TROPICAL SAVANNAS - INTRODUCTION

Gerhard Gottsberger and **Ilse Silberbauer-Gottsberger**
Botanischer Garten and Herbarium, Universität Ulm, D-89081 Ulm, Germany

Keywords: definition of savannas, Central Brazilian cerrado, origin of cerrado and paleoecological changes, the physical environment, vegetation and plant physiognomy, floristic diversity and community structure, reproduction, pollination and seed dispersal.

Contents

Summary

The problems of definition of savannas are indicated and the senses in which different authors use the term savanna are given. The Central Brazilian cerrado is used as an example of a Neotropical savanna, woodland and grassland type of vegetation. General subjects are treated, such as the development of cerrado, its history, the physical environment and its influence upon plants. Also, cerrado is defined, described and distinguished from other vegetation types. It is explained that cerrado appears to have had a relatively late origin in the Tertiary as compared to moist mesophytic forest biomes such as the Atlantic and Amazon forests. During the Pleistocene, relatively rapid climatic changes introduced a new factor into forest and cerrado dynamics and it appears that the cerrados and other South and Central American savanna regions were in some way connected and experienced floristic exchange. In modern times, cerrado is

nearly exclusively a seasonal upland vegetation on deep and well-drained soils and has a much richer floristic composition than other Neotropical savannas or savanna-like vegetation types. An introduction is given to phenological events, reproduction and seed formation of cerrado plants, their pollination modes and seed dispersal. The cerrado exhibits nearly all pollination and seed dispersal phenomena to be expected in the Neotropics, and it is certainly as rich in this respect as any mesophytic rainforest. This is also a reflection of the floristic richness of cerrado, especially the high number of woody species, which is neither found in any other South American savanna nor for that manner approached by any other savanna flora in the world.

1. Introductory Remarks

Authors, worldwide, do not agree at all on the definition of savannas and savanna is a term which is used for very different vegetation types. It is necessary, therefore, to discuss what different authors mean when they speak or write about "savannas". Moreover, our comments on tropical savannas are largely based on the Central Brazilian cerrado vegetation as example, and on further Central and South American savanna vegetation types. This is the vegetation we know best and where we have worked most intensively. We have seen and visited sites of savannas also in Australia and Africa and occasionally will refer to Paleotropical savannas as well.

2. Definition of Savanna

To draw a clear dividing line between savanna and other vegetation types worldwide is not easy and not at all clear and depends on the criteria used to define savanna. The term savanna seems to be of Amerindian origin, denoting an area covered with a grass layer and lacking trees. This original meaning was later extended by several authors to mean grassland on which grow tall woody plants. Most, but not all, authors would agree with the following definition: "Savannas are ecologically homogenous grasslands upon which woody plants are more or less evenly distributed." Specialists of savannas know that the grasses and ground-layer species on the one hand and the woody species on the other hand are competing plant types, which may be mutually exclusive. Having a different root system and a different water economy the two vegetation layers can be in an ecological equilibrium or not.

However, there are many senses in which different authors use the term savanna. Most North American botanists and geographers employ the term savanna for a general physiognomic-structural category of an open or sparse tree layer, or tree and shrub layer, over a grassy ground layer. In their definition savannas occur in any climate and on any substrate and have any floristic composition. Almost all European, Latin American, African and Australian authors, use the term savanna for a large-scale grassland vegetation type restricted to the wet/dry tropics, with rains only or predominantly in the summer months, and most allow any physiognomy. Authors indicate these by phrases like "savanna grassland", "low tree and shrub savanna", "savanna woodland" or "savanna forest". A third group of authors, ourselves included, combine both definitions and consider not only physiognomy, but also floristic composition and habitat factors, such as climate, seasonality, and/or substrate. We use the word savanna to mean a tropical/subtropical vegetation type with a grassy ground layer and a woody-layer intraperimetral crown-cover of less than 40% or less, but not zero. In different regions, countries or continents there is a long tradition to use a certain name for a particular vegetation type, and there is no indication that any author who has traditionally used the term “savanna” in one of the senses mentioned above is going to change to the other. It is therefore always necessary to see how an author is using the word.

A useful classification of natural tropical savannas, based on climatic and edaphic factors, recognizes four main savanna types:

- Climatic, when there is not enough rainfall to support closed forest on drained upland sites even on the most favorable, deep soils;
- Nonseasonal, when edaphic factors of any kind (except for permanent water saturation which would produce a marsh) prevent forest development in a climate without a dry season;
- Seasonal, when there is a definite dry season and the soil is well-drained, but other edaphic factors such as shallow soil, infertility and/or a high aluminum content prevent closed forest; the soil does not become saturated for long periods in the rainy season;
- Hyperseasonal, when the soil becomes saturated continuously for weeks or months during the wet season (by inundation, poor vertical drainage through the soil, or by water from higher terrain flushing out to or close to the surface) but dries out for weeks or months in the dry season. The term "hyperseasonal" was coined because soil water saturation for long periods in the wet season exaggerates the effect of rain and causes poor soil aeration. These soils are usually gleyed. Forest usually cannot grow under this regime; in fact, no woody plants at all can establish themselves, except for certain palms and a very few special species of shrubs or small trees.

Natural savannas grow under almost every tropical climate with more than 18°C average annual temperature and more than 500 mm average annual rainfall, independent of the seasonality of rainfall distribution. The natural non-derived "savannas" of Africa and Australia seem to be almost all climatic. With very few exceptions of negligible total area, all "savannas" of South America are edaphic. The northern tropical American "savannas" consist of a number of different associations on wet/dry white sands, and on wet/dry heavier soils. The water table in these northern American savannas may reach the surface in the wet season.

Conversely, cerrado is a seasonal upland vegetation on deep and well-drained soils, with a permanent, usually very deep water table. This situation is quite unique and usually does not occur in tropical American savannas. Cerrado also does not develop when the soil becomes flooded or saturated for any appreciable period in the rainy season. Another difference between most northern tropical American savannas and the Central Brazilian cerrados is the richness of species per unit area (alpha diversity). Cerrados may contain between 250 and 350 (-450) vascular plant species per hectare, whereas in South American savannas this number is very significantly lower, usually only a quarter as much by area or by number of trees/shrubs counted. The probable reason for the floristic poverty of the northern tropical American savannas as compared to cerrados is that in most of those savannas the water table during the rainy season, or at least towards its end, reaches the surface of the soil or is close to it, a physiologically stressful situation which but a few specially evolved species can withstand.

In conclusion, the Central Brazilian cerrado should be considered as a distinct vegetation type, distinguished from other physiognomically similar Central and South American vegetation types by its ecology, species composition and floristic diversity. Cerrado occurs frequently in savanna-like forms, but also as forest (closed arboreal canopy), woodland (open arboreal canopy), scrub and open grassland forms. Floristic similarities of cerrado and Central and South American savannas and savanna-like vegetation are the result of a common origin of all these vegetation types and also testify to floristic exchange between Neotropical savannas during the Tertiary and the Quaternary.

3. Location and Extension of Tropical Savannas

In total, tropical savannas are said to cover nearly a third of the world's land surface, over half of the surface of Africa and Australia, 45% of South America, and about 10% of India and South-East Asia. This is true, however, for South America only when savannas are considered in the broadest possible sense, and when the northeastern Brazilian caatinga, the whole Chaco of Bolivia, Paraguay and Argentina, and other open vegetation types are considered. Excluding these vegetation types, which is ecologically and floristically more sound, the "savannas" of tropical South America cover less than 20%, or more precisely only 16% of the whole land surface

In southern Mexico, in several parts of Central America from Guatemala to Panama, and in the Carribbean Islands there are the same, principally seasonal and hyperseasonal, types of savannas as found in South America. A distinct formation in Central America and the Caribbean Islands, which does not occur in South America, are the pine savannas, either on lowlands or highlands, where *Pinus caribaea* forms a tall tree layer.

4. Cerrado and Neotropical Savannas

The Portuguese word "cerrado", meaning "dense" or "closed", is used for a special vegetation type which covers most of Central Brazil. Although there exists a wide variety of physiognomic forms, from closed-canopy forests or open-canopy woodlands to savanna-like forms (with a sparse woody layer) and even to open grasslands having no woody-layer plants ("campo limpo"), the most common form of cerrado in Central Brazil is a tree-scrub woodland.

Prior to being evaluated, the large-scale vegetational province of cerrado had suffered considerable destruction such that its exact geographical location and extension must remain a matter of speculation. Estimates speak of an original extension covering approximately 20% to 25% of the Brazilian territory, or an area of 1.5 to 2 million sq. km. Data on the original (meaning the last several thousand years) extension of the cerrado are vague, partly also because of the difficulty of classifying vegetation, especially in the case of transitional forms, such as between cerrado and caatinga or between cerrado and various semi-deciduous forest types. When, incorrectly, Amazonian savannas are included in the cerrado concept, the area is larger.

A calculation of the area of the total cerrado biome gives 1.91 million sq. km. If we subtract the ca. 20% of other vegetation types which occur in the cerrado biome the original area of cerrado *sensu lato* is approximately 1,528,000 sq. km. The other savanna-like landscapes in South America, such as the Llanos, the Gran Sabana, and the savannas of Colombia, Guiana and Amazon, by our calculation comprise about 579,020 sq. km, whereas the Pantanal and the Beni biome together extend about over 332,435 sq. km. All South American savanna-like landscapes together, as mentioned above, including cerrado, therefore have an extension of about 2,821,660 sq km. This is 16% of the total area of South America, which has 17,840,000 sq. km of land surface.

5. Paleoclimate, Paleoecological Changes and Origin of Cerrado and South American Savannas

In the Tertiary (the last 65 million years) there were two alternating climatic cycles. During most of the Paleogene there was a long phase of humid tropical climate. From the beginning of the Oligocene onwards, a lowering of the global temperatures and precipitation set in. Beginning about the middle of the Oligocene and during the Neogene, this trend stabilized and the global climate became drier and cooler. During the Paleocene and the Eocene, apparently both poles were unglaciated. However, with the beginning of the Antarctic glaciation during the Oligocene, the long warm period was interrupted. During the Miocene, at about 9 million years before present, the Antarctic reached its climax of glaciation with approximately 50% more ice volume than today. The Arctic region was still without ice at that time. The glaciation of the Antarctic region caused a lowering of the sea level of about 40-50 m. Cold Antarctic surface water reached far to the north. In consequence, a shift of the intertropical convergence zone 9-12° further to the north occurred. The tropical rain belt probably was more accentuated in the northern hemisphere, and large more or less arid regions were formed between 0° and 20° south. Thus, the Tertiary, the Paleocene and Eocene periods were characterized by a tropical humid climate. As a result of increasing Antarctic glaciation during the Oligocene and Neogene, cooler, semi-arid to arid climates and more xeric vegetation began to dominate large parts of South America including Brazil. During the warm parts of the Paleogene, tropical rainforests apparently expanded enormously. In the Eocene, they covered a region twice as large as today and reached far into the southern portion of South America. Probably beginning about the Oligocene, and certainly during the drier and cooler climate of the Neogene, rainforests became more reduced and partly displaced. In concert with this shrinkage and displacement of rainforests, several central and northern parts of South America became covered by non-rainforest vegetation. Either already during the Oligocene or at the Oligocene/Miocene boundary arid-adapted herbs were present in sufficient abundance in formations similar to savannas of present-day South America. Therefore, it seems likely that South American savannas originated between 25 to 28 million years B.P. The development of savannas in Central America is believed to have occurred more recently, that is in the middle of the Pliocene. Probably, the savanna elements which originated in South America were not able to invade Central America prior to the establishment of the landbridge between South and North America during the Pliocene.

So, during the Miocene-Pliocene (between 25-2 million years B.P.), dry forests and more open vegetation, probably savanna-like with typical elements still found today, were widespread. This also must have been the period when cerrado as a large-scale vegetation became established. The evolutionary history of some elements of the savanna flora, especially that of the grasses, might be older, possibly dating back to the Middle Eocene (ca. 50 million years).

The grasses in late Oligocene ecosystems of South America apparently were of the C_3 metabolic type. Evidence suggests that C_4 grasses, better adapted to the open and sunny savanna landscapes, developed later. The first C_4 grasses are detectable by isotopic analysis as a dietary component of large grazing herbivores in South America at about 10 million years B.P. In fossils of grazers from that time mixed C_3/C_4 diets could be found. By about 7.6 million years B.P., C_4 grasses became dominant over C_3 grasses. The C_4 dietary component steadily increased until 3.7 million years B.P., when C_4 grasses comprised approximately 70% of ingested biomass. Compatible with the idea of a more extensive savanna landscape in the past, fossils from the Neogene bear testimony of a vertebrate fauna in several parts of the Amazon region, nowadays covered by mesophytic forests.

The climatic environment of the tropics during the Pleistocene is a matter of dispute among geomorphologists, climatologists and biologists. Some geomorphologists affirm that the Quaternary enjoyed relative climatic stability or at most the climatic changes were much less drastic than in extratropical regions, while others suggest that there were marked modifications and changes of climate with shifts toward semi-arid and arid conditions. Extensive aridity in the tropics seems to be correlated with glaciation maxima in extra-tropical regions. As a consequence, there must have been strong fluctuations in all landscape-forming factors, such as geomorphodynamics, soil dynamics, vegetation and fauna.

The more arid periods during the Pleistocene and supposedly also the Holocene (and earlier in the Tertiary) might have led to fragmentation of the Amazon rainforest, resulting in the formation of isolated forest refuges in the more humid parts of lowland Amazonia and peripheral mountain ranges. There is an ongoing debate about the significance of these postulated former forest refuges with respect to speciation phenomena of Amazonian rainforest flora and fauna. For some authors, it seems an open question whether the refuge theory is plausible, others consider it necessary at least to explain species distribution patterns and speciation processes. The theory postulates that the repeated oscillations of dry and moist climatic periods, which supposedly caused an alternating fragmentation and coalescence of lowland tropical rainforest vegetation, have led to the genetic differentiation and speciation of rainforest organisms in isolated populations, the "refugia", and in this way accounts for the high diversity found in these places. Some critics of the forest refuge theory point out that postulated forest refuges in the Amazon region coincide nicely with places of intensive collecting activity and hence may be artifacts. Other authors even doubt that the Amazon lowlands could have been sufficiently arid to allow savanna-like vegetation to replace rainforest in these places. These workers base their objections upon results of palynological profiles wherein no indication of savanna plants during ice-age periods were found.

In spite of the divergence of opinions among authors, the existing data demonstrate convincingly that, during the Tertiary and Quaternary, climatic changes have occurred in the Amazon basin and have caused a change in the vegetation cover. It is also clear that existing palynological data are still too few and geographically isolated to allow accurate reconstruction of the former extent of savanna-like and dry forest vegetation in the Amazon basin during the Quaternary. Notwithstanding, the geomorphological and paleoecological data provide strong evidence in support of the prior existence of large areas of savanna-like vegetation in Amazonia. The floristic affinities between presently separate Neotropical savannas and cerrado may be explained by former connections. For example, the savannas of Humaitá, nowadays islands within the Amazon rainforest, show strong floristic overlap with northern savannas in Surinam and the Central Brazilian cerrados, suggestive of a former connection between these islands and savannas outside the Amazon basin.

As previously outlined, Neotropical and Paleotropical savanna-like vegetation apparently developed and was established during the Upper Tertiary, the Neogene or, more precisely, during the cool and arid Upper Oligocene; the floristic composition of this vegetation continued to develop during the Miocene, Pliocene and the Quaternary. The origin of this vegetation in the Neotropics most likely are traced to the Brazilian Shield and to large parts of the Amazon basin up to the equator or even north of it. It can be further assumed that during the colder climatic events, the present day cerrados, as well as the northern South American savannas, including many of the Amazonian savannas, either were connected by a savanna belt across the Amazon basin, or at least were close enough for floristic exchange. Several species are common to disjunct savannas in Central America, northern South America, the Amazon, as well as Brazilian cerrados, places presently separated by extensive forest regions. These widely distributed species testify to former yet relatively recent connections between the savannas.

The debate concerning the distribution of Amazonian and other Neotropical plant communities during the Quaternary and before will doubtless continue. At the moment there are at least two major schools of thought. One group, relying on limited sampling of pollen data, argues that the lowlands of the Amazon basin were continuously forested throughout the glacial cycles and that there were no arid land surfaces. Consequently, in Amazonia there was no past enlargement of the savanna landscape and the Amazon forests have been stable since at least the start of the Pleistocene or even the end of the Miocene. On the other hand, other authors re-evaluated the Neogene and Quaternary vegetation history, climate, and plant diversity in Amazonia also on the basis of pollen and radiocarbon data and came to an entirely different interpretation. In their view, plant diversity during the Miocene was considerably higher than today. The general decrease of temperature during the Upper Neogene and especially of the Quaternary glacial periods may have caused considerable extinctions in the lowlands. Rainforest (especially the drier type) was locally replaced by savanna, savanna forest, and by extensive semi-desert dune formations. The present-day centers of higher rainfall (>2500 mm) surrounded by areas of lower rainfall, were previously places of refuge for very wet rainforest and centers of very high plant diversity. The arguments in favor of a continuous rainforest during glacial times in Amazonia are refuted in favor of the original idea which suggests that the vegetation pattern in the Amazon basin and surrounding lands was comprised of large, continuous open savanna, dry forest landscapes and rainforest refuges.

6. Climate

The present climate of Central Brazil is influenced by the South Atlantic high pressure center, the polar anticyclones and the Chaco low pressure center. The continent is dominated by warm winds from the edges of the great semi-permanent anticyclones in the Atlantic, the so-called SE trade winds, which blow toward Brazil during much of the year. From the beginning of spring onward (August-November) the SE trades from the South Atlantic high pressure center dominate the region. The continuous warming-up of the continent during summer (November-January), together with a build-up in intensity of the Chaco low pressure center, and a shift of the tropical high pressure centers towards the east, leads to an increasing influence of equatorial-continental west winds (bearing warm humid air) from the Amazon basin on weather patterns. At the end of autumn, the influence of these west winds diminishes, and the SE trades again, in combination with periodic cold polar fronts from the south, determine the weather during winter (May-July).

The Brazil Current, a component of the warm South Equatorial Current, contributes moisture to the trade winds. The Brazilian Shield along the Atlantic coast rises from sea level fairly continously and abruptly, blocking the onshore winds along nearly its whole length. The coastal escarpment collects so much orographic rainfall that this extensive coastal strip is ± humid throughout the year and covered with tropical evergreen rainforests, except between northern Rio de Janeiro State and Vitoria where the forest is semideciduous. Inland from the Atlantic coast, a series of higher S-N mountain ranges create still more rainshadow for the incoming trade winds, often leaving the leeward side with a semi-arid climate. Particularly during winter, the intensified "winter" trade winds exert a stabilizing effect, maintaining a dry season. During summer, however, the trades weaken enough to allow sufficiently strong convective activities to bring continental warm, humid air and summer rains.

The precipitation and temperature regime of the larger part of the Brazilian Shield, excluding the northeast Brazilian caatinga region, is classified as tropical savanna type (Aw) climate having average monthly temperatures always above 18°C and a winter dry season.

The average annual temperature of the cerrado region is 20°-26°C. Only in southern São Paulo may it reach as little as 18°C, the lower limit of an "A" climate. The southern parts of cerrado at moderately high altitudes (800-1000 m) in Minas Gerais, São Paulo or Paraná, may experience frosts in some years and at irregular intervals, while frost very rarely occurs in other parts of the cerrado region.

Considering rainfall, the cerrado as a whole occupies an intermediate pluviometric position when compared with rainfall values in surrounding regions. Cerrado occurs in regions with an average yearly rainfall ranging from 750 or 800 mm on the dry side to about 2000 mm on the wet side. In the Northeast, the cerrado is bordered by the semi-desert thorn-scrub caatinga of Northeast Brazil, a region with usually less than 800 mm annual rainfall. In the Southwest, the cerrado again borders a drier region which is covered by the Chaco vegetation of Paraguay, southeastern Bolivia and adjacent Argentina. Regions with rainfall over 2000 mm per year support continuous mesophytic forest, such as the Amazon forest in the west and the Atlantic forest in the east.

The cerrado region has a single dry period of almost always five months (May to September) and the driest months (July or August) may have on average as little as 5 mm a month or as much as 40 mm a month.

7. Soil Properties and Relationships among Soil, Vegetation and Plants

There is a striking diversity of soil types having significantly different properties in different parts of the cerrado, but most cerrado soils are well-drained, mostly reddish or yellowish in color and mostly quite deep (up to over 50 m). Most of them have a poorly developed mineral portion and are acidic with low cation exchange capacities and high levels of aluminum saturation --- these last two factors directly affect root systems and indirectly inhibit calcium and phosphorus uptake. The major soil groups are Oxisols, or in Brazilian terminology "Latosols", which are characteristically deep, well-drained, red or yellow, clay-rich, structurally strong but nutrient-poor. There are also extensive areas covered by Entisols (e.g., Quartz sand soils, concretionary soils and Lithosols) and Inceptisols (Cambisols), and others. Cerrado Oxisols are thought to be older, probably of Tertiary age, while other soils, such as the Cambisols are considered to be of more recent origin.

A minimum soil depth of at least three meters is necessary for the development of typical woodland and scrub cerrados. In many places in Central Brazil the soil is 20-30 m deep or more. On the other hand, less than 1% of all cerrado occurs on Lithosols, soils usually much less than 1 m deep over solid bedrock or a solid laterite pavement. In a valley near Brasília, for instance, such a shallow Lithosol supports a "campo sujo" (a dwarf to low scrub savanna form of cerrado) on valley sides having very thin stony soil over the bedrock, while nearby a low-tree woodland cerrado form develops on a soil layer 3 m thick.

Typical cerrado requires not only a deep but also a well-drained soil and there must be no long-term accumulation of water at the surface during the rainy season. Typical cerrado cannot tolerate a water-logged site, not even temporarily, and the few upper meters of the soil must dry out completely in the dry season.

Soil moisture is the principal factor influencing the distribution of vegetation formations all over Central Brazil. Within the cerrado region there are sharply defined geomorphological boundaries between three distinctive types of vegetation, cerrado, seasonally marshy campo, and gallery forest. Their distribution patterns, though showing some variations, are largely determined by soil moisture conditions. Gallery forests line water courses, marshy campos occupy the somewhat higher but still poorly drained sites fringing the outer margin of the gallery forests, and cerrado covers the well-drained interfluves.

Cerrado may also occur intermixed with dry forest. In the Serra do Roncador in northeastern Mato Grosso State mesophytic dry forest and cerrado occur side by side obviously under identical climatic conditions. The soils supporting both vegetation types have similar chemical and mineralogical properties, with the single difference that forest soils were found to be finer in texture than the cerrado soils; the former are sandy clay loams while the latter are sands or loamy sands. Authors concluded that in this region ...soil texture, through its influence on soil moisture status or possibly in chemical behavior, is an important factor controlling the distribution of cerrado and dry forest in the tension zone between these two regional types of vegetation.

There is an ongoing discussion concerning the major factors determining establishment and distribution of cerrado vegetation. First it was thought that a seasonal shortage of water, and later that not water shortage but the nutrient-poor soil probably is responsible for cerrado formation. Further, xeromorphic aspects of cerrado plants were explained as a consequence of nutrient poverty causing xeromorphic characteristics such as sclerophylly. As the xeromorphic features apparently are unrelated to water stress, the theory of "oligotrophic scleromorphism" was proposed. This concept gained greater acceptance after it was discovered that aluminum ions occurred in cerrado soils at a level considered toxic for most plants; in addition, aluminum is known to further decrease the availability of several nutrients. It was then suggested that nutrient deficiency and aluminum toxicity of the soils might be responsible for the density and low height of the vegetation as well as the twisted appearance of trees and shrubs, their thick bark and sclerophyllous leaves.

-
-
-

Bibliography

Bourlière, F. (ed.) (1983). Tropical Savannas. - Elsevier, Amsterdam. [A comprehensive discussion on vegetation, plants and animals of savannas worldwide.]

Eiten, G. (1972). The cerrado vegetation of Brazil. - Bot. Rev. 38: 201-341. [A classical and thorough account of the vegetation and its physiognomic forms.]

Eiten, G. (1997). Uso do termo savana. - Portug. Acta Biol., Sér. B, Sist. 17. 189-263. [An important discussion of the use and the meaning of the term "savanna" worldwide.]

Gottsberger, G., Silberbauer-Gottsberger, I. (2006). Life in the Cerrado: a South American Tropical Seasonal Ecosystem. Vol. I. Origin, Structure, Dynamics and Plant Use. - Reta, Ulm. [A synthesis of origin, structure, dynamics, floristics, phenology and plant use in cerrado.]

Gottsberger, G., Silberbauer-Gottsberger, I. (2006). Life in the Cerrado: a South American Tropical Seasonal Ecosystem. Vol. II. Pollination and Seed Dispersal. - Reta, Ulm. [A synthesis of plant-animal interactions, pollination and seed dispersal in cerrado.]

Huntley, B.J., Walker, B.H. (eds.) (1982). Ecology of Tropical Savannas. - Springer, Berlin, Heidelberg, New York. [A profound discussion on structure, determinants, function, dynamics and management of savannas worldwide.]

Oliveira, P.S., Marquis, R.J. (eds.) (2002). The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. - Columbia Univ. Press, New York. [A detailed account of the natural history and ecology of cerrado.]

Solbrig, O.T., Medina, E., Silva, J.F. (eds.) (1996), Biodiversity and Savanna Ecosystem Processes. A Global Perspective. - Springer, Berlin, Heidelberg, New York. [A broad account on biodiversity, structure, function and the future of savannas, with emphasis on the Neotropics.]

Warming, E. (1892). Lagoa Santa. Et Bidrag til den Biologiske Plantegeografi. - Bianco Lunos, Kjøbenhavn. [The first and classical work on vegetation and plants of cerrado.]

Warming, E. (1908). Lagoa Santa. Contribuição para a Geographia Phytobiologica. - Portuguese translation by A. Löfgren. Imprensa Official do Estado de Minas Geraes, Bello Horizonte. Reprint 1973. Editora Univ. São Paulo, São Paulo, Livraria Itatiaia Editora, Belo Horizonte. [Portuguese translation of Warming's classical work of 1892.]

Biographical Sketches

Gerhard Gottsberger was born 30 December 1940 in Judenburg, Austria. He studied biology, geology, chemistry, pedagogy and philosophy at the University of Graz (1959-1963). His Ph.D. thesis (defended in 1966) dealt with the biology, reproduction and phytogeography of Myxomycetes in the province of Styria. From 1966 to 1968, funded by several grants from Brazilian institutions, he worked at the University of São Paulo (USP) and the Botanical Institute of the Secretary of Agriculture of São Paulo State. At the end of 1968, he became a professor of Systematic Botany in the Department of Botany at the University of Botucatu (UNESP), where he remained until 1981 when he moved to the Federal University of Maranhão in São Luís as a professor in the Biology Department. Two years later, he accepted a position as professor and director of the Botanical Garden in the Institute of Botany and Plant Physiology at the University of Giessen, Germany (1983-1993). From 1993 to 2006 he held the chair of the Department of Systematic Botany and Ecology at the University of Ulm, where he was also director of the Botanical Garden and the herbarium (ULM). He was a visiting scientist (1971) at the University of Nijmegen and a visiting professor at the Universities of Vitória (1979), Rio de Janeiro (1979) and Vienna (1974, 1976, 1980). Since 1980, he has been a professor and an associated member of the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Federal University of Amazonas in Manaus. His research interests center on plant evolution, reproductive biology (pollination and seed dispersal), and tropical ecosystems.

Ilse Silberbauer-Gottsberger was born 11 June 1940 in Graz, Austria. She studied biology, mineralogy, geology, pedagogy, psychology and physical education at the University of Graz (1958-1963) and earned a teacher's diploma (Master of Science). Her Ph.D. thesis (defended in 1965) dealt with vertebrate cerebellum neurotransmitters. From 1965 to 1967, she taught biology at a secondary school in Leibnitz, Styria, and from 1967 to 1969, biology, physics and chemistry at the Colégio Humboldt in São Paulo. From the end of 1969 to 1981, she was a professor of Systematic Botany in the Department of Botany at the University of Botucatu (UNESP), and from 1981 to 1983, professor in the Biology Department at the Federal University of Maranhão in São Luís. Moving to Germany in 1983, she became an Associate Scientist at the Institute of Botany and Plant Physiology at the University of Giessen. Since 1993, she has been working as a researcher and staff member in the Department of Systematic Botany and Ecology at the University of Ulm and as a curator in the herbarium (ULM). Her research interests center on phytosociology and phytogeography of tropical vegetation, and reproductive biology (including pollination and seed dispersal).