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CHAPTER 16

A Critical Consideration of the Environmental Conditions Associated with the Occurrence of Savanna Ecosystems in Tropical America

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The Savannas Problem

The savannas cover extensive areas of the American tropics, and, together with rain forests, are the most extended neotropical plant formations. Ecological interpretation of these savannas has been quite divergent due partly to the word "savanna" being applied to completely different ecosystems. Even when limited by a definition like Beard's (1953), it still includes a wide variety of physiognomic types and floristic units under different climatic, topographic, soil conditions, and degrees of human interference. Furthermore, the difficulty in distinguishing secondary herbaceous communities from primary savannas, as well as delimiting savannas and open forests, helps make the interpretation more confused.

It is remarkable that savanna is the only ecosystem in the entire warm tropical region whose origin and permanence have been considered unanimously as a fundamental ecological problem. This is partly due to its peculiar physiognomy, interrupting the continuity of forest formations and suggesting by contrast that it is a secondary or unstable system. A common question is, if rain forests occur under wet tropical conditions and dry deciduous and thorn forests under drier environments, why do grass- and herb-dominated formations appear in the middle of this water gradient?

Almost every savanna region in the American tropics has been the subject of analysis, but each work has been specific in terms of area and viewpoint. Thus most generalizations and their extrapolations to other savanna regions have led to contradictory conclusions. This is even more evident when comparisons are made between savannas on different continents or when the conclusions from the study of African, Asian, or Australian savannas are applied to tropical America.

As a starting point, we will adopt a concept of tropical savanna widely accepted in America, the American savanna being the only region considered here. Following Beard, tropical savanna is defined as a natural and stable ecosystem occurring under a tropical climate, having a relatively continuous layer of xeromorphic grasses and sedges, and often with a discontinuous layer of low trees or shrubs. This definition includes physiognomy (a relatively continuous herb layer, with or without sparse trees or shrubs), floristics (predominance of grasses and sedges in that layer), and ecology (a tropical climatic regimen, a natural, stable ecosystem, and xeromorphic nature of the herbs).

This definition excludes all herbaceous communities where grasses and sedges are not dominant or xeromorphic, as in high mountain vegetation in the Andes (*paramos*), the vegetation of the high Guianan plateau, and the communities of seasonal or permanent swamps. The definition also excludes seral communities as well as obvious man-made systems as pastures and fields. On the other hand, the concept includes pure grasslands, without woody species, as well as plant formations with an almost continuous tree cover, provided that the herb layer is still a continuous, ecologically dominant vegetation stratum.

Other authors have used a broader concept of savanna, as, for example, Dansereau (1957) and Walter (1971), who divide grasslands from mixed communities of herbs, trees, and shrubs. These authors also include in their savanna concept all mixed communities from extratropical regions. Both criteria are fruitless when applied to tropical American savannas. First, because these ecosystems are fundamentally different in rhythmicity from communities of similar physiognomy in subtropical and temperate regions. Second, because in the neotropical region there are closely related ecosystems differing only in the presence or absence of a sparse tree cover, and according to a purely physiognomic definition, these would constitute completely different units. Thus it is neither useful nor convenient to separate pure grasslands from tree grasslands, at least in the American tropics.

Some other authors, like Jaeger (1945) and Lauer (1952), have employed a radically different savanna concept, considering as a "savanna belt" a tropical or subtropical region with a marked seasonal climate. Savanna, then, becomes a geographic unit, defined by its climatic regimen, independent of the actual ecosystems occurring in each area. A substantial part of savanna belts thus defined is in fact covered with various forest types.

The geographic distribution of tropical American savannas, together with a description of the major physiognomic and floristic types, has been reviewed by Sarmiento and Monasterio (1974). Figure 16–1 reproduces the map from that paper showing the main regions of savanna in South and Central America.

Here, the major aim is to discuss the environmental and/or historical factors related to the occurrence of tropical American savannas. We will refer to savanna ecosystems in the plural, because sufficient ecological diversity exists between types to make it impractical to consider all types as one ecosystem. As we will see later, it is necessary to differentiate at least three types of savanna ecosystems.

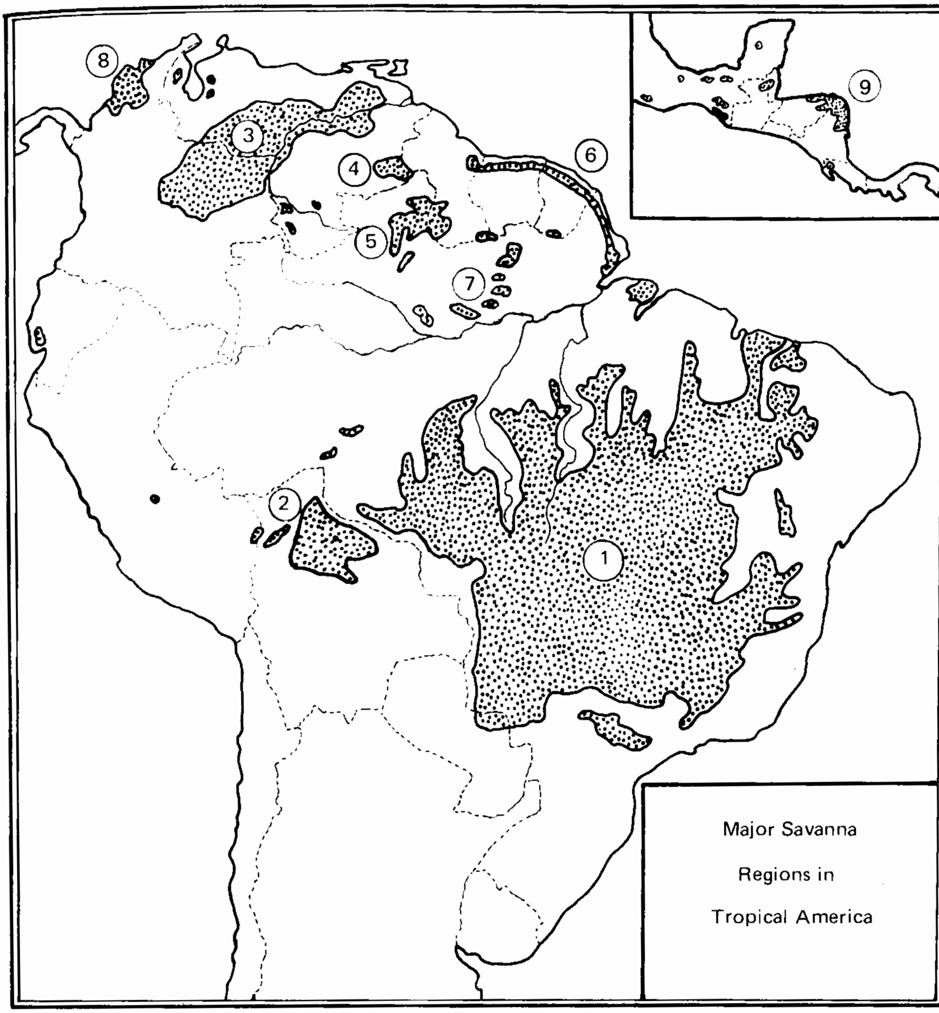

Fig. 16–1. Major savanna regions in tropical America. (*1*) Cerrado region; (*2*) Bolivian llanos; (*3*) Orinoco llanos; (*4*) Gran sabana; (*5*) Rupununi-Rio Branco savannas; (*6*) coastal Guianan savanna belt; (*7*) Amazonian campos; (*8*) Magdalena region; (*9*) Miskito region.

A thorough ecological study of the full range of tropical American savannas is still lacking. The first essay on this problem was Beard's (1953). Considering only the savannas extending from Central America and the West Indies to the northern part of the Amazon basin, Beard concluded that these savannas were edaphically determined, appearing in regions of strongly seasonal climate as a consequence of maldrainage problems during the rainy season and acute water deficiency during the dry season.

Hills and Randall (1968) summarize the conclusions of an international symposium held in Caracas in 1964 on the savanna-forest border, emphasizing the points made above. Van Donselaar (1965), considering the savannas only in northern Surinam, critically discussed the origin and evolution of the northern South American savanna flora and vegetation. He speculates about the possible origin of that savanna flora on the ancient plateau of the Guiana Shield. Blydenstein (1967), in Colombia, concluded that several factors acted concurrently, because savannas and forests occurred under identical climatic and soil conditions. Hills (1969) summarizes the studies of a McGill University research team in the Rupununi savannas in Guyana, which considered a hierarchy of operative factors, such as length of dry season, soil fertility, occurrence of laterites, fire, depth of water table, and landscape evolution. Eiten (1972) reviews the major savanna area of South America, the *cerrado* region in central Brazil, concluding that the *cerrado* vegetation is a climatic topographic and edaphic climax, with biotic factors having a much smaller influence. Our team in Venezuela (Monasterio, 1971; Sarmiento and Monasterio, 1969, 1974; Sarmiento et al., 1971; Silva and Sarmiento, 1973) has also considered a variety of factors in the occurrence of the various savanna types, emphasizing the wide diversity of savanna communities and the importance of the evolution of the whole landscape in understanding the distribution of forests and savannas.

In summary, the literature emphasizes the fragmentary knowledge on this subject. The occurrence of savannas in tropical America still remains one of the big biogeographic and ecological problems of the neotropical area. In the following sections we will consider the major ideas encountered in the literature, discussing them in the light of our direct experience.

The Main Theories on Factors Associated with Savanna Ecosystems

The various explanations of the occurrence of tropical American savannas may be grouped into six categories according to the external factor to which the most emphasis is given. We will consider these theories consecutively without giving a comprehensive list of all supporters, taking into account the fact that many researchers changed their opinions as new evidence became available.

Climatic Factors

Perhaps the oldest explanation (Grisebach, 1872; Schimper, 1903; Warming, 1908; Bouillene, 1926; Myers, 1936; Jaeger, 1945; Sarmiento, 1968) is that tropical savannas are the result of a particular climate. This climate is defined by Koeppen (1931) as tropical wet and dry, or savanna climate (Aw). The key operative factor in selecting the savanna ecosystem is the regimen of constantly high temperature throughout the year, with alternation of a very rainy season and a prolonged, almost completely rainless season. During the rainy season a large water surplus occurs (Thornthwaithe, 1948), while during the rainless season a strong water deficit prevails, with rainfall much lower than potential evapotranspiration. According to supporters of the theory, savanna is better adapted than any other plant formation to withstand this cycle of alternating soil-water conditions. Rain forests could not resist the extended period of extreme drought, while dry forests could not compete successfully with perennial grasses during the equally extended period with large water surplus.

Extensive areas of tropical America with an Aw climate (Figure 16–2), such as Cuba, the Colombian-Venezuelan llanos, the Bolivian llanos, and the interior Brazilian plateau, have in fact, a plant cover with a predominance of savannas.

Soil Factors

Several soil features have been postulated as major determinants of savannas. These include soil drainage, soil-water-retention capacity, and mineral supply.

Soil Drainage

According to this theory (Bennett and Allison, 1928; Charter, 1941; Beard, 1944, 1953; Richards, 1952; Miranda, 1952; Walter, 1971), the existence of savanna is related to a soil-water regimen where excessively wet

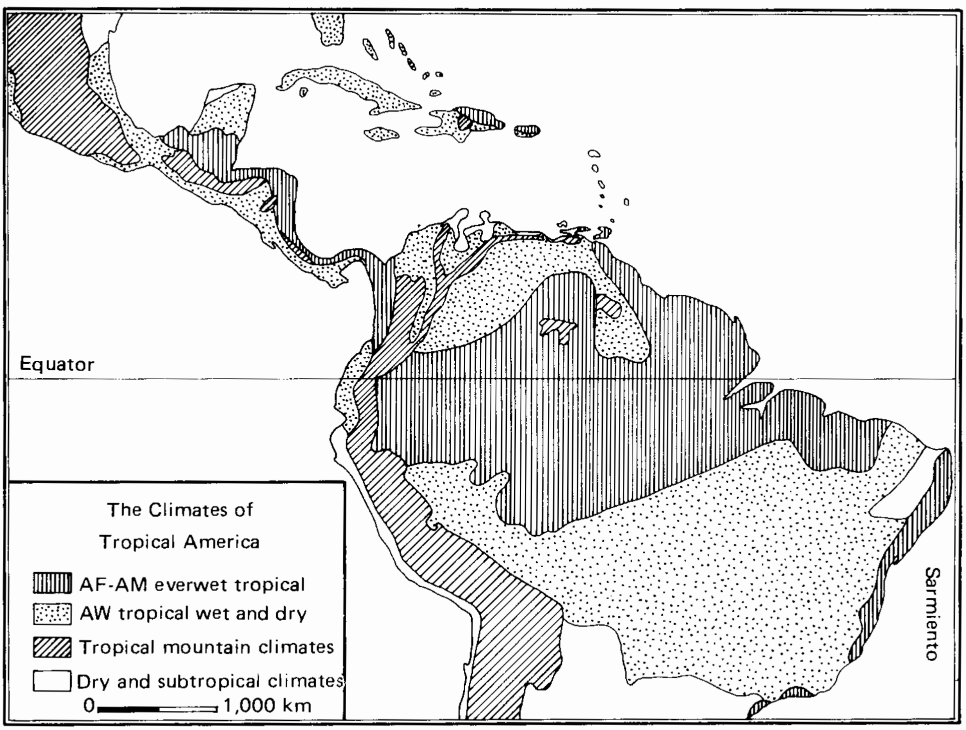

Fig. 16–2. The climates of tropical America.

conditions, with anaerobic horizons at or near the surface, alternate with periods where these same soil horizons become dry below the permanent wilting point. This annual cycle can be found under an Aw climate in physiographic and topographic situations with difficult external and internal soil drainage. For instance, seasonally hydromorphic soils frequently occur in alluvial floodplains where a combination of very gentle slopes and superposition of sedimentary layers of different permeability induces a slow drainage during the season of heavy rainfall. As these conditions of impeded drainage are generally associated with impermeable and poorly structured clay horizons, the previously saturated soils not only lose their water rapidly immediately after the end of the rainy season but very soon become physiologically dry, remaining in this state until the beginning of the next rainy season.

Another slightly different situation occurs in well-drained soils with a water table rising near the surface during several months. In both cases the alternation of wet and dry soil phases resembles the annual cycle produced by a savanna climate, and in this sense the explanation is similar to the climatic theory. Nevertheless, the ecological conditions of seasonally saturated or waterlogged soils are more complex, since the biological impact of the climatic cycle is reinforced by the soil-water cycle, resulting in an additional environmental stress on plant life. The potential for various life forms to exploit each soil horizon become significantly different, therefore causing important changes in the structure and composition of the corresponding savanna ecosystems.

Dry Soil

This explanation (Santamaria and Bonnazzi, 1963; Walter, 1969) is completely opposite the previous one, and constitutes a further demonstration of the contradictory interpretations of savanna ecosystems. In this case, the main operative factor is supposed to be an excessively dry soil, determined either by (1) a low water-retention capacity in the upper soil horizons originating in unfavorable texture, as in coarse deposits of gravel or sand; (2) a shallow soil profile as on hard-weather-resistant rocks (quartzites, some sandstones and limestones); or (3) a secondary shallow profile due to the development of a lateritic cuirass near the surface. In each case during a rainless period the soil profile is subjected to a rapid loss of available water.

If these conditions appear under a strongly seasonal climate, the vegetation will suffer from a water stress for almost the entire rainless period. Under an ever-raining climate, a complete soil drought will only occur during short periods between heavy rains, but the level of available soil water will often approach the permanent wilting point.

Low Nutrient Supply

According to this theory (Pulle, 1906; Lanjouw, 1936; Waibel, 1948; Arens, 1958), savanna soils are too poor nutritionally to maintain forest. This deficiency in mineral elements may originate in (1) a very poor parent material such as a pure quartz sand or any long transported alluvial or eolian deposit; and (2) a soil material impoverished through the soil-forming process, such as rapid weathering of ferromagnesian minerals, rapid mineralization of organic matter, the neosynthesis of kaolinitic clays of very low cation exchange capacity, a thorough leaching of soluble elements, increasing desaturation of the cationic complex, and the immobilization of elements in soil complexes.

If both a poor parent material and an extended evolution of the soil profile are concurrent, the resulting soils will be extremely poor, with a critical low level of most essential elements. In less extreme situations, only certain nutrients may be limiting.

Two other factors contributing to soil impoverishment are soil erosion and fire. Erosion with heavy rainfall, open vegetation, and steep slopes may lead to a total loss of the upper soil horizons. Fire results in the accumulation of mineral elements on the soil surface after burning as ash, which can be lost by water or wind erosion.

In any case, be it a senile soil profile, original poverty, or secondary losses, savanna soils in tropical America have in fact an extreme oligotrophic character.

Fire

Many workers (Rawitscher, 1948; Ferri, 1955; Parsons, 1955; Vareschi, 1960; Tamayo, 1964; Schnell, 1971) maintain that frequent fires in savanna prevent the establishment or persistence of plant formations not resistant to burning. Fire may originate by natural phenomena or by human origin. Some believe that any forest may be degraded to savanna provided that it is burned frequently enough; others think that only some particularly sensitive vegetation types may be transformed into savannas.

Whatever the case, burning will act like a selective filter through which only fire-tolerant or -resistant species pass, and these species are precisely those encountered in present-day savannas.

The Human Factor

This viewpoint (Aubreville, 1949; Budowski, 1956; Johannessen, 1963; Taylor, 1963; Walter, 1971; Puig, 1972) considers savannas to be relatively recent ecosystems originating from human action upon different forest types. Savannas could have originated and been maintained by aboriginal man through deforestation by burning or with tools to obtain open areas for hunting and later for cattle-raising and crop production. Once the forest has been destroyed and its reestablishment prevented over an extended time, several ecosystem characteristics vital for forest regeneration are irreversibly altered. The normal secondary succession is changed toward savanna, which is maintained as a permanent disclimax.

This explanation, although similar to the fire theory, differs in the fact that fire can be natural and not man induced, while man may resort to other deforestation methods besides burning. According to the anthropic theory, savanna communities would not be older than the first arrival of man in tropical America, that is, they would be postglacial and probably no more than 20,000 years old (Hester, 1966).

Historicogeographic Changes

Several authors (Aubreville, 1962; Hueck, 1966; Schnell, 1971) have considered the savannas as relics from previous periods when another set of ecological determinants was at work. Similarly, others have considered savannas as the final product of landscape evolution under conditions that are not comparable to the present ones, appearing only in habitats disintegrating under attack by the present morphogenetic agents (Cole, 1960; Egler, 1960). Thus the occurrence of savannas would be additional evidence of dramatic geologic, geomorphologic, and climatic change during the Quaternary Period in tropical American lowlands. These changes have been reported for Brazil, Guyana, Venezuela, and Colombia (see Vuillemier, 1971) and they alter previous ideas about the relative stability of the humid tropical environments.

The savannas problem however remains. What could the environmental conditions be in places where savannas originated and where they actually prevail? If these conditions exist now in any region, savannas would sooner or later become established there, and to explain this establishment we must certainly resort to one of the previous theories. If, on the contrary, these conditions have not been produced again, then the savannas become a paleoecologic puzzle.

An opposite argument is that savannas occur in such a geologically and evolutionarily young environment, that tree species capable of colonizing and forming a closed forest have not yet evolved, or reached these areas. This theory is reinforced by the apparent absence of a fauna of vertebrates from South American savannas. In this way, savannas would belong to the postglacial age, and represent early successional stages in a slow evolution toward a new forest type.

Holocenotic Theories

Most recent authors (Cole, 1960; Eden, 1964; Hills, 1965, 1969; Goodland, 1970; Monasterio, 1971; Monasterio and Sarmiento, 1971; Eiten, 1972) cite the interaction and concurrence of several factors in the origin and maintenance of savanna ecosystems. Some may be simply conditioning or predisposing factors, others may be a necessary but not sufficient determinant, while others may be important in the genesis of the ecosystem but not in its maintenance. Because these theories always include a set of simultaneous or successive agents, we have called them "holocenotic," to emphasize the interaction of many environmental and evolutionary factors and the holistic nature of their influences.

An example of a holocenotic theory is that, within a region of tropical wet and dry climate, in flat areas with heavy soils of impeded drainage that dry off completely during the long rainless season, the savannas displace any other possible formation not able to withstand the alternation of both water deficiency and water surplus. Another sequence of events leading to a savanna ecosystem would be a tropical rainy climate, with continuous water excess producing intensive soil leaching. Thus well-drained, coarse-textured soils would suffer almost complete loss of critical elements. On these impoverished soils the zonal rain forest is replaced by a lower, more open, and more scleromorphic forest that is also more susceptible to burning. After repeated burnings a savanna becomes established and is maintained by fire.

Discussion

Climate

In tropical America a high proportion of savannas occurs under tropical wet and dry climates—Koeppen's Aw climatic type (see Figures 16–1 and 16–2). In this climatic type annual rainfall amounts to 1,000 to 2,000 mm, and 80 to 90 percent of this total falls in a wet season five to eight months long. This climate is produced by the annual cycle of the tradewinds and the seasonal displacement of the Intertropical Convergence Zone between both hemispheres. Most savannas in the Colombian, Venezuelan, and Bolivian llanos, in Cuba, and in the interior plateau of the Guianas and Brazil occur under this climatic type. In contrast, the savannas of the Atlantic coast of Honduras and Nicaragua, Trinidad, the northern coast of Brazil, and the Guianas, as well as the savanna "islands" within the Amazon lowlands, do not occur under seasonal climates but in tropical wet climates (Af-Am types of Koeppen). In these regions annual rainfall generally exceeds 2,000 and even 3,000 mm, and there are at the most three months with rainfall lower than 100 mm.

A first climatic limit evident in the distribution of the tropical American savannas is a drought limit, since there are no savannas in this region with yearly rainfall figures under 800 to 1,000 mm. This is a major difference between America and other continents, where savannas occur under arid and semiarid climates (Walter, 1971). In the neotropical region, with dry climates (B types of Koeppen) and even with Aw climates near the dry limit, dry deciduous and thorn forests occur, and savannas are absent. Only in the subtropical and temperate regions of South and North America do semiarid savannas exist, as in the Chaco region of subtropical South America and the mesquite woodlands of southern United States and northeastern Mexico.

A second climatic limit of savannas in tropical America is altitude. Most savannas appear below 1,000 to 1,200 m above sea level. Along the Andes chain savannas never surpass these elevations. The only American areas where savannas are found at higher elevations are in the isolated ranges and plateau in the interior of the Guianas, where they may reach more than 2,000 m (Myers, 1936). Here they form a shrubby vegetation characterized by its peculiar, highly endemic flora, typical of the "rocky fields" of this region. This altitudinal limitation of tropical savannas could be explained as a thermal limit, not due to low temperatures being unfavorable to growth or establishment of savanna species but constituting a handicap in competition with other growth forms. The latitudinal limit of tropical savannas appears to be a coincident with a frost boundary and with the occurrence of a cold winter season in subtropical regions.

These two climatic limitations reduce the area of tropical savannas to the warm, tropical, rainy climates, the A types of Koeppen classification. According to Koeppen's system the A climates are divided in two main types: the tropical wet climates (Af), where rainfall of the driest month is at least 60 mm; and the tropical wet and dry climates (Aw) with a distinct dry season or at least one month having less than 60 mm. A third type, the monsoon, or Am, climate, is intermediate between Af and Aw, having a short dry season and a total annual rainfall greater than that of Aw climates.

Within the extensive region of Af-Am climates (Figure 16–2), the predominant plant formations are the rain forests (tropical rain forest *sensu stricto*, as well as seasonal evergreen forest and semideciduous forest; see Beard, 1944). Formations other than rain forests appear as islands dispersed in the rain forest matrix; these include savannas, swamps, and open, low forests called "savanna forests," or *caatingas*,[1] in the Amazon region. These three types are undoubtedly controlled by nonclimatic factors, since the wet climate is optimum for rain forest development.

In the tropical American region with wet and dry climates (Aw), the preceding pattern is reversed; here the forests appear as islands surrounded by a more or less continuous savanna matrix. Only in restricted cases do some forest types, mainly semideciduous and deciduous forests, appear over more continuous surfaces. Under these conditions savannas could be considered as "climatic," and the remaining formations could represent soil or topographic climaxes, but we must point out that the disjunction between savannas and dry deciduous forests does not rely primarily on regional climate. For further details about vegetation patterns under different climates in tropical America, see Sarmiento and Monasterio (1974).

Soils

Most tropical American savannas occur on flat topography, either on Quaternary alluvial plains (as in the llanos of Colombia, Venezuela, and Bolivia) or on ancient, very gently undulating peneplains (as in the Brazilian *cerrados*). A part of these savannas occupies low topographic positions where

[1] It is necessary not to confuse these Amazon *caatingas*, which are sclerophyl, evergreen forests, with the northeastern Brazilian *caatingas*, which are dry, deciduous forests.

rainwater accumulates during the rainy season, leading to the development of hydromorphic soils. However, savannas do not occur on soils that remain water saturated or waterlogged most of the year. In the latter case swamp communities become established, or if the underground water circulates, gallery forests may be maintained.

Savannas occur on ill-drained soils only in conditions of seasonal water saturation, when periods of oxidation and reduction within the soil profile alternate during the year, giving to the soil the characteristic red, yellow and gray mottled colors. These soils are unfavorable for plant growth almost the whole year, remaining anaerobic during the wet season, and then quickly drying shortly after the rains end. On the other hand, even when they are waterlogged, the subsoil at a depth of 0.5 to 1 m may be completely dry, since a clay hardpan near the surface greatly reduces water percolation to deeper horizons. In this way, under a seasonal wet and dry climate, in certain topographic positions, the soil features reinforce the two contrasting climatic extremes, giving rise to a drier habitat in the dry season and a wetter habitat during the rain period. A similar situation occurs in river floodplains when the river water volume changes seasonally and floods its plain almost yearly.

At the other extreme, frequently in savanna regions soils have low water-retaining capacity, due to coarse texture or shallow depth. Many of these soils have developed on coarse alluvial gravels or on alternating depositions of gravels and sands, while in other cases savannas occur on thin soils developed on weather-resistant rocks, such as sandstones, quartzites, and old lateritic cuirasses. Under a seasonal climate these soils are drier during the rainy period than more normal soils, and during the rainless season they remain ecologically dry for a longer time.

Considering nutrients, soils in tropical humid regions (A climates) are usually poor in mineral nutrients, as a direct consequence of the dominant soil genesis processes leading to an increasing elimination of soluble and interchangeable elements from the soil profile. Under particular circumstances the soil may be exceptionally poor in comparison with other tropical soils, as when the parent material is deficient in nutrients, the soil is very permeable, the clay and organic matter content is low, or the soil genesis has been prolonged.

Tropical podzols developed on pure "white sands" (Klinge, 1965; Sioli and Klinge, 1962) are undoubtedly the poorest soils in the American tropics (Stark, 1970). However, the vegetation they maintain is usually an open and low forest and rarely a savanna. In these forests the mineral cycling follows almost entirely biotic pathways through the well-developed organic horizons covering the soil surface where the tree roots are most developed. In this way the nutrient cycles bypass the mineral soil. When this deep humus layer is destroyed, either by fire or human activity, the rupture of the nutrient cycles may be responsible for the lack of regeneration of the forest and the perpetuation of a scrub vegetation or shrub savanna.

Other tropical soils do not show the extreme oligotrophic nature and the labile equilibrium in the nutrient cycles of podzols. However a significant difference exists between forest and savanna soils, not only in turnover rates and total amounts of nutrients in the system but also in the relative importance of the A horizons as nutrient reservoirs. If the soil organic matter content under forests and savannas is roughly equivalent, in a forest ecosystem soil litter plays a first-order role in the annual liberation of the mineral elements accumulated in the aerial parts of vegetation. In contrast, litter production in the savannas is insignificant. The only organic material incorporated directly in the soil originates in underground organs, while the mineral elements of aboveground biomass normally reach the soil as ashes after burning.

In summary, all humid tropical soils seem to be highly oligotrophic, some of them, like podzols, to an exceptional degree. Forests may occupy even the poorest soils. The cycling of nutrients in forests is labile and sensitive to external disturbance.

Fire

All savannas burn repeatedly at intervals varying from a few months to several years, and the great majority of them burn at least once every one or two years. The main period of burning is during the last half of the dry season or during short rainless intervals. It is difficult to find savannas that have not been burned for long periods, even in small savanna islands surrounded by rain forests. However, in everwet climates without a distinct dry season, fire frequency may be so low as to be unable to hamper woody growth, especially of those fast-growing trees that colonize open sites. Therefore, in this climate, if the savannas are a result of deforestation through fire, it is difficult to understand why the natural regeneration of forest does not proceed. Actually the savanna-forest border remains clean and stable for decennia.

In the case of wet and dry climates, it is obvious that fire does not affect the establishment of woody species in the savannas, and that tree density in these ecosystems is not basically dependent on fires but on certain soil factors (Mooney et al., 1974). If only fire were controlling woody growth and propagation, a forest of woody pyrophytes would become established in a rather short time. Fire in the savannas acts as a filter through which only adapted or tolerant species pass. Thus all woody and herbaceous savanna species are pyrophytes, with different methods of avoiding, resisting, or tolerating recurrent burning. But the grassland or open woody physiognomy of most savannas is not directly related to fire frequency.

In temperate and subtropical regions there are fire-tolerant ecosystems characterized by a closed cover of shrubs or low trees where perennial grasses play, at best, only an accessory role, as for example, the chaparral, *garrigues* and the *Quercus-Pinus* low, evergreen forests of Mediterranean climate of Europe and North America. Why, then, in a tropical savanna, would burning be responsible for an open, grassy physiognomy, while in ecosystems of comparable fire frequency of extratropical regions, closed tree or shrub formations are maintained? Considering also the additional fact that burning woody cover, often of highly resinous wood, produces much higher temperatures for a longer time than savanna fires, which very quickly pass over the herb layer and only reach lower temperatures (Vareschi, 1962).

In present-day conditions, fires are more frequent in tropical savannas than in any other natural system elsewhere in the world. This high frequency is due to the use of savannas for cattle-raising, and is a phenomenon of the last few centuries. However, we have no evidence that these savannas were different 400 to 500 years ago, before European colonizers arrived in tropical America, when they might have been subjected to a much lower fire frequency by the aboriginal population.

In tropical zones natural fires occur mostly in a seasonal wet and dry climate, since commonly in dry climates the vegetation fuel on and near the soil is not continuous enough to propagate the flames, and in everwet climates the standing plant material and the litter are rarely dry enough to become flammable. In everwet climates only the savannas may be easily burned, providing that a long enough dry period has desiccated the standing biomass of the herb layer. Semideciduous forests also are not easily burned, and natural fires are not likely; but if they are intentionally burned, secondary grasslands quickly occupy the former forest land. These herbages differ from natural savannas in both composition and ecology, being dominated by alien grasses like the African species *Panicum maximum, Hyparrhenia rufa*, and *Melinis minutiflora* (Vareschi, 1969; Sarmiento et al., 1971; Parsons, 1972). Through frequent fires these grasslands may be maintained indefinitely without further forest regeneration. Usually the differentiation of these secondary herbaceous communities from primary savannas on the basis of a floristic analysis is not difficult.

Human Interference and Historic Factors

Human action has and continues to produce vast extensions of herbaceous secondary communities in tropical America. Some of these secondary communities will be maintained by annual burning. On the other hand, many primary savannas have been modified by overgrazing or ploughing, thus changing their original composition and structure, altering the herb-woody equilibrium, and favoring many weeds. Primary savannas, modified savannas, and secondary herbaceous communities may be separated easily by their composition. Without further consideration of secondary systems, we now have much evidence to support the statement that savannas did exist in tropical America before the arrival of the Europeans, before the development of aboriginal cultures, and most probably before the arrival of *Homo sapiens*—even before the birth of this species on the planet.

Palynological evidence, though fragmentary, shows the occurrence of savannas in the Orinoco plains, 5,000 years ago and in the Guianas 14,000 years ago, in both cases comprising the full extent of the available pollen records (van der Hammen, 1963; Wijmstra and van der Hammen, 1966). Palynological records reaching older Quaternary strata show that savannas have occurred in the Amazon basin from the last glacial period, having a probable age of 13,000 to 30,000 years (van der Hammen, 1972). This latter evidence is particularly interesting because the savanna pollen period is located between two forest pollen periods and in an area (near the Brazilian-Bolivian border) where there are no savannas at all.

Indirect evidence of a savanna-like vegetation under a strongly seasonal climate may be obtained by geomorphologic and pedologic data from Quarternary deposits in the Venezuelan plains, since only some soil and erosive paleoprocesses dating from middle Quarternary were possible under this type of climate and vegetation (Zinck and Stagno, 1965; Blanck et al., 1972).

The differentiation of a rich savanna flora in tropical America, distinct from any existing forest flora, is more evidence of the considerable age of the savanna formation. It is very difficult to explain the evolution of hundreds of species with complex and multiple adaptations to wet and dry climates, frequent fires, and low nutrient supply without continuous and prolonged operation of these selective forces. In pollen records from northern South America many savanna species already are present in the middle Eocene (van der Hammen, 1972).

Climatic, orogenic, and geomorphologic Quaternary changes led to dramatic changes in the distribution of lowland tropical ecosystems, with periodic replacement in any given place of savannas, forests, and swamps. These changes are documented in the pollen records from several localities in Colombia, Guyana, and Brazil.

In summary: First, the existence of savannas in tropical America during most of the Quaternary and the very ancient evolution of its flora have been established beyond any reasonable doubt. Second, the replacement of savannas and forests is also well documented. An immediate consequence is that the area of savanna has changed in the past concurrently with major environmental changes. The interpretation of savannas as human-induced ecosystems may be entirely discarded, without ignoring the fact that human action may be partly responsible for the maintenance of savannas.

Conclusions

We have concluded that the operation of several factors result in and maintain savannas; that is, we have developed a holocenotic interpretation of savanna ecosystems. We now wish to analyze three problems. First, if savannas are sufficiently heterogeneous to be conditioned by a different combination of external factors, the holocenotic interpretation will not be applicable to each type but only to all savannas in a single heterogeneous ecological category. Second, supposing that the holocenotic interpretation is valid for each major savanna type, how will the various factors be arranged in order of importance or in causal sequence? Third, is the impact of the environment on the ecosystem similar in every case, and are the living organisms under similar environmental stresses and identical selective forces?

Savannas and Rain Forests Under Tropical Rainy Climates

Let us consider first the situation under tropical rainy climates where long water stress periods do not occur. Under these climates three main types of ecosystems occur (disregarding swamp and other semiaquatic communities): (1) evergreen tropical rain forests; (2) low, open, scleromorphic forests (the Amazon caatingas); and (3) savannas. We have also seen that the pattern of these three types is that of a more or less continuous rain forest, with occasional patches or islands of the other formations.

Most rain forests in this area are climatic climaxes, and the differentiation between various forest formations depends upon the presence or absence of short drier periods (see Beard, 1944, for a classification of tropical American vegetation types). The scleromorphic forests appear in the Amazon region and in the Guianas where they have been called by the unfortunate names of "savanna forests" and "savanna woods" (Heyligers, 1963). They are always associated with white sands and are determined by the highly oligotrophic podzols developed on this parent material (Sioli and Klinge, 1962; Hueck, 1966) or by the constantly dry nature of these soils (Heyligers, 1963).

The savannas appear under two different sets of conditions: (1) on white sands, possibly as a final product of the natural evolution of the *caatinga* forest when the closed nutrient circulation within the ecosystem is no longer possible, or by irreversible rupture of this equilibrium through man-induced fires; and (2) on senile soils of latosolic evolution developed on old sediments of Plio-Pleistocene age. In contrast to podzols, these latosols are neither excessively drained, nor do they have seasonal deficits or surplus of water for long periods, but they have a very low fertility, though not to the advanced degree shown by podzols.

The occurrence of savanna on white sands may be associated with soil mineral deficiency as a determining factor for the open forest and a predisposing factor for savanna, while the natural evolution of the soil profile and/or fire may be the direct cause of savanna establishment and permanence. However, on highly laterized profiles the problem is how is the side-by-side coexistence of rain forest and savanna possible on soils of similar parent material, age, and topographic position, and therefore similar water budget and initial stock of plant nutrients.

Within the wet climate regions of tropical America savanna patches are almost constantly associated with flat alluvial surfaces, slightly elevated over the actual relief, formed by loose and rather coarse material, with frequent occurrences of iron hardpans or disintegrating lateritic cuirasses. These landforms, apparently of late Pliocene or early Pleistocene age, appear as reduced relictual forms in several regions of Central and South America, and are covered to varying degrees by typical savannas. Their soils are, in general, very leached latosols, or, in some cases, podzolized profiles developed on an ancient lateritic soil. Parsons (1955) described this landform in the *misquito* savannas of Nicaragua and Honduras; van Donselaar (1965) recognized this old surface as the main savanna belt in northern Surinam, and Bouillenne (1926) and Egler (1960) report that Amazon savannas appear on these elevated surfaces.

Our hypothesis, to explain the coexistence of rain forests and savannas in the humid regions of tropical America, is as follows: During a climatic period drier than the present one, with a clearly seasonal rainfall regime (an Aw climate), probably during the last glaciation, the Amazon basin and the neighboring regions were covered mostly by savannas, while rain forests were localized along or near the bordering mountains. As the climate became wetter and warmer from 15,000 years ago to the present, the seasonal regime disappeared and everwet climates became generalized in the whole region. Along with this gradual change of climate toward a nonseasonal regimen, rain forests gradually displaced the savannas. This colonization by rain forests proceeded first along river valleys and young terraces that were covering most of the Amazon depression between the old Brazilian and Guianan Shields and were slower on older deposits and landforms with senile soils. This process was certainly not continuous but probably followed the postglacial climatic oscillations. Finally, the rain forest reached the limits of the wet climatic region and only some isolated savanna patches remained where there were the least favorable conditions for forest growth, such as coarse sediments of low water-retaining capacity where lateritic iron pans were frequent and the soils very poor.

Man's arrival in the forest regions of Central and South America stopped forest advance in most areas, since primitive man chose open sites to settle, and savanna areas near the forest border offered him a most suitable environment for protection and hunting. As he employed fire as a hunting tool, savanna burning became more frequent and forest advancement receded. The late intervention of European man completely stopped the process, most markedly during the last century, bordering the former savannas with belts of secondary herbaceous communities.

This hypothetical reconstruction of vegetation displacements in the now wet tropical America is supported by several pieces of evidence. The extreme reduction of the Amazon rain forest area 15,000 to 20,000 years ago seems well documented on the basis of independent biological and biogeographic evidence (Haffer, 1969; Vuillemier, 1971). The corresponding climate was drier and colder, as is suggested by geomorphologic and pedogenetic processes then at work. Consequently, it seems quite probable that a vegetation more or less similar to present-day savannas covered most of this region. As we pointed out earlier, van der Hammen (1972) reported a long savanna phase between two forest periods in the southern Amazonas. Finally, the savanna patches inside this region correspond quite well to the senile soils in old peneplains.

Savannas, Rain Forests, and Dry Deciduous Forests Under Tropical Seasonal Climates

We have already noted that under a seasonal wet and dry tropical climate three physiognomic units coexist: semideciduous rain forests, deciduous forests, and savannas. These three types form complex vegetation patterns, where as a rule savannas make the dominant continuous matrix and forest appear as more discontinuous patches of varying extension.

Swamps and Hyperseasonal Savannas

In flat plains, rain or flood river water accumulates in low topographic situations during the rainy season, depositing the finest sediments carried in suspension. Heavy deposits are thus formed or, in many cases, a sequence of layers of different grain size according to the water-carrying capacity in each period. Heavy textured and poorly structured soils evolve with slow drainage, remaining waterlogged during most of the rainy season. At the end of the rainy season, external drainage and high evapotranspiration begin to desiccate these soils. In a couple of months they become completely dry, very hard, and the surface cracks, resulting in conditions of high water stress for living organisms. The corresponding soil profile is a pseudogley with descending hydromorphism (Zinck and Stagno, 1965; Monasterio and Sarmiento, 1971).

This type of soil-water annual cycle, under the joint action of climate relief and soil, produces a particular kind of savanna, which we have called "hyperseasonal savannas." This type is characterized by an extreme seasonality in vegetative and reproductive activities, a relatively open herb layer even in the period of maximal development (ground cover around 50 percent), a high proportion of xeromorphic sedges besides the grasses, and an almost completely absent tree layer with the noteworthy exception of palms such as species of *Copernicia* in South America and Cuba. Such communities and their habitats have been described in many regions of tropical America (Beard, 1953; Ramia, 1959; Cole, 1960; Blydenstein, 1967; Monasterio and Sarmiento, 1971). In his review, Beard considers that in this habitat the woody species cannot successfully compete with herbs, since, with the possible exception of some palms, most trees are unable to survive alternate periods of soil-water saturation and soil drought.

When the soil remains waterlogged for a longer period or a high water table occurs throughout the year, hyperseasonal savannas are replaced by swamp communities. These later formations vary widely in composition and structure; they may be exclusively herbaceous or have woody elements, in particular some palms such as species of *Mauritia*; but, in any case, they are not seasonal ecosystems. Some intermediate situations arise when the permanent water table remains at a certain depth during the dry season (around 1 m) and in this case some communities appear that are difficult to classify as swamps or savannas.

Gallery and Semideciduous Forests

On more normal soils of the seasonal climatic region, where waterlogging and desiccation do not occur, semideciduous or evergreen seasonal forests may form complex patterns with savannas (Monasterio and Sarmiento, 1971; Silva et al., 1971; Monasterio et al., 1971). Forests always appear under the most favorable annual water budgets. In fact, these two forest types only occur in seasonal climate regions where the soil constantly has available water or where it remains below or near the permanent wilting point only for a very short period at the end of the dry season. This shortening of the dry period is not due to climate but to an additional source of soil water available to trees.

The clearest case is gallery forests, which have a permanent water table within the reach of tree roots. When the forests occur further away from rivers, there is evidence that the trees also reach a water table, not only during the rainy season but also during a part of the dry season. In these cases water tables have been shown to oscillate between 1 and 3 to 8 m in depth, and as there is a lag period between the end of rainfall and the downward movement of the water table, the lowest levels are reached not at the end of the dry season (which otherwise could be a critical period for tree water supply) but during the first months of the next rainy season, when again trees have enough water available in the upper soil layers.

In some situations, as in the central Venezuelan plains (Monasterio and Sarmiento, 1971), the source of underground water supply for trees is a perched seasonal water table lying on an impermeable soil layer, or an iron hardpan, or an old lateritic cuirass. This perched water table, although neither permanent throughout the year nor continuous in space, provides an additional water source for certain localized forest patches during the first months of the rainless season, shortening in this way the length of the unfavorable period to no more than two or three months. This discontinuous water table is responsible for the complex vegetation pattern of forest groves in a savanna matrix, leading some authors to believe that this parkland physiognomy is evidence of a formerly continuous forest recently reduced by man's action. But the distribution of forest islands is not at random within the savanna matrix, as we would expect if they were relicts from a former continuous forest, being instead associated with factors favoring the occurrence of perched water tables.

Seasonal Savannas and Deciduous Forests

When in a lowland region of tropical America under seasonal wet and dry climate, there is neither accumulation of rainwater nor an extra water supply through a high water table, only two primary ecosystems may occur: tropical deciduous forest and savanna. This particular savanna type will be called "seasonal savanna" to distinguish it from the previously considered "hyper-seasonal savanna." We will consider this forest-savanna antinomy and the circumstances favoring the occurrence of one or the other ecosystem. If we analyze the situation in regions where both formations form vegetation mosaics, as in the central Venezuelan plains (Sarmiento and Monasterio, 1969; Monasterio & Sarmiento, 1971) or in the middle San Francisco basin in central eastern Brazil (Azevedo, 1966), we see that each formation appears under a different set of habitat conditions.

In the Venezuelan plains deciduous forests occur on middle Tertiary geological formations formed by clay and shale that give rise to rather heavy soils of moderately low internal drainage and good water-retaining capacity. These medium-textured soils have a high cation exchange capacity, considering the humid tropics, and also a medium base saturation, since the drainage somewhat hampers soil leaching. All these features contribute to maintain soil fertility in medium ranges. The same forest type also occurs in river terraces of similar granulometry and physical and chemical characteristics. In both cases, though internal drainage is slow, the soil does not remain waterlogged or water saturated for long periods, because of adequate external drainage. Otherwise the forest would be replaced by hyperseasonal savannas, as it does in low topographic positions.

In the same region of the Venezuelan plains, seasonal savannas occur over Plio-Pleistocene alluvial sands of coarse texture, often with intercalation of gravel layers, and a less important silt and clay content. These soils are well to moderately well drained, with low water retention, low cation exchange capacity, rather unsaturated, and therefore drier and poorer than the neighboring deciduous forest soils.

In the middle valley of the San Francisco River, in the state of Minas Gerais in Brazil, Azevedo shows a comparable situation in the wide contact area between *cerrados* (seasonal savannas) and *caatingas* (dry, deciduous forests and scrubs). Savannas only occur over sandstones where coarse textured, well-drained, and poor soils develop; deciduous forest appears over limestone, with finer and more fertile soils; and the deciduous scrub, a transition type to more xerophyllous formations, is found over clay-lime alluvium, of intermediate texture and nutrient content.

In both situations of coexistence of deciduous forest and savanna, two main factors seem to control the differential occurrence of each ecosystem. First is the water factor. Deciduous forest has more water available in the upper soil horizons during the wet season, because of higher water-retaining capacity and slower drainage; in contrast, savannas appear on soils with less available water in the upper soil during this same period. Second is the nutrient factor. Forest occurs on richer soils, because a high nutrient content apparently favors deciduous trees in competition with perennial grasses (Mooney et al., 1974).

Dynamic Relationships Between Different Ecosystems Under Seasonal Climates

Summarizing the preceding discussion, we may consider not only the vegetation but the whole landscape as a dynamic system varying according to long-term climatic fluctuations, geomorphogenesis, and soil evolution. As one example of this landscape evolution, take the case of an alluvial floodplain in a seasonal climate where rivers show great seasonal changes in water volume and almost yearly overflood the adjoining plains.

Figure 16–3*a* is a representation of the initial situation of a portion of a plain between two rivers. Sedimentary processes tend to accumulate coarser sediments near the water courses, forming more or less high sandy banks, while finer materials are transported and deposited further away from the river in the central portion of the plain. Two gradients are then formed outward from

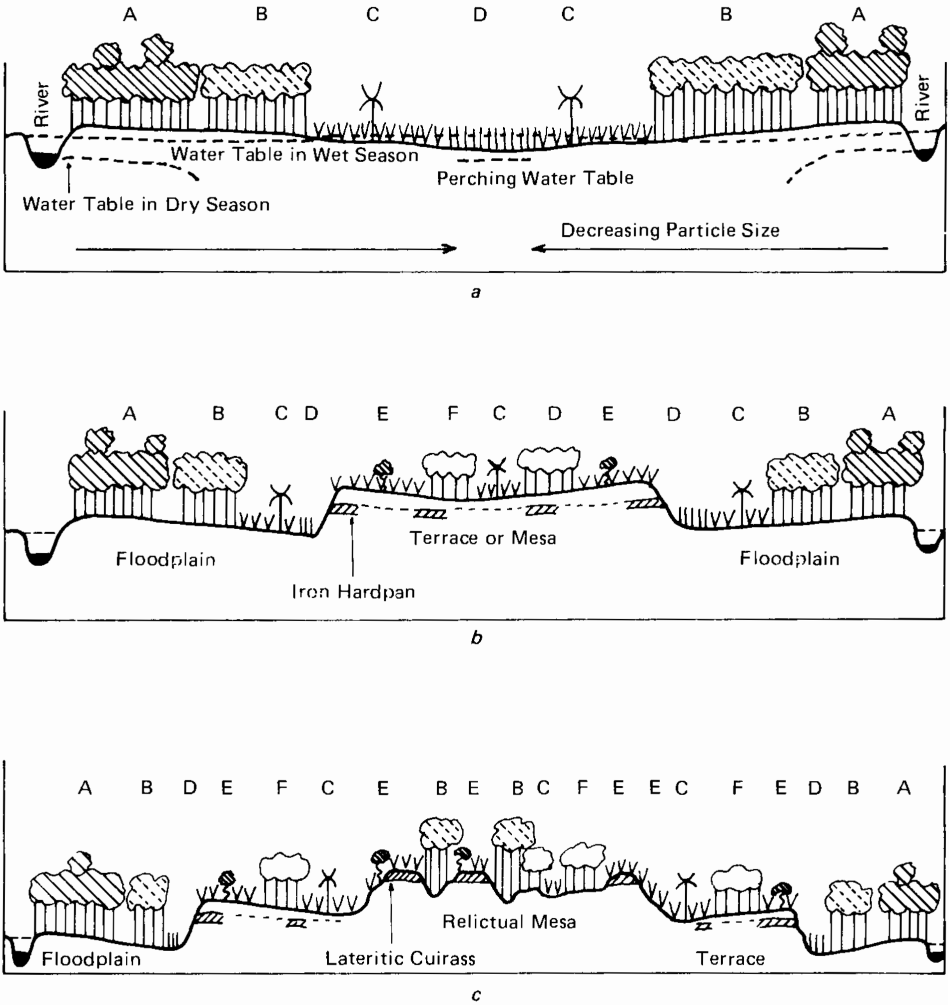

Fig. 16–3. Hypothetical reconstruction of landscape and vegetation changes in an alluvial plain under seasonal wet and dry climate along two rejuvenation cycles. (*a*) Wide alluvial plain where vegetation pattern depends on depth of water table in the wet and in the dry seasons, occurrence of perched water tables, and existence of seasonally waterlogged areas. (*b*) After rejuvenation, a terrace or mesa is formed where an indurated iron hardpan occurs at the place of ancient water table level. In the floodplains vegetation pattern is similar to (*a*). In the terrace the pattern depends on drainage, soil-water-retaining capacity, and mineral status of the soil. (*c*) A new rejuvenation cycle has taken place, thus forming two levels of terraces; the oldest has been eroded. The iron hardpan in the old mesa has become a distinct lateritic cuirass acting as a resistant layer to erosion. Vegetation pattern there depends on drainage, occurrence of seasonal or permanent water tables along small channels and rivulets, soil-water-retaining capacity, and mineral status of the soil. *A* = gallery forest; *B* = semideciduous forest; *C* = hyperseasonal savanna; *D* = swamp; *E* = seasonal savanna; *F* = deciduous forest.

the river margin, one of decreasing particle size and another of increasing bad drainage. In such a way the central bottomlands will be more frequently and extensively waterlogged; whereas the banks will be relatively well drained and will have a permanent high water table. The sequence of communities corresponding to these conditions is: A—gallery forest, generally of the evergreen seasonal type; B—semideciduous forest; C—hyperseasonal savanna; D—seasonal semipermanent swamps.

What happens if a new geomophologic cycle of erosion/sedimentation starts because of a climatic change toward wetter conditions? The former floodplain is first desiccated and eroded, forming a new floodplain at lower level and converting the old one into a river terrace (see Figure 16–3*b*). In the newly formed floodplain, the environmental conditions and the vegetation sequence will follow the same previously described pattern, but on the terrace the habitat conditions have been drastically changed. As the external drainage has improved as a result of river dissection, it is possible for the ancient iron- and clay-enriched illuvial soil horizons to change to hardpans or indurated cuirasses. The best drained places in this old but recently raised surface (raised relatively with reference to the new base level) will be occupied by seasonal savannas, while the less well-drained and richer soils could be covered by deciduous forests, restricting the former hyperseasonal savannas and swamps to a few localized habitats with impeded drainage.

If further rejuvenation occurs similar to the previous one, with a like erosion of the former floodplain and consequent formation of a new one, three levels will appear with different water regimens, soil age, soil evolution, intensity of erosion and, therefore, quite divergent vegetation (see Figure 16–3*c*). The first and second levels (the youngest) will repeat the previous process already depicted in the former rejuvenation, while on the oldest and highest level, retrogressive erosion will gradually reduce the primitive flat surface to a hilly landscape, with lateritic capped disorganized hills and many small drainage lines, creeks, and rivulets creeping between. This vestigial mesa will continue to be mostly covered by seasonal savanna and deciduous forests, but semideciduous forests will advance through the drainage network, gradually reducing the surface occupied by other formations. The general picture of community displacement is shown in Figure 16–3*c*. It is interesting to note that a complete "inversion" of the primitive relief has been produced, with resistant hills occupying the former place of bottomlands.

This hypothetical reconstruction of events related to a succession of environmental and vegetational changes would not have much practical value if there were not much evidence to support and document its reality in many lowlands areas of tropical America. During the dramatic climatic changes of the pluvial and interpluvial periods, and also as a result of the spectacular series of uplifts that gave rise to the neighboring mountains in the American *cordilleras*, vegetation changes have undoubtedly occurred. The first palynologic analysis began to disclose some of them while morphogenetic study of landscapes has permitted a reconstruction of ancient soils and ecosystems. In many tropical American lowlands four successive levels of alluvial terraces or rock pediments have been reported (Zinck and Stagno, 1965; Bigarella and Andrade, 1965; Monasterio and Sarmiento, 1971), suggesting that a yet more complex sequence than that depicted in Figure 16–3 took place.

According to this dynamic approach, at the same time that the major landscape features change, ecosystems are displaced and replaced, reflecting changes in drainage, depth of water table, leaching of nutrients, development of soil hardpans, and so on. At any given moment in this dynamic cycle the landscape will be composed not only of the ecosystems already considered but also, and significantly, by numerous more or less transitional forms. By contrast, in areas with an extended evolution or less labile landscape, as in the ancient plateau of Guiana and Brazil, the ecosystem pattern is more stabilized, senile forms become more widespread, and a clear tendency toward predominance of seasonal savannas is evident, the forests being restricted to younger surfaces or richer soils. The Venezuelan plains are a good example of the former situation and the Brazilian *cerrado* area of the latter. In the Amazon basin, which is already under a nonseasonal climate, the previous situation has been entirely reversed; rain forests predominate, and savannas only appear on small relictual landforms.

If to this complex pattern of primary communities we add the evolutionary recent, but impressive, human interference, we get a confused picture in the form of secondary ecosystems, which makes the interpretation of heavily disturbed landscapes quite problematic. Fortunately, the lowland regions of tropical America have not yet changed so much as to be unintelligible, making the interpretation of ecological facts simpler than in other tropical places.

The Three Major Types of Savanna Ecosystems

After considering the occurrence of several ecosystems under various environmental conditions, we now have the necessary elements to answer the three initial questions asked at the beginning of this section. In the first place, there are at least three main ecological types of savannas, each one associated with a given combination of external factors. One single factor plays a different role in each case, giving rise to quite different global environmental stresses and selective forces on living organisms.

The first type comprises those savannas not subjected to a strong seasonal variation on soil-available water. They are met with only in everwet tropical climates, on well-drained, deep, medium- to coarse-textured soils, with a water table that is far from the rhizosphere at any time of the year. This nonseasonal savanna appears on two different soils: white sands and red sands. The nonseasonal savannas on white sands are less related physiognomically and floristically to all other savanna types, being closely related through their common woody species to the dry Amazon caatingas, or savanna forests and woods. Fragmentary knowledge of these white-sand communities suggests that soil-related factors are considered the main determinants of the series from a high, closed, xeromorphic forest to a low and open savanna (Heyligers, 1963). Their soils have in common two major ecological features: they are the driest and also the poorest soils found in this wet climatic region. On the other hand, the most open communities in the series, some formed by low bushes and an almost bare soil in between, are apparently maintained by a high fire frequency.

The nonseasonal savannas on red soils are intermediate in composition between the white sand and seasonal savannas. Some of them could result from fire action on scleromophic forests, but most have been interpreted as relictual formations in the least favorable environments for forest colonization.

The second type of savanna ecosystem is the most widespread under the wet and dry climates of tropical America, and on the basis of this regional character we have called them *seasonal savannas*. Previously, most authors have referred to them as "dry savannas," in comparison with the "wet savannas" here termed hyperseasonal; but we think that the terminology proposed here is more precise and meaningful from an ecological viewpoint. Seasonal savannas occur on well or moderately well-drained soils, of medium to coarse texture, low availability of nutrients, and deep water table. We hypothesize that this ecosystem represents the biotic response to a seasonal climate with a long rainless period, where the upper part of the soil profile maintains intermediate water levels during the rainy season and dries out slowly after the rains end, reaching a level of ecological drought during the final part of the dry season. The water budget in deeper layers, where most woody species find their water supply, is different (see Mooney et al., 1974). Two factors are necessary for the persistence of this ecosystem: well-drained, deep soils and low soil fertility. Frequent burning contributes to low fertility and is a major selective pressure for savanna species but seasonal savannas could maintain themselves even with a very low fire frequency, as could be the case if only natural fires were considered.

The third type of ecosystem, the *hyperseasonal savanna*, is under the additional environmental stress of an extended period of soil-water saturation. The species in this ecosystem pass from a water-deficient period to another equally long period of water excess. These savannas only occur in regions of seasonal climate, on heavy, ill-drained soils, poor to very poor in nutrients, and are also subjected to periodical fires. As we pointed out earlier, they are mostly grass savannas with no woody cover except the occasional presence of palms. The herb layer has many exclusive species and many others shared in common with seasonal savannas.

The distinction between seasonal, hyperseasonal, and nonseasonal savannas makes the savanna concept more useful and clarifies the ecological context of each type. Many controversies about savannas have been caused by the lack of distinction between these three basically different types of ecosystems.

Some Essential Factors Acting Upon Different Ecosystems in the Humid Lowland Tropics

In the last part of this chapter we want to summarize in a very concise form the major features associated with the occurrence of various ecosystems in the lowlands of tropical America.

1. With a constantly wet climate, rain forests constitute the zonal climatic formations, disregarding any additional source of plant water supply.

2. In soils with a high water table during the whole year, but with no waterlogging or water saturation in the upper part of the profile, evergreen rain forest is found, independent of the rainfall regimen.

3. In sites with a high water table saturating the upper soil layers for more or less extended periods, swamp-forests develop.

4. On permanently or almost permanently saturated soils, swamp communities occur under any type of rainfall regime.

5. Under an ever-raining climate on very permeable and infertile soils, scleromorphic forests and woods appear, forming a series of plant physiognomies from moderately tall, closed forests to open, patchy, savanna-like vegetation.

6. Under an ever-wet climate in very poor and excessively drained soils a non-seasonal savanna may be maintained, its permanence depending on the burning frequency.

7. In wet and dry climatic regions (Aw climates) on well-drained sites, with poor soils of low water-retaining capacity in the upper horizons, seasonal savannas occur.

8. Under wet and dry climates, in moderately drained soils, with high water-retaining capacity in upper soil layers and medium levels of fertility, dry deciduous forest occurs.

9. On ill-drained, heavy soils, where water saturation and water deficiency periods alternate during a yearly cycle, hyperseasonal savannas are found.

A graphic representation of some of these facts in the particular case of wet and dry climates is shown in Figure 16–4. In that graph the ecological complexity of these environments has been reduced to two major axes of environmental variation, one reflecting soil-water conditions during the most unfavorable period of the year (the end of the dry season) and the other representing soil-water content at the wettest point of the year (the end of the rainy season).

This graphic representation shows the position of eight types of ecosystems in the plane determined by those two axes. Some points of this figure are worth considering: The two axes can discriminate seven out of the eight ecosystems; only the dry deciduous forest overlaps with the seasonal savanna, since their respective occurrence is, as we have already discussed, determined by other factors. Some transitional zones exist, but their nature and precise ecological range could only be established when more quantitative data are available.

In the preceding pages we have postulated the existence of fundamental correspondences between factors and features of the physical environment, mainly those related to annual water budget and nutrient cycling, and the occurrence of different ecosystems in the humid lowland American tropics. Other factors, such as fire, human interference, and paleoecological changes, have been considered under this perspective as agents or processes whose action completes the picture of the present-day distribution of these ecosystems. While additional information is necessary in order to accept or reject our hypotheses, we are convinced that they will help point out precisely the critical data pertinent to the problem, serving as a guideline in establishing priorities for future research.

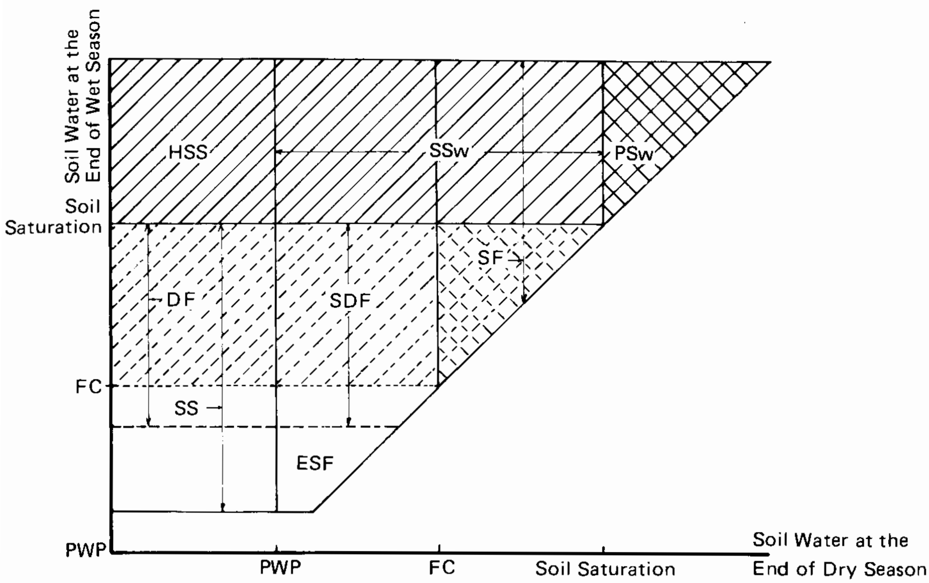

Fig. 16–4. Ideal distribution of ecosystems under a tropical wet and dry climate, according to maximal water stresses in the two contrasting rain seasons. Note overlapping of seasonal savanna and deciduous forest, and of seasonal swamp and seasonal forest. *HSS* = hyperseasonal savanna; *SSw* = seasonal swamp; *PSw* = permanent swamp; *DF* = deciduous forest; *SDF* = semideciduous forest; *SS* = seasonal savanna; *ESF* = evergreen sclerophyllous forest. [////] = area of seasonal waterlogging; [XXX] = area of permanent waterlogging; [////] = area of seasonal soil saturation; [XXX] = area of permanent soil saturation. *PWP* = permanent wilting point; *FC* = field capacity.

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