Citar como:

THE MAIN ECOLOGICAL AND PHYTOGEOGRAPHIC 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 km². 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 regions, 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 unites 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 phyto-geographic 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 Montesinos, 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.](Image)
nations occurs by a constantly or mostly wet climate. In this case one or two short dry seasons may represent the main rhythmic environmental strain. Under those 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-fed cover.

A second type, and the most widespread in tropical America, is the seasonal savanna. Here, an extended wet season increases the probabilities of dry season fires, and both cacti, 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 rainy season, and an extended period of water excess during all or part of the rainy season, when soils become waterlogged and aphytotrophic. 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 epero, using a common Spanish term widely adopted to these ecosystems in several Latin American countries.

Another useful criterion in differentiating savannas 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

<table>
<thead>
<tr>
<th>Savanna Type</th>
<th>Total cover of woody layers (%)</th>
<th>Average tree density (trees/ha)</th>
<th>Brazilian Name</th>
<th>Spanish-American Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Savanna</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Savanna grassland</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree and shrub savanna</td>
<td>&lt; 2</td>
<td>500</td>
<td>campo leão</td>
<td>sabana pastazal</td>
</tr>
<tr>
<td>Wooded savanna</td>
<td>2-15</td>
<td>1000</td>
<td>campo cerrado</td>
<td>sabana cerrada</td>
</tr>
<tr>
<td>Savanna woodland</td>
<td>15-40</td>
<td>3000</td>
<td>cerrado</td>
<td>sabana bravaes</td>
</tr>
<tr>
<td>Woodlands or open forest</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sclerocephalous woodland</td>
<td>&gt;40</td>
<td>4000</td>
<td>cerrado</td>
<td></td>
</tr>
<tr>
<td>Savannas dotted with groves</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Savanna parkland</td>
<td>&lt; 40</td>
<td></td>
<td></td>
<td>sabana palmarosa</td>
</tr>
</tbody>
</table>
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 10%. A wooded savanna has an open tree cover ranging between 20% and 30%, which corresponds to a total density of about 1000 trees ha⁻¹. A savanna woodland has a tree cover above 30%, reaching cover values of 40%, to 50%, 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 santo, 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 cerrado or 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 of the four previous 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.

116. BRAZILIAN CERRADO

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 km² in the Brazilian Shield. Ab'Sabre (1973) considering the major morphophenological 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 plantation surface of Middle Teriary age. The formerly continuous surface of these extensive tablelands has been deeply dissected and fragmented, now appearing as isolated high plateaux or cerras, separated by wide interfluvies. 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 nearly 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).
The cerrado vegetation has been reviewed by Fren (1972), and four symposia have been devoted to different aspects of its floristics, ecology, environmental conditions, etc. (Ferris, 1964, 1971, 1977; Habermann, 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 "campo" 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 most extensive, will be considered first, and then the other types.

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.

Fig. 10.3. The core area of the cerrados in central Brazil and its neighboring formations (after AhNather, 1971).
restricted to small areas of particular habitat conditions.

Four structural types of cerrado vegetation have been recognized and designated by popular names (Enc. 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 30 ‰, and the ground layer of grasses, forbs and half-shrubs is in¬versely 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 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 m² ha⁻¹ in the most treeless grassland to 51.3 m² ha⁻¹ in the cerradão; canopy cover ranges from 0 to 85%; ground cover from 0% 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 217. The importance of most species, either trees, shrubs or grasses, also shows continuous variation along the physiognomic gradient. In a later paper (Goodland and
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 contrast the two extremes. The precise phytosociology of cerrado communities still needs to be studied; it may be 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 x 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

| *Astronium fraxinifolium* | *Manilkara zapota* |
| *Anadenanthera peregrina* | *Maytenus balsamifera* |
| *Anisomeles argentea* | *Melia azedarach* |
| *Apicarpa parviflora* | *Prosopis advertens* |
| *Apicips sartorum* | *Psidium guajava* |
| *Bauhinia variegata* | *Psophocarpus tetragonolobus* |
| *Bixa orellana* | *Passiflora edulis* |
| *Brassica oleracea* | *Passiflora quadrangularis* |
| *Cassia fistula* | *Quercus myrtifolia* |
| *Casuarina equisetifolia* | *Quercus similis* |
| *Celtis aurantia* | *Raphia hookeri* |
| *Cotinus coggyria* | *Salix matsudana* |
| *Copalina laurifolia* | *Salix purpurea* |
| *Corymbia citrifolia* | *Strychnos pinnata* |
| *Dalbergia voigtii* | *Strychnos toxifera* |
| *Dipteryx odorata* | *Tabebuia coryne* |
| *Dipterocarpus alatus* | *Tabebuia rosea* |
| *Erythrina vespertilio* | *Terminalia arjuna* |
| *Enterolobium contortisiliquum* | *Terminalia superba* |
| *Ficus carica* | *Trichilia ecklonis* |
| *Ficus glomerata* | *Vochysia ferruginea* |
| *Flacourtia indica* | *Yelena eiffeliana* |
| *Fremontia americanafolia* | *Zeyheria aromatica* |
| *Guazuma ulmifolia* | *Zizyphus jujuba* |
| *Haematoxylum campechianum* | *Zzyphora digitata* |
TABLE 10.3
Some of the commonest species in the ground layer of the cerrado community.

SHRUBS

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Andropogon bracteatus</em></td>
<td>Bracteate Andropogon</td>
</tr>
<tr>
<td><em>Andropogon odoratus</em></td>
<td>Odoriferous Andropogon</td>
</tr>
<tr>
<td><em>Andropogon virginicus</em></td>
<td>Virginian Andropogon</td>
</tr>
</tbody>
</table>

HALF-SHRUBS OR HALE-WOODY SPECIES

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Borago officinalis</em></td>
<td>German Blueweed</td>
</tr>
<tr>
<td><em>Borago glabrata</em></td>
<td>Glabrous Borago</td>
</tr>
</tbody>
</table>

GRASSES

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bromus riparius</em></td>
<td>Riparian Bromus</td>
</tr>
<tr>
<td><em>Bromus tectorum</em></td>
<td>Field Bromegrass</td>
</tr>
</tbody>
</table>

Sedges

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Carex leucantha</em></td>
<td>Lance-leaved Sedge</td>
</tr>
<tr>
<td><em>Carex stricta</em></td>
<td>Strict Sedge</td>
</tr>
</tbody>
</table>

To give a further picture of a cerrado community, the description given by Eiten (1975) of an undisturbed cerrado on the west of the Serra do Roncador in Matto 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 the rest of the space, but woody plants do not form definite layers. Among the most common trees, Eiten lists *Apidia pumila* spp., *Curatella americana*, *Delicia elliptica*, *Kleinheimia circaea*, *Paliocarya rigida*, *Qualea grandiflora*, *Savilla vasculata*, 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*, *Amphora*, *Schinaphis*, and *Paepalanthus* are the most common grasses. They reach 0.5 to 1.25 m tall when in flower. Open colonies of a low terrestrial *Bromus* 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, consisting either of 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 cerrado. The *Himile galindii* cerrado is a "low savanna woodland in which the taller trees vary from 3 to 10 m in height; there is no continuous casapate and the ground vegetation is very dense and difficult to walk through". Characteristic trees of this community, besides *Himile glindii*, are *Andropogon macrocarpus*, *Boudica virgata*, *Sclerolobium paniculatum*, *Xylopia sericata*, 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 *Mogoua subsecens-Calliclome fasciculata* cerrado, in which the largest trees attain 15 m high and the ground layer is quite dense. As may be realized from these descriptions,
even the dew-extracted types of woodlands have structural and floristic characteristics that relate them to the other savannas. Several authors, like Rizzini and Heringer (1962) and Rizzini (1968a), have considered the cerrado 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. Bergomovii and Chiari (1969) presented a map showing these southernmost strivulations of cerrado. They reach the border between the States of São Paulo and Paraná, at about 24° S. Silberbauer-Goutsberger et al. (1977) analyzed the effects of the exceptional 1973 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 distinct cerrados among the prevailing caatinga vegetation (Valverde et al., 1962; Eiten, 1972). They occupy sandy stone plateaus and tablelands. Their floristic and physiognomy are similar to those of typical cerrado in its central core area. Byromia caatinga, Caatinga longiflora, Hancornia species, Hirtella xanthina and Orthanthera flagelliformis are the commonest trees (Favaras, 1964).

The hyposeasonal 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. Asew 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 ‘tampo’ or savanna grassland. Their heathaceous 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.
some seasonal savannas and esteros generally occur as treciôs grasslands or wetlands as palm savannas with *Mauritia enriquii*. They occupy wet sites on valley sides or tableland margins throughout the area, though they became 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 few 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 Guayana 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 intergrades 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 Aparue, 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 about 2000 mm at the Guaviare River on the southwestern 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 southward from the Cordillera de la Costa and approaches the Orinoco. This is the major area of tropical deposits within the llanos.
On well-drained sites, the whole range of tropical soils appears, from Entisols on young alluvial 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 localized areas, raising crops like rice, cotton, sorghum, corn and sesame.

Almost every ecological and physiographic 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 physiography 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 Blydensten (1967). Tarnayo (1964), Romo (1967) and Medina and Sarmiento (1979) give a general picture of the 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 formation and overall vegetation patterns. These four subregions — the piedmont, the high plains, the alluvial overflow plains and the aquatic 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. Semi-deciduous tropical forests are widespread on these...
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, according to Tracart and Millies-Lucot (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 halof chips (Table 10.4 and Fig. 10.10). The Q, terrace maintains wooded savannas intermixed with semideciduous forests. The more extensive Q, 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,) is the domain of pinyon forests, though on sandy soils seasonal savannas may occur with Ellymospermos trachycalci as the dominant grass. Hyperseasonal savannas, on the other hand, are restricted to a few localized bottom lands, in this piedmont region.

<table>
<thead>
<tr>
<th>TABLE 10.4</th>
<th>Some of the commonest species in the seasonal savannas of the piedmont region of the Venezuelan llanos.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>TPES</strong></td>
<td></td>
</tr>
<tr>
<td>Acacia zelleri</td>
<td><em>Caesalpinia sappan</em></td>
</tr>
<tr>
<td>Bougainvillea oxylobus</td>
<td><em>Grevillea americana</em></td>
</tr>
<tr>
<td>Bougainvillea macrostachya</td>
<td><em>Boisiea elegans</em></td>
</tr>
<tr>
<td>Bursera simaruba</td>
<td><em>Cassia spectabilis</em></td>
</tr>
<tr>
<td>Canavalia rosea</td>
<td><em>Kigelia aromatica</em></td>
</tr>
<tr>
<td>SHRUBS AND HALF-SHRUBS</td>
<td></td>
</tr>
<tr>
<td>Calycophyllum brasilianum</td>
<td><em>Patersonia glabrinervia</em></td>
</tr>
<tr>
<td>Guazuma ulei</td>
<td><em>Psidium guajava</em></td>
</tr>
<tr>
<td><em>Leucaena leucocephala</em></td>
<td><em>Salix guianensis</em></td>
</tr>
<tr>
<td><em>Leucaena reticulata</em></td>
<td><em>Tephrosia utilis</em></td>
</tr>
<tr>
<td>GRASSES AND SEDGES</td>
<td></td>
</tr>
<tr>
<td>Andropogonella nivea</td>
<td><em>Leptadenia hexagona</em></td>
</tr>
<tr>
<td>Andropogon sibiricus</td>
<td><em>Pipturus decussatus</em></td>
</tr>
<tr>
<td>Axonopus compressus</td>
<td><em>Pipturus pteris-panis</em></td>
</tr>
<tr>
<td><em>Berthoudia capitata</em></td>
<td><em>Pipturus plicatus</em></td>
</tr>
<tr>
<td>Buchloea dactyloides</td>
<td><em>Spermacoce rubescens</em></td>
</tr>
<tr>
<td>Buchloea integrifolia</td>
<td><em>Thespesia populnea</em></td>
</tr>
<tr>
<td>Cenchrus ciliaris</td>
<td><em>Trachypogon panicum</em></td>
</tr>
<tr>
<td>Elymus riparius</td>
<td><em>Trachypogon plumosus</em></td>
</tr>
<tr>
<td>Elymus trachycaulus</td>
<td><em>Trachypogon testaceus</em></td>
</tr>
</tbody>
</table>
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 Q₀, Q₁, or Q₂ terraces. Each soil series was found to carry a chaetosereatic community, but that the composition and importance of the species varied continuously, from the drier seasonal savannas on coarse soils developed on the Q₁ terrace, to the wetter hyposeasonal savannas on poorly drained sites of the Q₂ terrace. Only a few species were restricted to narrow parts of this gradient, while most of them occurred in more than one community (Fig. 16.11). This phytosociological continuum reflects environmental gradients related to soil-water conditions during the dry and wet season.

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 hyposeasonal savanna, in this piedmont area of the western Venezuelan llanos. Seasonal formations attained a maximum standing crop of 222 to 604 g m⁻², without showing significant differences between communities and among different years. The hyposeasonal savanna reached a maximum of 305 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 Q₂ 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.
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 relèves mesas remain in some places, 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 Pfitzer (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. vestibii*, with *Andropogon selloanus, Acoplos canescens* and *Leptoceras plumatun* as subdominant grasses. The low, scattered trees belong almost exclusively to the species *Bovelichia virgillioi, Byrsonima extrafolia* and *Curatella americana*. A wooded savanna occurs on the steep slopes of the incised valleys, with the mentioned species plus a few others, like *Byrsonima coccoloba*, *Piptadenia peregrina* or *Bosque composita*, 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, Acoplos* and *Trachypogon*. The wide valleys dissecting the mesas have a system of river terraces of different ages. Seasonal savannas, mostly treeless grasslands, occupy the
A seasonal saxuma with very scattered trees on the mesa of the eastern high plains in the Yucatan Peninsula. Cassia abbreviata is almost the only tree species over a ground layer dominated by species of Anacampseros, Asparagus, and Trichopogon.

A savanna parkland on the high plains (mesa) of the central Yucatan Peninsula (Calabozo Biological Station). The seasonal saxuma is a Trichopogon-Asparagus community with scattered trees (Broclavia vespertilio, Bersema exangifolia, Cassia abbreviata). The grasses are dominated by high trees like Cassia abbreviata, Cynodon radicans and Tunbergia vexillifolia.
SAVANNAS OF TROPICAL AMERICA

drier habitats, while hyperseasonal savannas occur on waterlogged sites, where they may either be grasslands dominated by Leersia hexandra, Manihot esculenta, Sorghastrum parviflorum and several species of Andropogon and Panicum, or the palm Cephalostachyum may be locally abundant as the simple 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 mossoom formation in this region is a seasonal tree savanna, with low trees mostly Brachystegia rufescens and Isoberlinia virgulifera and a ground layer dominated by species of Bulnesia, Lepisanthes, Psidium, and Trichogynum. 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 Trichogynum savannas with sparse trees, including the common species mentioned previously.

Primary production of the savannas on the mesas of the central Venezuelelano 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 Trichogynum 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 dependant 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 above-ground standing crop (San José and Medina, 1977). Apparently, this community is more productive than the seasonal savanna of the same region.

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 Rumet (1959, 1974b). FAO (1966), Blydenstein (1967) and Surmento et al. (1971b). Vegetation varies along topographic contours, 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 mantle corresponds to natural levees or banks that border the streams, where sandy alluvium has been de-

**Fig. 10.14.** A hyperseasonal savanna with palms (Cephalostachyum on a low alluvial terrace in the upper valley dissecting the mesas in the Venezuelan llanos.
posed. These sandy banks appear as narrow strips gently dipping away from the river to a wide flat area where silt alluvium predominates. The lower part of the cutaneus is formed by slowly draining decantation cutanes, 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 levels support a treeless grassland. In the first case, Asparagus purpureus and Fynbos plicatum are the dominant species in the ground layer. In the treeless savannas the main grasses are Sporobolus indicus and Imperata cylindrica. 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 silt expanses between successive banks. These are mostly treeless savannas (Fig. 10.16), or less frequently palm savannas with Copernicia americana 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 Antheropygium and Miconia. 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).

<table>
<thead>
<tr>
<th>Woody and Half-Woody Species</th>
<th>GRASSES AND SEDGES</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bridelia uliginosa</em></td>
<td><em>Brachiaria ramosissima</em></td>
</tr>
<tr>
<td><em>Cassia fasciculata</em></td>
<td><em>Eleusine indica</em></td>
</tr>
<tr>
<td><em>Eleusine indica</em></td>
<td><em>Eragrostis curvula</em></td>
</tr>
<tr>
<td><em>Eragrostis curvula</em></td>
<td><em>Glycyrrhiza glabra</em></td>
</tr>
<tr>
<td><em>Glycyrrhiza glabra</em></td>
<td><em>Guizotia abyssinica</em></td>
</tr>
<tr>
<td><em>Guizotia abyssinica</em></td>
<td><em>Helianthus annuus</em></td>
</tr>
<tr>
<td><em>Helianthus annuus</em></td>
<td><em>Kermesina viscosa</em></td>
</tr>
<tr>
<td><em>Kermesina viscosa</em></td>
<td><em>Lippia alba</em></td>
</tr>
<tr>
<td><em>Lippia alba</em></td>
<td><em>Melilotus albus</em></td>
</tr>
<tr>
<td><em>Melilotus albus</em></td>
<td><em>Miscanthus sinensis</em></td>
</tr>
<tr>
<td><em>Miscanthus sinensis</em></td>
<td><em>Parthenium hysterophorus</em></td>
</tr>
<tr>
<td><em>Parthenium hysterophorus</em></td>
<td>* Panicum miliaceum*</td>
</tr>
<tr>
<td><em>Panicum miliaceum</em></td>
<td><em>Pennisetum purpureum</em></td>
</tr>
<tr>
<td><em>Pennisetum purpureum</em></td>
<td><em>Rhamnus cathartica</em></td>
</tr>
<tr>
<td><em>Rhamnus cathartica</em></td>
<td><em>Raphanus sativus</em></td>
</tr>
<tr>
<td><em>Raphanus sativus</em></td>
<td><em>Ricinus communis</em></td>
</tr>
<tr>
<td><em>Ricinus communis</em></td>
<td><em>Sesamum indicum</em></td>
</tr>
<tr>
<td><em>Sesamum indicum</em></td>
<td><em>Sorghum bicolor</em></td>
</tr>
<tr>
<td><em>Sorghum bicolor</em></td>
<td><em>Trachypogon pygmaeus</em></td>
</tr>
<tr>
<td><em>Trachypogon pygmaeus</em></td>
<td><em>Trachypogon nigricans</em></td>
</tr>
<tr>
<td><em>Trachypogon nigricans</em></td>
<td><em>Trachypogon setosus</em></td>
</tr>
</tbody>
</table>

### TABLE 10.6
Some of the commonest species in the savannas of the alluvial overflow plains in the Colombian Llanos (from FAO, 1966).

<table>
<thead>
<tr>
<th>Woody and Half-Woody Species</th>
<th>GRASSES AND SEDGES</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Baccharis pilularis</em></td>
<td><em>Andropogon virginicus</em></td>
</tr>
<tr>
<td><em>Caragana arborescens</em></td>
<td><em>Andropogon virginicus</em></td>
</tr>
<tr>
<td><em>Caragana arborescens</em></td>
<td><em>Andropogon virginicus</em></td>
</tr>
<tr>
<td><em>Caragana arborescens</em></td>
<td><em>Andropogon virginicus</em></td>
</tr>
<tr>
<td><em>Caragana arborescens</em></td>
<td><em>Andropogon virginicus</em></td>
</tr>
<tr>
<td><em>Caragana arborescens</em></td>
<td><em>Andropogon virginicus</em></td>
</tr>
<tr>
<td><em>Caragana arborescens</em></td>
<td><em>Andropogon virginicus</em></td>
</tr>
<tr>
<td><em>Caragana arborescens</em></td>
<td><em>Andropogon virginicus</em></td>
</tr>
</tbody>
</table>

---

**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 associations of one or another hydrophilous species, like Iponema crassicaulis, Ludovigia lithostephanifolia, 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 gradient. During the year of data collection, the seasonal savanna on the sandy bank reached a maximum green biomass of 42.7 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 areal 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 Cumaruco River in southern Venezuela (Fig. 10.17). 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.](image-url)
dune fields superimposed on larger areas of less-like material that was partly covered by younger alluvia.

A dry-seasonal savanna occurs on the dunes, with a few trees or entirely treeless. *Bysonima crassifolia* is almost the single tree species over a quite open ground layer, dominated by *Trachypogon nigricans* and *Perajodium carinatum* (Fig. 10.18). A *Mamurea* hyperseasonal savanna occupies the depressions between the dunes and the extensive silty plains. In some areas, *Carapa flamarion* 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 flexuosa*) as its only tree. These marshes may be fairly good grazing lands since the grasses remain green throughout the dry season.

**Other savannas related to the llanos**

Seasonal savannas 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 occur 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 trees 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 depressions of the lower Magdalena in northern Colombia, intermingled with permanent swamps and other types of hydrophytes 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 alluvial plains in the region between the Caura and the Meta rivers. In the foreground is a *Mamurea* hyperseasonal savanna grassland; in the background a dune covered by a seasonal savanna woodland. *Bysonima crassifolia* is the only tree species over a ground layer dominated by *Trachypogon nigricans* and *Perajodium 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 original stages stabilized as fire climax 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, Acomyris, Elymus, Paspalum, Trachypogon, together with some naturalized species like Hierochloe ontario and Melinis minutiflora.

Denevan and Chestowski (1970) and Scott (1977) studied one isolated savanna area on an uplaid 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, Bremisoma crusfolia is the most conspicuous woody species, together with some shrubby Melastomataceae and Rubiaceae. Andropogon lanatus, A. leucotrichus, and Leptocorys lanatus 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 GUAYANA PLATEAUX AND THEIR SOUTHERN BORDERS

In the Guiana region of southeastern Venezuela, there is a large area where the sandstones of the Precambrian Paraima Formation form landscapes of tablelands at different altitudes, with a relief of large horizontal slabs. They appear as a complex arrangement of flat-topped plateau 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 plateaus called tepuis. The Auyán Tepuy, Roraima, Duida, Jaua, Cerro de la Nebina, are some of the major tepuis. Lower tablelands, from 800 to 1200 m above sea level, connect the higher plateaus. They extend as much smaller and isolated areas to Guayana and Surinam. The Venezuelan part of these lower-level plateaus is known as the Gran Sabana (Grand Savannah) and is almost entirely a savanna land. To the south, these highlands descend and penetrate the Brazilian and Guyanese territories where they form other 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 Tepui 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 Macasai River, where the Amazonian forests begin rather abruptly. Climatic conditions on the higher tepuis 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 (1933) travelled 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/Carinaria 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 sial 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. Styermark (1967) presented floristic information for the Auyan Tepui savannas and related vegetation formations. Van Donkelaar (1968, 1969) extended his phytosociological and phytogeographic analysis of northern Surinam savannas to the restricted savanna patches in the Surinam-Brazil border, comparing the areas floristically and phytosociologically, but the most comprehensive ecological analyses 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 Guyana (Guiana). Several papers on plant communities (Goodland, 1984), ecology (Eden, 1964; Hills, 1969), geomorphologic evolution of the landscape (Sinhu, 1968) and other aspects were produced. The Ratum Brazil Project (Proyecto 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 will remain unpublished.

**Main savanna types**

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

1. Herbaceous swamps on the tepuis, 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 tepuis. In the Auyan Tepui, for instance, Styermark (1967) described several communities dominated by sedges (Cephalocarpos, Euerardia, Laguncularia), Xyridaceae (Ahibeboda, Xyris), Eriocaulaceae (Eri- ocolpus, Paspalanthus, Synetrum), Bromeliaceae (Boechonina, Costealla-frit), Rapateaceae, Vellozio- ceae, Orchidaceae, together with many species of shrubs.

2. (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 tepuis 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 Acanthoschoenus, Panicum, Rychinospora, Scleria, Trachypogon, etc. (Styermark, 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 rainy season is rather short,
Fig. 10.20: The landscape of high tablelands in the Gran Sabana region. A savanna grassland on shifting 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*, *Boucheia virgata var. virgata*, *Brosimum occidentale*, *B. crassifolium*. *Couratella americana*, *Genipa americana*, *Phoradendron tomentosum*, *Raphia conjugata* and *Salvadora persica* as the woody components. The ground layer is dominated by *Trachypogon plumosus*, with *Artisia sericea*, *A. tineae*, *Ayous cumanensis*, *Bulbostylis paradoxa*, *Echinolaena incisa*, *Lepidozyphium lanatum* and *Thysan pusillum* as codominant species. The main half-woody species are *Brosimum verbascifolium*, *Casuarina sylvestris*, *Pithecoloea rigida* and *Pseudum spp.*. A similar type of seasonal savanna occurs on dune bunds in southern Rapunning (Simha, 1968).

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

(5) Hypersaline savannas on river flats. These are either pure grasslands, or areas where small trees occur onterrestrial mounds. The drier communities are dominated by *Andropogon selvaticus*, *Panicum laxum*, *Paspalum pulchellum* and *Sporobolus cumbensis* and some other grasses and sedges. In the wetter sites, the most frequent species are *Andropogon bicolor*, *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 swampland 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](https://via.placeholder.com/150)
of Brazil to the mouth 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 3000 mm, and two to four months with less than 60 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 (Lanjon, 1936; Heyligers, 1963; Van Donnelaar, 1965), and a detailed analysis of French Guiana savannas was performed by Hook (1971). Benoist recognized three main formations: dry savannas, with scattered trees (Brosimum cassinifolia and Canella americana) over a grass layer dominated by Ardisia, Annonas and Trachypogon; intermediate savannas, dominated by sedges (Laguncularia racemosa, Rhynchospora, Scirpus) with Mauritia flexuosa patches, and wet savannas or herbaceous swamps. Lanjon (1936) differentiated three savanna formations in northern Surinam: a flat-wet type of dry grass savanna with shrubs, a type of wet, sedgaira 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 40 km 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 Laguncularia racemosa and Rhynchospora venosa 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 Donnelaar (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 Donnelaar distinguished three Orders, eight Alliances and 27 Associations. These phytosociological units, defined on the basis of their characteristic and different 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 Tecticornia pumila and Muehlab 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 Paragayl pachellii. On white sand, sedges together with Axonopus and Eriocaulaceae prevail, while a treeless community characterized by the sedges Bulbostylis and synonyms, some times with bushy islands of Licania urva, Tectaria speciosa and Tibouchina aspera occurs on red loamy sand and sandy loam. An Imperata brasiliensis-Micranthus cayennensis grassland appears on sandy loam and heavier soils, sometimes with sparse trees (Brosimum cassinifolia and Boudia montana). Finally, on very wet soils, the Associations of the Panicum scitulum Order occur either as pure grass and sedge savannas or with Mauritia flexuosa groves along the rivulets.

Hook (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 sedge tree and Axonopus purpureus, Leptocoryphium la-
naturally and Tachypogon plumosus as the dominant grasses. The grass savannas have a similar ground layer but no trees or shrubs. Two savanna communities occur on colluvial gray sands with podsols, a low savanna with nanophaserophytes and a low herbaceous savanna. In the first type, Bynoma verticillifolia appears as a characteristic half-woody species scattered in a Tachypogon plumosus-Leptochloa lanatina grass layer. An ecological group of hygrophytes becomes important in the second type, on wetter sites, with species like the grasses Echinolaena palustris and Panicum sternodes and the sedges Rhynchospora globosa and R. graminacea. Two communities occur on podzolized white sands: a low shrub savanna with scattered trees (Bynoma verticillifolia) over a ground layer of sedges, Juncus and other herbs; and a shrub formation of the type Heyligers (1963) called "scrub savanna" with Chusia forrestana, Hirtella strioglaba, Teucrium capitata 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 Guiana 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 Amazonian 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 laterization, 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-seasatorial savannas, on well-drained sites, or hypersesatorial 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 Boullene (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 interfluvies, 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 Putum-Humaita campos (after Lauer and Ramos, 1959); 2 = the Aesvalo campos (after Egler, 1960); 3 = the Amapá cerrados and campos (after Aesvalo, 1965); 4 = the campos and swamps of the Marajo island (after Muggers 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 *Ceratopetalum gummiferum*, scattered in a grass carpet of *Aristida capillacea*, *Elymus sp.*, *Lippia geniculata*, *Panicum repens* 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 relics surfaces of an old tabland 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 *Bactrodium confertum*, *B. lancastre*, *Lippia geniculata*, *Paspalum curatilum*, *P. barbattum*, *Teechypagnosta* sp., etc. The isolated trees are mostly *Ceratopetalum gummiferum*, *Qualea grandiflora* and *Salvietia callistophyllum*. 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 Rupiaceae, Xyridaceae, Ericaceae, Bromeliaceae and Orchidaceae. Floristic relationships may thus be established with the savannas on sandstones and those on the white sand of the interior Guianan region.

Azevedo (1967) also found a gradient of savanna formations in the Amazon Basin (Fig. 9.23). Three main types of open vegetation occur there: cerrado, campos and seasonal swamps. The cerrado savannas have tree species like *Byrsonima crassifolia*, *Ceratopetalum gummiferum*, *Panicum vittatum* and *Salvietia curatilum*. The campos are treeless grasslands (biannual savannas) that, besides grasses and sedges, have many representatives of the monocotyledon families already mentioned. Seasonal swamps on flood plains (campo 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 interfluvial areas, 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 *Ceratopetalum gummiferum* and *Byrsonima crassifolia*, over a ground layer of *Acanthospermum*, *Lippia geniculata* and *Teechypagnosta*, appear as isolated patches on well-drained sites in several parts of the upper Orinoco. Waterlogged savannas dominated by species of *Andropogon*, *Paspalum* and *Rheichsocarpus* occur in poorly drained areas. Sometimes a few palms (*Mauritia flexuosa*) appear as the single woody component of these grasslands. As may be realised from all these descriptions, similar vegetation gradients and mosaics appear in widely separated areas within the Amazonian region. Seasonal savannas occupy well-drained sites, while hyperseasonal savannas and estuaries occur on poorly drained areas. Eden (1978) believes that most of these non-forest ecosystems have to be excluded from the cerrado concept, but it must be remembered that Eden's delimitation of the cerrado is essentially floristic. According to Eden, 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-type, on hilly land with latosols; an Amazonian type on flat areas with white sands and podolic 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 *Bouleochia* trigloides, *Ceratopetalum gummiferum* and *Xylopia aromatica*, together with *Platycentrum orinocoense*, a species restricted to this type of savanna in the Venezuelan Amazonia. Due to its highly permeable soil, the white sand savannas almost never remains waterlogged for long. According to Huber, this formation must be even older, since in its still poorly known flora he found several new species of tropical African and Asian affinity. There are also open formations.
called *Ambra humilis*, 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 llanos 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 ever-wet 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 relics from a former extension of open formations throughout the Amazonian region. It seems logical to suppose that these relic savanna patches will tend to remain on the sites least suitable for reclamation by rain forests.

2. Hypersaline 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 Guiana 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 relics from more widespread grassland formations connecting the main savanna areas of Southern America during earlier climatic phases (Eden, 1974; Serrante 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 km², 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 relicual 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 pools of C. C. and T. aurea, constitute the only trees on a campo ground layer. A mosaic of cerrados, cerradões 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 tropical prairie landscape of extensive flat landl Lans, 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 terrestrial grasses, the other where the cerrado groves show a distinct 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 affinities, 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 Adamo (1974) analyzed the distribution and the ecological characteristics of these esteros (also called pajonal or) in the eastern Chaco. The esteros are concretions of tall and coarse species of Paspalum ven P. punctatum and P. agristodes is the dominant grass in hyperseasonal formations. Frequently there is a sparse cover of Cenopira 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 impractically 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 km² 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 sabulosa as the two commonest trees (Denevan, 1966). This savanna type is popularly known as arboleda, while the name chaparal 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, Paniceae and Paepalanthus. Sporobolus-Armosus-Antiphyllon-Trichocline grasslands or palm savannas with Cenopira alba and Acmenia spinola 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 pattern 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
The savannas of southern Mexico, Central America, and the Caribbean Islands

Neotropical savannas cover 20,000 km² 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 strikes their ecological interpretation difficult (Miuenda, 1952). This same type of interior savanna extends to Honduras (Ohannessen, 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 latesols. Corallia inselbergs, Duguetia leucocarpa, Passpalum poecilephalum, P. floridanum, P. purpureum, Trachypogon angustifolius, etc.

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

To the three trees mentioned above, Puig adds species of Acaia, Calliandra, Cynipterum, Cidemia, Chloropetalum, etc. The soils are apparently similar to the previous type, but as overgrazing has presented times, an invasion of woody species has been induced.

3. Tannalea or palm swamps, with the palm Pauropsis (Aeolochryson) whitei over grass and sedges (Antrozono, Passpalum, etc.)

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

Gómez Pompa (1972), 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 Aeolochryson mexicanum, Brosimum crassifolium, Coelodora huebneri, Coryphena yucateca and Corallia 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, Caisia, Dichromena, Passpalum, Rhynechostachys, etc. Finally, Pauropsis whitei forms pure stands of palm savannas on wet soils corresponding to the drier parts of swamps.

It is clear, then, that these types of savanna formations occur as more or less large patches in the coastal regions of tropical Mexico: a seasonal savanna on latesols 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 Pauropsis whitei, 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 Corallia-Brosimum community, and finally to a pine woodland (Pinus caribaea). On level terraces flooded for long periods, the vegetation is a sedge (hyperorsonal) savanna, dotted with cramps of the palm Pauropsis
weightii and isolated trees of Crescentia ujagre and Camaruna 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 Byronima 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 (1953) described the environment and vegetation of this Miskito savanna. It is a park-like savanna where pasture is widely spaced, intermingled with a sparse tree cover of Byronima crassifolia, Calliandra hirsuta, Curatella americana, Micocas spp., and less commonly Crescentia, Mimosa and Quercus. The ground layer is rich in sedges (Rhychochalam, Bulbostylis, etc.) with Trachypogon sp. is the most important grass, followed by species of Andropogon, Aristida, Leptocoryphium and Paspalum. The highest layer, open to very open, up to 25 ft. high, has Pinus caribaea as its single species. On poorly drained soils Parsons reports the occurrence of palm groves (Pentox).

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 exception- 
ally high rainfall (2600–3500 mm, with three dry months). He pointed out that even in the area of deciduous tropical forest there are secondary sau-
vannas with Crescenta alata and several species of Acacia, Haematoxylon, Pithecellodium, etc., over a grass cover of Aristida and Brachiaria.

Seasonal savannas of the Curatella type have also been reported on upland soils of coastal Costa Rica and Panama. Porter (1973) listed Anacamptan ovate, Byronima crassifolia, Curatella americana, Pidium guajava, Xylela aromaticum and Xylela fruitescens as the dominant trees in the Panaman savanna. Among the species of the ground layer he cites Andropogon angustifolius, Aristida longilima, Rhyncosperma amorphoides, etc. These, in several parts of Central America from Guatemala to Panama (Fig. 10.25), 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 plateaus (Beard, 1953). A treeless savanna covers an extensive area of the coastal plain with poorly drained soils. A tree savanna, either with pines (P. occidentalis) or with the typical orchard trees (Byronima, Curatella) covers a broken surface, remnants of a dissected plateau in the same area.

In several of the Lesser Antilles, there are redu-
ced patches of savanna, such as the Gran Sabana of Dominica, with Byronima and Sporobolus (Beard, 1935; 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 (Bennett, 1928; Wajct, 1943; Sotir, 1943; Beard, 1935; Borhidi and Herrera, 1977), between 30 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 serpentinite. An open formation with palms (Sabal parriffloa) and other low trees (Acacia, Curatella, Pinus) occurs on shallow soils, with lauret pebbles or hardpan (locally called maccarenos). The ground layer includes several species of Andro-
pogon, Panicum, Paspalum, Rnychosperma, Scirca and Setaria (Borhidi and Herrera, 1977). Siliceous sandy soils, in western Cuba and the Isla de Pinos are covered by open woodlands of Pinus trojpalus, or sometimes P. caribaea, with scattered palms, such as Colophonix weightii, Copernicia curvispina and Paspalum weightii. The herb layer includes species of Andropogon, Bulbostylis, Cypero, Embryopas, and Paspalum, as well as many typical neotropical savanna species like Leptocoryphium.
Savannas of Tropical America

Savannas, Mesauccola laurifolia and Trachypogon biflorus. Serpentine soils typically maintain a tree savanna that has as a distinctive physiognomic feature the abundance of low palms, like Coccothrinax nigritana, C. pseudovigida, Copernia monteana, C. pauciflora, C. ramontssima, C. ype, etc. (Boividi and Herrera, 1977). Other trees are Arecsina crassifolia, Caratella americana, Rondoniaria crassifolia, Tabebuia lepidophylla, T. lepidota, etc. The ground layer has several species of Andropogon and Aristida, besides Imperata brasiliensis, Hyparrhenia longirostris and other widespread Neotropical savanna grasses and sedges.

On the highlands of the Sierra de Iipe in eastern Cuba, at 400 to 600 m above sea level, Carabia (1941) reported open pine woodlands on limonitic soils derived from serpentine. According to him, grases and sedges represent the most dominant species in these pines. Pinea cabrerina, 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 pine. Carabia suggested that these pineless savannas are fire-induced. Hyposeasonal savannas occupy hydromorphic soils on the flood plains of several of the main rivers of the island. Several palms of the genus Ceporfia and various shrubby legumes of the genera Acacia, Guazuma and Cassia form the open woody layer, while the ground vegetation includes species of Andropogon, Arceidea, Balbisia and Rhynchospora. Seasonal savannas have two distinctive palms: Paronas virgatae and Salitri prifoliorum. In the grass and sedge layer, up to 2 m high, the more frequent species are Calidium jamacense, Hyparrhenia annua, Andropogon virgatus and several species of Ceporfia, Eleosclera, Flourensia and Rhynchospora.

In summary, in the Caribbean area, particularly in the two major islands Cuba and Hispaniola, seasonal and hyposeasonal 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 variants 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 Palmer, where several genera reach a remarkable specific diversification within these savanna formations.
The flora of the Neotropical savannas is specific and affiliative.

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 Viuilleumier (1971), Van der Hammen (1974), and Brown and AtSaber (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 wetclimatic phases. During the Late Glacial a dramatic contraction of rain forests took place, with a parallel expansion of savannas and to a lesser degree of thorn forests as well. [AtSaber (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 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 generic 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 floristic savanna flora evolved into 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 subshrubry flora peculiar to savannas; and an accessory 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 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. Coccoloba purpusii has two Neotropical species, one C. reginae is a half-woody plant exclusive to the cerrado, the other C. veitchii is a tree occurring in savannas of northern South America and Central America and in seral stages of tropical deciduous
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 evolutionary 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 *Anacardiaceae* or *Verbenaceae*.

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 vicarants 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*, *Copatia* or *Vochysia*, are common to both savanna and forest, but their representatives in the two ecosystems are not closely related.

Apparently the Brazilian rain forest trees 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 10K

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
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 distinction 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 pecular 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, other monotypic or with few species, like Brassia, Orthopappus and Hedyotis among the Asteraceae, Dichorisandra in the grasses and Torreya in the legumes. Other genera show a wider diversification in Neotropical savannas, like the genera Annona, Macrotyloma and Trichogyne, or the seeds Balanites, Lagerstroemia and Rhynchophora (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 certain 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 wider 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 particular to Neotropical savannas. Many of these species appear among the common in the herb layer of ever-wet Neotropical savanna. Nevertheless, it is a rather difficult trick 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 Lepotecropsis lanata — whose evolutionary 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 Clelman, Echinochloa, Trigonaria and Trichogyne.

The palms constitute a particular case within the savanna flora since a few genera, like Coccoloba, Colpodocarpus, Copernicia and Mauritia, have attained a significant diversification within savanna ecosystems as characteristic elements of hyperseasonal savannas and esteros (Table 10.12).
### TABLE 10.11
Some large plant genera having some representatives in Neotropical savannas (total number of species and distribution after Wills, 1973)

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Total number of species</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acacia</td>
<td>Fabaceae</td>
<td>150</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Andropogon</td>
<td>Poaceae</td>
<td>113</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Aristolochia</td>
<td>Aristolochiaceae</td>
<td>310</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Aster</td>
<td>Asteraceae</td>
<td>500</td>
<td>cosmopolitan</td>
</tr>
<tr>
<td>Bauhinia</td>
<td>Anacardiaceae</td>
<td>400</td>
<td>American</td>
</tr>
<tr>
<td>Boronia</td>
<td>Rubiaceae</td>
<td>150</td>
<td>warm</td>
</tr>
<tr>
<td>Cassia</td>
<td>Fabaceae</td>
<td>600</td>
<td>tropical and warm temperate</td>
</tr>
<tr>
<td>Centaurium</td>
<td>Fabaceae</td>
<td>550</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Crassula</td>
<td>Euphorbiaceae</td>
<td>750</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Cuphea</td>
<td>Lythraceae</td>
<td>250</td>
<td>American</td>
</tr>
<tr>
<td>Dombeya</td>
<td>Fabaceae</td>
<td>450</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Erythrina</td>
<td>Fabaceae</td>
<td>140</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Euphorbia</td>
<td>Euphorbiaceae</td>
<td>2000</td>
<td>cosmopolitan</td>
</tr>
<tr>
<td>Evolvulus</td>
<td>Convolvulaceae</td>
<td>100</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Galenia</td>
<td>Fabaceae</td>
<td>140</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Gomphocarpus</td>
<td>Amaranthaceae</td>
<td>190</td>
<td>American</td>
</tr>
<tr>
<td>Hiptage</td>
<td>Loxantarpaceae</td>
<td>400</td>
<td>warm American</td>
</tr>
<tr>
<td>Heliotropium</td>
<td>Fabaceae</td>
<td>700</td>
<td>warm</td>
</tr>
<tr>
<td>Ilex</td>
<td>Verbenaceae</td>
<td>150</td>
<td>tropical, American, African</td>
</tr>
<tr>
<td>Lippia</td>
<td>Verbenaceae</td>
<td>220</td>
<td>tropical, American, African</td>
</tr>
<tr>
<td>Mimosia</td>
<td>Mimosaceae</td>
<td>500</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Pentaclethra</td>
<td>Malvaceae</td>
<td>200</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Pluchea</td>
<td>Fabaceae</td>
<td>240</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Polygala</td>
<td>Polygalaceae</td>
<td>600</td>
<td>cosmopolitan</td>
</tr>
<tr>
<td>Rhynchosia</td>
<td>Fabaceae</td>
<td>300</td>
<td>tropical and subtropical</td>
</tr>
<tr>
<td>Sabul</td>
<td>Lamiaceae</td>
<td>700</td>
<td>tropical and temperate</td>
</tr>
<tr>
<td>Senecio</td>
<td>Asteraceae</td>
<td>9000</td>
<td>cosmopolitan</td>
</tr>
<tr>
<td>Sida</td>
<td>Malvaceae</td>
<td>200</td>
<td>warm</td>
</tr>
<tr>
<td>Stylospermopsis</td>
<td>Verbenaceae</td>
<td>160</td>
<td>American</td>
</tr>
<tr>
<td>Stylospermopsis</td>
<td>Verbenaceae</td>
<td>160</td>
<td>American</td>
</tr>
<tr>
<td>Stylospermopsis</td>
<td>Verbenaceae</td>
<td>160</td>
<td>American</td>
</tr>
<tr>
<td>Stylospermopsis</td>
<td>Verbenaceae</td>
<td>160</td>
<td>American</td>
</tr>
</tbody>
</table>

### TABLE 10.12
Palm genera with representatives in Neotropical savanna formations

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Tropical and subtropical American</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acrocomia</td>
<td>Aristolochiaceae</td>
<td>300</td>
</tr>
<tr>
<td>Aristolochia</td>
<td>Rubiaceae</td>
<td>300</td>
</tr>
<tr>
<td>Aristolochia</td>
<td>Rosaceae</td>
<td>300</td>
</tr>
<tr>
<td>Aristolochia</td>
<td>Sapindaceae</td>
<td>300</td>
</tr>
<tr>
<td>Aristolochia</td>
<td>Urticaceae</td>
<td>300</td>
</tr>
<tr>
<td>Aristolochia</td>
<td>Verbenaceae</td>
<td>300</td>
</tr>
</tbody>
</table>

The 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. espeletia* in the dry formations of Northeastern Brazil (caatingas); *C. tepetum* and *C. santae-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...
savana palms show a particularly rich diversi-
ification, often with quite peculiar growth forms like
the aculeocent dwarf palms (see Ch.5). On the
other hand, palms appear among the primeval
floristic elements of Neotropical savannas. Van der
Hamm (1972) reported Maurisia pollen in the
Palocene of northern Southern America as an indica-
tion of the early occurrence of wet savanna-like
formations in this area. Other palms, such as
species of Astrocaryum, Syagrus and some other
genere, appear instead as more recent additions to
the savanna flora from rain-forest stocks, where
these genera have a large number of species. Some
Another interesting point to notice concerning
the relationships of the Neotropical savanna flora is
its almost total lack of affinity with some nearby
dry forests. In the cerrado, for instance, it is sur-
prising 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 struc-
ture. Though certain transitional communities exist
(Eiten, 1972), they seem to be rather impoverished
types of each formation than ecotones where cer-
rado and caatinga elements mix with each other.
Similarly, a savanna thorn forest contact occurs in
Venezuela between the llanos and the semi-arid
drainage patterns of the Caribbean coast (Sarmiento,
1976), but the distinction between them always
remains clear-cut. Floristically the number of com-
mon species is almost nil, while the genera common
to both are large genera of the type referred to
previously as unspecialized or ubiquitous, like
Cosia, Coscia, Guapumia, Mimos and Sida.
Quite exceptionally an entire characteristic of the
dry forests 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
savana/thorncrumb border in northern South
America. Similarly a few floristic elements common
to savannas and arid formations are really rain-
forest 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 Agaveae,
are almost unrepresented in savannas. Thus, the
only savanna cactus, Cerocajacaruru, does not
have close relationships with species of dry forma-
tions, 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 (campinar
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
of the scrub, low forest, and herbaceous
swamps that characterize the high sandstone plate-
aux of the Roraima Formation (tepuys). Steyer-
mark (1966, 1967) analyzed these isolated highland
formations from both floristic and phytos-
geographical 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, par-

cularly among the monocotyledons, characterizes
the tepuis as well as the open lowland communities.
Among the herbaceous flora may be mentioned
species in the families Bromeliaceae, Cyperaceae,
Eriocaulaceae, Marantaceae, Orchidaceae,
Rutaceae, Thurniaceae, and Yriddiaceae. The
most characteristic genera among the woody flora
are: Antonia, Chiasa, Cupania, Hamirina, Mashaya,
Rupanu, Termstroemia, 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
Amazonian Territory, where several highly inter-
esting floristic connections with Palaeotropical areas
are becoming evident with the advancing knowl-
edge of their flora, suggesting the considerable
antiquity of this particular kind of savanna.
Outside the white sand areas, the plant com-
unities exhibiting the greatest number of Guianan
elements undoubtedly are certain types of esteros
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 Laguna Sante in Minas Gerais alone. Ellen (1963) analyzed the cerrado flora in a restricted region in eastern São Paolo, at 22 S — that is, near the southern border of this formation. In an area of about 500 km² 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 cerradão and those species exclusive of the open campos. Goddall (1970) gave a list of 600 species and 336 genera in the flora of an area of about 5,000 km² 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 (Hertringer et al., 1977) a total of 774 woody species are recorded, with a complementary list of 127 herbaceous and subshrubby species, 106 grasses and 34 orchids — that is, an overall figure of 1106 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 Hertringer 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 Birkart (1969) and Cabrera (1970).
| Formation | Area (km²) | Number of trees and shrubs | Number of substrates, half-shrubs, herbs, vines, etc. | Number of grass species | Total number of species* 
|-----------|-----------|---------------------------|-----------------------------------------------------|-------------------------|------------------
| cerrado in northeastern São Paulo (Eiten, 1963) | 90 | 45 | 175 | 17 | 257
| cerrado in western Minas Gerais (Goeldi, 1970) | 15,000 | ~240 | ~330 | 33 | ~600
| Wajtap cerrado region (Stemper et al., 1977) | 2,000,000 | 429 (74%) | 181 | 108 | 718 (1963)²
| Rio Branco savannas (Rodriguez, 1971) | 40,000 | 40 | 87 | 9 | 136
| Rupununi savannas (Goeldi, 1966) | 12,500 | ~50 | 201 | 90 | 431
| Northern Surinam savannas (Van Donkelaar, 1965) | ~900 | 15 | 213 | 44 | 272 (445)²
| Central Venezuelan llanos (Ariegueta, 1960) | 3 | 69 (36%) | 175 | 44 | 266
| Venezuelan llanos (Rumia, 1974a) | 250,000 | 43 | 312 | 200 | 555
| Colombian llanos (FAO, 1960) | 150,000 | 4a | 174 | 88 | 306

*Total flora including other plant formations.
²Total flora including barks.
³Number of savanna tree excluding grasses.

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 northeastern São Paulo, while Andrade Lima (1959) for the savannas near Monte Alegre and Egler (1960) in his floristic inventory of the Aïrangaš 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 campos. Rodriguez (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 shrubs, 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.

Goeldi (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 is a total of 398 herbaceous and subshrubby species, including more than 90 grasses, together with 53 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 São Raimundo (coastal savanna), Van Donselaar (1963) 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 São Raimundo savannas include 314 species collected so far (Van Donselaar, 1963).

In the seasonal savannas of the central Venezuelan llanos, Aristigueta (1966) reported 34 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 graces (tororas) 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, Ramírez (1974b) listed 555 species, including in this figure any type of savanna as well as many widespread weeds. The grass family is the largest, with 299 species; trees and high shrubs including palms total 43 species. In the Colombian llanos (FAO, 1966), a total of 88 grasses, 30 species, 144 herbaceous 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 different types of parent material including some unusual substrata such as siliceous sands and serpentine rocks which are responsible for an endemism of 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 (Aristigueta, 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 herbacea 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 Guayan formation.

A possible explanation of these contrasting gradians 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 interval 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 a 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 also may 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 Bondichia virescens, Berbsinaea crucifolia and Chamaele australis, and also for grasses and sedges like Leptochloa phiala, Trachypogon plumosus and several species of Andropogon, Aegypoc, Bahiocalis, Phalacra, 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 physiognomological systems is difficult due to the lack of adequate floristic knowledge and to the intrinsic weaknesses of physiognomological methodological approaches. In general, one may notice that physiognomological classifications, like those already discussed (Van Domselaar, 1965, Hoek, 1971), seem to be successful at a regional level. But extrapolation to regions further away from the areas of origin becomes rather problematical.

REFERENCES


