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TREE SPECIES MONODOMINANCE OR SPECIES-RICH SAVANNAS? THE INFLUENCE OF ABIOTIC FACTORS IN DESIGNING PLANT COMMUNITIES OF THE BRAZILIAN *CERRADO* AND PANTANAL MATOGROSSENSE *A REVIEW*

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Resumo. Duas vegetações de savana sulamericanas foram revistas e comparadas: o diversificado *cerrado* do planalto central e a monodominância arbórea de *Tabebuia aurea*, em campos semi-inundados do Pantanal de Miranda, no Pantanal Matogrossense. Tentou-se determinar um cenário ecológico que poderia explicar como e porque espécies arbóreas tropicais podem manter populações monodominantes em áreas semi-inundadas, considerando um certo conjunto de condições abióticas capazes de inibir herbivoria e competição. A revisão e compilação de dados aqui apresentada objetiva fornecer evidências circunstanciais em suporte a duas hipóteses previamente testadas: (1) de que a estocasticidade de fatores abióticos no Pantanal do Miranda poderia favorecer populações grandes de plantas pioneiras por limitarem o grau de herbivoria, ao contrário do que aconteceria no *cerrado* devido às condições predominantemente constantes; (2) de que a associação de diferentes dinâmicas de inundação, anual regular a plurianual estocástica, poderia retornar o processo sucessional constantemente para um estágio inicial, no qual *T. aurea* seria o melhor competidor. Uma descrição breve dos biomas e suas comunidades vegetacionais é apresentada, baseada em literatura amplamente disponível no Brasil, porém pouco conhecida internacionalmente. Séries temporais e dados publicados sobre fatores abióticos foram analisados de forma a demonstrar a validade das premícias das hipóteses acima. As dinâmicas de inundação do Pantanal foram descritas, e padrões de precipitação e variação de temperatura foram comparados entre o *cerrado* e o Pantanal do Miranda. Enquanto o *cerrado* apresentou um clima sazonal e previsível, o Pantanal do Miranda apresentou um clima extremamente estocástico, resultando em condições ambientais que podem vir a ser negativas para insetos herbívoros, e portanto favoráveis a plantas pioneiras. A ocorrência de inundações sobrepostas e severas podem de fato contribuir para manter a sucessão em um estágio inicial. Desta forma, os dados de clima corroboram as hipóteses apresentadas anteriormente, e representam assim um passo na direção de entender a monodominância de *T. aurea* no Pantanal. Implicações para conservação são discutidas.

Abstract. Two South American savanna vegetations are reviewed and compared: the diverse *cerrado* in center of Brazil, and the monodominant woodlands of *Tabebuia aurea*, in semi-flooded fields in the Pantanal of Miranda, within the wetlands of Pantanal Matogrossense. We attempted to picture an ecological scenario that could explain, at least partially, how and why tropical tree species can maintain monodominant populations within semi-flooded areas, given a certain set of abiotic conditions constraining herbivory and competition. The review and data compilation here presented aim to provide circumstantial evidence in support of two previously tested hypotheses: (1) that stochasticity of abiotic factors in the Pantanal of Miranda could favor large populations of pioneer plants species by limiting the levels of herbivory, the opposite of the predominantly constant conditions in the *cerrado*; (2) that an association of different flood dynamics, annual regular and pluriannual stochastic, could return the successional process in the Pantanal permanently to an earlier stage, in which *T. aurea* would be one of the most competitive species. Short descriptions of both biome and plant communities are presented, based on literature, widely available in Brazil but not well known internationally. Available time series and published data of abiotic factors for these biomes are analyzed in order to demonstrate the validity of the assumptions of the above hypotheses. Flood dynamics of Pantanal are described, and patterns of precipitation and temperature variation are compared between *cerrado* and Pantanal of Miranda. While *cerrado* has a seasonal, predictable climate, Pantanal of Miranda has a very stochastic climate, thus resulting in several environmental conditions which could be detrimental to ins-

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ect herbivores, but favorable to pioneer plant species. The occurrence of severe and overlapping floods may contribute to keeping this floodplain constantly in an early successional stage. Therefore, climate data corroborate the hypotheses presented previously, and thus represent a step forward in the understanding of such extensive monodominance of *T. aurea* in the Pantanal of Miranda. The implications for conservation is discussed. *Accepted 07 April 2002.*

Key words: Cerrado, flood dynamics, friagem, monodominant stands, Pantanal Matogrossense, rainfall, Pantanal of Miranda, Paratudal, Tabebuia aurea.

INTRODUCTION

Great ecosystems of South America, such as the Brazilian *cerrado* and the wetlands of Pantanal Matogrossense, evolved closely with large-scale geomorphological processes. For instance, the Brazilian Crystalline Plateau which is composed of old, leached, Pre-Cambrian soils, was raised twice, over a long geological period, by the time of the Andes Cordillera formation. The raising of the Crystalline Plateau was followed by increasing erosion and leaching, between the Tertiary and Quaternary Periods (Freitas 1951, King 1956). The resulting poor soils, on average at 800 m above sea level, defined most of the 1800000 km² distribution of the *cerrado* ecosystem (Sarmiento 1983), which most likely evolved during the Tertiary. The *cerrado* vegetation is composed of a complex gradient of plant communities, ranging from grasslands to open woodlands but dominated by a savanna-type vegetation (Warming 1908, Sarmiento 1983, Rizzini 1997). In addition, small enclaves of calcareous rocky relief, and other richer geomorphological zones, provide habitats for forests which have several species in common with the coastal Atlantic rainforest, or with the dry Chaco further to the southwest (Adámoli 1986a). Finally, there are gallery forests that border the rivers and streams, and form a network of mesic habitats pervading most of the xeromorphic *cerrado* vegetation. This mosaic of mesic patches and gallery forests within xeric habitats form the complex domain of the *cerrado*, the phytogeographic division "Sub-province of the Central Plateau" (Rizzini 1997).

Regardless of its poor soil, the *cerrado* is a very diverse ecosystem. Various adaptations to the harsh conditions have evolved in this plant community. Sclerophylly (chemical and mechanical protection against desiccation) and an ability to absorb nutrients in poor soils heavily contaminated by aluminum are typical traits of plant species of the *cerrado* (Goodland 1971, Goodland & Pollard 1973, Goodland & Ferri 1979, Salatino 1993, Haridasan 2000). The subsequent evolution of insect herbivore strategies to cope with these plants, and to survive and feed in extreme conditions, resulted in unique, complex ecological communities, rich in exquisite strategies of survival of both plants and animals (Goodland & Ferri 1979; Fernandes & Price 1988, 1991, 1992; Ribeiro *et al.* 1994, 1998, 1999; Lara & Fernandes 1996). This particular vegetation type, with high species diversity accompanied by increasing human impacts, resulted in the selection of *cerrado* as one of the hottest of Conservation International's hotspots (Myers *et al.* 2000).

While the *cerrado* vegetation covers most of the territory in the center of Brazil, further to the west there lies an important and unique region of 138183 km², the wetlands of Pantanal Matogrossense (Fig. 1). The Pantanal is a recent floodplain formed by sedimentary soils in a geographic depression at 80 m above sea level, which is much lower than any geomorphology surrounding it. These sediments accumulated after the orogenesis of the Andes, and alongside this process many different plant communities colonized the area, including semi-arid vegetation during the Pleistocene (Ab'Sáber 1988). In modern times, it is covered with a mosaic of pioneer plant species and communities influenced by all surrounding ecosystems (Ab'Sáber 1988).

Pantanal is a continuous but complex floodplain. It is a heterogeneous landscape which has been constantly modified by orogenic processes, and affected by distinct climatic conditions. According to the contrasting geomorphology, vegetations, and hydrology, the Pantanal is divided into subregions, or "Pantanais" (Adámoli 1986a, Vila da Silva 1991). According to Duds (1992) and others, it is the most important wetland for conservation in the world. Indeed, it is a MAB Reserve of Biosphere, and in 2000 the Pantanal was named by UNESCO as a natural world heritage site.

As a plant community, perhaps one of the most peculiar regions within the Pantanal is in south Pantanal Matogrossense, in the Miranda river basin. In contrast to the species-rich *cerrado*, this region is covered by large monodominant stands of a few plant species, which replace each other along differing soil patches. Among these monodominant plant populations, the most impressive are the woodlands of *Tabebuia aurea* (Manso) Bentham & Hooker (Bignoniaceae), hereafter called "Paratudal" woodlands. Like most *Tabebuia* species, *T. aurea* has an explosive flowering season, when the trees are covered by many yellow tubiform flowers, resulting in a large seed production. In the present case, such a synchronous reproductive strategy also results in several kilometers of yellow-flowered trees, presenting an amazing landscape. Although it is clearly a pioneer species, with several invasive traits (fast growth rate, low density wood, high reproductive investment), *T. aurea* is of great relevance for conservation and has a strong aesthetic appeal, as do most of the species in this genus (for instance, the genus was chosen as the national symbol of both Brazil and Venezuela).

FIG. 1. Location of the Pantanal (fine, gray doted area) and the central Brazilian *cerrado* (coarsely doted area) in South America. The two squares show the regions of the Paratudal woodland and the study sites in the *cerrado*.

Tabebuia aurea occurs in its largest stand as the only tree species over an area of 1200 km² in the Pantanal. In the *cerrado* the species occurs only in sparse and discontinuous populations. Ribeiro & Brown (1999) showed that *T. aurea* is intensively attacked by herbivorous insects in the *cerrado*, but not in the Pantanal. Their data indicates that high herbivory levels in the *cerrado* is important in preventing the establishment of individuals of *T. aurea*. For instance, genotypes of this species from the *cerrado* were less vigorous while those from the Pantanal grew faster, but suffered greater herbivory damage if planted in the *cerrado* (Ribeiro 1999, Ribeiro & Brown, unpubl. data). On the other hand, tree species which are ecologically successful in the *cerrado*, such as the congeneric *Tabebuia ochracea* (Chamisso) Standley, are those that have low growth rates and great investment in defenses against herbivores and diseases (Salatino 1993; Ribeiro *et al.* 1994, 1999; Bittencourt 1995; Ribeiro & Brown 1999).

Ribeiro (1999) showed that, in the *cerrado*, the number of insect herbivore species associated with *T. ochracea* (whether chewing, sap-sucking, or gall-forming species) was significantly greater than with *T. aurea*. However, the former species had slower growth rates, but greater seed production and seedling establishment than the latter, which is clear evidence that *T. ochracea* can better cope with a diverse *cerrado* insect fauna than *T. aurea*. Considering that herbivory pressure plays an important role in shaping tree species populations and plant diversity patterns, the question remains: why are there so many insect species and associated damage on *Tabebuia* trees in the *cerrado* but not in the Pantanal? What kind of abiotic factors could be negatively influencing insect populations in the Pantanal? And, in addition, does the lack of herbivory pressure favor monodominant populations of pioneer tree species?

In this article we compare two extreme regions between the *cerrado* and Pantanal: the mid-valley of the São Francisco river basin, in the state of Minas Gerais, and the Miranda river floodplain (Pantanal of Miranda), in the state of Mato Grosso do Sul, in south-east and Western Brazil, respectively (Fig. 1). The former was chosen because it is a typical *cerrado* (*sensu strictu*), with low trees in an open savanna vegetation type. Moreover, it is a region where there are various small populations of *T. aurea*, and also of its congener *T. ochracea*. The Miranda river floodplain is dominated by *T. aurea*. Actually, it is influenced in its species composition by the *cerrado*, and can be considered an enclave of *cerrado* vegetation under a strong regime of natural disturbance (Adámoli 1986a). Geomorphology, soil composition, and plant communities of these two regions were reviewed and compared. Climatic factors were analyzed, with emphasis on rainfall and temperature. For the Pantanal, the inundation dynamics were reviewed and the importance of their stochasticity explored.

Ribeiro (1999) and Ribeiro & Brown (1999) coined two hypotheses to explain the considerable monodominance of *T. aurea* in the Pantanal. Firstly, that the stochasticity of abiotic factors in the Pantanal of Miranda could favor large populations of pioneer plant species, the contrary of the predominantly constant conditions in the *cerrado*. Secondly, that an association of different flood dynamics, annual regular and pluriannual stochastic, could constantly return the successional process to an earlier stage in the Pantanal, in which *T. aurea* is one of the most competitive species. The unpredictability of flood intensity happens in association with a within-year unpredictable rain regime, and then with equally unexpected long dry periods that alternate with severe floods. In a short period of evolutionary time, the selection of life cycles of insect herbivore species able to cope with such unpredictability has a low probability of occuring. Moreover, the environmental stochasticity could increase tree seedling mortality in years with severe conditions. In the present scenario, *T. aurea* seems the best pioneer species, since the large number of seeds produced every year by established adult trees could compensate for the negative effect of years with severe floods or extremely long dry seasons. Young individuals survive and grow on mounds, above the influence of floods. On the other hand, although there is evidence that *T. aurea* cannot survive below the floodline (Pott & Pott 1994), the species must be able to cope with and benefit from the floods. Unfortunately, there is no study on the eco-physiology of this species, thus how adult individuals respond to the water stress in their roots is unknown.

The present work aims to describe plant communities of the Pantanal of Miranda and the *cerrado* of Minas Gerais, along with abiotic data comparisons, in order to provide circumstantial evidence of environmental conditions consistent with those expected in the hypotheses above. The importance of this system in explaining the evolution of large-scale plant community patterns, the limitations of this paper for the understanding of other floodplain plant communities, and the relevance of the work for forming strategies for conservation are discussed.

METHODS

This article presents a short description of the biomes of the *cerrado* and the Pantanal of Miranda, based on a literature review. Firstly, these biomes are characterized according to their abiotic factors, and then their plant communities are described in general terms. The description as presented is original, and aims to provide the context in which the abiotic factors will be discussed. Moreover, as most of the descriptive literature on *cerrado* and Pantanal has been published in Brazil and written in Portuguese (but see Eiten 1972, 1978; Sarmiento 1983), this short review is also a contribution to the broader dispersal of such information outside Brazil.

Each abiotic factor will be analyzed according to its likely effects on *Tabebuia* species and associated herbivores. The flood dynamics of the Pantanal of Miranda, and its consequence for the Paratudal woodland are presented. Patterns of precipitation and temperature variation are compared between the *cerrado* and the Pantanal of Miranda, and their likely effects on insect herbivores and plant population dynamics are discussed. Data on insect herbivores, herbivory, and seed/seedling mortality of *Tabebuia* species are published elsewhere and cited data are used in this review.

Description of abiotic factors. In the *cerrado*, the study sites were set up between 800 and 900 m above sea level in the eastern montane boundaries of the *cerrado* with the Atlantic rainforest (Fig. 1). Natural reserves in the following four locations were chosen for sampling soils, and collecting rainfall and temperature data: EFLEX/Paraopeba (PA; 44°20'W, 19°20'S), EMBRAPA/CNPMS (SL; 44°15'W, 19°28'S), National Park of Serra do Cipó (CP; 43°55'W, 19°40'S), Estação Ecológica UFMG/BH (BH; 43°58'W, 19°52'S). PA and BH are sites on deep sedimentary soils, while CP and SL lie on slopes that have been eroded more intensely, thus having shallower soils than other sites. The CP site lies on an alluvial sandy soil in a mountainous area, while all the others are situated on clay latosols, which is the characteristic leached soil occurring throughout most of the *cerrado* (King 1956, Goodland & Ferri 1979). In the Pantanal, two study sites were set up at two locations 10 km apart, around the core area of the largest Paratudal woodland (57°10'W, 19°40'S, Fig. 1). These sites are on a very compact clay soil, with hummock-type mounds occuring all over.

Although the soil types of *cerrado* and Pantanal are well known, there are large variations among sites, and so it is necessary to characterize soil nutrients from some specific locations where *T. aurea* may occur. Soil traits were quantified for the four study sites in *cerrado* and for the two sites near the core distribution of the Paratudal woodland in the Pantanal. Soil was sampled within nature reserves where there is no record of agricultural activity, and thus original conditions are preserved. From each study site, five soil samples were randomly collected. A sample comprised soil taken from the surface to a depth of 30 cm, homogenized, and analyzed for pH, phosphate, potassium, aluminum, calcium, magnesium, capacity of cation exchange, and micronutrients, at the Department of Soils of the Federal University of Viçosa, MG, Brazil.

Regional climatic data and, for the Pantanal, variation in the river levels were taken from a national database compiled and made available by ANEEL (National Agency of Electric Energy, Brazil). Rainfall data were provided by local meteorological stations. A series of 40 years of rainfall readings from PA (EFLEX/IBAMA, Brazil) was used to describe the rain regime in the *cerrado* region studied here. In the Pantanal, meteorological data were obtained from the cattle company that owns the land where Paratudal woodland occurs. These data span 12 years, with only one year missing. Nevertheless, the data were collected at the center of the Paratudal, where a permanent field camp ("Retiro") has been set up. Comparative data from other sites surrounding the Paratudal woodland, within the company's property, were available. The reliability of these data was confirmed by the Center of Agriculture Research of Pantanal (CPAP/EMBRAPA), Corumbá, Brazil.

RESULTS

The Brazilian cerrado: evolution, geology, and soils. Cerrado is a persistent, mature ecosystem, occurring in a geologically old region (Sarmiento 1983). There is strong evidence that this vegetation has covered the Central Brazilian Plateau since the Tertiary Period (Freitas 1951, Rizzini 1997). *Cerrado* vegetation is frequently affected by fires, and one of its most evident characteristics is xeromorphism. However, the xeromorphism in the *cerrado* is accepted as being caused by adaptation to dystrophic soils rather than to water stress or fire impact (see below). Therefore, the *cerrado* is better described as oligotrophic, and sclerophyllous, than xeromorphic (Goodland & Ferri 1979, Salatino 1993).

In the mid-valley of the São Francisco river, the four study sites had acidic soils (pH < 5.0). In comparison with other tropical soils, the site PA had a high concentration of aluminum, while the other sites showed medium concentrations of aluminum (Table 1). However, PA, CP, and SL had high aluminum saturation. Everywhere soils were sampled, low cation exchange capacity, and thus, low fertility, was found, which is typical for most of soils in this ecosystem.

Nevertheless, the great variety of physiological responses to low nutrient contents means that poor soils cannot be considered as stressful condition to *cerrado* plant species (Haridasan 2000). Similarly, plants in *cerrado* have evolved various strategies to respond to fire impact, and many species cope, and even depend on, fire occuring at low frequency (Oliveira *et al.* 1996, Sato & Miranda 1996, Silva *et al.* 1996, Hoffmann 2000a). Nevertheless, fire events can drastically change the relative density of plant species in a community (Moreira 1996; Hoffmann 1998, 1999), even though the effect of fire may vary according to its interaction with other atmospheric conditions (Silva *et al.* 1996, Hoffmann 2000b).

Plant communities in the cerrado. Despite the poor soils, *cerrado* is a very diverse ecosystem. For instance, in an area of 100 km², within 23000 km² of preserved *cerrado*, Goodland & Ferri (1979) found more than 600 plant species, distributed among 300 genera and 83 families. Some of the common woody plant families are Anacardiaceae, Annonaceae, Apocynaceae, Asteraceae, Bignoniaceae, Caryocaraceae, Compositae, Euphorbiaceae, Erythroxylaceae, Guttiferae, Leguminosae, Malphighiaceae, Melastomataceae, Myrcinaceae, and Vochysiaceae. Although the commonest species have a relatively wide distribution, measures of dominance, such as abundance, density, and IVI (Importance Value Index, which is an indirect measure of species biomass) vary strongly between areas. Therefore, the relative importance of a family will depend on the specific region, and the most representative families will change significantly (Goodland & Ferri 1979, Sarmiento 1983, Gontijo 1991, Felfili & Silva Jr. 1993).

Although *cerrado* falls within the broad meaning of a savanna by having a continuous herbaceous strata with a discontinuous arboreal canopy (Sarmiento 1986, Gontijo 1991), Eiten (1972) and others do not agree with the definition of savanna as applied to the *cerrado*. The term savanna aggregates many different plant communities with roughly similar physiognomy, most of them being characterized by xeromorphism. By contrast, *cerrado* can be defined as a sclerophyllous vegetation, *sensu* Loveless (1962), since it is the result of nutrient-poor soils rather than of drought (Goodland 1971, Goodland & Pollard 1973, Eiten 1978, Goodland & Ferri 1979). The oligotrophism of this vegetation is a consequence of high solar radiation (thus high photosynthetic levels) and a deficiency of nitrogen and phosphate, which result in a high C/N ratio (Loveless 1962, Salatino 1993). Goodland & Ferri (1979) proposed the widely accepted hypothesis of "aluminotoxic oligotrophism", which suggested that the soil poverty would be increased by high concentrations of aluminum, despite the adaptative response of many species to such conditions (Haridasan 2000). Sclerophylly, high concentration of phenolic compounds, dense indumentum, and epidermic waxes are amongst the commonest traits related to oligotrophism found in *cer-*

TABLE 1. Chemical characteristics of soils in the cerrado of Minas Gerais, and in the Paratudal woodland, Miranda river floodplain. For location codes see text.

Sites	Organic Carbon (%)	pH in 1N KCl	P (mg/dm³)	K (mg/dm³)	Al (mg/dm³)	Ca (mg/dm³)	Mg (mg/dm³)
Cerrado/PA	2.5	4.2	2.8	90.4	1.9	0.6	0.5
Cerrado/ SL	4.1	4.9	8.0	170.8	0.5	2.5	1.0
Cerrado/ CP	2.3	4.4	4.0	37.0	0.9	0.3	0.4
Cerrado/ BH	3.2	4.9	3.6	61.2	0.2	1.7	0.6
Paratudal woodland	2.7	6.1	78.0	133.8	0	4.6	1.1

rado plants (Sarmiento 1983, Giullieti & Pirani 1988, Salatino 1993, Ribeiro *et al.* 1999). The so-called "*cerrado sensu strictu*" (Rizzini 1997) predominates in the study sites. In these sites, most adult trees vary in height from 3 to 6 m and are commonly distributed in dense patches, separated by areas which are covered predominantly by grass.

The Pantanal, the Miranda river floodplains, and the "Paratudal" monodominance: evolution, geology, and soils. The Pantanal is a Quaternary sedimentary basin, occupied by a chronically disturbed ecosystem, thus dominated by pioneer species (Ab'Sáber 1988). The Depression of the Pantanal developed over a short interval of between a few thousand and three million years. The most relevant geological changes that led to the appearance of the current ecological community and its dynamics date from the Pleistocene (Ab'Sáber 1988).

The Pantanal is the largest inundated plain on the planet, composed of various wetlands, but mainly temporally flooded habitats, shaped by different fluvial systems and their geomorphological characteristics (Adámoli 1986a, Ab'Sáber 1988). Habitat dynamics are influenced by cyclic variations in the flooding systems and gradual changes in the river beds and channels (Adámoli 1986b; Ab'Sáber 1988; Vila da Silva 1991, 1995; Duds 1992; Prado *et al.* 1992; Vila da Silva & Kux 1992). The Pantanal was subdivided into seven (Adámoli 1986a) to 11 (Vila da Silva 1995) macroregions in attempts to explain its geomorphological heterogeneity. In addition, the Pantanal subregions are influenced by many surrounding ecosystems: Amazonian forest to the north, white forest to the west and south, *cerrado* vegetation to the east.

These surrounding ecosystems evolved in geomorphological regions that are older than the Pantanal. In fact, due to a post-Pleistocene increase in humidity (a dramatic change from semi-arid subtropical to wet tropical climate) associated with a widespread fluvial transformation, no modern habitat or ecological community is thought to have existed in the Pantanal lowlands before the last 12000 or, in some cases, 6000 years (Ab'Saber 1988). Therefore, the Pantanal is a mosaic ecosystem resulting from an entangled mix of pioneer species, with patches of persistent species in more stable habitats (see also Prance & Schaller 1982 for description of surrounding vegetation, in the hilly regions bordering the southern Pantanal). Most of these plant colonizations were very recent, probably taking place after the last dry interglacial period in the Pleistocene (Adámoli 1986a, Ab'Sáber 1988). This hypothesis is supported by a nearly complete absence of endemic and habitat specialist species in the Pantanal, at any taxonomic scale, in both flora and fauna (Brown 1986).

The Pantanal of Miranda, in the southern region of the Pantanal Matogrossense, is a large floodplain formed by sedimentary deposits from the Miranda river. The southern side of the river, where there are Paratudal woodlands, is composed of a combination of soils with different clay compositions (in a gradient from greater than 60% clay to patches of sandy soils with less than 15% clay), varying from well to poorly drained, according to the "National Survey and Soil Conservation Service", SNLCS/EMBRAPA (Vila da Silva 1991). Eight classes of soils can be distinguished in this region: Planisol eutrophic, solonetz solodised, and vertisol are found in the Paratudal woodland. The Paratudal woodland borders on hydromorphic quartz sands (Vila da Silva 1991). The study sites had soil pH > 6, no aluminum, and high cation exchange capacity, therefore these are highly fertile soils (Table 1).

The richer soils in the Pantanal than in the *cerrado* should explain the faster plant growth in the former. However, herbivory and other negative interactions should be favored in a more productive tropical habitat (Coley *et al.* 1985, Herms & Mattson 1992). Nevertheless, for trees in the Paratudal woodland only rapid plant growth has been observed, and thus other factors must be preventing negative interactions with, for instance, insect herbivores.

Plant communities of the Pantanal of Miranda. The vegetation types are distributed in discrete patches throughout this floodplain, depending on vulnerability to seasonal floods, soil types, and the draining characteristics. Grassland communities occupy semi-inundated, and temporally inundated plains. Fragments of forests occur in calcareous patches, the "capões", which are suppose to be of anthropogenic formation, by the Guaicurus tribes in the past. This habitat, varying from hundreds to 1–2 thousand meters in extent, occurs always above the inundation level. Finally, several savanna-type monodominances occur on different soils patches: (1) "Espinheral", the stands of a small bush of *Bauhinia bauhinioides* Mart., occurring on sandy soils; (2) "Canjiqueiral", of *Byrsonima orbignyana* A. Juss., which is a pioneer shrub found in temporarily flooded fields (Pott & Pott 1994); (3)

"Carandazal," large patches of the palm *Copernicia alba* Morong., typical of the chaco vegetation, which occurs on salty or basic soils, and is a pioneer species favored by fire (Pott & Pott 1994).

The most impressive and widespread monodominance, though, is the Paratudal woodland. The monodominant *T. aurea* savanna occurs on very compact clay soil, where there are so-called mounds or "murunduns". The mounds in this area are elevated soil patches, normally one meter high and one to two meters in diameter. Usually the germination and establishment of *T. aurea* occurs only on the mounds, a pattern that suggests *T. aurea* is not a flood-resistant species, as the mounds stay above the flood level. Prance & Schaller (1982) showed that *T. aurea* is an abundant, but not dominant tree species in the *cerrados* of hilly regions on the border of southern Pantanal.

Flood dynamics in the Pantanal and their effect on the Paratudal woodland. The flood dynamic in the Pantanal of Miranda is influenced by a superposition of different hydrological processes (Adámoli 1986b, Vila da Silva 1991, Hamilton *et al.* 1996): (1) a long flood cycle that causes strong and widespread river floods for a series of years, followed by another similar period without strong floods; (2) annual river floods, which last for a few to several weeks, varying from year to year in intensity; and finally, (3) floods caused directly by rains, which are not too intense but result from storms. The result for the Paratudal woodland is that most of the mounds are not covered during low-flood cycles, but rain floods cover the floodplain, killing the seedlings of *T. aurea* not growing on the mounds. On the other hand, very intense river floods can have a catastrophic effect on the whole ecosystem. Floods may kill established seedlings and young trees by covering most of the mounds. Furthermore, such intense floods can disrupt fish migration, and cause the rapid death and decomposition of terrestrial plants and trapped fish (S.P. Ribeiro, unpubl. data; R. A. Mauro - Embrapa/CPAP; pers. comm).

The annual flood dynamic in the Miranda river floodplain can be summarized as follows: (1) the Miranda river first floods in December and peaks in February, as a result of a combination of different interactive floods. This inundation usually finishes before the end of March (Adámoli 1986b, Vila da Silva 1991). Depending on the year this flood can be preceded by floods directly caused by rains, starting in November. (2) The second flood occurs in May-June due to the influx of an enormous volume of water from the floods in the northern region of the Pantanal, many kilometers away. This water volume affects the area directly (mainly in exceptional years with high floods), but also dams the Miranda river, which floods again.

The Paratudal woodland is affected by two independent river flood systems. For instance, sampling site I is mainly affected by the flood of the Miranda river, while site II is affected by the flood of the Miranda river plus the late flood of the Paraguay river, in May. The dynamics of the Miranda river are the most influential for the Paratudal woodland. Vila da Silva (1991) showed that the inundation in the study area is highly correlated with the water level measured in the Miranda river (Pearson R = 0.85). However, as the Miranda basin is composed of a very complex drainage system, predictions concerning levels and time-lag of floods are rather difficult to make (Adámoli 1986b, Vila da Silva 1991, Vila da Silva & Kux 1992).

The best descriptive data for the Miranda river comes from the nearest hydrographic station of "Tição de Fogo" (ANEEL, Brazil). At this station, the river overflows its banks when it reaches the height of 449 cm. The mean flood level in the study areas when the river reaches this level was 96 cm. This represents a normal river inundation, not able to kill or remove seedlings from the top of most of the mounds. Rearranging the data in Vila da Silva (1991), it was possible to obtain an expected time interval of occurrence of floods exceeding 514 cm in "Tição de Fogo", with a probability of 95%. Such a water level was the maximum estimate, corresponding to catastrophic inundations in the Paratudal. The data leads to the expectation of catastrophic floods, on average, once every 20 years (Ribeiro 1999). To some extent this probability is equivalent to the cycles of low and high inundation previously described (Adámoli 1986b, Carvalho 1986), even though their occurrence is rather stochastic.

Cerrado versus *Pantanal. Precipitation.* The Pantanal is affected by an extremely variable climate (Vila da Silva & Kux 1992). The impact of this phenomenon on the biota seems particularly pronounced in the Pantanal of Miranda. The variable climate factors considered here for the Pantanal, in comparison with the *cerrado*, are: (1) a wet season based on highly concentrated stormy rains, and (2) several sudden drops in temperature at the beginning of the dry season.

The Pantanal of Miranda has a continental tropical climate, with well defined dry (May to September) and wet (October to April) seasons. From 1985 to 1997, the mean annual rainfall in the core area of the Paratudal woodland was 915 mm. In the Miranda river basin, this precipitation level was consistently the lowest within an area of 2038.3 km², sampled at up to 10 different sites througout these years (Fazenda Bodoquena, unpubl. data). It was also lower than the mean annual rainfall in the Pantanal of Nhecolândia (1353 mm), a nearby subregion to the north (Soriano 1997). Most importantly, this precipitation was also lower than in the *cerrado* of Minas Gerais State for the same period (1280 mm).

Fig. 2 shows that the studied *cerrado* had a greater volume of rain during the wettest months than the Paratudal woodland, while the precipitation in the dry season matched more closely. However, the number of rainy days per year was disproportionately higher in the *cerrado* than in the Paratudal (Fig. 3a). Therefore, the mean rainfall per rainy day was higher in the latter, regardless of the lower mean annual rainfall (Fig. 3b). For instance, in December 1994 it rained an average of 50.6 mm per rainy day in the Paratudal compared 16.7 mm per rainy day in the *cerrado*. The converse situation occurred with the total rainfall: 152.0 mm in the Paratudal versus 267.0 mm in the *cerrado*. Hence the wet season in the Paratudal woodland could be defined as long dry periods interrupted by intense storms. For example, in November 1996, 100 mm rain fell during just 12 hours, and accounted for 12.5% of all rainfall for that year.

Conversely, the rainfall for the wet season in the *cerrado* is more constant and evenly distributed. However, the *cerrado* also showed exceptionally wet seasons, with extremely high amounts of rain, which happened in approximately 10% of the years from 1959 to 1997. Years of low rainfall also occurred during this period. Nevertheless, even during the driest years the *cerrado* had higher levels of rainfall than the mean annual rainfall in the Paratudal woodland (915 mm). The driest rainy season in the *cerrado* was 1968-69, with a total annual rainfall of 1080 mm. Table 2 shows recent rainfall data, for 1996, in both Paratudal and *cerrado*.

Temperature variation. Climatic instability is intense in the southern Pantanal due to its geography. The Pantanal is a geographical depression ranged longitudinally at 80 m above sea level. It is surrounded by the mountains of the Andes Cordillera to the west (up to 3000 m), and the Brazilian Plateau to the east and

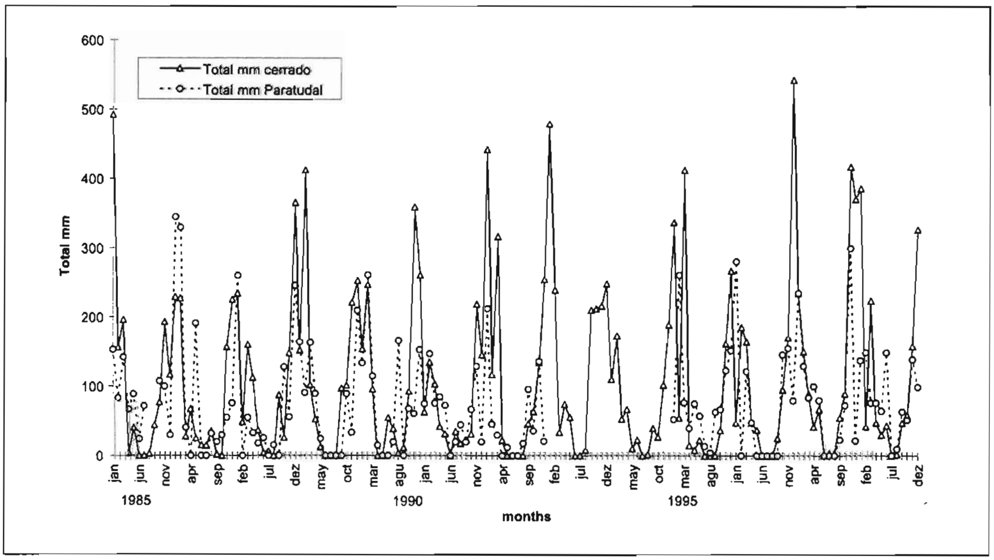
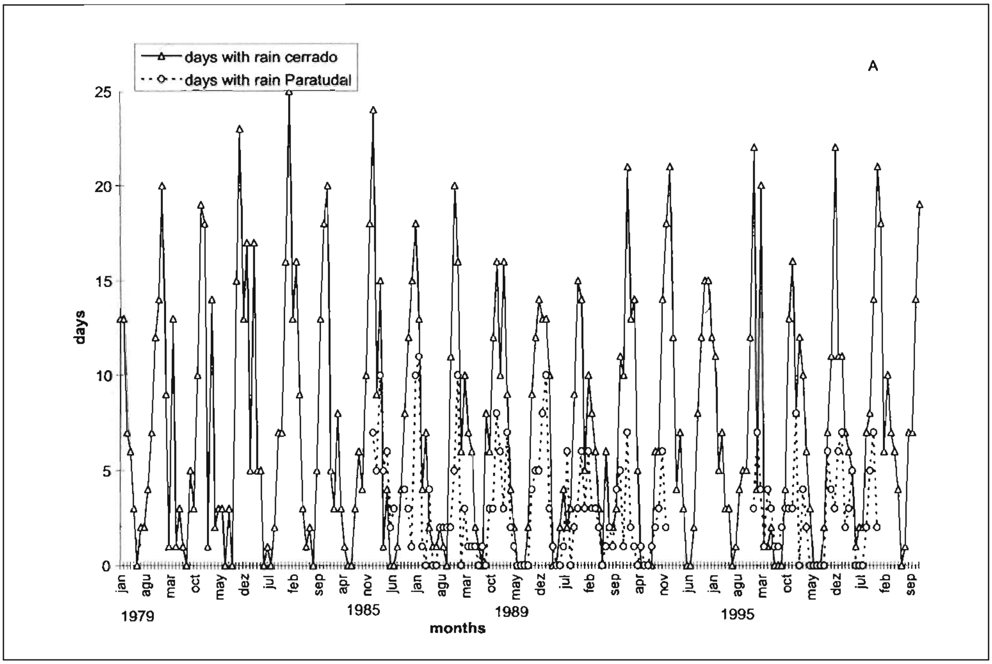


FIG. 2. Total monthly rain in the *cerrado* of Paraopeba and in the Paratudal woodland, from 1985 until 1997. Note the lack of data for the Paratudal woodland in 1994.



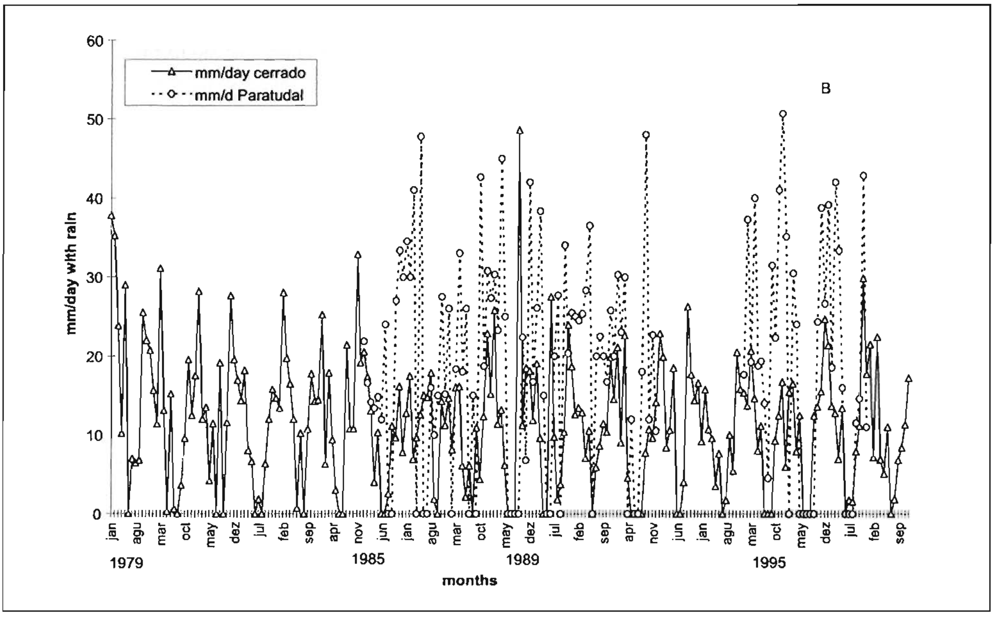


FIG. 3. Distribution of rain in the *cerrado* of Paraopeba and in the Paratudal woodland. (A) Number of days with rain per month, showing a higher proportion of rainy days in the *cerrado* during the wet season. (B) Mean rainfall (mm) per number of rainy days, showing a greater concentration of rain in a few days in the Paratudal, which most of the time represent stormy intervals within long dry periods in a wet season. Note the lack of data for the Paratudal woodland before 1985 and in 1994.

TABLE 2. The rainfall regime in the *cerrado* and in the Paratudal woodland, 1996.

Rain regime	*Cerrado*	Paratudal
Total annual rainfall (mm)	1,202.5	848.0
CV annual rainfall (%)	11.9	19.8
Mean mm/day	10.1	8.2
Mean monthly rainy days (%)	23.0	3.7
Mean number of rainy days/year	82.0	30.7

north (up to 950 m). By contrast the southern border of the Pantanal is a continuation of the lowlands of the Gran Chaco, which, in its turn, extends to the Argentinean pampas. Therefore there is a straight corridor of open lowlands that meets the Atlantic Ocean near the extreme south of the continent, towards Antarctica. This particular geography favors a north-south exchange of air masses (Tarifa 1986), which expose the south of the Pantanal to the strongest "friagem" observed in the continent. "Friagem" is a winter phenomenon in which there is a drastic drop in temperature. It is a consequence of sudden upward movements of the stationary continental warm air mass, from the center of the continent towards the Caribbean Sea. This air movement allows the entrance of polar anticyclones into the center of the continent, instead of their usual progression along the coast of Brazil (Nimer 1979, Tarifa 1986). The "friagens" happen randomly four to five times every year, between April and September. In the Paratudal woodland, the temperature can drop from + 20 to 30°C to + 0.5 to 2°C in less than 24 hours. Low temperatures and strong winds last for two to four days (Tarifa 1986). This phenomenon occurs in many other regions in the *cerrado* (and also in the Amazon), but the highest frequency and thermal amplitude are in the Pantanal. In terms of mean annual temperature, the Pantanal is warmer (27.4°C) than the *cerrado* (22°C), and daily temperature is more constant. Published mean annual daily amplitude in temperature was lower in the Pantanal (6°C) than in the *cerrado* (10°C), reflecting the stronger winter (dry season) in the *cerrado* (Goodland & Ferri 1979, Garcia 1984, Tarifa 1986). An average high and constant temperature in the Pantanal strengthens the impact of sudden decreases of temperature on the biota, during the "friagem".

DISCUSSION

Tropical monodominant woodlands and environmental unpredictability. Pantanal Matogrossense is a geologically recent region, where there is a great deal of environmental variation. In addition to the unpredictability of annual climatic conditions, there are large cycles of drought and severe flooding. The south of Pantanal is particularly susceptible to climatic and flooding fluctuations. For this region even the mildest annual flooding variations mean prolonged flooded periods, due to the recurrence of floods at the beginning of dry season. During this time, slow water movement from the northern parts of the Pantanal cause a new influx of water over the entire Miranda river floodplain. Regarding the Paratudal woodland, it is important to consider that it happens to be in the driest part of this subregion, which could strengthen the consequences of any water stress regime.

The young geological age and the stochastic climate of the Pantanal contrast with the geologically old and stable, and climatically constant *cerrado* domain. Furthermore, the existence of a considerable monodominance of *T. aurea* in the Pantanal may be related to a species-poor guild of insect herbivores on the trees (Ribeiro 1999), which also contrasts with the high diversity of plant species and insect herbivores in the *cerrado* (Fernandes & Price 1988, Gontijo 1991, Price *et al.* 1995, Ribeiro *et al.* 1998, Ribeiro 1999, Ribeiro & Brown 1999). On the one hand, it is hard to prove that lack of herbivory is a predominant cause of this monodominance, but on the other there is sufficient evidence to support the idea that a highly stochastic environment retains an early successional community in the Pantanal, where *T. aurea* performs best. In a lattice model, the rapid growth and high reproductive rates of *T. aurea*, based on wind-dispersed seeds, favored the recolonization of large areas from a few adult trees (based on tree survivorship only on the scattered mounds), and gave this species the best competitive ability after having been established (Ribeiro 1999, Ribeiro *et al.* unpbl. data).

The rationale behind the hypotheses here discussed is that unpredictability and high frequency of disturbance, due to climatic oscillations and flooding, could create an unfavorable scenario for insects and other parasites, thus allowing the positive selection of host plants that invest in fast growth and high reproduction in the Pantanal (Ribeiro 1999, Ribeiro &

Brown 1999). In addition, a high seed production and efficient dispersal strategy may provide a mechanism by which the first species with these traits established on the mounds could garantee its own colonization of other empty mounds (Ribeiro 1999). In this sense, the Paratudal woodland could be understood as a window of opportunity for a tree species in a semi-flooded grassland community. The ecological patterns of insect herbivores distribution and herbivory damage, tree species reproduction, seed yield and establishment, which are in accordance with the hypotheses above, are presented elsewhere (Ribeiro 1999, Ribeiro & Brown 1999).

Concluding remarks: the relevance of cerrado and Pantanal for species conservation. In Ribeiro (1999) and Ribeiro & Brown (1999) we presented data supporting the hypotheses related to the negative effects of a stochastic climate on parasites and competition, which thereby favor monodominant populations. These hypotheses contribute to explaining the existence of a substantial monodominance of *T. aurea* in the Pantanal of Miranda. It is worthwhile remarking that the mechanisms we pointed out as probably being important for the maintenance of the Paratudal woodland are not exclusive of any other explanation. Likewise, the fact that an extremely stochastic environment can favor plant monodominance does not necessarily mean that it explains every tropical monodominance. The role of a low-competition community and the lack of diseases in favoring pioneer, aggressive plant species is well known and has been discussed in various articles on ecology and evolution (see Christiansen 1974, 1975; Clarke 1979; Coley *et al.* 1985; Hamilton *et al.* 1990; Hamilton 1991; Frank 1993, 1997).

The true mechanisms behind species relative abundance remain to be discovered (Hubbell 2001). Nonetheless, it is likely that the interaction between soil fertility and atmospheric conditions could provide the framework for many combinations of species community composition and diversity. Certainly, the set of conditions here described are likely to be intimately connected to the ecological processes that trigger the establishment of the monodominance of *T. aurea* and other species in the Pantanal of Miranda.

Although the Paratudal woodland is an early successional process, it is strictly habitat-dependent, and thus fragile. The typical economic activities in the Pantanal, based on extensive cattle raising and ecotourism, are compatible with the conservation of its plant communities. The same could not be said for the enlargement of the Waterway Paraguay-Parana, which could seriously affect the flooding dynamics, drying out large parts of the floodplains (Hamilton 1998). As the monodominance of *T. aurea* seems to be closely linked to the inundation dynamics, the waterway could have catastrophic consequences for this impressive plant community and its habitat. Such an enterprise has been proposed by the governments of Brazil, Argentina, and Bolivia, but has, so far, been legally prevented from being constructed, after intervention by non-governmental organizations in Brazil.

The Pantanal Matogrossense is dominated by only a few, but abundant, populations of plants and animals (Brown 1986). An important aspect of preserving these populations is the protection of a large genetic pool of species that are endangered in other parts of the continent, such as in the *cerrado*. Contrasting with the Pantanal, the Brazilian *cerrado* has been drastically changed by human activities. Modern agriculture, such as soya bean monoculture, urbanization, and logging for charcoal production are having the greatest impacts on biodiversity, habitat, and species loss in the *cerrado* (Klink *et al.* 1993). Many tree species will have their population sizes seriously decreased and fragmented in the next decades. For some pioneer species, the Pantanal represents an important genetic and population reservoir. However, the ecological interactions and processes that have evolved with the diverse ecological community in the *cerrado* cannot be preserved elsewhere, but only in the remaining fragments. Various of these fragments are preserved in National Parks. Nevertheless, without a broad, efficient policy for proper land use, a great loss of species can be expected in the future of the Brazilian *cerrado*. Unfortunately, such a loss will occur well before science has properly understood the *cerrado*, or even before we learn the importance of tropical ecosystems other than rainforest or African savanna.

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