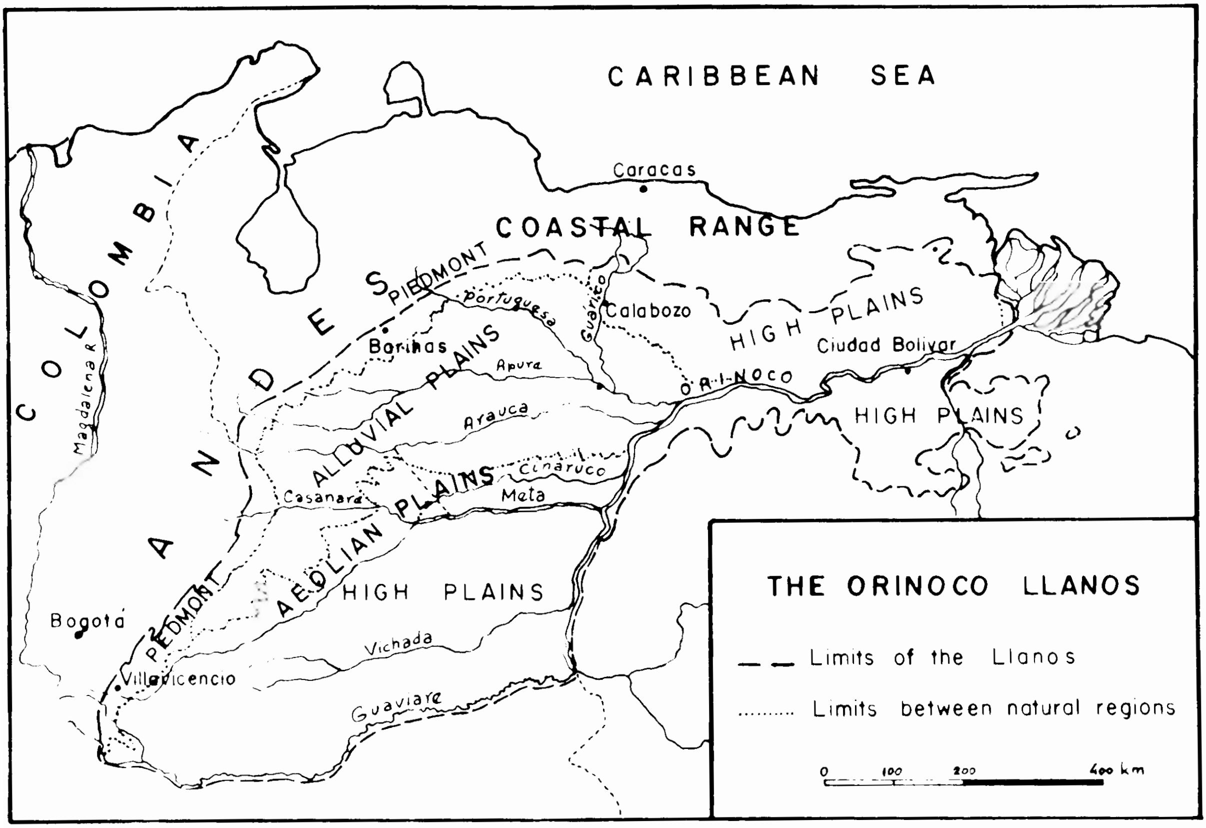


Fig. 10.7. The Orinoco llanos in Colombia and Venezuela. Four major regions have been distinguished: the piedmont, the high plains, the alluvial overflow plains and the aeolian plains.

On well-drained sites, the whole range of tropical soils appears, from Entisols on young alluvia surfaces, to Oxisols on the more ancient ones; but Alfisols and Ultisols are the two most widespread types. On badly drained terrains, Vertisols and Alfisols predominate.

Savannas are used as extensive rangelands for cattle raising, but modern agriculture penetrates a region extending from the best soils, near the piedmont, to the hinterlands. Some large irrigation programs already allow an intensive agriculture in lozalized areas, raising crops like rice, cotton, sorghum, corn and sesame.

Almost every ecological and physiognomic type of savanna occurs in the llanos, the dominant formations depending on topography and soil. Except in some quite inaccessible areas, such as parts of the Meta and Vichada Departments in Colombia, the physiognomy and main floristic types of savannas are fairly well known. An overall account of savanna vegetation in the Colombian llanos may be found in FAO (1966) and Blydenstein (1967). Tamayo (1964), Ramia (1967) and Medina and Sarmiento (1979) give a general picture of this vegetation in the Venezuelan llanos. Indeed, the Venezuelan llanos are perhaps one of the more thoroughly analyzed and best known areas of neotropical savannas.

Four main subregions may be distinguished within this natural region, differing from each other in age of parent materials, land forms and soil, and as a consequence in types of savanna formations and overall vegetation patterns. These four subregions — the piedmont, the high plains, the alluvial overflow plains and the aeolian plains — will be briefly considered in turn.

**The piedmont savannas**

The piedmont region is characterized by large alluvial fans and a system of alluvial terraces. Semideciduous tropical forests are widespread on these

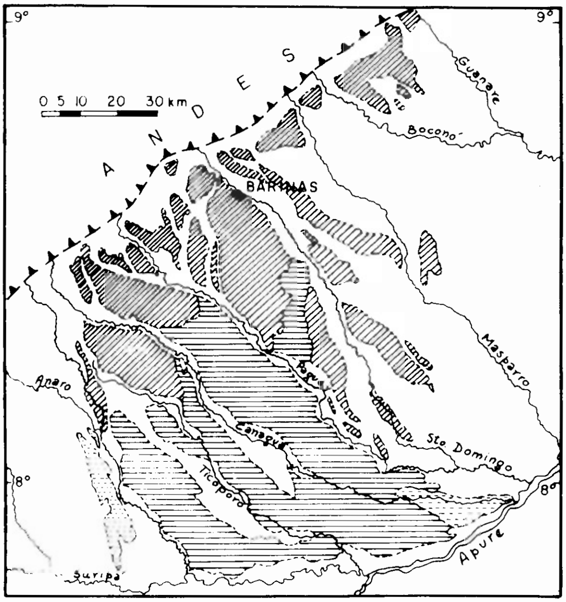


Fig. 10.8. Vegetation pattern in the piedmont region of the Venezuelan llanos. Oblique hatching indicates the areas with seasonal savannas; horizontal hatching shows the areas of hyperseasonal savannas; discontinuous horizontal hatching indicates the esteros; the white areas correspond to various types of rain forests. (After Sarmiento et al., 1971a.)

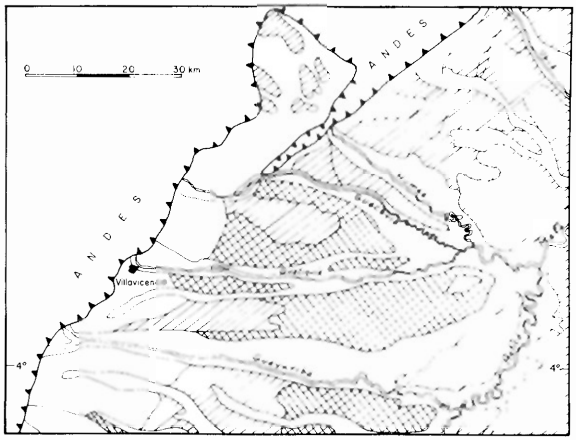


Fig. 10.9. Vegetation pattern in the piedmont region of the Colombian llanos. Oblique hatching indicates areas of seasonal savannas (savannas of *Melinis minutiflora*, *Trachypogon ligularis*, *Trachypogon vestitus*, *Trachypogon vestitus–Axonopus purpusii*; and savannas of *Paspalum pectinatum*); cross-hatching refers to areas with hyperseasonal savannas (*Leptocoryphium lanatum* savanna); white areas correspond to various types of rain forests. (After FAO, 1966.)

land forms, but savannas occupy a major portion of the landscape (Figs. 10.8 and 10.9). In the western Venezuelan llanos, the distribution, ecology and composition of the piedmont savannas were analyzed by Sarmiento et al. (1971a), Silva et al. (1971) and Monasterio et al. (1971).

A savanna woodland occupies the oldest Quaternary deposits, $Q_{iv}$ according to Tricart and Millies-Lacroix (1962). Just a few species form the low and open tree layer, while the ground vegetation is dominated by hard tussock grasses and sedges and by halfshrubs (Table 10.4 and Fig. 10.10). The $Q_{iii}$ terrace maintains wooded savannas intermingled with semideciduous forests. The more extensive $Q_{ii}$ terrace was formerly covered by seasonal savannas that have now been replaced by croplands or grazing lands of introduced grasses, mainly the African *Hyparrhenia rufa*, covering large areas. The lowest and youngest terrace level ($Q_i$) is the domain of gallery forests, though on sandy soils seasonal savanna may occur with *Elyonurus tripsacoides* as the dominant grass. Hyperseasonal savannas, on the other hand, are restricted to a few localized bottom lands, in this piedmont region.

TABLE 10.4

Some of the commonest species in the seasonal savannas of the piedmont region of the Venezuelan llanos

| | |
|---|---|
| TREES | |
| *Acrocomia sclerocarpa* | *Cochlospermum vitifolium* |
| *Bowdichia virgilioides* | *Curatella americana* |
| *Byrsonima coccolobaefolia* | *Genipa americana* |
| *Byrsonima crassifolia* | *Roupala complicata* |
| *Casearia sylvestris* | *Xylopia aromatica* |
| SHRUBS AND HALF-SHRUBS | |
| *Clitoria guianensis* | *Palicourea rigida* |
| *Desmodium pachyrrhizum* | *Pavonia speciosa* |
| *Galactia jussieana* | *Psidium guianense* |
| *Ichthyothere terminalis* | *Tephrosia adunca* |
| GRASSES AND SEDGES | |
| *Andropogon selloanus* | *Leptocoryphium lanatum* |
| *Andropogon semiberbis* | *Panicum olyroides* |
| *Axonopus canescens* | *Paspalum gardnerianum* |
| *Axonopus purpusii* | *Paspalum plicatulum* |
| *Bulbostylis capillaris* | *Sporobolus cubensis* |
| *Bulbostylis junciformis* | *Thrasya petrosa* |
| *Bulbostylis paradoxa* | *Trachypogon montufari* |
| *Dichronema ciliata* | *Trachypogon plumosus* |
| *Elyonurus adustus* | *Trachypogon vestitus* |

Fig. 10.10. A savanna woodland in the piedmont region of the Venezuelan llanos. *Byrsonima crassifolia*, *B. coccolobaefolia* and *Bowdichia virgilioides* are the main components of the tree layer, while the ground layer is dominated by *Andropogon semiberbis*, *Trachypogon plumosus* and various halfwoody species. (Photo from Vera, 1979.)

Silva and Sarmiento (1976a, b) analyzed the floristic composition and ecological relationships of these savannas as they occur on seven different soil series either on the $Q_{iv}$, $Q_{iii}$ or $Q_{ii}$ terraces. Each soil series was found to carry a characteristic community, but that the composition and importance of the species varied continuously, from the drier seasonal savannas on coarse soils developed on the $Q_{iv}$ terrace, to the wetter hyperseasonal savannas on poorly drained sites of the $Q_{ii}$ terrace. Only a few species were restricted to narrow parts of this gradient, while most of them occurred in more than one community (Fig. 10.11). This phytosociological continuum reflects environmental gradients related to soil-water conditions during the dry and wet seasons.

Sarmiento and Vera (1979a) followed the changes in soil water content during an annual cycle, in various sites along that gradient, confirming that soil-water availability was very different at the two extreme sites, though varying continuously along the gradient.

Sarmiento and Vera (1979b) measured the annual production of the ground layer by the harvesting method, in three seasonal and one hyperseasonal savanna, in this piedmont area of the western Venezuelan llanos. Seasonal formations attained a maximum standing crop of 522 to 604 g $m^{-2}$, without showing significant differences between communities and among different years. The hyperseasonal savanna reached a maximum of 705 g $m^{-2}$. As all these savannas were burned each year, the maximum above-ground biomass may be taken as a rough estimate of the aerial net primary production of the ground layer. Maximum below-ground biomass to a depth of 2 m ranged from 1148 to 1891 g $m^{-2}$, giving an estimated below-ground annual production of about 500 to 1300 g $m^{-2}$. In a savanna woodland on the $Q_{iv}$ terrace, where total tree density was about 1000 trees $ha^{-1}$ Vera (1979) determined an annual litter production of about 120 g $m^{-2}$. Sarmiento (1978) discussed some methodological and conceptual problems derived from these estimates of annual production,

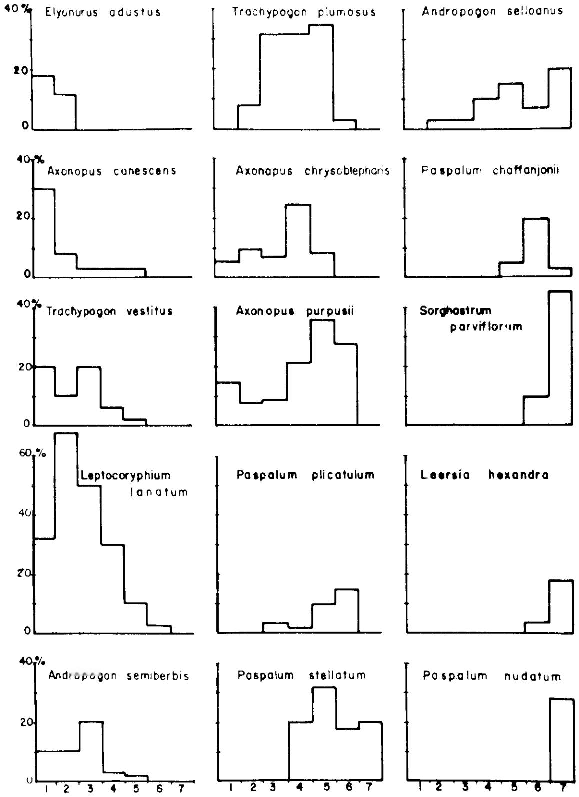


Fig. 10.11. The representation of different grasses in seven savanna communities along a humidity gradient in the piedmont region of the Venezuelan llanos. Number *1* corresponds to the driest savanna and number *7* to the most humid type. The vertical axis indicates total cover of the species in each of the seven ecosystems. Notice how most species show a wide range of occurrence, though with different cover in each community. Species like *Paspalum nudatum* restricted to a single community are rather the exception. (From Silva and Sarmiento, 1976a.)

concluding that the real production figures might be about 100% higher than these figures, if other variables like differential growth and mortality rates were taken into account.

## The high plains

The high plains, or mesas, constitute a second subregional unit within the llanos. They occupy two distinct areas in the south and east, separated by a central tectonic depression (Fig. 10.7). These high plains appear as remnants of a former continuous tableland of Late Pliocene or Early Pleistocene age. The isolated mesas may show either a gently undulating surface or their surface may have been dissected giving rise to a hilly relief. A few relict mesas remain in some places, generally protected from erosion by hard lateritic layers. The parent material on the tablelands is rather coarse alluvium on which light-textured soils have evolved.

The savanna on the mesas in the eastern Venezuelan llanos was considered in a pioneer paper by Pittier (1942). He described this characteristic landscape of low plateaus, 200 to 300 m above sea level, deeply dissected by rivers flowing to the Orinoco. The savanna is a seasonal tree savanna (Fig. 10.12) dominated by *Trachypogon plumosus* or by *T. vestitus*, with *Andropogon selloanus*, *Axonopus canescens* and *Leptocoryphium lanatum* as subdominant grasses. The low, scattered trees belong almost exclusively to three species: *Bowdichia virgilioides*, *Byrsonima crassifolia* and *Curatella americana*. A wooded savanna occurs on the steep slopes of the incised valleys, with the forementioned species plus a few others, like *Byrsonima coccolobaefolia*, *Piptadenia peregrina* and *Roupala complicata*, while the valley bottoms are occupied either by *Mauritia flexuosa* palm swamps or by gallery forests.

The savanna on the mesas in the central Venezuelan llanos has been described by Blydenstein (1962) and Sarmiento and Monasterio (1969a, b, 1971). Here, isolated mesas remain as dissected remnants of a formerly continuous upland. As the denudation of these mesas left just a few meters or even less of coarse alluvium, underlying materials may appear at the surface, introducing a further diversity of habitats. As a result, these seasonal savannas are more varied than those in the eastern mesas, and they frequently form intricate patterns with forests and hyperseasonal savannas. On the mesas, seasonal savannas vary from tree savannas to savanna woodlands. Tree density and height, as well as floristic composition of the ground layer, depend on soil depth, occurrence of lateritic crusts and fire frequency (Sarmiento and Monasterio, 1969a, 1971). A savanna parkland prevails in areas where water shortage is less restrictive (Fig. 10.13). All these communities have a rather closed ground layer dominated by species of *Andropogon*, *Axonopus* and *Trachypogon*.

The wide valleys dissecting the mesas have a system of river terraces of different ages. Seasonal savannas, mostly treeless grasslands, occupy the

Fig. 10.12. A seasonal savanna with very scattered trees on the mesas of the eastern high plains in the Venezuelan llanos. *Curatella americana* is almost the only tree species over a ground layer dominated by species of *Andropogon*, *Axonopus* and ***Trachypogon***.

Fig. 10.13. A savanna parkland on the high plains (mesas) of the central Venezuelan llanos (Calabozo Biological Station). The seasonal savanna is a *Trachypogon–Axonopus* community with scattered trees (*Bowdichia virgilioides*, *Byrsonima crassifolia*, *Curatella americana*). The groves are dominated by high trees like *Cassia moschata*, *Copaifera officinalis* and *Vochysia venezuelana*.

drier habitats, while hyperseasonal savannas occur on waterlogged sites, where they may either be grasslands dominated by *Leersia hexandra*, *Mesosetum loliiforme*, *Sorghastrum parviflorum* and several species of *Andropogon* and *Panicum*, or the palm *Copernicia tectorum* may be locally abundant as the single woody species (Fig. 10.14). Savanna parklands occur in some areas where the hyperseasonal savannas are dotted with groves of deciduous tropical forest (Fig. 10.15). On the younger terraces, a fairly continuous deciduous forest prevails, while the stream borders are mostly covered by gallery forests.

The high plains also occupy large extensions of the Colombian llanos, particularly between the Meta and Guaviare Rivers. They extend unchanged to southern Venezuela, and end at the Cinaruco River. The most common formation in this region is a seasonal tree savanna, with low trees mostly *Byrsonima crassifolia* and *Bowdichia virgilioides* and a ground layer dominated by species of *Bulbostylis*, *Leptocoriphium*, *Paspalum* and *Trachypogon*. Table 10.5 gives a list of the most frequent species in these savannas according to FAO (1966).

The Guiana Shield in southern Venezuela is bordered to the east and north by a fringe of seasonal savannas on uplands that represent a southern extension of the mesas. Williams (1942) and Tamayo (1964) give descriptions of these formations. They are mostly *Trachypogon* savannas with sparse trees, including the common species mentioned previously.

Primary production of the savannas on the mesas of the central Venezuelan llanos, in the Calabozo area, has been estimated in several papers (Blydenstein, 1962, 1963; San José and Medina, 1975, 1977; Medina et al., 1977). According to San José and Medina (1975), the *Trachypogon* savanna shows a peak of green biomass that ranges from 320 to 420 g $m^{-2}$, being higher when burned than when protected from fire. These figures were obtained during a year when rainfall was well above the mean, and the total standing crop of the ground layer reached a maximum of 730 g $m^{-2}$. In drier years, total standing crop scarcely surpasses 300 or 400 g $m^{-2}$, the figures are dependent on the precise date of burning. There are no data available on biomass or annual production of the woody layers. The *Andropogon* hyperseasonal savanna on the terraces reaches a peak of 653 g $m^{-2}$ for the aboveground standing crop (San José and Medina, 1977). Apparently, this community is more productive than the seasonal savanna of the same region.

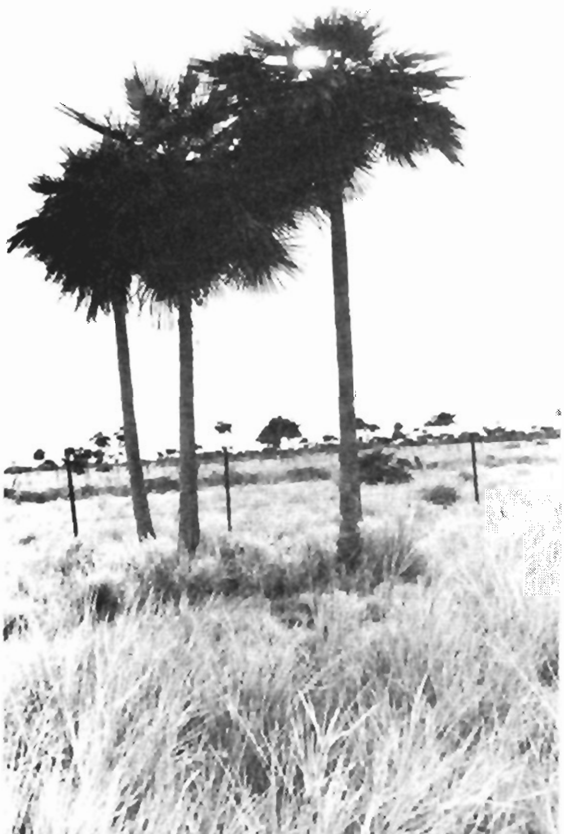

Fig. 10.14. A hyperseasonal savanna with palms (*Copernicia tectorum*) on a low alluvial terrace in a wide valley dissecting the mesas in the Venezuelan llanos.

### The alluvial overflow plains

The alluvial overflow plains occupy a vast depression in the central part of the llanos, between the piedmont and the high plains. These savannas have been considered by Ramia (1959, 1974b), FAO (1966), Blydenstein, (1967) and Sarmiento et al. (1971b). Vegetation varies along topographic catenas, which show differences of only 1 or 2 m between their highest and lowest points in this flat area. The upper part of the vegetation soil catena corresponds to natural levees or banks that border the streams, where sandy alluvium has been de-

Fig. 10.15. A hyperseasonal savanna parkland on alluvial soils of the Venezuelan llanos. Besides the palm *Copernicia tectorum*, the most frequent trees are *Annona jahnii*, *Platymiscium pinnatum*, *Pterocarpus podocarpus* and *Spondias mombim*.

posited. These sandy banks appear as narrow strips gently dipping away from the river to a wide flat area where silty alluvium predominates. The lowest part of the catena is formed by slowly draining decantation cuvettes, where clay particles have settled leading to the development of Vertisols. During the rainy season, only the levees remain unflooded, all the rest of the area being waterlogged for periods ranging from a few weeks to several consecutive months. The terrain is not flooded by overflowing streams but by the accumulation of rain water that drains quite slowly. Towards the end of the dry season the waters have receded, except from the permanent swamps.

Either gallery forests or seasonal savannas may occur on banks, according to the depth of the water table. On the higher banks tree savannas predominate, while the lower levees support a treeless grassland. In the first case, *Axonopus purpusii* and *Paspalum plicatulum* are the dominant species in the ground layer. In the treeless savannas the main grasses are *Sporobolus indicus* and *Imperata contracta*. Since cattle gather on these higher areas during the rainy season, most savannas are heavily overgrazed, with a marked decrease in all palatable species and a corresponding increase in herbaceous and woody weeds.

Hyperseasonal savannas are the most widespread ecosystems in this low region, occupying the wide silty extensions between successive banks. These are mostly treeless savannas (Fig. 10.16), or less frequently palm savannas with *Copernicia tectorum* as the single woody species. The ground flora is rather rich, with many species of annual and perennial grasses and sedges (Table 10.6). The two main savanna communities occurring on this landform produced by slack waters are dominated respectively by species of *Andropogon* and *Mesosetum*.

The bottom lands support a vegetation either of esteros or of permanent swamps. Both types of ecosystems remain under 1 m or more of water during the rainy season, while they slowly dry out as the dry season approaches. The esteros are probably the best grazing lands of the whole llanos, since they can support a heavy carrying capacity during the critical dry months of the rainless season. Though these treeless savannas are rather

TABLE 10.5

Some of the commonest species in the savannas of the high plains region of the Colombian llanos (after FAO, 1966)

| | |
|---|---|
| WOODY AND HALF-WOODY SPECIES | |
| *Bowdichia virgilioides* | *Jacaranda lasiogyne* |
| *Byrsonima crassifolia* | *Lantana moritziana* |
| *Byrsonima verbascifolia* | *Palicourea rigida* |
| *Cassia flexuosa* | *Pavonia speciosa* |
| *Clitoria guianensis* | *Psidium eugenii* |
| *Curatella americana* | *Psidium guianense* |
| *Ichthyothere terminalis* | *Xylopia aromatica* |
| GRASSES AND SEDGES | |
| *Andropogon selloanus* | *Panicum versicolor* |
| *Andropogon hypogynus* | *Paspalum carinatum* |
| *Andropogon virgatus* | *Paspalum minus* |
| *Aristida capillacea* | *Paspalum multicaule* |
| *Axonopus canescens* | *Paspalum pectinatum* |
| *Axonopus pulcher* | *Rhynchospora barbata* |
| *Axonopus purpusii* | *Rhynchospora globosa* |
| *Bulbostylis junciformis* | *Scleria hirtella* |
| *Dichronema ciliata* | *Setaria geniculata* |
| *Eriochrysis holcoides* | *Sorghastrum parviflorum* |
| *Leptocoryphium lanatum* | *Thrasya petrosa* |
| *Mesosetum rottboellioides* | *Trachypogon ligularis* |
| *Panicum rudgei* | *Trachypogon plumosus* |
| *Panicum stenodes* | *Trachypogon vestitus* |

TABLE 10.6

Some of the commonest species in the savannas of the alluvial overflow plains in the Colombian llanos (from FAO, 1966)

| | |
|---|---|
| WOODY AND HALF-WOODY SPECIES | |
| *Buettneria jaculifolia* | *Melochia villosa* |
| *Caraipa llanorum* | *Mauritia minor* |
| *Ipomoea crassicaulis* | *Rhynchanthera grandiflora* |
| *Ludwigia lithospermifolia* | |
| GRASSES AND SEDGES | |
| *Andropogon bicornis* | *Panicum laxum* |
| *Andropogon hypogynus* | *Panicum parvifolium* |
| *Andropogon selloanus* | *Panicum stenodes* |
| *Andropogon virgatus* | *Panicum versicolor* |
| *Axonopus purpusii* | *Paratheria prostrata* |
| *Cyperus haspan* | *Paspalum pulchellum* |
| *Eriochrysis holcoides* | *Rhynchospora barbata* |
| *Eriochrysis cayennensis* | *Rhynchospora globosa* |
| *Leersia hexandra* | *Scleria hirtella* |
| *Leptocoryphium lanatum* | *Setaria geniculata* |
| *Mesosetum chaseae* | *Sorghastrum parviflorum* |
| *Mesosetum rottboellioides* | *Trachypogon ligularis* |

Fig. 10.16. An *Andropogon–Sorghastrum* hyperseasonal savanna grassland during the dry season in the alluvial overflow plains of the Venezuelan llanos. A gallery forest appears at the background.

poor in species, the two commonest grasses, *Leersia hexandra* and *Hymenachne amplexicaulis*, are both highly palatable. Swamps appear as more or less pure consociations of one or another hydrophilous species, like *Ipomoea crassicaulis*, *Ludwigia lithospermifolia*, *Thalia geniculata* or one of several species of sedges.

The areas annually flooded by the overflow of rivers and streams support another type of estero, a tall grassland dominated by *Paspalum fasciculatum*, a tussock grass that reaches 2.5 m high (Figure 10.17). This is a widespread formation in the lowest parts of the llanos, such as those near the Apure River and in the lowlands bordering the eastern mesas and merging into the Orinoco Delta.

González Jiménez (1979) measured above-ground production of the herb layer in the three main types of savannas along the topographic catena. During the year of data collection, the seasonal savanna on the sandy bank reached a maximum green biomass of 425 g m$^{-2}$ and a maximum above-ground standing crop of almost 700 g m$^{-2}$. The hyperseasonal savanna in the loamy basin reached maximum figures of 550 and 800 g m$^{-2}$ respectively for green and total biomass, while the estero had a peak green biomass of 900 g m$^{-2}$, almost equivalent to the peak standing crop (916 g m$^{-2}$). As these figures were obtained in savannas under their normal regime of annual burning, they represent rough estimates of the net aerial production of the ground layer. The figures may vary somewhat according to burning or fire protection, and also according to the precise time of burning.

**The aeolian plains**

An aeolian landscape extends as a continuous belt from the upper Meta River in central Colombia to the Cinaruco River in southern Venezuela (Fig. 10.7). It continues eastwards forming sparse reduced patches within the eastern high plains. This aeolian landscape represents the remnant of a former arid morphogenesis that took place during the Würm glacial period according to Tricart (1974). Its characteristic land forms are extensive

Fig. 10.17. An estero during the rainy season on the alluvial overflow plains of the Venezuelan llanos. *Paspalum fasciculatum* is the dominant grass. In the background a gallery forest.

dune fields superimposed on larger areas of loess-like material that was partly covered by younger alluvia.

A dry seasonal savanna occurs on the dunes, with a few trees or entirely treeless. *Byrsonima crassifolia* is almost the single tree species over a quite open ground layer, dominated by *Trachypogon ligularis* and *Paspalum carinatum* (Fig. 10.18). A *Mesosetum* hyperseasonal savanna occupies the depressions between the dunes and the extensive silty plains. In some areas, *Caraipa llanorum* appears as a characteristic tree, occurring only on this type of habitat and forming a wooded savanna. Along rivulets or on slowly draining lowlands, a grass and sedge estero occurs, with the *moriche* palm (*Mauritia minor*) as its only tree. These *morichales* may be fairly good grazing lands since the grasses remain green throughout the dry season.

**Other savannas related to the llanos**

Several savanna patches closely related to the seasonal savannas of the piedmont region of the llanos occur in various areas of northern Colombia and Venezuela. In some cases, such as along the middle Magdalena Valley, they occupy high terraces with coarse soils. In other areas they cover extensive alluvial fans, such as in the eastern piedmont of the Perijá Cordillera or in the northwestern piedmont of the Venezuelan Andes, in the Maracaibo Lake basin, where tree and wooded savannas occur in old terraces of Early Pleistocene age. All these seasonal savannas have some species of *Trachypogon* as the leading species of the ground layer, while the trees belong to the three or four commonest tree species in the llanos.

Hyperseasonal savannas and esteros are widespread in the swampy depression of the lower Magdalena in northern Colombia, intermingled with permanent swamps and other types of hygrophyllous formations. Small patches of hyperseasonal savannas have also been described in Trinidad (Beard, 1953; Richardson, 1963) where they occur on an old poorly drained terrace of Late Pleistocene age, as small savanna islands encircled by a seasonal swamp forest.

Fig. 10.18. The aeolian plains in the region between the Cinaruco and the Meta rivers. In the foreground a *Mesosetum* hyperseasonal savanna grassland; in the background a dune covered by a seasonal savanna woodland. *Byrsonima crassifolia* is the only tree species over a ground layer dominated by *Trachypogon ligularis* and *Paspalum carinatum*.

Seasonal savannas extend widely over the low mountains of the Caribbean cordillera that border the llanos along their northern edge. They cover the ridge crests and mid-slopes, while semi-deciduous forests occupy creeks and valleys. These mountain savannas, as some other isolated patches that occur along the eastern Andean slopes, seem to represent seral stages stabilized as fire disclimax long ago (Vareschi, 1969; Sarmiento and Monasterio, 1969b). They are mostly tree savannas, sometimes with relict clumps of forest trees. The widespread species of seasonal savannas also occur here, and even the ground layer is dominated by widespread grasses and sedges, mostly species of *Andropogon*, *Axonopus*, *Elyonurus*, *Paspalum*, *Trachypogon*, together with some naturalized species like *Heteropogon contortus* and *Melinis minutiflora*.

Denevan and Chrostowski (1970) and Scott (1977) studied one isolated savanna area on an uplifted plateau, 1000 to 1200 m above sea level, in the eastern chains of the Peruvian Andes. This area, known as the Gran Pajonal, supports several associations that range from pure grasslands to tree and shrub savannas. *Byrsonima crassifolia* is the most conspicuous woody species, together with some shrubby Melastomataceae and Rubiaceae. *Andropogon lanatus*, *A. leucostachys*, and *Leptocoryphium lanatum* are the three dominant grasses. The introduced *Melinis minutiflora* may also be locally abundant. Scott (1977) emphasized the crucial influence of the local Amerindians in the origin and maintenance of these savannas.

As may be realized, the savannas on mountain slopes and other highlands that occur in various parts of tropical South America, are plant communities closely related to the upland formations of the llanos, in spite of the great differences between the habitats on which the two types of savannas occur. This similarity may reflect the fact that both types are fairly young ecosystems, the one colonizing relatively recent alluvial or aeolian materials, the other a product of human influences from pre-Spanish times.

## SAVANNAS OF THE GUIANA PLATEAUX AND THEIR SOUTHERN BORDERS

In the Guiana region of southeastern Venezuela, there is a large area where the sandstones of the Precambrian Roraima Formation form landscapes of tablelands at different altitudes, with a relief of large horizontal stairs. They appear as a complex arrangement of flat-topped plateau levels bounded by very steeply sloping scarps and divided by broad and swampy river flats. The highest levels, with altitudes from 2000 to 3000 m, appear as solitary plateaux called *tepuys*[1]. The Auyan Tepuy, Roraima, Duida, Jaua, Cerro de la Neblina, are some of the major tepuys. Lower tablelands, from 800 to 1200 m above sea level, connect the higher plateaux. They extend as much smaller and isolated areas to Guyana and Surinam. The Venezuelan part of these lower-level plateaux is known as the Gran Sabana (Grand Savanna) and is almost entirely a savanna land. To the south, these highlands descend and penetrate the Brazilian and Guyanan territories where they form another extensive savanna land known as the Rio Branco-Rupununi savannas (Fig. 10.19). This savanna

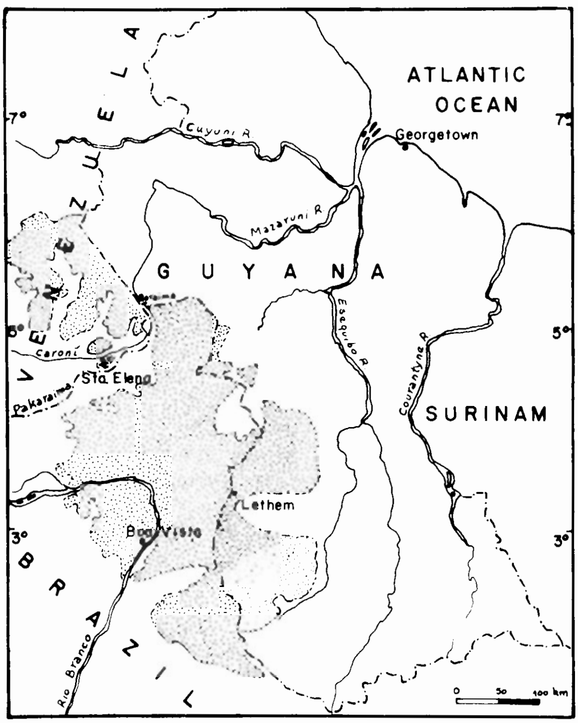


Fig. 10.19. The Rio Branco–Rupununi region in Brazil and Guyana. The Gran Sabana area in southeastern Venezuela is also shown.

[1]Tepuy is an Amerindian name used for a high tableland in the Guianas.

country, with altitudes from 300 to 100 m above sea level, extends to the Mucajai River, where the Amazonian forests begin rather abruptly. Climatic conditions on the higher tepuys are practically unknown, though they seem to be areas of heavy rainfall. The lower tablelands and the adjacent low-altitude regions have an annual rainfall of 1500 to 2000 mm, with three to five dry months.

Myers (1936) traveled through this area of the Venezuelan/Brazilian/Guyanan border and he gave one of the first accounts of its vegetation. He described several types of savanna formations. A *Trachypogon/Curatella* tree savanna was recognized as the most extensive type, apparently quite homogeneous floristically throughout the area. Myers also referred to the occurrence of moister flats with treeless sedge savannas, and seasonal swamps where the palm *Mauritia flexuosa* forms open stands. Savannas were recorded on the Roraima and Pakaraima highlands up to more than 2000 m above sea level.

Beard (1953) also presented a first-hand description of this area and its savannas. He recognized two principal types of site under savanna, which he termed the alluvial and the residual, repeated either on the valleys or on the uplands. The alluvial sites are treeless and dotted with termite mounds. The residual sites, with soils developed *in situ* or from ancient alluvia, frequently have a stony surface layer of ironstones and quartz pebbles. Here the savannas may have sparse low trees. Beard indicated that *Trachypogon plumosus* was the dominant grass in all savannas on well-drained soils. In swampy depressions, that as Beard remarked are similar to the esteros of the llanos, a different grass cover occurs, with isolated groves of *Mauritia flexuosa*.

Takeuchi (1960) gave a short description of the savannas in the Roraima Territory of Brazil, as Tamayo (1961) did for the Gran Sabana area. Steyermark (1967) presented floristic information for the Auyan Tepuy savannas and related vegetation formations. Van Donselaar (1968, 1969) extended his phytosociological and phytogeographic analysis of northern Surinam savannas to the restricted savanna patches in the Surinam/Brazil border, comparing both areas floristically and phytosociologically. But the most comprehensive ecological analysis of savanna lands in this area is that of a research team from McGill University that worked on the Rupununi savanna of the former British Guiana (Guyana). Several papers on plant communities (Goodland, 1964), ecology (Eden, 1964; Hills, 1969), geomorphologic evolution of the landscape (Sinha, 1968) and other aspects were produced. The Radam Brazil Project (Projeto RADAMBRASIL, 1973–78) inventoried geology, soils and vegetation formations in the whole area of the Rio Branco savannas. Finally, I had direct acquaintance with this area during a field trip in 1976, whose results still remain unpublished.

## Main savanna types

Summarizing all the forementioned information, the following picture of the main savanna formations in this area emerges:

(1) Herbaceous swamps on the tepuys, above an altitude of 1500 m. Though they scarcely could be considered as savannas, since grasses do not play any significant role in this formation, this ecosystem may be taken as a useful reference point for comparison with the savannas. The same type of formation appears on sandy soils developed on the Roraima Sandstones in all known tepuys. In the Auyan Tepuy, for instance, Steyermark (1967) described several communities dominated by sedges (*Cephalocarpus*, *Everardia*, *Lagenocarpus*), Xyridaceae (*Abolboda*, *Xyris*), Eriocaulaceae (*Eriocaulon*, *Paepalanthus*, *Syngonanthus*), Bromeliaceae (*Brocchinia*, *Cottendorfia*), Rapataceae, Velloziaceae, Orchidaceae, together with many species of shrubs.

(2) Savannas and seasonal swamps on white sands, at levels around 900–1200 m. This is the main level of the tablelands of the Gran Sabana. On white sands derived from the Roraima sandstones, an intermediate formation between the high tepuys and the savannas on the lower levels occurs (Fig. 10.20). The wetter communities are dominated by the families and genera of monocotyledons mentioned above, but with a greater representation of grasses. The drier areas maintain a treeless grass and sedge savanna (Fig. 10.21), with species of *Axonopus*, *Panicum*, *Rhynchospora*, *Scleria*, *Trachypogon*, etc. (Steyermark, 1967). Although the phenological changes of these species and communities have not been followed, one is apparently dealing with a dry type of semi-seasonal savanna, since the rainless season is rather short,

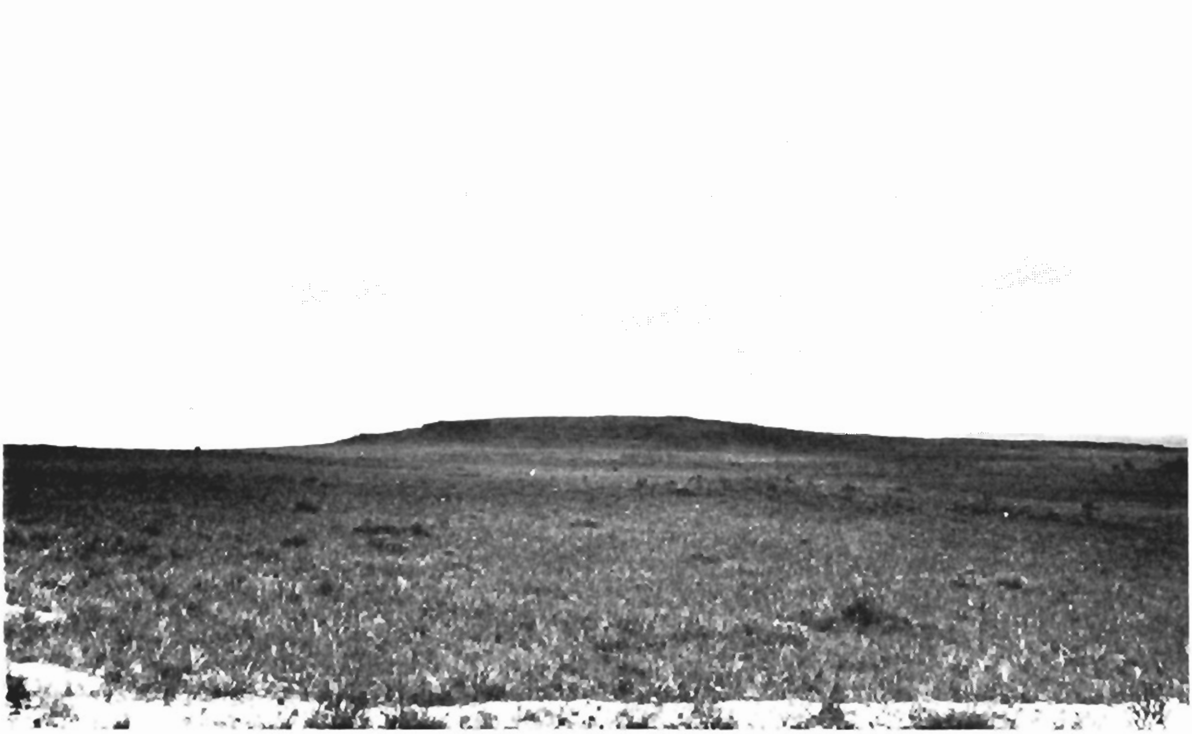

Fig. 10.20. The landscape of high tablelands in the Gran Sabana region. A savanna grassland on white sands appears in the foreground.

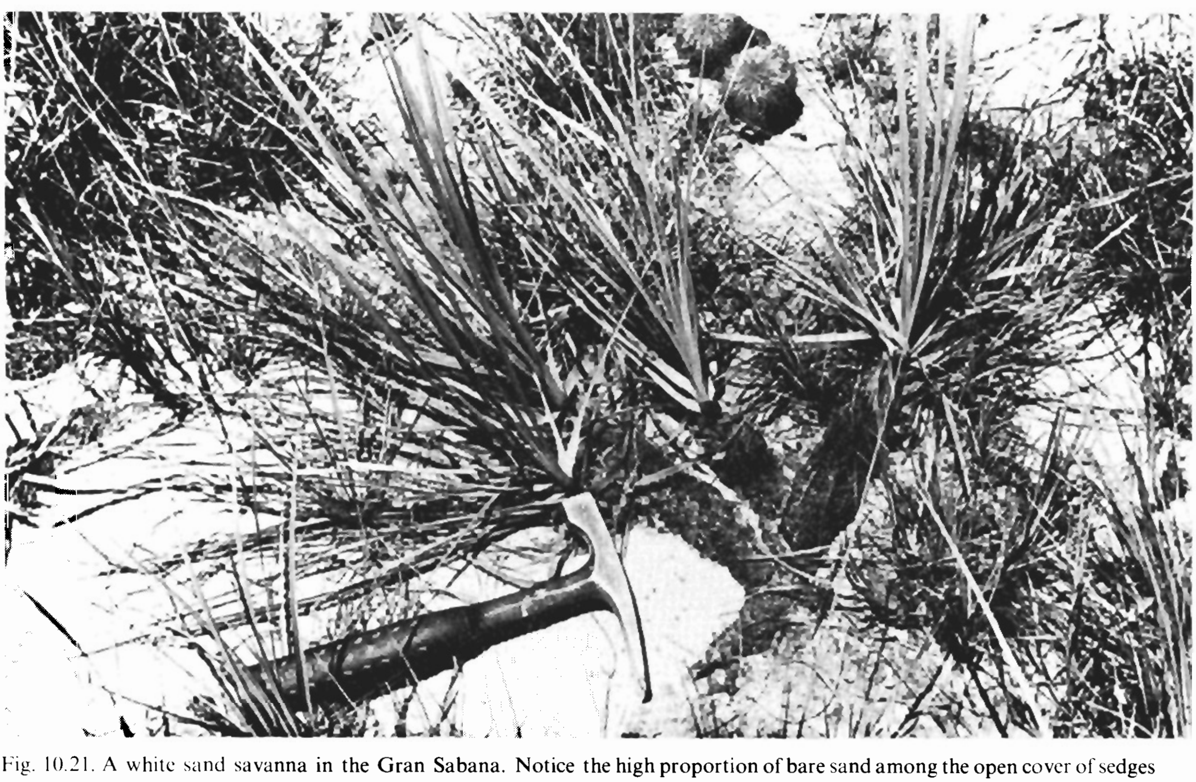

Fig. 10.21. A white sand savanna in the Gran Sabana. Notice the high proportion of bare sand among the open cover of sedges and grasses.

but soils permanently maintain conditions of suboptimal humidity due to their coarse textures.

(3) Seasonal savannas on the lower tablelands, on alluvial fans and upper river terraces, at altitudes between 100 and 500 m. These are mostly open tree savannas with *Antonia ovata*, *Bowdichia virgilioides*, *Byrsonima coccolobaefolia*, *B. crassifolia*, *Curatella americana*, *Genipa americana*, *Plumeria inodora*, *Roupala complicata* and *Salvertia convallariodora* as the woody components. The ground layer is dominated by *Trachypogon plumosus*, with *Aristida setifolia*, *A. tincta*, *Axonopus canescens*, *Bulbostylis paradoxa*, *Echinolaena inflexa*, *Leptocoryphium lanatum* and *Thrasya paspaloides* as codominant species. The main half-woody species are *Byrsonima verbascifolia*, *Casearia sylvestris*, *Palicourea rigida* and *Psidium* spp. A similar type of seasonal savanna occurs on dunelands in southern Rupununi (Sinha, 1968).

(4) Savanna woodlands and woody savannas in the piedmont zone of the Kanuku Mountains and on the lower slopes of the Pakaraima Mountains. Here, the woody species are practically the same as in the tree savannas, though they have a much greater density. In many cases, *Curatella americana* seems to be the most important tree.

(5) Hyperseasonal savannas on river flats. These are either pure grasslands, or areas where small trees occur on termite mounds. The drier communities are dominated by *Andropogon selloanus*, *Panicum laxum*, *Paspalum pulchellum* and *Sporobolus cubensis* and some other grasses and sedges. In the wetter sites, the most frequent species are *Andropogon bicornis*, *Paspalum densum*, *P. millegrana*, *P. pulchellum*, etc.

(6) Morichales and seasonal swamps. These are open stands of *Mauritia flexuosa* palms (Fig. 10.22) with a sedge and grass undergrowth in the swampier parts of river flats.

## THE COASTAL SAVANNAS IN THE GUIANAS

In the coastal region of the three Guianas (Guyana, Surinam and French Guiana) there is a belt of lowland savanna country quite distinct from the llanos and from the interior of Guiana. It extends further south across the Amapa Territory

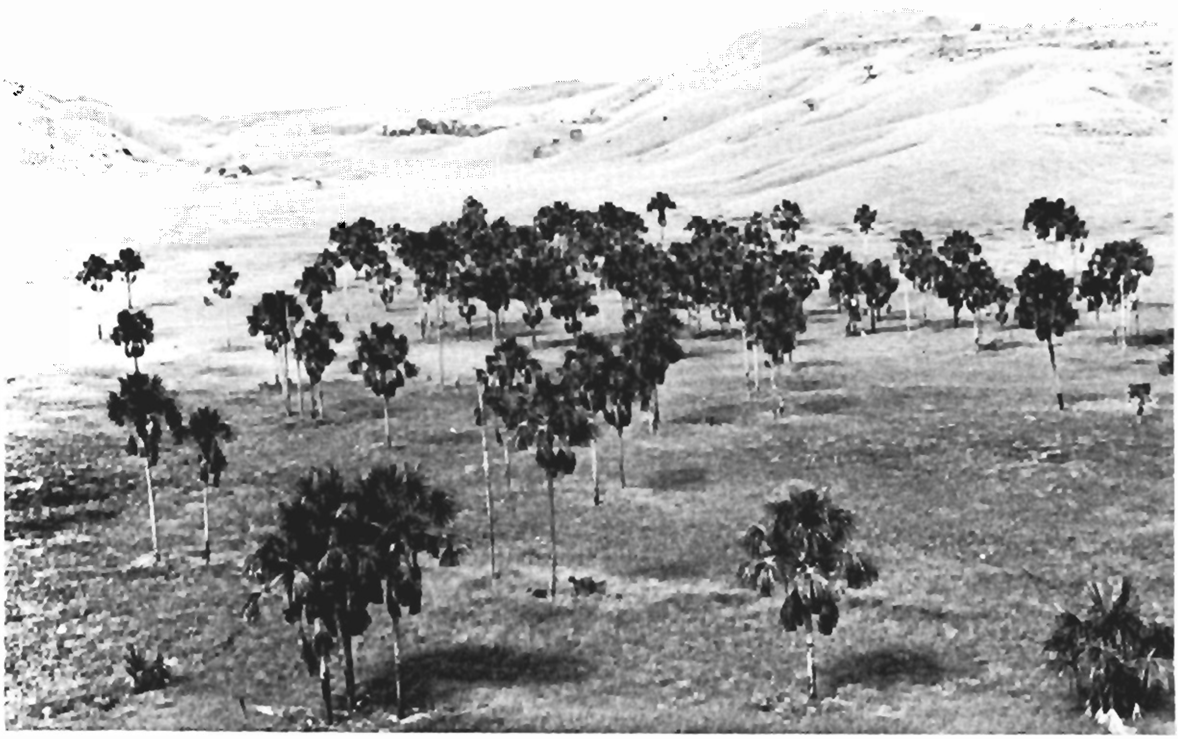

Fig. 10.22. A stand of *Mauritia flexuosa* palms (morichal) on a river flat between the high tablelands of the Gran Sabana region.

of Brazil to the mouths of the Amazonas, thus establishing a link with the Amazon savannas which will be considered later.

The coastal savannas occupy a narrow and discontinuous belt on Plio-Pleistocene alluvial deposits, mainly coarse sands, located between the littoral swamps and mangroves and the continuous rain forest that covers most of the hinterland in these countries. The coastal climate is tropical and constantly wet, with annual rainfall from 2000 to 3800 mm, and two to four months with less than 50 mm rainfall.

The savanna formations of this coastal belt are relatively well-known. The first descriptions were made by Benoist (1925), a comprehensive study was carried out by Dutch workers in Surinam (Lanjouw, 1936; Heyligers, 1963: Van Donselaar, 1965), and a detailed analysis of French Guiana savannas was performed by Hoock (1971). Benoist recognized three main formations: dry savannas, with scattered trees (*Byrsonima crassifolia* and *Curatella americana*) over a grass layer dominated by *Aristida*, *Axonopus* and *Trachypogon*; intermediate savannas, dominated by sedges (*Lagenocarpus*, *Rhynchospora*, *Scleria*) with *Mauritia flexuosa* patches; and wet savannas or herbaceous swamps. Lanjouw (1936) differentiated three savanna formations in northern Surinam: a flat-watershed type of dry grass savanna with shrubs; a type of wet, sedge savanna on impermeable clays; and a type on leached soils and impermeable iron pans, where patches of bushes and small trees occur interspersed with open areas.

Heyligers (1963) analyzed the vegetation and soil of a white sand savanna in northern Surinam. These white sands form a low plateau consisting of coarse sands 30 m above sea level. Low types of forest, which Heyligers called "savanna forest" and "savanna wood", develop on this parent material. Besides these formations, Heyligers referred to a "savanna scrub" and "thicket" as more open and lower woody formations. Neither of these four types could really be considered as a savanna, but they are related to a last formation of true savanna in which small patches of bushes and woods appear intermingled with open stretches of grasses, sedges and herbs. *Trachypogon plumosus* is the dominant grass in this formation, while in wetter habitats the sedges *Lagenocarpus tremulus* and *Rhynchospora tenuis* become more important. Heyligers maintained that the *Trachypogon* savanna owed its origin to the destruction of the savanna woods and the prevention of its regeneration by repeated burning.

Van Donselaar (1965) established a formal classification of the Surinam savannas according to the Braun-Blanquet phytosociological system. All savannas in the area were grouped in a single class, which he named after the two most frequent and widespread species: *Trachypogon plumosus* and *Leptocoryphium lanatum*. Within this class, Van Donselaar distinguished three Orders, eight Alliances and 27 Associations. These phytosociological units, defined on the basis of their characteristic and differential species, reflect differences in soil moisture and type of parent material.

On very dry to moist sites a *Trachypogon–Axonopus* savanna is found. On white sand, this type appears as a grassland dotted with bushes dominated by *Terstroemia punctata* and *Matayba opaca*. The *Curatella–Trachypogon* savanna, so widespread throughout northern South America, occurs on red sand and loamy sand. On red sandy loam, this tree savanna becomes enriched with some additional tree species, while sedges become more abundant in the ground layer. Wet to very wet sites maintain savannas grouped in a second Order, named after the grass *Paspalum pulchellum*. On white sand, sedges together with *Xyris* and Eriocaulaceae prevail, while a treeless community characterized by the sedge *Bulbostylis lanata*, sometimes with bush islands of *Licania incana*, *Tetracera asperula* and *Tibouchina aspera* occurs on red loamy sand and sandy loam. An *Imperata brasiliensis–Mesosetum cayennense* grassland appears on sandy loam and heavier soils, sometimes with sparse trees (*Byrsonima crassifolia* and *Roupala montana*). Finally, on very wet soils, the Associations of the *Panicum stenodes* Order occur either as pure grass and sedge savannas or with *Mauritia flexuosa* groves along the rivulets.

Hoock (1971) recognized seven savanna types and biotypes in the savanna belt of French Guiana. Each type is characterized by the presence of certain ecological groups of species. On yellow sands, he distinguished one forest and two savanna types: a tall shrub savanna and a tall grass savanna. The shrub savanna, characterized by a mesophilous group of species, is an open tree savanna with *Curatella americana* as the most frequent sparse tree and *Axonopus purpusii*, *Leptocoryphium la-*

*natum* and *Trachypogon plumosus* as the dominant grasses. The grass savanna has a rather similar ground layer but no trees or shrubs. Two savanna communities occur on colluvial gray sands with podzols, a low savanna with nanophanerophytes and a low herbaceous savanna. In the first type, *Byrsonima verbascifolia* appears as a characteristic half-woody species scattered in a *Trachypogon plumosus–Leptocoryphium lanatum* grass layer. An ecological group of hygrophytes becomes important in the second type, on wetter sites, with species like the grasses *Echinolaena inflexa* and *Panicum stenodes* and the sedges *Rhynchospora globosa* and *R. graminea*. Two communities occur on podzolized white sands: a low shrub savanna with scattered trees (*Byrsonima crassifolia*) over a ground layer of sedges, *Xyris* and other herbs; and a shrub formation of the type Heyligers (1963) called "scrub savanna" with *Clusia fockeana, Hirtella strigulosa, Tetracera aspersa* and other common white sand shrubs. Finally, an hygrophilous herbaceous savanna occurs on hydromorphic soils, of the type called here hyperseasonal savanna, with tall species of *Andropogon* and *Paspalum* as its dominant grasses.

To summarize all the data heretofore presented on the coastal savannas of the Guianas, it may be emphasized that several savanna types occur in this narrow belt that extends from Guyana to Amapa (Brazil). They may be distinguished either on a phytosociological basis or major site features. A double distinction becomes evident, one based on type of parent material, the other on moisture conditions. White sand communities form a very special type of savanna that, as will be seen later, is ecologically and floristically related to the Amazon caatinga forests and their derived savannas occurring on the same type of parent material. By contrast, savanna formations on red soils with a more or less advanced latosolization, are more akin to the widespread types of savanna formation occurring in other areas of northern South America, particularly in the llanos and the interior Guiana highlands. Both types, savannas on white sand and on red soils, may be further subdivided either according to structural features forming a continuum from treeless savannas to savanna woodlands, or on the basis of a seasonality gradient. In the ever-wet climates of the Guiana savanna belt, these formations are semi-seasonal savannas, on well-drained sites, or hyperseasonal savannas and esteros on poorly drained areas.

## THE SAVANNAS IN THE AMAZONIAN REGION

Though the Amazonian lowlands are really the domain of the continuous tropical rain forest, open vegetation, either savannas or swamps, is by no means absent from this huge natural region. These vegetation types appear either as narrow fringes along the flood plains or as scattered patches within a nearly continuous forest cover. As the knowledge of the region advances, a picture emerges of a landscape dotted with numerous natural clearings occupied by different types of savannas and swamps.

After the pioneer work of Bouillene (1926) and the first overall picture given by Ducke and Black (1953), several authors dealt with the Amazonian open vegetation as it occurs in various parts of this area. Braun and Ramos (1959) described the campos in the region of the Madeira, Purus and Ituxi Rivers in southwestern Amazonia (Fig. 10.23). In this zone, savannas are a part of topographic catenas that extend from cerrado-like savannas on the narrow interfluves, pass through the wet campos and end in the rain forest on the alluvial soils.

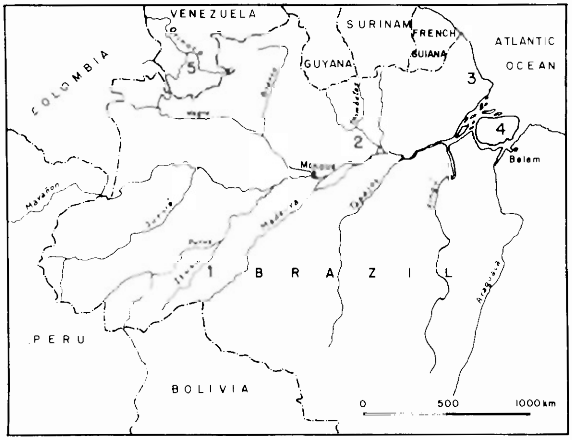


Fig. 10.23. Location of some savanna areas (campos) within the Amazonian region: *1* = the Puciari–Humaitá campos (after Braun and Ramos, 1959); *2* = the Aribamba campos (after Egler, 1960); *3* = the Amapá cerrados and campos (after Azevedo, 1967); *4* = the campos and swamps of the Marajo Island (after Meggers and Evans, 1957); *5* = the upper Orinoco savannas in southern Venezuela (after Eden, 1974).

The upper surface seems to be the remnant of an ancient tableland of Tertiary age. *Hancornia speciosa* is the characteristic savanna tree on well-drained latosols, where it occurs, together with *Curatella americana*, scattered in a grass carpet of *Aristida capillacea*, *Elyonurus* sp., *Leptocoryphium lanatum*, *Panicum rudgei* and other herbs and sedges.

Egler (1960) gave one of the first detailed accounts of the vegetation mosaics in the Lower Amazon region, near the mouth of the Trombetas River (Fig. 9.23). Here, both cerrado-like savannas and wet campos occur, besides gallery forests and a type of evergreen dry forest. The seasonal savannas occupy relict surfaces of an old tableland that has been preserved by hard lateritic crusts. The ground, paved with lateritic pebbles, has an open cover of grasses and sedges, with species like *Bulbostylis conifera*, *B. junciformis*, *Leptocoryphium lanatum*, *Paspalum carinatum*, *P. gardnerianum*, *Trachypogon* sp., etc. The isolated trees are mostly *Curatella americana*, *Qualea grandiflora* and *Salvertia convallariodora*. Seasonally waterlogged areas, on level sandstones, show a mosaic of open savannas (campos) and swamps. Besides grasses and sedges, these communities have many representatives of the families Rapataceae, Xyridaceae, Eriocaulaceae, Bromeliaceae and Orchidaceae. Floristic relationships may thus be established with the savannas on sandstones and those on the white sands of the interior Guiana region.

Azevedo (1967) also found a gradient of savanna formations in the Amapa Territory, in the northeastern part of the Amazon Basin (Fig. 9.23). Three main types of open vegetation occur there: cerrados, campos and seasonal swamps. The cerrado savannas have tree species like *Byrsonima crassifolia*, *Curatella americana*, *Palicourea rigida* and *Salvertia convallariodora*. The campos are treeless grasslands (hyperseasonal savannas) that, besides grasses and sedges, have many representatives of the monocotyledon families already mentioned. Seasonal swamps on flood plains (*campos de varzea*) are dominated by tall grasses and sedges, particularly by species of *Panicum* and *Paspalum*. The same three formations occur in Marajo Island nearby (Meggers and Evans, 1957).

In the upper Xingu area of Mato Grosso, Setzer (1967) reported that cerrados cover most of the interfluves, flat tablelands of about 400 m in elevation; while the flood plains, 100 m lower, are the domain of rain forests.

A mosaic of seasonal and hyperseasonal savannas has also been described in the Venezuelan Amazonas Territory. Eden (1974) reported that wooded savannas with *Curatella americana* and *Byrsonima crassifolia*, over a ground layer of *Axonopus*, *Leptocoryphium* and *Trachypogon*, appear as isolated patches on well-drained sites in several parts of the upper Orinoco. Waterlogged savannas dominated by species of *Andropogon*, *Paspalum* and *Rhynchospora* occur in poorly drained areas. Sometimes a few palms (*Mauritia flexuosa*) appear as the single woody component of these grasslands.

As may be realized from all these descriptions, similar vegetation gradients and mosaics appear in widely separated areas within the Amazonian region. Seasonal savannas occupy well-draines sites, while hyperseasonal savannas and esteros occur on poorly drained areas. Eiten (1978) believes that most of these non-forest ecosystems have to be excluded from the cerrado concept, but it must be remembered that Eiten's delimitation of the cerrado is essentially floristic. According to Eiten, only the drained savannas and the campos on well-drained soils or on soils with lateritic pebbles, contain a flora having affinities with the cerrado.

In a recent unpublished presentation covering the savannas in the Venezuelan Amazonas Territory, Huber (1979) considered three types of savannas: a llanos-like type, on hilly land with latosols; an Amazonian type on flat areas with white sands and podzolic soils; and flooded savannas on the poorly drained bottom lands. The llanos-like communities occur in small patches spread throughout the northern part of that Territory. They are tree savannas ecologically and floristically related to the savannas of the neighboring llanos. Their most common trees are *Bowdichia virgilioides*, *Curatella americana* and *Xylopia aromatica*, together with *Platycarpum orinocense*, a species restricted to this type of savanna in the Venezuelan Amazonia. Due to its highly permeable soil, the white sand savanna almost never remains waterlogged for long. According to Huber, this formation must be quite ancient, since in its still poorly known flora he found several new species of tropical African and Asian affinity. There are also open formations called *sabanetas*, transitional to the caatinga forest, dominated by the monocotyledon genera characteristic of white sands in the Guiana region. They remain flooded under half a meter of water over long periods.

To summarize the information presented in this short review, the same ecological and structural types already known from the llanos or from the Guianas do occur as isolated patches throughout the Amazonian region, with the possible exception of the upper Amazon in Peru and Brazil, where savannas have not yet been reported. Some new types, as yet unreported for other Neotropical regions, have also been described. The following savanna formations occur in the Amazonian region:

(1) Seasonal savannas, most of them with a structure of tree savannas. Apparently, wooded savannas or woodlands do not exist in this area. The tree savannas are quite similar to the seasonal formations occurring in the llanos, with perhaps a few additional species. The ground flora is quite similar both to that of the seasonal savannas in the llanos and to the herbaceous flora of the cerrados. The occurrence of seasonal savannas under an everwet climate may be explained in the following two ways. First, even in the Middle and Lower Amazonia, there are two or three months with reduced precipitations which simulate a short dry season. Second, these savannas might also represent relicts from a former extension of open formations throughout the Amazonian region. It seems logical to suppose that these relict savanna patches will tend to remain on the sites least suitable for recolonization by rain forests.

(2) Hyperseasonal savannas on periodically waterlogged lowlands. They seem to be equivalent to the wet campos of the cerrado region.

(3) Seasonal swamps, particularly of the varzea (flood-plain) type, dominated by tall grasses and sedges. They are closely related to the esteros of the llanos.

(4) Savannas on pure white sand with podzolized soils. This unit refers to a vegetation series occurring on this very special kind of substratum, that extends from a low sclerophyllous forest (Amazonian caatinga) to scrub and grass formations. Ecologically, they could be considered as semi-seasonal savannas. They extend throughout the whole area of white sand in the Amazonian and the Guianan regions without major floristic or structural changes.

These various savanna formations scattered throughout the Amazonian region constitute a link in the chain of savanna ecosystems which connects the Brazilian cerrados with the llanos and the interior Guiana savannas on one side, and with the coastal savanna region on the other side. Many authors have been reluctant to consider them as cerrados, and from a purely floristic viewpoint they are not; but they surely represent relicts from more widespread grassland formations connecting the main savanna areas of South America during earlier climatic phases (Eden, 1974; Sarmiento and Monasterio, 1975; Brown and Ab'Saber, 1979).

## THE GRAN PANTANAL, THE LLANOS DE MOJOS AND THE CONNECTIONS WITH THE CHACO FORMATIONS

In the very center of the South American continent, where Brazil, Bolivia and Paraguay meet, there is a large lowland of more than 100 000 km$^2$, known as the Gran Pantanal ("great swampland"). This northernmost part of the Paraguay–Plata Basin is a tectonic depression where the Quaternary climatic fluctuations produced an intricate mosaic of actual and relictual landforms, either of alluvial or aeolian origin.

The main consequence of these changes is that the drainage network has not yet reached a state of equilibrium with the present-day climate, causing most of the area to be waterlogged during the rainy season.

The Gran Pantanal vegetation is a mosaic of forests, cerrados and campos (Valverde, 1972; Eiten, 1975). The cerrado savannas dominate the interfluves with sandy soils and a deep water table. Campos de varzea (esteros) occupy the flood plains, either as pure grasslands of tall, coarse grasses and sedges, or intermingled with palmlands of *Copernicia alba*. This is a typical formation of the Chaco lowlands that reaches its northern limit in this area. Wet campos occur on somewhat higher sites, with woody species restricted to termite mounds. Here two species of Bignoniaceae, *Tecoma* (*Tabebuia*) *caraiba* and *T. aurea*, constitute the only trees on a campo ground layer. A mosaic of cerrados, cerradãos and forest islands of Chacoan affinities occurs on higher ground.

Eiten (1975) noticed that a totally intergrading series may be formed in the pantanal from a typical cerrado to the typical pantanal landscape of extensive flat lowlands, periodically inundated or badly drained, with a grass cover and large cerrado groves on high platforms. This series, correlated with a gradient of drainage conditions, includes, besides the two extreme types, two intermediate vegetation patterns, the one previously discussed (see p.253) with small cerrado groves on raised platforms with termitaria, the other where the cerrado trees show a definite tendency to clump in circular groves while the rest of the landscape is left treeless.

Two different floristic stocks meet in the Gran Pantanal, forming mosaics of plant formations, some of them of definite cerrado affinity, others closely related to the Chaco vegetation. Upland types may be more or less clearly differentiated according to their relationships with the cerrado or the Chaco, as is the case with campos and palmlands. Hyperseasonal savannas and esteros show instead a more gradual transition. These formations, that dominate the landscape throughout the eastern border of the Paraguayan and Argentinian Chaco, have species in common with the corresponding communities in tropical America. Morello and Adamoli (1974) analyzed the distribution and the ecological characteristics of these esteros (also called *pajonales*) in the eastern Chaco. The esteros are consociations of tall and coarse species of *Paspalum* or *Panicum*, while *Sorghastrum agrostoides* is the dominant grass in hyperseasonal formations. Frequently there is a sparse cover of *Copernicia alba*.

In northern Bolivia, there is another large plain mostly covered by seasonally flooded savannas. This area, known as the Llanos de Mojos, extends between the Andes and the Brazilian Shield, being bounded to the south by the Chiquitos highlands. To the north, the imprecisely known border with the continuous Amazonian forest seems to be located near the Madre de Dios River (Fig. 10.24). According to Denevan (1966), 50% of this 180 000 km$^2$ area is grassy savanna, about 30% tree or palm savanna, and the remaining 20% is under forest.

Seasonal and hyperseasonal savannas and esteros seem to occur in the area, depending on the length of the flooding period. Savanna woodlands cover the ground rarely attained by flooding, with *Curatella americana* and *Tabebuia suberosa* as the

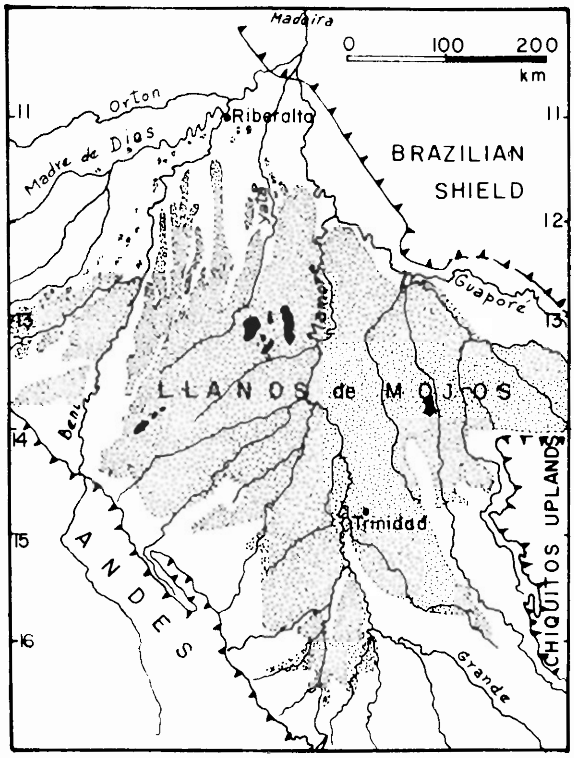


Fig. 10.24. The Llanos de Mojos in northern Bolivia. They occupy a large depression between the Andes, the western border of the Brazilian Shield and the Chiquitos Uplands (after Denevan, 1966).

two commonest trees (Denevan, 1966). This savanna type is popularly known as *arboleda*, while the name *chaparral* refers to a dense woodland with species of *Acacia*, *Cassia* and *Mimosa*. In some areas of arboledas, trees only grow on termite mounds as is the case in areas of Pantanal. Where flooding lasts for five to ten months, pure grasslands occur with species of *Leersia*, *Panicum* and *Paspalum*. *Sporobolus–Axonopus–Andropogon–Trichachne* grasslands or palm savannas with *Copernicia alba* and *Acrocomia totai* cover higher ground, with a shorter flooding period. Esteros with tall grasses and sedges occur on the ever-wet bottom lands.

Southeast of Mojos, along the continental divide between the Amazon and the Plata Basins, there is another poorly known region with various patterns of savannas and forests. Here, too, the Amazonian and Chacoan floras meet, resulting in a mosaic of formations of one type or another. According to

Hueck (1972), palm savannas with *Acrocomia totai* and *Attalea princeps* are common on dry soils near Santa Cruz, in eastern Bolivia. *Mauritia vinifera* appears instead as the characteristic palm of flooded savannas on the northern border of the Sierra de Velazco.

## THE SAVANNAS OF SOUTHERN MEXICO, CENTRAL AMERICA AND THE CARIBBEAN ISLANDS

Neotropical savannas cover 20 000 km$^2$ in the States of Tabasco, Chiapas, Veracruz, Campeche, Oaxaca and Guerrero in southern Mexico (Flores Mata et al., 1971). They occur on coastal plains both of the Gulf of Mexico and the Pacific Ocean (Fig. 10.25), as well as in interior valleys, where a strong human influence makes their ecological interpretation difficult (Miranda, 1952). This same type of interior savanna extends to Honduras (Johannessen, 1963).

Puig (1972) analyzed the savannas of Tabasco, in the coastal plain of the Gulf, where he recognized four main types:

(1) An open tree savanna on upper topographic positions with ill-drained latosols. *Curatella americana*, *Byrsonima crassifolia* and the palm *Acrocomia mexicana* form the woody layer, while the commonest grasses and sedges are *Dichronema ciliata*, *Digitaria leucites*, *Paspalum pectinatum*, *P. plicatulum*, *P. punctatum*, *Trachypogon angustifolius*, etc.

(2) A denser wooded savanna, which is really a mosaic of areas of tree savanna and scrub patches.

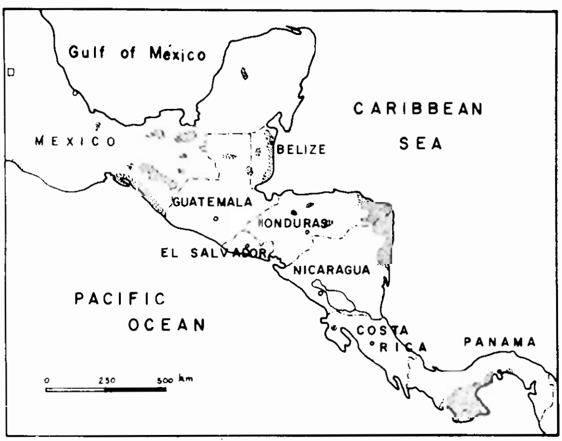


Fig. 10.25. The major savanna regions of southern Mexico and Central America.

To the three trees mentioned above, Puig adds species of *Bauhinia*, *Calliandra*, *Calyptranthus*, *Clidemia*, *Cochlospermum*, etc. The soils are apparently similar to the previous type, but as overgrazing has prevented fires, an invasion of woody species has been induced.

(3) *Tasistales* or palm swamps, with the palm *Paurotis* (*Acoelorraphe*) *wrightii* over a grass and sedge cover of *Andropogon*, *Paspalum*, etc.

(4) *Encinares* or open woodlands of *Quercus oleoides*, with forest trees (*Vochysia*, *Terminalia*) and savanna trees (*Byrsonima*, *Xylopia*). The herb layer is poorly developed, with some grasses, sedges and legumes.

Gómez Pompa (1973), in his analysis of the vegetation of Veracruz (Mexico), recognized a special type of savanna woodland strongly related to lowland oak forest. Its tree species are *Acrocomia mexicana*, *Byrsonima crassifolia*, *Coccoloba barbadensis*, *Crescentia cujete* and *Curatella americana*. The upland savannas have many species in common with this type of savanna woodland, but they have a close ground cover of *Andropogon*, *Bulbostylis*, *Cassia*, *Dichronema*, *Paspalum*, *Rhynchospora*, etc. Finally, *Paurotis wrightii* forms pure stands of palm savannas on wet soils corresponding to the drier parts of swamps.

It is clear, then, that three types of savanna formations occur as more or less large patches in the coastal regions of tropical Mexico: a seasonal savanna on latosols with just a few tree species, apparently quite similar to other seasonal savannas of northern South America and Central America; a hyperseasonal savanna characterized by the palm *Paurotis wrightii*; and a third type not previously found elsewhere — a woodland formation apparently related to the tropical oak forests, though it is not yet clear if it should be considered as a secondary seral stage of that forest formation.

In British Honduras (Belize), Charter (1941) reported the occurrence of a series of savanna formations related to soil evolution on river terraces and on the coastal plain. At a certain stage of soil differentiation, when an impervious clay develops under a sandy layer, a *Quercus* savanna appears, later changing to a *Curatella–Byrsonima* community, and finally to a pine woodland (*Pinus caribaea*). On level terraces flooded for long periods, the vegetation is a sedge (hyperseasonal) savanna, dotted with clumps of the palm *Paurotis* *wrightii* and isolated trees of *Crescentia cujete* and *Cameraria belizensis*. There also are pine savannas in hilly areas on soils similar to the pine savanna soils of the plains. Charter compared these pine woodlands to those of the southeastern United States and the Bahamas.

Stretches of seasonal savannas are scattered through the Peten Province of Guatemala, either with *Pinus caribaea*, *Curatella americana* or *Byrsonima crassifolia* (Lundell, 1937). On the Caribbean coast of Honduras and Nicaragua, an extensive area of deeply weathered quartz gravel and sand supports a savanna vegetation. Parsons (1955) described the environment and vegetation of this Miskito savanna. It is a park-like savanna where pines are widely spaced, intermingled with a sparse tree cover of *Byrsonima crassifolia*, *Calliandra houstoniana*, *Curatella americana*, *Miconia* spp., and less commonly *Crescentia*, *Mimosa* and *Quercus*. The ground layer is rich in sedges (*Rhynchospora*, *Bulbostylis*, etc.) with *Trachypogon* sp. as the most important grass, followed by species of *Andropogon*, *Aristida*, *Leptocoryphium* and *Paspalum*. The highest layer, open to very open, up to 25 m high, has *Pinus caribaea* as its single species. On poorly drained soils Parsons reports the occurrence of palm groves (*Paurotis*).

Taylor (1963) analyzed these coastal pine savannas of Nicaragua, favoring the hypothesis that they represent secondary formations of the tropical rain forest, since they occur in an area of exceptionally high rainfall (2600–3500 mm, with three dry months). He pointed out that even in the area of deciduous tropical forest there are secondary savannas with *Crescentia alata* and several species of *Acacia*, *Haematoxylon*, *Pithecellobium*, etc., over a grass cover of *Aristida* and *Bouteloua*.

Seasonal savannas of the *Curatella* type have also been reported on upland soils of coastal Costa Rica and Panamá. Porter (1973) listed *Anacardium occidentale*, *Byrsonima crassifolia*, *Curatella americana*, *Psidium guajava*, *Xylopia aromatica* and *Xylopia frutescens* as the dominant trees in the Panamian savanna. Among the species of the ground layer he cites *Andropogon angustatus*, *Aristida jorullensis*, *Rhynchospora armerioides*, etc.

Thus, in several parts of Central America from Guatemala to Panama (Fig. 10.25), there are the same types of savannas already found in Mexico and northern South America. However a quite interesting new formation appears: the pine savanna, either on lowlands or highlands, where *Pinus caribaea* form a high tree layer. These tall trees are absolutely unknown in all other types of Neotropical savanna formations. Whether these pine savannas are secondary to rain forests or whether they constitute original types determined by soil evolution under particular conditions of climate and parent material, is not yet clear. A similar type of pine savanna occurs in Cuba, including the Isla de Pinos, and Hispaniola.

In Hispaniola, one of the Greater Antilles, there are savannas on the plains and plateaux (Beard, 1953). A treeless savanna covers an extensive area of the central plain with poorly drained soils. A tree savanna, either with pines (*P. occidentalis*) or with the typical orchard trees (*Byrsonima*, *Curatella*) covers a broken surface, remnant of a dissected plateau in the same area.

In several of the Lesser Antilles, there are reduced patches of savanna, such as the Gran Sabana of Dominica, with *Byrsonima* and *Sporobolus* (Beard, 1953; Howard, 1973). But it is in Cuba, the largest of the Antilles, that tropical savannas reach regional importance. Though there is no agreement among authors about the extent of natural savannas as opposed to man-induced open formations (Bennet, 1928; Waibel, 1943; Seifriz, 1943; Beard, 1953; Borhidi and Herrera, 1977), between 10 and 20% of the island seems to be covered by original or by semi-natural savannas (Fig. 10.26).

Seasonal savannas occur on three different types of habitats: shallow soils, often with an ironstone hardpan; quartz sands; and red soils developed on serpentine. An open formation with palms (*Sabal parviflora*) and other low trees (*Acacia*, *Caesalpinia*, *Pisonia*) occurs on shallow soils, with lateritic pebbles or hardpan (locally called *mocarrero*). The ground layer includes several species of *Andropogon*, *Panicum*, *Paspalum*, *Rhynchospora*, *Scleria* and *Setaria* (Borhidi and Herrera, 1977). Siliceous sandy soils, in western Cuba and the Isla de Pinos are covered by open woodlands of *Pinus tropicalis*, or sometimes *P. caribaea*, with scattered palms, such as *Colpothrinax wrightii*, *Copernicia curtissii* and *Paurotis wrightii*. The herb layer includes species of *Andropogon*, *Bulbostylis*, *Cyperus*, *Fimbristylis* and *Paspalum*, as well as many typical neotropical savanna species like *Leptocoryphium*

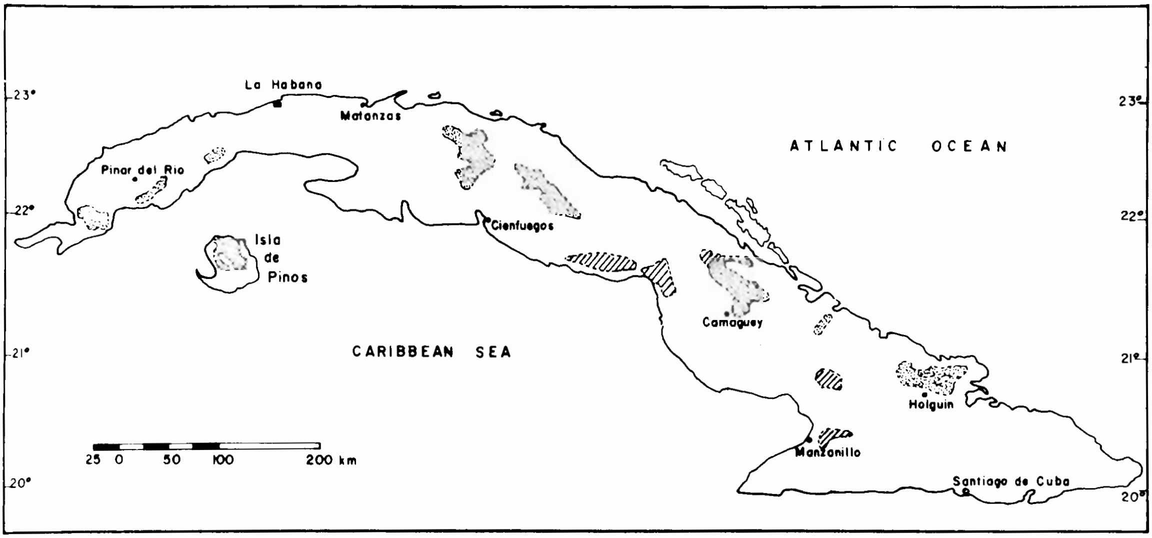


Fig. 10.26. The distribution of natural savannas in Cuba. Dotted areas correspond to seasonal savannas, hatched areas to hyperseasonal savannas. (Adapted from Borhidi and Herrera, 1977.)

*lanatum*, *Mesosetum loliiforme* and *Trachypogon filifolius*. Serpentine soils typically maintain a tree savanna that has as a distinctive physiognomic feature the abundance of low palms, like *Coccothrinax miraguama*, *C. pseudorigida*, *Copernicia macroglossa*, *C. pauciflora*, *C. ramosissima*, *C. yarey*, etc. (Borhidi and Herrera, 1977). Other trees are *Byrsonima crassifolia*, *Curatella americana*, *Rondeletia correifolia*, *Tabebuia lepidophylla*, *T. lepidota*, etc. The ground layer has several species of *Andropogon* and *Aristida*, besides *Imperata brasiliensis*, *Leptocoryphium lanatum* and other widespread Neotropical savanna grasses and sedges.

On the highlands of the Sierra de Nipe in eastern Cuba, at 400 to 600 m above sea level, Carabia (1945) reported open pine woodlands on limonitic soils derived from serpentine. According to him, grasses and sedges represent the true dominant species in these *pinares*. *Pinus cubensis*, a tree up to 25 m high, is the single tree species, with a density of about 200 trees $ha^{-1}$. A similar community occurs in the same area, but without pines. Carabia suggested that these pineless savannas are fire-induced.

Hyperseasonal savannas occupy hydromorphic soils on the flood plains of several of the main rivers of the island. Several palms of the genus *Copernicia* and various shrubby legumes of the genera *Acacia*, *Caesalpinia* and *Cassia* form the open woody layer, while the ground vegetation includes species of *Andropogon*, *Aristida*, *Bulbostylis* and *Rhynchospora*. Seasonal swamps have two distinctive palms: *Paurotis wrightii* and *Sabal parviflora*. In the grass and sedge layer, up to 2 m high, the more frequent species are *Cladium jamaicense*, *Hymenachne amplexicaulis*, *Panicum virgatum* and several species of *Cyperus*, *Eleocharis*, *Fimbristylis* and *Rhynchospora*.

In summary, in the Caribbean area, particularly in the two major islands Cuba and Hispaniola, seasonal and hyperseasonal savannas, as well as seasonal swamps, occupy substantial areas. Some of these savanna formations are floristically quite similar to continental savannas, either considering the tree or the ground flora. But it is in this insular region where pine savannas, also occurring in Central America, reach their greatest diversification, with various lowland or medium-altitude types occurring on different soil types, either silicious or derived from serpentine. Another point to note about Cuban savannas is the high degree of endemism shown by this flora. This fact appears clearly in palms, where several genera reach a remarkable specific diversification within these savanna formations.

**THE FLORA OF THE NEOTROPICAL SAVANNAS: ITS SPECIFICITY AND AFFINITIES**

The savanna formations in tropical America, as every series of plant formations spreading over an extensive geographical range, include a complex mixture of floristic elements of various provenance, age and affinity. This fact follows from the continuous paleogeographical and paleoecological changes that have taken place in the two continents of North and South America and their related islands. Since the Middle Mesozoic, when the Atlantic Ocean began to spread, pushing apart the continental masses hitherto united in a single supercontinent, the South American and to a lesser degree the Central American flora began to evolve more or less isolated from each other and from other floristic realms. In the Late Cenozoic their evolution culminated under the impacts of the cataclysmic changes induced by the still active Andean orogeny, the periodic climatic oscillations of the Glacial Ages, and their associated fluctuations in sea level. These events influenced decisively the present-day distribution of plant formations and their corresponding floras and faunas. [See Simpson Vuilleumier (1971), Van der Hammen (1974), and Brown and Ab'Saber (1979) for a general consideration of the paleogeographical evolution of South America and its ecologic consequences.]

The two major vegetation types of tropical lowlands in the Americas, rain forests and savannas, seem to have suffered successive expansions and contractions in their areas during the alternating dry and wet climatic phases. During the Last Glacial a dramatic constriction of rain forests took place, with a parallel expansion of savannas and to a lesser degree of thorn forests as well. [Ab'Saber (1977) presented a paleogeographic map with the natural domains of South America between 13 000 and 18 000 years ago.]

These frequent displacements of whole biomes along continental distances provided ample opportunities for speciation in isolation in forest and savanna refuges, during the drier and more humid climatic phases respectively. Furthermore, these disruptions of the vegetation equilibrium also facilitated wide interchanges between the floristic stocks of the various interacting and interconnecting plant formations. In this way one may suppose that a vast genetic flow took place, along with the diversification of characteristic taxa in each ecosystem at various moments of these cycles.

In spite of the resulting inherent heterogeneity in age, origin and evolutionary history of the component species, a characteristic savanna flora evolved in tropical America. In fact, the overall floristic picture provided by these formations is that of a rich flora in which at least half of the species appear to be largely restricted to savanna ecosystems, while the other half consists of more ubiquitous components. A first distinction can thus be made at the species level between a floristic stock mostly exclusive to Neotropical savannas, and the remaining alien species representing a more or less opportunistic, occasional and often more recent component of this flora.

One further distinction has to be made within the Neotropical savanna flora between the woody and half-woody elements on the one side and the herbaceous species on the other side, since the two groups seem to represent rather divergent evolutionary situations. Four different groups must therefore be considered separately: a cohort of woody species exclusive to these savannas; a numerous group of trees closely related to rain-forest species; a herbaceous and subshrubby flora peculiar to savannas; and an accesory non-woody flora without much ecological specificity arriving in these ecosystems from different sources.

In order to go more deeply into the analysis of the affinities of the Neotropical savanna flora, attention must now be shifted to the main patterns of distribution of plant genera within and between savanna formations. Genera are a more adequate analytical tool for providing a wider evolutionary perspective of floristic changes and relationships.

Among the woody species peculiar to Neotropical savannas are a number of taxa, phylogenetically more or less isolated, that do not have non-savanna species in the same genus. Table 10.7 lists some of these species. This list is rather limited, but several of the species are quite abundant and frequent savanna trees. All of them occur in the cerrados, though several extend to other formations. *Cochlospermum* has two Neotropical species, one *C. regium* is a half-woody plant exclusive to the cerrado, the other *C. vitifolium* is a tree occurring in savannas of northern South America and Central America and in seral stages of tropical deciduous

TABLE 10.7

Woody species belonging to the characteristic floristic element of Neotropical savannas (isolated species, sometimes monotypic)

| Species | Family |
|---|---|
| *Antonia ovata* | Loganiaceae |
| *Austroplenckia populnea* | Celastraceae |
| *Bowdichia virgilioides* | Fabaceae |
| *Bowdichia major* | Fabaceae |
| *Cochlospermum regium* | Cochlospermaceae |
| *Cochlospermum vitifolium* | Cochlospermaceae |
| *Curatella americana* | Dilleniaceae |
| *Diptychandra glabra* | Caesalpiniaceae |
| *D. aurantiaca* | Caesalpiniaceae |
| *Hancornia speciosa* | Apocynaceae |
| *Harpalyce brasiliana* | Fabaceae |
| *Magonia pubescens* | Sapindaceae |
| *Magonia glabrata* | Sapindaceae |
| *Pamphilia aurea* | Styracaceae |
| *Pterodon pubescens* | Fabaceae |
| *Pterodon polygalaeflorus* | Fabaceae |
| *Riedeliella graciliflora* | Fabaceae |
| *Salvertia convallariodora* | Vochysiaceae |
| *Spiranthera odoratissima* | Rutaceae |

forests as well. *Bowdichia virgilioides*, *Curatella americana*, *Hancornia speciosa*, *Magonia pubescens* and *Salvertia convallariodora* occur to a varying extent outside the cerrado region. It may be postulated that their taxonomic isolation reflects an evolution within these ecosystems which has continued long enough to allow a differentiation at the generic level, while the lack of diversification may suggest an advanced specialization. They probably represent a floristic paleoelement well adapted to the savanna environment.

There is another small group of genera of woody plants in which, even though each genus has several rain-forest species, many of their species belong exclusively to the savannas. Among the genera in this group may be mentioned *Anacardium*, *Bombax*, *Byrsonima*, *Kielmeyera*, *Stryphnodendron* and *Sweetia*. Several species in these genera are quite common savanna trees, like *Byrsonima crassifolia* and *B. coccolobaefolia* throughout the South American savannas, or *Kielmeyera coriacea* and *Stryphnodendron barbadetimam* in the cerrados. The genus *Bombax* has even reached a high degree of diversification in the cerrado, with more than ten species.

These two groups of genera of woody plants together constitute the characteristic floristic element of Neotropical savannas, either by their exclusive occurrence or by their greater evolutive radiation in these ecosystems. As may be seen in Chapter 5 on growth forms, a hypothetical chain of architectural and functional changes may have derived from ancestral forest trees some half-woody or even subterranean tree forms peculiar to savannas, such as *Anacardium humile* or *Byrsonima verbascifolia*.

A different situation occurs in many woody genera that have diversified mostly in the Amazonian or the Atlantic rain forests where they have many species. But in these genera, one or two species, quite closely related morphologically and taxonomically to some of the rain-forest representatives, occur exclusively in the cerrados. These savanna vicariants of rain-forest species constitute an important component of the rich woody flora of the Brazilian cerrados (Table 10.8). A comparable situation does not occur elsewhere. Several genera of forest trees, like *Hymenaea*, *Copaifera* or *Vochysia*, are common to both savanna and forest, but their representatives in the two ecosystems are not closely related.

Apparently the Brazilian rain forests have been the ecosystems where all these genera accomplished their greatest evolutionary radiation. The very fact of the existence of closely related species in the neighboring savannas suggests a long interplay between both types of ecosystems, as well as a relatively more recent speciation of the representatives in the savannas. One may speculate that the savanna vicariant species probably originated during the glacial periods of rain-forest contractions when savannas spread over large areas of the tropical American lowlands. The occurrence in some cases of a diversification below the species level suggests that this process is still actively proceeding (Table 10.8).

Another situation is represented by many genera of wide distribution in tropical areas which have representatives in several plant formations, including a few savanna species (Table 10.9). These species may be considered part of a less specific floristic stock able to adapt to many different ecological situations, including those of tropical savannas.

To summarize this discussion about the phyto-

TABLE 10.8

Some examples of pairs of closely related species (vicariants), one growing in the Brazilian rain forests, the other in the cerrados (from Heringer et al., 1977)

| Tropical rain forests (Amazonian and Atlantic) | Cerradão and cerrado |
|---|---|
| *Aegiphila arborescens* Vahl | *A. lhotzkyana* Cham. |
| *Agonandra silvatica* Ducke and *Agonandra brasiliensis* Miers f. *silvestre* | *A. brasiliensis* Miers f. *campestre* |
| *Andira retusa* H.B.K. | *A. humilis* Mart. |
| *Aspidosperma duckei* Huber and *Aspidosperma pallidiflorum* M. Arg. | *A. tomentosum* Mart. |
| *Brosimum discolor* Schott. | *B. gaudichaudii* Trec. |
| *Callisthene dryadum* A. Duarte | *C. fasciculata* (Spr.) Mart. |
| *Caryocar villosum* (Subl.) Pers. | *C. brasiliense* Camb. |
| *Cenostigma tocantinum* Ducke | *C. gardnerianum* Tul. |
| *Connarus cymosus* Planch. | *C. suberosus* Planch. |
| *Copaifera lucens* Dwyer | *C. langdorffii* Desf. |
| *Copaifera trapezifolia* Hayne | *C. oblongifolia* Mart. |
| *Dalbergia nigra* Fr. All. | *D. violacea* (Vog.) Malme |
| *Dalbergia foliolosa* Benth. | *D. spruceana* Benth. |
| *Dimorphandra parviflora* Benth. | *D. mollis* Benth. |
| *Dioclea megacarpa* Rolfe | *D. erecta Hoehne* |
| *Diospyros hispida* DC | *D. hispida* var. *camporum* Warm. |
| *Emmotum glabrum* Benth | *E. nitens* (Benth) Miers |
| *Enterolobium contortisiliquum* (Vell.) Morong | *E. gummiferum* (Mart.) Macbr. |
| *Erythrina verna* Vell | *E. mulungu* Mart. |
| *Ferdinandusa speciosa* Pohl | *F. elliptica* Pohl |
| *Hymenaea altissima* Ducke and *Hymenaea stilbocarpa* Mart. | *H. stigonocarpa* Mart. |
| *Kielmeyera excelsa* Camb. | *K. petiolaris* (Spr.) Mart. |
| *Lafoensia glyptocarpa* Koehne | *L. densiflora* Pohl |
| *Machaerium villosum* Vog. | *M. opacum* Vog. |
| *Mapronnea guianensis* Aubl. | *M. brasiliensis* St. Hil. |
| *Mimosa obovata* Benth. | *M. laticifera* Rizz. & Matt. |
| *Peschiera affinis* (M. Arg.) Miers | *P. affinis* var. *campestris* Rizz. |
| *Piptadenia peregrina* (L.) Benth. | *P. falcata* Benth. |
| *Plathymenia foliolosa* Benth. | *P. reticulata* Benth. |
| *Psittacanthus decipiens* Eichl. | *P. robustus* Mart. |
| *Qualea jundiahy* Warm. | *Q. multiflora* Mart. |
| *Sclerolobium rugosum* Mart. | *S. aureum* (Tul.) Benth. |
| *Stryphnodendron polyphyllum* Benth. | *S. barbatimam* (Veu.) Mart. |
| *Swartzia macrostachya* Benth. | *S. grazielana* Rizz. |
| *Tabebuia chrysotricha* (Mart.) Standl. | *T. ochracea* (Cham.) Standl. |
| *Terminalia hylobates* Eichl. | *T. argentea* Mart & Zucc. |
| *Tragia amoena* M. Arg. | *T. lagoensis* M. Arg. |
| *Vochysia tucanorum* (Spr.) Mart. | *V. thyrsoidea* Pohl. |
| *Zeyhera tuberculosa* (Vell.) Bur. | *Z. digitalis* (Vell.) Hoehne |

geographical significance of the woody flora in the American savannas, one may first point out that the overall pattern of speciation in this flora suggests a persistent contact between rain forests and savannas, with a heavy interchange of floristic stocks from the former to the latter over a rather extended period. In this way the Amazonian and the Atlantic rain forests appear as the main sources nourishing primarily the cerrados and through them the other American savannas. But evidently this has not been

TABLE 10.9

Woody genera with most of their species in rain forests but with a few savanna species

| | |
|---|---|
| *Agonandra* (Opiliaceae) | *Ilex* (Aquifoliaceae) |
| *Andira* (Fabaceae) | *Jacaranda* (Bignoniaceae) |
| *Annona* (Annonaceae) | *Laplacea* (Theaceae) |
| *Aspidosperma* (Apocynaceae) | *Licania* (Rosaceae) |
| *Astronium* (Anacardiaceae) | *Lonchocarpus* (Fabaceae) |
| *Bauhinia* (Fabaceae) | *Matayba* (Sapindaceae) |
| *Blepharocalyx* (Myrtaceae) | *Ouratea* (Ochnaceae) |
| *Brosimum* (Moraceae) | *Palicourea* (Rubiaceae) |
| *Calliandra* (Fabaceae) | *Platycarpum* (Rubiaceae) |
| *Caraipa* (Hypericaceae) | *Pinus* (Pinaceae) |
| *Caryocar* (Caryocaraceae) | *Qualea* (Vochysiaceae) |
| *Chaunochiton* (Olacaceae) | *Quercus* (Fagaceae) |
| *Clusia* (Hypericaceae) | *Roupala* (Proteaceae) |
| *Diospyros* (Ebenaceae) | *Symplocos* (Symplocaceae) |
| *Esenbeckia* (Rutaceae) | *Vochysia* (Vochysiaceae) |
| *Ficus* (Moraceae) | *Xylopia* (Annonaceae) |
| *Hirtella* (Rosaceae) | |

TABLE 10.10

Some characteristic herbaceous species in Neotropical savannas

| | |
|---|---|
| *Axonopus* (Poaceae) | *Lagenocarpus* (Cyperaceae) |
| *Brasilia* (Asteraceae) | *Leptocoryphium* (Poaceae) |
| *Bulbostylis* (Cyperaceae) | *Mesosetum* (Poaceae) |
| *Curculigo* (Amaryllidaceae) | *Orthopappus* (Asteraceae) |
| *Chaetium* (Poaceae) | *Polycarpaea* (Caryophyllaceae) |
| *Ctenium* (Poaceae) | *Rhynchospora* (Cyperaceae) |
| *Diectomis* (Poaceae) | *Thrasya* (Poaceae) |
| *Echinolaena* (Poaceae) | *Trachypogon* (Poaceae) |
| *Gymnopogon* (Poaceae) | *Tristachya* (Poaceae) |
| *Hoehnephyton* (Asteraceae) | *Torresea* (Fabaceae) |
| *Kyllinga* (Cyperaceae) | |

the only floristic source of the savanna flora; other tropical, subtropical and even temperate formations have also contributed, as seems to be indicated by the distribution of numerous genera listed in Table 10.9. Moreover, in the case of the northernmost formations occurring in Mexico, Central America and the Caribbean, some boreal genera have contributed a few species to the peculiar flora of the savannas, as for instance, some large temperate genera like *Quercus* and *Pinus*.

The case appears somewhat different with the herbaceous and subshrubby savanna flora. A few of these genera are more or less restricted to tropical American savannas or to tropical savannas in general. This is the case with certain small genera, either monotypic or with few species, like *Brasilia*, *Orthopappus* and *Hoehnephyton* among the Asteraceae, *Diectomis* in the grasses and *Torresea* in the legumes. Other genera show a wider diversification in Neotropical savannas, like the grasses *Axonopus*, *Mesosetum* and *Trachypogon*, or the sedges *Bulbostylis*, *Lagenocarpus* and *Rhynchospora* (Table 10.10).

However, these two groups of herbaceous genera concentrated in tropical savannas only include a minority of the herbaceous savanna flora. Most of the remaining species, composing by far the bulk of this flora, belong to widespread and non-specialized taxa whose species occur in almost every type of ecosystem, though with a concentration in seral communities, transitory niches and disturbed habitats. These genera undoubtedly represent more opportunistic evolutionary strategies; thanks to this behavior they have been able to occupy the widest geographical ranges and to show the richest diversification. Table 10.11 lists some of these taxa, all of them with 100 or more species, only a few of which are peculiar to Neotropical savannas. Many of these species appear among the codominants in the herb layer of every Neotropical savanna. Nevertheless, it is a rather difficult task to identify with any acceptable degree of certainty the origin and affinities of this more opportunistic floristic stock. Because of the lack of adequate factual data, this point remains for the moment highly speculative.

If one's purpose were to elucidate the center of origin and diversification of the herbaceous savanna flora as a means of reconstructing its history, a more suitable research object could be certain monotypic elements restricted to, but of widespread occurrence, in these formations — like *Leptocoryphium lanatum* — whose evolutive steps might be followed through the morphological, functional and biochemical variability of its populations among the different ecosystems where it occurs. The same may be said of some other small grass genera, such as *Ctenium*, *Echinolaena*, *Thrasya* and *Trachypogon*.

The palms constitute a particular case within the savanna flora since a few genera, like *Coccothrinax*, *Colpothrinax*, *Copernicia* and *Mauritia*, have attained a significant diversification within savanna ecosystems as characteristic elements of hyperseasonal savannas and esteros (Table 10.12). The

TABLE 10.11

Some large plant genera having some representatives in Neotropical savannas (total number of species and distribution after Willis, 1973)

| Species | Family | Total number of species | Distribution |
|---|---|---|---|
| *Aeschynomene* | Fabaceae | 150 | tropical and subtropical |
| *Andropogon* | Poaceae | 113 | tropical and subtropical |
| *Aristolochia* | Aristolochiaceae | 350 | tropical and subtropical |
| *Aster* | Asteraceae | 500 | cosmopolitan |
| *Baccharis* | Asteraceae | 400 | American |
| *Borreria* | Rubiaceae | 150 | warm |
| *Cassia* | Fabaceae | 600 | tropical and warm temperate |
| *Crotalaria* | Fabaceae | 550 | tropical and subtropical |
| *Croton* | Euphorbiaceae | 750 | tropical and subtropical |
| *Cuphea* | Lythraceae | 250 | American |
| *Desmodium* | Fabaceae | 450 | tropical and subtropical |
| *Eriosema* | Fabaceae | 140 | tropical and subtropical |
| *Eupatorium* | Asteraceae | 1200 | cosmopolitan |
| *Euphorbia* | Euphorbiaceae | 2000 | cosmopolitan |
| *Evolvulus* | Convolvulaceae | 100 | tropical and subtropical |
| *Galactia* | Fabaceae | 140 | tropical and subtropical |
| *Gomphrena* | Amaranthaceae | 100 | American |
| *Hyptis* | Lamiaceae | 400 | warm American |
| *Indigofera* | Fabaceae | 700 | warm |
| *Lantana* | Verbenaceae | 150 | tropical, American, African |
| *Lippia* | Verbenaceae | 220 | tropical, American, African |
| *Mimosa* | Mimosaceae | 500 | tropical and subtropical |
| *Pavonia* | Malvaceae | 200 | tropical and subtropical |
| *Phaseolus* | Fabaceae | 240 | tropical and subtropical |
| *Polygala* | Polygalaceae | 600 | cosmopolitan |
| *Rhynchosia* | Fabaceae | 300 | tropical and subtropical |
| *Salvia* | Lamiaceae | 700 | tropical and temperate |
| *Senecio* | Asteraceae | 3000 | cosmopolitan |
| *Sida* | Malvaceae | 200 | warm |
| *Stachytarpheta* | Verbenaceae | 100 | American |
| *Stevia* | Asteraceae | 150 | tropical and subtropical American |
| *Tibouchina* | Melastomataceae | 200 | tropical American |
| *Vernonia* | Asteraceae | 1000 | cosmopolitan |
| *Viguiera* | Asteraceae | 150 | warm American |

TABLE 10.12

Palm genera with representatives in Neotropical savanna formations

| | |
|---|---|
| *Acanthococos* | *Copernicia* |
| *Acrocomia* | *Diplothemium* |
| *Astrocaryum* | *Mauritia* |
| *Attalea* | *Orbignya* |
| *Bactris* | *Paurotis* |
| *Butia* | *Sabal* |
| *Coccothrinax* | *Syagrus* |
| *Colpothrinax* | |

genus *Copernicia*, for instance, has several South American species extensively occurring in tropical savannas and extending to dry forests and subtropical grasslands. Thus *C. alba* occurs in the subtropical grasslands of the Gran Chaco; *C. cerifera* in the dry formations of northeastern Brazil (caatingas); *C. tectorum* and *C. sanctae-martae* in northern South American savannas. But this genus has attained a most remarkable speciation within the island of Cuba, where about ten species occur in its savannas. Moreover the Cuban savannas and the cerrados are the two Neotropical areas where savanna palms show a particularly rich diversification, often with quite peculiar growth forms like the acaulescent dwarf palms (see Ch.5). On the other hand, palms appear among the primeval floristic elements of Neotropical savannas. Van der Hammen (1972) reported *Mauritia* pollen in the Paleocene of northern South America as an indication of the early occurrence of wet savanna-like formations in this area. Other palms, such as species of *Astrocaryum*, *Syagrus* and some other genera, appear instead as more recent additions to the savanna flora from rain-forest stocks, where these genera have a large number of species.

Another interesting point to notice concerning the relationships of the Neotropical savanna flora is its almost total lack of affinity with some nearby dry floras. In the cerrado, for instance, it is surprising that, even though this formation borders the dry caatinga for thousands of kilometers, all along this border the two types remain quite distinct, either floristically or in vegetation structure. Though certain transitional communities exist (Eiten, 1972), they seem to be rather impoverished types of each formation than ecotones where cerrado and caatinga elements mix with each other. Similarly, a savanna thorn forest contact occurs in Venezuela between the llanos and the semi-arid and arid formations of the Caribbean coast (Sarmiento, 1976), but the distinction between them always remains clear-cut. Floristically the number of common species is almost nil, while the genera common to both are large genera of the type referred to previously as unspecialized or ubiquitous, like *Cassia*, *Croton*, *Gomphrena*, *Mimosa* and *Sida*. Quite exceptionally an element characteristic of the dry floras enters into the savannas, such as one species of *Plumeria* in the Rio Branco–Rupununi savannas or *Prosopis juliflora*, a ubiquitous tree in areas with seasonal water shortage, that may occasionally enter the savannas along the savanna/thornscrub border in northern South America. Similarly a few floristic elements common to savannas and arid formations are really rainforest genera that not only have a few savanna representatives, but also extend to dry vegetation types. Among them are *Aspidosperma*, *Tabebuia*, and a few other woody genera. Typical elements of arid formations, like the Cactaceae and Agavaceae, are almost unrepresented in savannas. Thus, the only savanna cactus, *Cereus jacamaru*, does not have close relationships with species of dry formations, but with species of tropical deciduous and subtropical forests.

A particular case worth separate consideration concerns communities occurring on pure white sand, either in the Amazonian region (*campinas* or Amazonian caatingas) or in the Guianas. These white sand formations — bush, open woodlands and savannas — have a peculiar woody flora, in which, besides a few common savanna species that sometimes may occur, there is a new floristic element, unrelated to the savanna flora of other formations. This characteristic component shows the closest affinity with the flora of the Guiana highlands (Maguire, 1971), mainly with species typical of the scrub, low forest, and herbaceous swamps that characterize the high sandstone plateaux of the Roraima Formation (tepuys). Steyermark (1966, 1967) analyzed these isolated highland formations from both floristic and phytogeographical viewpoints. He stressed not only the high degree of endemism within this flora, but also the relationships with the Amazonian lowlands, particularly with the open formations referred to previously.

A whole set of peculiar plant families, particularly among the monocotyledons, characterizes the tepuys as well as the open lowland communities. Among the herbaceous flora may be mentioned species in the families Bromeliaceae, Cyperaceae, Eriocaulaceae, Marantaceae, Orchidaceae, Rapataceae, Thurniaceae, and Xyridaceae. The most characteristic genera among the woody flora are: *Antonia*, *Clusia*, *Cupania*, *Humiria*, *Matayba*, *Rapanea*, *Ternstroemia*, etc. The grass family, on the other hand, is conspicuously underrepresented, even in the herbaceous formations, and for this reason it is hard to apply to most of them the name of savannas, the denomination of campinas being preferable (Lisboa, 1975).

Huber (1979) stressed the floristic peculiarities of the Amazonian-type savannas in the Venezuelan Amazonas Territory, where several highly interesting floristic connections with Paleotropical areas are becoming evident with the advancing knowledge of their flora, suggesting the considerable antiquity of this particular kind of savanna.

Outside the white sand areas, the plant communities exhibiting the greatest number of Guianan elements undoubtedly are certain types of esteros and morichales occurring throughout tropical America on permanently wet, sandy soils (Aristiguieta, 1969; Egler, 1960). When discussing the origin and evolution of the savanna flora in Surinam, Van Donselaar (1965) suggested that most of its species originated from an ancestral savanna stock living on the high plateaus of the Roraima Formation and migrating to and evolving in the lowlands as the plateaus were lifted, broken and isolated from one another. The small southern Surinam savannas have a strong floristic bond with those of Northern Surinam, and also with those of central Amazonia (Van Donselaar, 1968).

The flora of the savannas on siliceous sands in the Caribbean and Central America (eastern Cuba, Isla de Pinos, Belize, Honduras, etc.), though it also appears quite rich in exclusive species, has a definite boreal affinity as indicated not only by the pines but also by numerous shrubs and subshrubs (Seifriz, 1943; Carabia, 1945). In Cuba these savannas also have certain remarkable endemics like the dwarf cycads of the genus *Zamia*.

A final point to mention refers to the genera shared in common by American and African savannas. Disregarding the man-induced recent acquisitions of the Neotropical savannas, there are several typical genera common to both areas. Outstanding examples are the grass genera *Ctenium*, *Sorghastrum*, *Trachypogon* and *Tristachya*, as well as certain other genera in various families. These continental disjunctions at the generic level sharply point out the antiquity of savanna-like formations. Some kinds of proto-savannas must certainly have been in existence before the splitting apart of South America and Africa, since the alternative hypothesis of an independent parallel evolution with a later adaptation to savannas in both sets of species seem much harder to maintain. In any case, it is interesting to notice that these disjunctions only occur in herbaceous genera, the woody savanna component having evolved independently in each continent. A corollary is that the primeval savannas were mostly herbaceous or with a poor woody flora.

## FLORISTIC DIVERSITY IN NEOTROPICAL SAVANNAS

The seasonal savannas of the cerrado region have one of the richest savanna floras in the world. This is particularly true of the woody flora. Already in the last century, Warming (1892) gave a list of more than 700 cerrado species for the area of Lagoa Santa in Minas Gerais alone. Eiten (1963) analyzed the cerrado flora in a restricted region in eastern São Paulo, at 22°S — that is, near the southern border of this formation. In an area of about 50 km$^2$ he recorded 237 species, including several weeds but excluding many of the common woody species because they were not in bloom when the area was visited. Rizzini (1963b) gave the first comprehensive floristic list for the whole cerrado region, which included 537 species of trees and shrubs alone. In this flora Rizzini differentiated between forest species (227), cerrado elements (226) and species from the campos (84), thus making distinctions between the proper and the alien flora as well as between the woody species of the more closed-canopy types of cerrados and those species exclusive of the open campos. Goodland (1970) gave a list of 600 species and 336 genera in the flora of an area of about 15 000 km$^2$ in western Minas Gerais, in the core area of the cerrados. This list includes 73 species of grasses. Rizzini (1971) enlarged his list of cerrado woody plants to 653, and in the latest inventory of the flora in the whole cerrado region (Heringer et al., 1977) a total of 774 woody species are recorded, with a complementary list of 127 herbaceous and subshrubby species, 108 grasses and 54 orchids — that is, an overall figure of 1063 species (Table 10.13), 718 of which pertain to the floristic element specific to savannas.

As may be realized from these figures, the woody flora of the cerrados, referring exclusively to the seasonal savannas in this area, appears to be impressively diversified. According to Heringer et al. (1977), of the 774 woody species, 429 compose the proper floristic stock of the savannas, 300 species belong to forest formations and the remaining 45 to other vegetation types. This figure of 429 woody savanna species is not approached by any other savanna flora in the world. On the other hand, the herbaceous flora, including the grasses, is not so rich as the woody one, with something more than 300 listed species of which about one third are grasses. These figures are much lower than those of temperate South American grasslands (*pampas*) where the number of grass species is well above 400, according to the floras of Burkart (1969) and Cabrera (1970).

TABLE 10.13

Floristic richness of various Neotropical savanna formations

| Formation | Area ($km^2$) | Number of trees and shrubs | Number of subshrubs, half-shrubs, herbs, vines, etc. | Number of grass species | Total number of species |
|---|---|---|---|---|---|
| Cerrado in northwestern São Paulo (Eiten, 1963) | 50 | 45 | 175 | 17 | 237 |
| Cerrado in western Minas Gerais (Goodland, 1970) | 15 000 | ~200 | ~330 | 73 | ~600 |
| Whole cerrado region (Heringer et al., 1977) | 2 000 000 | 429 (774)[1] | 181 | 108 | 718 (1063)[1] |
| Rio Branco savannas (Rodriguez, 1971) | 40 000 | 40 | 87 | 9 | 136 |
| Rupununi savannas (Goodland, 1966) | 12 000 | ~50 | 291 | 90 | 431 |
| Northern Surinam savannas (Van Donselaar, 1965) | ~3000 | 15 | 213 | 44 | 272 (445)[2] |
| Central Venezuelan llanos (Aristeguieta, 1969) | 3 | 69 (16)[3] | 175 | 44 | 288 |
| Venezuelan llanos (Ramia, 1974a) | 250 000 | 43 | 312 | 200 | 555 |
| Colombian llanos (FAO, 1966) | 150 000 | 44 | 174 | 88 | 306 |

[1] Total flora including other plant formations.
[2] Total flora including bushes.
[3] Number of savanna trees excluding groves.

Similarly, the flora of the wet campos, either within the cerrado region or in neighboring areas of Amazonia, appears as relatively much less diversified. Eiten (1963) recorded 108 species in this community type in northwestern São Paulo, while Andrade Lima (1959) for the savannas near Monte Alegre and Egler (1960) in his floristic inventory of the Ariramba campos, both areas in lower Amazonia, each record about 300 species, including 26 grasses, but these inventories correspond to several formations occurring in those small areas: wet campos, esteros, cerrados and campinas. Rodríguez (1971) gave a first list, certainly far from comprehensive, of the flora of the Rio Branco savannas in the Roraima Territory of northern Brazil. His list includes a total of 136 species: 87 herbs and subshrubs, 9 grasses and 40 woody species. Incidentally, it is interesting to note how the woody flora of these savannas, though not at all comparable in richness to the cerrado woody flora, seems to be at least equally or perhaps even more varied than the tree and shrub flora of the Orinoco llanos.

Goodland (1966) presented a more complete inventory of the flora in the Rupununi savannas of Guyana, an extension of the Rio Branco savannas in the same country. There are a total of 398 herbaceous and subshrubby species, including more than 90 grasses, together with 33 trees — that is, a global figure of 431 species. Thus, this rather well-known formation has a rich herbaceous flora, but the number of woody species remains much lower than those recorded for the cerrados.

In the small savanna area of northern Surinam (coastal savannas), Van Donselaar (1965) records a list of 272 species, including 44 grasses and 15 trees and shrubs. These savannas, though diversified into several community types are floristically rather poor, particularly in respect of woody elements, but if the shrub communities on white sand were also taken into account, the total number of species increases to 445, with a significantly larger number of trees (Table 10.13). The small southern Surinam savannas include 314 species collected so far (Van Donselaar, 1968).

In the seasonal savannas of the central Venezuelan llanos, Aristiguieta (1966) reported 54 tree species, 15 shrubs, 35 vines, 44 grasses and 140 herbs and subshrubs, making a total of 228 species, for the 250 ha of the Los Llanos Biological Station. This is a long list for such a small area. However, most trees, shrubs and vines belong to the groves (*matas*) scattered within the savanna in the characteristic pattern called "savanna parkland". There are only 22 tree species in the actual savanna of this biological station.

Most other areas within the Venezuelan llanos are still poorer in woody species. In his preliminary account of the flora of the whole Venezuelan llanos, Ramia (1974b) listed 555 species, including in this figure any type of savanna as well as many wide-spread weeds. The grass family is the largest, with 200 species; trees and high shrubs including palms, total 43 species. In the Colombian llanos (FAO, 1966), a total of 88 grasses, 30 sedges, 144 herbs and subshrubs, and 44 trees, palms and shrubs are listed, for a grand total of 306 species in this savanna flora. But this was not a complete floristic inventory, which explains the lower number of species in comparison with the nearby Venezuelan llanos.

The floristic knowledge of savanna formations in Central America, Mexico and the Caribbean Islands still remains too fragmentary to make possible comparisons with South American formations. The only generalization possible is that, on the basis of actual knowledge, Cuban savannas seem to be richer than the other savannas in the area. This fact may be due to a greater ecological diversification on several different types of parent material including some unusual substrata such as silicious sands and serpentine rocks which are responsible for an endemic flora with remarkably high endemism (Seifriz, 1943; Carabia, 1945).

The various formations of hyperseasonal savannas and esteros are much more difficult to compare with each other, because of their more patchy distribution at a large ecological scale and their more continuous area at a small, continental scale. In fact, the fragmentation of these formations on the landscape renders dubious a comparison between vegetation types divided into patches of every possible size. On the other hand, the distribution of the habitats of these formations along rivers and bottom lands leads to greater floristic continuity without significant gaps that might induce great differences in composition. If only one particular type of community is considered, as for example the morichales in the llanos (Aristiguieta, 1969), a list of 193 species is obtained including 49 grasses and 21 woody species. These figures compare well with those reported for the wet Brazilian campos (Eiten, 1963).

To sum up all this information on floristic richness of different Neotropical savanna vegetations, it seems that the seasonal savannas have reached their highest floristic diversification in the cerrado area. This floristic richness heavily depends on the number of woody species, while the herbaceous and subshrubby flora does not seem to be more diversified in this formation than in other American areas. This conclusion could be biased by an imperfect knowledge of the herbaceous element, but though this factor may somewhat alter the previous figures, even in well-known families like the grasses the total number of species in the cerrados is scarcely one half that of the grass flora of the Venezuelan llanos. This latter region of northern South America harbors the richest herbaceous savanna flora, while on the other hand its list of woody species is surprisingly reduced. The Rupununi savannas in Guyana, located between the two areas mentioned, maintain an intermediate position concerning floristic diversity, since their herbaceous and woody floras show figures between those of the cerrados and the llanos, particularly taking into account the small area occupied by this Guyanan formation.

A possible explanation of these contrasting gradients of impoverishment in woody species and enrichment in herbaceous elements as one passes from the cerrado to the llanos, may rely on the more continuous interplay between savannas and rain forests in the Brazilian area, with a fluctuating record of replacements and displacements all along their evolutionary and paleogeographical history. The Orinoco seasonal savannas, on the other hand, besides being geologically younger, have been almost encircled by drier lowland formations, like tropical deciduous and thorn forests, or by middle-altitude montane rain forests that have a totally different floristic stock adapted to a wholly different set of environmental conditions.

## SUMMARY AND CONCLUSIONS

A wide variety of savanna ecosystems exists in tropical America. These ecosystems may be classified into several ecological and physiognomic types, or an ordination may be made along two main axes of variation: one structural, the other ecological. The structural gradient shows a continuous variation between two extreme types: a treeless grassland and a closed woodland that looks very much like a low, sclerophyllous forest formation. The other axis relates to seasonality gradients. It has semi-seasonal savannas as one extreme, where ever-wet climates determine a feeble seasonal water stress. The gradient continues with seasonal savannas, under climates or conditions leading to a rather long period of water shortage; and then with formations subjected to alternate periods of water deficiency and waterlogging during each annual cycle (hyperseasonal savannas). Finally, there are those ecosystems that remain under conditions of excessive soil water during a major part of the year (esteros), approaching the situation of permanently waterlogged swamps.

The occurrence of each type depends therefore both on climate and on topographic situation, but the parent material may also be important, particularly when it influences soil drainage, as is the case with coarse white sands. The physiognomic types depend more on soil fertility, depth of water table, occurrence and depth of hard plinthite, fire frequency, etc.

In each region the same savanna types appear on similar sites, generally disposed along equivalent environmental gradients or topographic catenas. All Neotropical savannas also share a common floristic stock. Many species occur in similar formations of neighboring areas, while a few extend practically throughout tropical America, occurring in related savanna types anywhere in the Neotropics. This is the case, for instance, for trees like *Bowdichia virgilioides*, *Byrsonima crassifolia* and *Curatella americana*, and also for grasses and sedges like *Leptocoryphium lanatum*, *Trachypogon plumosus* and several species of *Andropogon*, *Axonopus*, *Bulbostylis*, *Paspalum*, *Rhynchospora*, etc. But even considering this floristic similarity that homogenizes Neotropical savannas, two particular areas show a much more diversified savanna flora. These are the cerrados and, perhaps to a lesser degree, the Cuban savannas, specifically the formations on serpentine and on siliceous soils.

To go further in the characterization of savanna communities following one or another of the widely used phytosociological systems is difficult due to the lack of adequate floristic knowledge and to the intrinsic weakness of phytosociological methodologies. In general, one may notice that phytosociological classifications, like those already discussed (Van Donselaar, 1965; Hoock, 1971), seem to be successful at a regional level. But extrapolation to regions further away from the areas of origin becomes rather problematical.

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