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Woody vegetation in the Pantanal of Mato Grosso, Brazil: a preliminary typology

by

C. Nunes da Cunha, W.J. Junk & H.F. Leitão-Filho

Prof. Dr. Catia Nunes da Cunha, Dept. of Botany and Ecology, NEPA, IB/UFMT, Av. Fernando Correia s/n, Coxipó, 78060-900 Cuiabá/MT, Brazil; e-mail: catianc@ufmt.br
Prof. Dr. Wolfgang J. Junk, Max-Planck-Institute for Limnology, Tropical Ecology Working Group, August-Thienemann Strasse 2, 24306 Ploen, Germany; e-mail: wjj@mpil-ploen.mpg.de
Prof. Hermógenes Freitas Leitão-Filho, Dept of Botany, IB-Unicamp, Campinas-SP, Brazil. In memoriam.
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Abstract

The ecological conditions of the Pantanal of Mato Grosso change during yearly and multi-years cycles because of pronounced water-level fluctuations. Differences in topography and related hydrological conditions allow the coexistence of specific vegetation units. This paper presents an analysis of the flora and vegetation types described in the scientific literature and based on our own observations in the Pantanal. It offers a unifying characterization of the vegetation of the Pantanal of Mato Grosso with respect to the characteristics of woody plants of the region. Grasslands and aquatic communities were not considered. Three floristic types with 19 units were distinguished: savannas (5 units), forests (2 sub-types and 10 units), and scrublands (4 units). The environmental parameters used to define these types, sub-types, and units are described, and information on species composition is given.

Keywords: **Pantanal, semi-deciduous and dry forest, savanna and *cerrado* vegetation, periodically flooded forests, typology.**

Resumo

As condições ecológicas do Pantanal de Mato Grosso mudam anualmente e em ciclos pluri-anuais devido às pronunciadas flutuações do nível das águas. Diferenças na topografia e nas condições hidrológicas relacionadas permitem a coexistência de unidades específicas de vegetação. Este artigo apresenta uma análise da flora e tipos de vegetação apresentada na literatura científica e em nossa experiência e oferece uma caracterização unificada da vegetação lenhosa do Pantanal de Mato Grosso. Campos e comunidades de plantas aquáticas não foram consideradas. Diferenciamos 3 tipos florísticos com 19 unidades: savanas (5 unidades), florestas (2 sub-tipos e 10 unidades) e *arbustal* (4 unidades). Os parâmetros ambientais que levam à formação dos tipos, dos sub-tipos e das unidades são descritos e a composição das espécies é apresentada.

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Introduction

The Pantanal is situated in a depression of the upper Paraguay River catchment area that developed as a consequence of the formation of the Andes. During the Pleistocene, at least four climate changes alternating between arid and semi-humid occurred. Torrential rains transported large amounts of sediments into the depression and formed a sediment layer called the Pantanal Formation (DEL'ARCO et al. 1982). Based on the region's evolution, the Pantanal Formation can be subdivided into three sub-units, representing the Pleistocene alluvial plain, sub-recent sediments, and recent sediments. During the Holocene, the Pantanal passed through different climatic episodes that are not yet fully understood (ASSINE & SOARES 2004). Nonetheless, the following climatic episodes have been distinguished: 40,000-8,000 BP, cool and dry; 8,000-3,500 BP, warm and wet; 3,500-1,500 BP, warm and dry; and 1,500-Present, warm and wet (IRIONDO & GARCIA 1993; STEVAUX 2000).

In the first article of the Ramsar Convention, wetlands are defined as "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salty, including areas of marine water the depth of which at low tide does not exceed six meters" (NAVID 2002). According to this definition, the Pantanal is a wetland, but the term "Pantanal" suggests an area of swamps. In fact, the Pantanal is a large floodplain that is periodically inundated during the rainy season by rainwater and transbording rivers but which is dry during the dry season (JUNK et al. 1989). Permanent lakes and swamps represent permanent aquatic or moist habitats inside the vast floodplain, which covers an area of 160,000 km^2. Elevated paleo-levees of former rivers serve as permanent terrestrial habitats.

Associated with the numerous types of habitats is a large variety of different vegetation types. These have been given specific local names and they are also used in the scientific literature. However, the local names are often not adequately defined, a fact that leads to confusion in comparative studies.

LUGO (1990) pointed out that inadequate characterization of forested wetlands hinders comparative studies but also the development of sustainable management and protection measures. The present study shows that a major portion of the woody vegetation of the Pantanal of Mato Grosso does not belong to the category of floodplain forests but colonizes small permanent dry areas inside the floodplain. These little or non-flooded forested habitats increase habitat and species diversity and play an important role as periodic refuge for terrestrial animal species during the flood season.

PRANCE (1989) proposed a classification of Amazonian wetland forests and differentiated between three major groups: permanent swamp forest (2 sub-groups), periodically flooded forest (5 sub-groups), and gallery forest. The applicability of this classification to the forested wetlands of the Pantanal remains to be tested. All flooded forests of the Pantanal of Mato Grosso belong to those categories describing seasonally flooded forests with the exception of the swampy woodland savanna, in which *Mauritia flexuosa* is found.

An analysis of 86 tree species that occur along the inundation gradient indicated that 26 species are restricted to terrestrial habitats and only four to habitats that are subject to long-term flooding. The other 56 species show a large ecological amplitude and occur under dry as well as flood conditions. This has been interpreted as an adaptation of the woody plants to the strongly varying hydrological conditions in the Pantanal, which

have favored the occurrence of these species under recent climatic conditions (NUNES DA CUNHA & JUNK 1999). A similar overlap of species occurs between deciduous and semi-deciduous forests.

The aim of the present study is the floristic and physiognomic characterization of the principal woody plant communities associated with specific habitats of the Pantanal, based on information in the literature and data from our own studies. While our knowledge of plant communities of the Pantanal is still insufficient to propose a phytosociologically correct classification according to international rules (BARKMAN et al. 1986), preliminary characterizations are urgently required to support sustainable management and ecological research. This article provides the basis for deriving a classification of wetland habitats of the Pantanal.

Study area

ADAMOLI (1982) divided the Pantanal of Mato Grosso into different sub-regions according to their ecological characteristics (Fig. 1). Large areas in the northern part are situated more than 130 m asl and are shallowly flooded. Near the Cuiabá River, flooding is intermediate. To the south, the altitude decreases to 100-110 m asl.), with annual rainfall reaching about 1,300 mm. The southern Pantanal is strongly inundated (HAMILTON et al. 1996). There is a pronounced dry season from June to August (winter), when the monthly rainfall is less than 10 mm, and a rainy season from December to February (summer), when the maximum monthly rainfall is 250-300 mm. The climate is Köppen's "savanna" subtype (AW).

In the northern Pantanal, flooding coincides with the rainy season (Fig. 2). During low-water periods, the Pantanal is dry and many of the floodplain lakes are decoupled from the rivers. Floodwater needs about 3 months to reach the southern end of the Pantanal. In addition to the annual flood cycle, there are multi-year periods of high floods and strong droughts.

The research area of this study was subdivided into the following geomorphologic units: elevations that reach 1-2 m above mean flood level (*murunduns, capões, cordilheiras*, and levees), flat plains periodically flooded to a depth ranging from a few decimeters to up to 3 m (*campos*), shallow natural channels that drain the *campos* but fall dry during low-water periods (*landis, vazantes*), depressions that continue to be swampy even during normal low-water periods, and permanent lakes and river channels. Woody vegetation grows mostly on elevations, in shallowly flooded areas, in the drying drainage channels, and along river and lake shores.

State of the art

Different denominations for the Pantanal vegetation are found in the literature. HOEHNE (1936) differentiated between xerophilous vegetation on dry and calcareous soils and hydrophilous vegetation on periodically flooded non-calcareous soils. The vegetation was described as a mixture of species from the Amazonian rain forest and the xerophilous vegetation (*caatinga*) of Ceará (NE Brazil). "The xerophilous flora is represented by the following species: *Cereus peruvianus, Opuntia stenarthra, Pereskia sacharosa, Cereus bonplandii, Novillea cavendishii, Jatropha urens, Cnidoscolus phyllanthus, Loasa* sp, *Ceiba pentandra, Ceiba pubiflora* and others".

Because of the extension of the climatic region of the boreal Chaco into the southern Pantanal, typical species of the flora of the eastern Chaco occur as far as Corumbá, such

as *Chorisia ventricosa, Schinopsis balansae*, and *S. lorentzi, Aspidosperma* sp. (WILHELMY 1958; RIZZINI 1963). Only a few species of the Chaco enter the entire Pantanal, such as *Jacaranda mimosifolia, Tecoma ocracea*, and *Piptadenia macrocarpa*.

AGUIRRE (1945) emphasized the existence of gallery forests along rivers and water bodies. KUHLMAN (1954) complemented this analysis with the observation that along the Paraguay River these formations are irregular and often very narrow. Resident species included "*Inga edulis, Inga nobilis, Tecoma caraiba, Attalea princeps, Triplaris formicosa*, and *Genipa americana*". HOEHNE (1936) referred to this as a hydrophilous formation on non-flooded ground (*terra firme*) when "*Desmoncus, Bactris*, and *Astrocarium*" were present. For WILHELMY (1958), these were not gallery forests, but river bank forests, in the sense of TROLL (1936), that grew on the highest levees.

Humid semi-deciduous forests that were green in summer (wet season) were found, according to WILHELMY (1958), "in every non flooded area in the Pantanal with species that occur in the Chaco: *Tecoma caraiba, Tecoma ipe, Tecoma ochracea, Jacaranda mimosifolia, Caryocar brasiliense, Attalea phalerata, A. princeps, Vochysia tucanorum, Curatella americana, Hancornia speciosa, Piptadenia macrocarpa, Hymenaea stignocarpa*, and *Acrocomia aculeata*".

Flooding savannas were mentioned by PAFFEN (1957). WILHELMY (1958) confirmed the authenticity of the flooding savannas for the Gran Pantanal, commenting that sometimes they were interspersed with islands of humid semi-deciduous forests. He mentioned a special savanna type, the termite savanna, which was first denominated by TROLL (1936) in Africa. Termite savanna is blanketed by small forested islands that cover termite mounds (*murunduns*).

Several authors, among them COLE (1960), KUHLMAN (1953, 1954), and RIZZINI (1979), considered the Pantanal as one vegetational complex because of the environmental variations resulting from alternating dry and flood periods. For COLE (1960), this complex included several not-specified types of savannas and forests. RIZZINI (1979) denominated the mosaic of hydrophilous, mesophilous, and xerophilous communities as the Pantanal Complex, a term that was dismissed by ADAMOLI (1982).

The first vegetation classification was elaborated by LOUREIRO et al. (1982), who defined five phytoecological sub-regions for the Pantanal: (1) savanna (*cerrado*), (2) savanna steppe (*chaquenha*), (3) semi-deciduous seasonal forest, (4) deciduous seasonal forest, and (5) areas of ecological tension, i.e., subject to anthropogenic modification.

PRANCE & SCHALLER (1982) described different floristic types in the Fazenda Acurizal, which covers an area at the border of the Pantanal. The authors characterized *cerrado*, semi-deciduous forest, swamp vegetation types, and xeric vegetation types. RATTER et al. (1988) carried out a phytosociological study of the *cerrado* and semi-deciduous forests of the region. An area near Poconé was found to contain many of the indicator species of the mesotrophic facies *cerradão*. The phytosociological studies of NASCIMENTO & NUNES DA CUNHA (1989) included stands of *Vochysia divergens* POHL in the Pantanal of Mato Grosso. In 1999, NUNES DA CUNHA & JUNK quantified the floristic composition of forests on termite mounds (*murunduns*) and paleo-levees (*capões* and *cordilheiras*); these authors related tree distribution to flooding patterns.

Further information on the vegetation of the Pantanal is found in POTT & POTT (1994), PRADO et al. (1994), DUBS (1994), NUNES DA CUNHA (1990, 1998), GUARIM-NETO et al. (1996), SCHESSL (1999), ZEILHOFER & SCHESSL (1999),

NUNES DA CUNHA. & JUNK (1999), POTT & POTT (2000), SALIS (2000), SILVA et al. (2000), NUNES DA CUNHA & JUNK (2001), NUNES DA CUNHA & JUNK (2004), DAMASCENO-JUNIOR et al. (2004), and DAMASCENO-JUNIOR et al. (2005).

NUNES DA CUNHA et al. (1996) elaborated a physiognomic vegetation map at a scale of 1:100,000 for the area north of Poconé, based on a modified classification of the results of VELOSO et al. (1991). Using satellite images, they delineated for the Pantanal: (1) one type of seasonal semi-deciduous forest; (2) four types of savanna (*cerrado*): (a) forested savanna (*cerradão*), (b) seasonally flooded low-tree and scrub woodland (*cerrado aberto*), (c) seasonally flooded savanna parkland, including *campos de murunduns, paratudal, piuval,* and *campos* with *capões*, and (d) seasonally flooded grass-wood savannas, including fields of *Thalia geniculata, Ipomoea carnea, Combretum lanceolatum*; (3) transition systems or ecological tension areas of two types: seasonally flooded evergreen forests, including *cambarazais* and floating aquatic vegetation (*batumes*); (4) secondary systems including deforested areas and bare soil.

SILVA et al. (2000) constructed maps of the vegetation of the Pantanal following an aerial survey. They used the management and protection of large animals, such as caimans, capybaras, jaguars, and swamp deer, as the basis for separating 16 vegetation classes and one class with miscellaneous structures.

Methodology

We characterized the woody vegetation in terms of three types: savanna, forests, and scrublands. These were further classified in different sub-types and units according to flooding regime, physiognomic aspects (e.g., degree of deciduousness), and the dominant species found in each one. The units were communities or groups of communities with similar characteristics.

There are several unresolved questions with respect to the definition of deciduous, semi-deciduous, and evergreen forests. In many species, leaf change is subject to a certain seasonality that may be intensified or weakened during very dry or wet years, respectively. Many species of the flooded forest are considered evergreen, for instance, *Calophyllum brasiliense* CAMBESS., and *Vochysia divergens* POHL., but may lose most of their leaves during very dry years (facultative deciduous). This behavior has also been described for trees of semi-evergreen lowland rain forests (RICHARDS 1996). Some flooded forest species are also deciduous, such as *Vitex cymosa* and *Cassia grandis*. While *Callistene fasciculata* and *Astronium fraxinifolium* of the semi-deciduous forest type are deciduous, they may retain some of their leaves in wet years. Due to the large multi-year variation in rainfall in the Pantanal, the behavior of the different forest types with respect to leaf fall and flush can also vary considerably.

The term semi-evergreen was defined by WALTER (1971) and was used to refer to those species in which the "upper tree layer is defoliated for some of the year (during drought), while the lower tree layer retains its foliage". Semi-evergreen forests have been described in non-flooded areas of Trinidad (RICHARDS 1996) and Sri Lanka (DITTUS 1977). In the Pantanal, semi-evergreen forests occur in areas that become inundated during the high-water period from December to April and are dry during the period of low water from June to November. The soil is in part denuded or covered by a dense litter layer, with few tree seedlings and very few herbaceous plants and shrubs. The upper story consists of both facultative deciduous and deciduous species. In wet years, most of the trees lose few leaves, while in very dry years the entire canopy may appear leafless.

Here, regional terms for habitats and vegetation have been used for the characterization of vegetation units. Botanical collections were carried out for the purpose of taxonomic characterization, and quantitative analyses were performed to describe community structure, as published in NUNES DA CUNHA & JUNK (1999) and NUNES DA CUNHA (1990). The data of BRAZIL MINTER (1979) and RADAMBRASIL (1982) were also included in this analysis. However, the scale and vegetation units used in the maps of

those authors were too small to be useful in the present context. In this study, we have used the term "savanna" according to the definition of the IBGE (1992), which positions the Brazilian *cerrado* in an international context.

Botanical names correspond to those listed at http://mobot.org/W3T/Search/vast.html and in POTT & POTT (1994, 1996).

Results

The Pantanal of Mato Grosso presents, in terms of its woody plants, three basic types of vegetation: savanna, forest, and scrubland. This vegetation grows on characteristic landscape units, some of which have local names. These are defined as follows:

Cordilheiras are sinuous remains of paleo-levees several kilometers in length and about 100 m wide, reaching 1-2 m above the surrounding seasonally inundated plains. These elevations are not subject to inundation (Fig. 3).

Capões are elevated remnants of eroded paleo-levees. They are elongated or round in shape and occur in seasonally flooded plains (the term *capão* comes from the aborigine Tupi word Káa pu'ã, round woods).

Murunduns are earth mounds up to 1.20 m high that reach above the mean high-water level and cover an area between 1 and 15 m^2. The mounds are built by termites to escape flooding during periods of high water (Fig. 3).

Levees are the highest recent sediment depositions along river channels. They become flooded only in years of exceptionally high water. Lower river terraces and low-lying areas opposite the levees are periodically flooded to varying extents, depending on their elevations (Fig. 4).

Morrarias are groups of hills a few hundred meters high that are located at the border or isolated inside the Pantanal. They are not discussed here further.

Aterros de bugre are artificial earth mounds of anthropogenic, often of pre-Columbian origin. They were constructed by the indigenous population for flood protection.

Inundated plains are defined as the flat areas between elevations and depressions in the floodplain that become periodically flooded by rain water or transbording rivers. The depth of inundation varies from a few decimeters to several meters, depending on the elevation of the plain.

Landis are continuous and sinuous depressions covered by trees in high-lying parts of the Pantanal. They provide drainage during the flood period but fall dry during low-water periods, while maintaining a rather high groundwater level (Fig. 3). When they are covered with grasses and herbaceous vegetation, they are called *vazantes*.

1. Type: Treeless vegetation (not characterized in this article)

(a) Treeless, periodically flooded savanna and grassland (*campo limpo*)
(b) Treeless vegetation on low-lying levees and river terraces
(c) Depressions with waterlogged soils that are covered with perennial herbaceous palustric vegetation even during dry periods (swamps)
(d) Extended belts of floating and submersed aquatic macrophytes along river and lake shores
(e) Dense floating islands (*batumes*) that drift on the lakes

2. Type: Savannas (*cerrado, chaco*)

"*Cerrado*" is the Brazilian term given to the xeromorphic woodland scrub savanna and

grass-field vegetation of central Brazil (EITEN 1978). According to COUTINHO (1982), "*cerrado* sensu lato" is formed by *campo limpo* (a grassland formation), *campo sujo, campo cerrado, cerrado* "sensu stricto" (intermediate savanna formations), and *cerradão* (a scleromorphic forest formation). The savanna formations may be considered ecotones between *campo limpo* and *cerradão*. The different phytophysiognomies and the floristic heterogeneity are determined by the mosaic pattern of fire action and hydrologic and edaphic factors (EITEN 1972; GOODLAND & POLLARD 1973; COUTINHO 1982; OLIVEIRA-FILHO et al. 1989; RATTER et al. 1997). The Pantanal, together with Mato Grosso, Goias, and Mato Grosso do Sul, is included in the central-western geographic region of the *cerrado* vegetation (RATTER & DARGIE 1992; CASTRO 1994; RATTER et al. 1996; RATTER et al. 1997).

According to EITEN (1990), the flat periodically inundated plains of the Pantanal are "hyper-seasonal savannas", the *cerrado*-covered non-inundated elevations are "seasonal savannas". Hyper-seasonal savannas occur on heavy, ill-drained soils and are characterized by alternating dry and very wet conditions. In the dry season, the vegetation dries out and is often burnt but in the wet season the ground becomes waterlogged or flooded (RICHARDS 1996). We include in this vegetation type a sub-type that, based on its floristic composition, belongs to the chaco (*carandazal*).

The savannas of the Pantanal of Mato Grosso include the vegetation that occurs mainly in the peripheral areas of the northern part, with the Pinxaim River as the southern border. Savanna vegetation in the southern end of the Pinxaim River occurs sporadically and the floristic richness of arboreal species is less. Some *cerrado* species form dense, almost homogeneous stands, which determine the physiognomies of the vegetation of some localities, for instance, *Curatella americana* L., *Callisthene fasciculata* MART., and *Tabebuia aurea* (MANSO) B. & H. ex S. MOORE, locally called *lixeiro*, *carvoal*, and *paratudal*, respectively. The great majority of the registered species has a wide geographic distribution.

2.1 Seasonally flooded termite savanna with *Curatella americana* (*campo de murunduns, lixeiral*)

The termite savanna, regionally known as *lixeiro or campo de murunduns*, is a seasonally inundated savanna covered by termite mounds (micromounds according to PONCE & NUNES DA CUNHA 1993). The density of the mounds may be more than 100 ha^{-1} (CASTRO 1999). They are covered with trees and their floristic composition is closely related to that of the *cerrado* flora. The characteristic tree species are *Curatella americana* L., *Andira cuyabensis* BENTH., *Simarouba versicolor* ST. HIL., *Vatairea macrocarpa* (BENTH.) DUCKE, *Tabebuia aurea* (MANSO) B. & H. ex S. MOORE, and *Sclerolobium aureum* (TUL.) BENTH, among others (NUNES DA CUNHA 1990). The plain between the termite mounds is covered by grasses and herbaceous plants.

2.2 Seasonally flooded woodland savanna with *Tabebuia aurea* (*paratudal*)

The *paratudal* designates a woodland savanna covered mainly with single trees of *Tabebuia aurea* (MANSO) B. & H. ex S. MOORE (Fig. 3). It occurs mainly on flat land that is shallowly flooded during the rainy season, mostly in the region of the Cassanges River, and in large extensions in the region of the Paraguaizinho River (NUNES DA CUNHA et al. 2006). Abundant herbaceous vegetation and grasses grow between the trees. Large areas of *paratudal* have also been described for the southern

Pantanal (OLIVEIRA 1993).

2.3 Seasonally flooded woodland savanna with *Copernicia alba* (*carandazal*)

The *carandazal* is a monodominant community of the palm tree *Copernicia alba* MORONG ex MORONG & BRITTON, which is present at varying densities. The palm reaches a height of about 10 m. The understory consists of a dense scrub layer, including *Celtis spinosa* SPRENG., *Mimosa hexandra* MICHELI, *Croton urucurana* BAILL., *Manihot carthaginensis*, (JACQ.) MÜLL. ARG., *Thevetia amazonica* DUCKE, and the grass *Panicum laxum* SWARTZ. (ALLEM & VALLS 1987). PRADO (1993) considered this community to be edaphic. *Carandazal* occurs in the humid Chaco (HUECK 1972; LEWIS 1991; PRADO 1993) and extends into the Pantanal on periodically flooded habitats of high salinity.

2.4 Open low-tree savanna with *Curatella americana* and *Tabebuia aurea* (*cerrado ss*)

SILVA et al. (1998) described this unit as comprising little-inundated plains in the region of the Miranda River. The vegetation of open, low-tree savanna is less dense than that of the *cerradão* (see Sect. 3.1.1) and consists of a continuous grass stratum that is frequently affected by fire. The trees are small, with thin and tortuous stems, and mixed with shrubs. In the area of Nhecolândia, ABDON et al. (1998) described this unit as *cerrado denso* or *savanna arborizada* (woody savanna), with a tree coverage of <70 %, a tree height of up to 12 m, and a herbaceous stratum. Frequent tree species are *Curatella americana* L., *Tabebuia aurea* (MANSO) B. & H., *Alibertia sessilis* (VELL.) SCHUM., *Andira cuyabensis* BENTH., *Byrsonima orbignyana* A. JUSS., *Casearia sylvestris* SW., *Hymenaea stigonocarpa* (MART.) HAYNE, *Caryocar brasiliense* CAMB., and *Tocoyena formosa* (CHAM. & SCHL.) SCHUM. In the Pantanal of Poconé, this vegetation is considered to be the result of *cerradificação* (savannization), which is the invasion of savanna tree species in the floodplain because of man-made or naturally reduced flooding.

2.5 Swampy woodland savanna with *Mauritia flexuosa*

In depressions at the edge of the Pantanal there are wetlands covered by grasses, sedges, and herbaceous plants (Poaceae, Cyperaceae, Xyridaceae, Eriocaulaceae). In higher-lying areas, a few shrub and tree species dominated by the palm *Mauritia flexuosa* L.F. are found. Soils are waterlogged or flooded over long periods and may contain high amounts of organic material. Similar formations occur in depressions in the *cerrado* of central Brazil, where they are called *veredas*. Frequently, streams rise from theses depressions (EITEN 1983, 1994).

3. Type: Seasonal forests

Seasonal forests can be divided into semi-deciduous and deciduous forests (PRADO 2000). They are related to climatic seasonality and undergo a well-defined dry season of variable length. Many species of deciduous forests also occur in semi-deciduous forests and vice versa. Here, seasonal forests also include seasonally flooded forests. Seasonality is induced by inundation with rain/river water and can coincide with the rainy season, for instance in the northern Pantanal. It may also be delayed, as in the southern Pantanal, where the flood curve follows the precipitation curve with a time

difference of about 3 months (hydrologically induced seasonality). While many species of this forest type are facultative evergreen, they lose most of their leaves during extremely dry periods. Some species are deciduous.

3.1 Sub-type: Seasonal semi-deciduous forests on dry ground

3.1.1 Semi-deciduous forest with *Curatella americana* and *Magonia pubescens*

This unit is the forested form of the *cerrado*, called *cerradão*, which is defined as a scleromorphic forest formation. Many authors consider it as a transition between savanna and forest. We have included it as a forest type, as did COUTINHO (1982). The floristic composition is influenced by different factors, such as surface area, topography, soil conditions, and grazing and trampling by cattle. This leads to a large heterogeneity between *cerradões* of the Pantanal with respect to floristic composition and vegetation structure. For the Pantanal of Poconé, COSTA (2002) described *Curatella americana* L. and *Magonia pubescens* A. ST.-HIL. as the characteristic species; in Nhecolândia, SALIS (2004) reported *Protium heptaphyllum* (AUBL.) MARCHAND and *Diptychandra aurantiaca* TUL. The *cerradão* normally shows two distinct tree strata. The upper stratum reaches a maximum height of 18 m, sometimes with emergent trees of 20 m. The lower stratum has a height of up to 7 m. The occurrence of *Bromelia balansae* MEZ, locally called *gravatá*, in the herbaceous stratum characterizes the beginning of the non-flooded area. Other common tree species in the Poconé region are *Qualea parviflora* MART., *Qualea grandiflora* MART., *Apidosperma macrocarpa* MART., *Tabebuia aurea* (MANSO) B. & H. ex S. MOORE, *Connarus suberosus* PLANCH., and *Kielmeyera coriacea* MART. In the Pantanal, the *cerradão* represents about 22 % of the vegetation cover (SILVA 2000). It is frequent on sandy soils in the sub-regions of Cáceres, Barão de Melgaço, Nhecolândia, Aquidauana, and Miranda.

3.1.2 Semi-deciduous forest with *Tabebuia* spp. and *Scheelea phalerata* (*Cordilheira de mata, capão de mata*)

Semi-deciduous forests occur in the central parts of *capões* and *cordilheiras* and on high levees along the rivers (Fig. 3). These dense forests consist of lianas and are without a layer of grasses, herbaceous plants, and shrubs. The first stratum, between 2 and 8 m, is closed and composed of *Trichilia stellato-tomentosa* KUNTZE, *Combretum leprosum* MART., *Cordia glabrata* (C. MARTIUS) A. DC., *Dilodendron bipinnatum* RADLK., and *Dipteryx alata* VOG. The upper stratum is open and contains specimens with heights up to 25 m. The typical species are *Scheelea phalerata* (MART. ex SPRENGEL) BURRET, *Tabebuia heptaphylla* (VELL.) TOLEDO, *Tabebuia impetiginosa* (MART. ex DC.) STANDL., *Tabebuia roseo-alba* (RIDL.) SANDWITH, *Enterolobium contortisiliquum* (VELL.) MORONG, *Anadenanthera colubrina* var. *cebil* (GRISEB.) REIS., *Anadenanthera falcata* (BENTH.), *Hymenaea courbaril* L., *Sclerolobium aureum* (TUL.) BENTH, *Terminalia argentea* (CAMB.) MART., *Vitex cymosa* BERTERO ex SPRENG., *Aspidosperma cylindrocarpon* MÜLL. ARG., *Casearia sylvestris* SW., *Acacia paniculata* WILLD., and *Inga marginata* WILLD., among others. Individuals of the palm tree *Scheelea phalerata* (MART. ex SPRENGEL) BURRET normally occur in larger numbers at the edges of these forests or in groups or as single specimen in the inner part. An increased density of palms inside the stands points to human impact.

3.1.3 Semi-deciduous forests on *aterros* de indio

Aterros de indio, also called *aterros de bugre* and *capão de aterro*, are artificial earth mounds with sizes up to 1 ha. They were constructed by pre-colonial indigenous settlers to provide protection against flooding. Excavations have revealed fragments of pottery and other archeological remnants, but also large deposits of mollusk shells (PONCE & NUNES DA CUNHA 1993). Soil fertility in the mounds is higher than in the surroundings. Most of the trees are useful for humans, suggesting former plantations of *Acrocomia aculeate* (JACQ.) LODD. ex MART., *Genipa americana* L., *Rheedia brasiliensis* (MART.) PLANCH. & TRIANA, *Sapindus saponaria* L., *Cassia grandis* L., *Unonopsis lindmannii* R.E. FR., and *Ficus* sp.

3.1.4 Deciduous forest with *Callisthene fasciculata* (*carvoal*)

The name *carvoal* refers to deciduous vegetation, with *Callisthene fasciculata* MART., locally called *carvoeiro*, as the dominant or even exclusive tree species. The soil is covered by a sparse vegetation of grasses and herbaceous plants, with dense stands of *Bromelia balansae* MEZ. and *Ananas ananassoides* (BAKER) L.B. SM. Some communities form dense canopies 8-14 m in height, with emerging specimen 15-18 m high. Other communities are lower, with canopies 2-8 m in height and emerging specimen 13-15 m high. RATTER et al. (1973, 1977) denominated this type of vegetation mesotrophic facies *cerradão*. The authors noted several frequent indicator species, such as *Callisthene fasciculata* MART., *Magonia pubescens* A. ST. HIL., *Lafoensia pacari* ST. HILAIRE., *Jacaranda cuspidifolia* MART., *Tabebuia aurea* (MANSO) B. et H. ex S. MOORE, *Terminalia argentea* (CAMB.) MART., *Pseudobombax longiflorum* (MART. et ZUCC.) ROB., *Bowdichia virgilioides* H.B.K., *Luehea paniculata* MART., *Dilodendron bipinnatum* RADLK., *Terminalia argentea* (CAMB.) MART., *Astronium fraxinifolium* SCHOTT. ex SPRENG., *Dipteryx alata* VOG., and *Myracodruon urudeuva* (ENGl.) FR. ALL. The carvoal occurs on *cordilheiras* and levees common in the regions of the Pinxaim, Claro, and Novo Rivers and less frequent in the region of the Cassanges River (NUNES DA CUNHA et al. 2006). Trees are slightly flood-resistant and drought-adapted. This vegetation type features the physiognomy of a forest and the floristic elements of a savanna (*cerrado* domain).

3.1.5 Deciduous forest with *Sebastiana brasiliensis* and *Seguieria paraguayensis* (*Cordilheira de mata, capão de mata*)

On the highest levels of these forests, which are flooded, if at all, only during extreme floods, the floristic composition is made up of deciduous species (Fig. 3). The herbaceous stratum is heterogeneous and shows, between areas of denuded soil, dense stands of *Bromelia balansae* MEZ up to 2 m high, patches of *Petiveria alliacea* L., and sparse shrubs of *Sebastiana brasiliensis* SPRENG. The first canopy stratum, which has a height of 5-6 m, is characterized by *Adelia membranifolia* (MÜLL. ARG.) CHODAT & HASSL. and *Trichilia pallida* SWARTZ. Large trees form the upper canopy, which reaches a height of up to ~30 m. The species found in this stratum are *Swartzia jorori* HARMS, *Sweetia fruticosa* SPRENG., *Pterogyne nitens* TUL., *Seguieria paraguayensis* MORONG, *Sideroxylon obtusifolium* (HUMB. ex ROEM. & SCHULT.) T.D. PENN., *Calycophyllum multiflorum* GRISEB., *Aspidosperma australe* MÜLL. ARG., and *Aspidosperma cuspa* (KUNTH) S.F. BLAKE ex PITTIER.

The deciduous forests of the Pantanal also contain many species found by RATTER

et al. (1988) on the hills (*morrarias*) of the Corumbá region, such as *Acacia paniculata* WILLD., *Anadenanthera colubrina* var. *cebil* (GRISEB.) REIS., *Myracodruon urundeuva* (ENGL.) FR. ALL., *Sideroxylon obtusifolium* (HUMB. ex ROEM. & SCHULT.) T.D. PENN., *Calycophyllum multiflorum* GRISEB., *Cereus peruvianus* MILL., *Combretum leprosum* MART., *Cordia glabrata* (MART.) A. DC., *Albizia samam* (JACQ.) F. MUELL., *Sebastiana brasiliensis* SPRENG., *Tabebuia heptaphylla* (VELL) TOLEDO, *Tabebuia aurea* (MANSO) B. & H. ex S. MOORE, and *Vitex cymosa* BERTERO ex SPRENG.

Typical species from forests of the central Brazilian highlands and southeast Brazil also occur in deciduous forest in cordilheiras, capões, and levees, such as *Pterogyne nitens* TUL., *Trichilia catigua* A. JUSS., *Astronium fraxinifolium* SCHOTT. ex SPRENG., *Trichilia pallida* SWARTZ., *Seguieria paraguayensis* MORONG, and *Vitex cymosa* BERTERO ex SPRENG, (HUECK & SEIBERT 1981).

Deciduous and semi-deciduous forests are frequent on soils of intermediate to high fertility and are located in peripheral areas that connect the Cerrado and Caatinga Provinces in the east to the Chaco Province at the western boundaries of the Pantanal (OLIVEIRA-FILHO & RATTER 1995). The indicator species are *Sterculia striata, Anadenanthera colubrina, Tabebuia impetiginoa, Myracrodruon urundeuva, Dilodendron bipinnatum, Maclura tinctoria, Cordia glabrata* and *Enterolobium contortisiliquum.*

3.2 Sub-type: Seasonally flooded semi-evergreen forests

3.2.1 Seasonally flooded semi-evergreen forests with *Calyptranthes eugenoides* and *Mouriri guianensis*

These forests occur in all areas subjected to flooding over several months. Normally, the soil is covered by a litter layer that lacks herbaceous plants. There exist several varieties of seasonally flooded semi-evergreen forests (NUNES DA CUNHA 1998). In the Pantanal of Poconé, the forests established in sandy soils are characterized by a sparse understory about 2 m in height, with *Unonopsis lindmanii* R.E. FRIES. and *Psychotria carthagenensis* JACQ. as the characteristic species. This is followed by a middle stratum, 4-7 m in height, containing *Calyptranthes eugenioides* CAMBESS., *Mouriri guianensis* AUBL., and *Thieleodoxa lanceolata* CHAM. The upper stratum, up to 13 m high, is occupied by *Calophyllum brasiliense* CAMBESS. and *Vochysia divergens* POHL. On soils with a higher clay content, *Zygia cauliflora* (WILD.) KILLIP ex RECORD, *Trichilia catigua* A. JUSS., *Salacia elliptica* (MART.) PEYR, *Aptandra liriosmoides* SPRUCE, *Buchenavia oxycarpa* (MART.) EICHLER, *Homalium guianense* (AUBL.) OKEN, *Inga vera* ssp. *affinis* (DC) T.D. PENN., *Crataeva tapia* L., and *Pouteria glomerata* (MIQ.) RADLK. are frequent in the middle stratum, and *Ceiba samauma* (MART.) K. SCHUM., *Cassia grandis* L.F. and *Tabebuia heptaphylla* (VELL.) TOLEDO in the upper stratum.

3.2.2 Seasonally flooded semi-evergreen forest with *Calophyllum brasiliense* (*landizal*)

Elongated and sinuous stretches of semi-evergreen forest in high-lying plains covered by *cerrado* vegetation point to the presence of *landizal*. This can be explained by the fact that, in periodically drying drainage systems, floods last longer and water availability during low-water periods is better because of a high groundwater level. *Landi* refers to the regional name of *Calophyllum brasiliense* CAMBESS. The following species,

which are also common in other seasonally flooded forests, are characteristic of this sub-type of forest: *Licania parvifolia* HUBER, *Erythroxylum anguifugum* MART., *Alchornea discolor* POEPP., *Calophyllum brasiliense* CAMBESS., *Mouriri guianensis* AUBL., *Ficus pertusa* L.F., *Sorocea sprucei* (BAILL.) MACBR., *Eugenia florida* DC., *Coccoloba ochereolata* WEED., and *Triplaris gardneriana* WEDD.

3.2.3 Seasonally flooded semi-evergreen forests with *Licania parvifolia* (*pimenteiral*)
This unit is characterized by *Licania parvifolia* HUBER. These trees, which are 5-8 m in height, grow in periodically flooded areas with a preference for drainage channels with intermittent water flow. The sandy soil is normally not covered with an herbaceous stratum (GUARIM NETO 1984; LORENZZI 1992; BRASIL 1997). According to POTT & POTT (1994), this species was favored during the multi-annual wet period lasting from 1974 until the middle of the 1990s, and invaded pasture areas. It has been described in the Pantanal de Poconé and in the Pantanal de Barão de Melgaço.

3.2.4 Seasonally flooded semi-evergreen forests with *Vochysia divergens* (*cambarazal*)
Cambarazais are dense forest formations in which *Vochysia divergens* POHL (*cambará*), sometimes occurring in monospecific stands, predominates. According to NASCIMENO & NUNES DA CUNHA (1989), *V. divergens* is a characteristic species of the Pantanal. Dense stands develop in low-lying humid areas. This species is flood-tolerant (ARIEIRA & NUNES DA CUNHA 2006) and in multi-year wet periods spreads into surrounding savannas, creating serious problems for ranchers. The expansion of *cambarazais* is counteracted by the wild fires of extremely dry years. Stands of *V. divergens* are also found in periodically flooded areas along the Rio das Mortes and the Araguaia River in the Amazon basin (MARIMON et al. 2001).

3.2.5 Seasonally flooded semi-evergreen forests with *Erythrina fusca* (*abobral*)
Along some river stretches, for instance the Paraguay River near Taiamã Island and the Caracará River in Pantanal National Park, the sediment load is low. Shores show no or little developed levees and are flooded for several months every year to a depth of 2 m and more. These shores are covered by old monospecific stands of *Erythrina fusca* LOURT. (*abobreiro*) that develop impressive stilt roots.

4. Type: Scrubland (*arbustal*)
Arbustal is a common plant community in the Pantanal and refers to the domination by shrubs (*arbusto* = shrub). Scrublands occur in periodically flooded areas and may be either naturally occurring or the result of human activity. In some regions, they remain stable over decades, while in others they are transitional communities that occur temporarily as the result of a disturbance, such as major fire events or deforestation. The shrub density can be very high, making some parts of the *arbustal* nearly impenetrable for humans.

4.1 Seasonally flooded scrubland with *Mimosa pellita* (*espinheiral*)
Scrubland with *Mimosa pellita* KUNTH ex WILLD. reaches a height of about 1.50 m. It dominates the large areas of the Cuiabá River floodplain that become flooded during several months. Sparsely scattered individuals of *Bonafousia siphilitica* (L.F.) L.

ALLORGE. rise above the canopy to a height of about 2.5 m. Mainly during the flood period, the *arbustal* is rich in annual and perennial vines, which cover the scrubs. During the dry period *Cissus* sp. dominates the upper stratum.

4.2 Seasonally flooded scrubland with *Combretum lanceolatum* (*pombeiral*)

Scrubland with *Combretum lanceolatum* POHL ex EICHLER, which reaches a height of about 4 m, is often monospecific. It is widespread in the Pantanal and occurs near permanent water bodies in areas subject to several months of inundation. Ranchers have tried to eradicate the vegetation because it invades natural and artificial pastures and reduces the carrying capacity for cattle.

4.3 Seasonally flooded scrubland with *Byrsonima orbignyana* (*canjiqueiral*)

Below the stratum of *Byrsonima orbignyana* (A. JUSS.), which is about 1-5 m high, there is a stratum of grasses, sedges, and herbaceous plants (SILVA et al. 2000). *Canjiqueiral* grows on sandy, little-flooded soils and expands during multi-annual dry periods into low lying areas, where it becomes problematic for ranchers because it occupies pasture. However, it is naturally eradicated in prolonged wet periods (POTT & POTT 1994). SILVA et al. (1998) denominated *canjiqueiral* as open scrubland or scrub savanna, depending on its density.

4.4 Seasonally flooded scrubland with *Byttneria filipes* and *Bauhinia bauhinioides* (*espinheiral*)

This type of scrubland, which is impenetrable for humans and cattle, was described by SILVA et al. (1998) as a scrub community dominated by *Byttneria filipes* MART. ex K. SCHUM., *Bauhinia bauhinioides* (MART.) J.F. MACBR., and *Cissus spinosa* CAMBESS. It occurs in areas of different levels of flooding.

Distribution of the units along the inundation gradient

Most woody species of the Pantanal have a broad ecological amplitude (NUNES DA CUNHA & JUNK 2001). This enables them to colonize a substantial portion of the inundation gradient and to adapt their ranges to multi-annual wet and dry periods. The geographical positions of the units listed in Table 1 therefore indicate only the core areas of distribution. The gradient comprises the entire aquatic terrestrial transition zone (ATTZ; JUNK et al. 1989) and varies from permanently terrestrial conditions on the one end to permanently aquatic conditions on the other. Inundation of the Pantanal is the result of flooding by transbording rivers, local rainfall, and geomorphology. Due to the Pantanal's characteristic flat relief, the hydrological conditions are very complex.

Woody vegetation colonizes the upper and middle parts of the gradient but is absent from the lowest part, which is instead colonized at low-water levels by grasses and herbaceous plants (natural *campos limpos*). The permanent terrestrial habitats that were part of the present study belong to the ATTZ because the vegetation is affected during extreme flood events, either by direct short-term flooding or an increase in the ground-water level to the rhizosphere, which eliminates those species sensitive to waterlogging of the soil. The length of the inundation period is often correlated with the depth of inundation, but depressions may be shallowly flooded and their soils can remain water-logged over long periods of time, independent of the level of the parent river or the amount of rainfall. Some species, such as *Copernicia alba* and *Mauritia flexuosa*,

tolerate long-term waterlogging of the soil but not very deep flooding.

Tab. 1: Characterization of the vegetation units according to the depth of flooding. Types with a broad distribution are mentioned several times. Occurs, respectively, frequently or exclusively in permanently waterlogged soils.

Permanently dry or shortly flooded in extreme flood periods	
3.1.1	Semi-deciduous forest with *Curatella americana* and *Magonia pubescens*
3.1.2	Semi-deciduous forest with *Tabebuia* spp and *Scheelea phalerata* (*Cordilheira de mata, capão de mata*).
3.1.3	Semi-deciduous forests on *aterros de indio*
3.1.4	Deciduous forest with *Callisthene fasciculata* (*carvoal*)
3.1.5	Deciduous forest with *Sebastiana brasiliensis* and *Seguieria paraguayensis* (*Cordilheira de mata, capão de mata*)
Little flooded habitats	
2.1	Seasonally flooded termite savanna with *Curatella americana* (*campo de murunduns, lixeiral*)
2.4	Open low-tree savanna with *Curatella americana* and *Tabebuia aurea* (*cerrado ss*)
4.3	Seasonally flooded scrubland with *Byrsonima orbignyana* (*canjiqueiral*)
Intermediate flooded habitats	
2.2	Seasonally flooded woodland savanna with *Tabebuia aurea* (*paratudal*)
2.3	Seasonally flooded woodland savanna with *Copernicia alba* (*carandazal*)
2.5	Swampy woodland savanna with *Mauritia flexuosa*
3.2.1	Seasonally flooded semi-evergreen forests with *Calyptranthes eugenoides* and *Mouriri guianensis*
3.2.2	Seasonally flooded semi-evergreen forest with *Calophyllum brasiliense* (*landizal*)
3.2.3	Seasonally flooded semi-evergreen forests with *Licania parvifolia* (*pimenteiral*)
3.2.4	Seasonally flooded semi-evergreen forests with *Vochysia divergens* (*cambarazal*)
4.2	Seasonally flooded scrubland with *Combretum lanceolatum* (*pombeiral*)
4.4	Seasonally flooded scrubland with *Byttneria filipes* and *Bauhinia bauhinioides* (*espinheiral*)
Deep flooded habitats	
2.3	Seasonally flooded woodland savanna with *Copernicia alba* (*carandazal*)
3.2.4	Seasonally flooded semi-evergreen forests with *Vochysia divergens* (*cambarazal*)
3.2.5	Seasonally flooded semi-evergreen forests with *Erythrina fusca* (*abobral*)
4.1	Seasonally flooded scrubland with *Mimosa pellita* (*espinheiral*)
4.4	Seasonally flooded scrubland with *Byttneria filipes* and *Bauhinia bauhinioides* (*espinheiral*)

Discussion

All ecological classification systems are inherently artificial, as they depend on the aim of the study and the parameters used by the respective authors. The typology proposed herein is based mostly on woody vegetation, physiognomic aspects (e.g., level of deciduousness), and hydrological parameters. Water is the driving force in floodplain

ecosystems. Plant and animal species are distributed in floodplains according to the length and depth of the flooding, as postulated by the flood pulse concept (JUNK et al. 1989). Climate clearly affects the level of deciduousness, whereas the impact of edaphic factors is still poorly understood. *Pantaneiros* (people living inside the Pantanal) have denominated certain landscape features, habitats, and plant communities with local names that refer to the respective environmental characteristics. We have adopted these local names as much as possible because one of the aims of our typology is to assist sustainable management and protection measures in the Pantanal. The inclusion of local terms facilitates discussions between *pantaneiros*, scientists, and politicians as well as the implementation of protective measures. The second aim of this typology is of a scientific nature, i.e., to provide a better overview of habitat diversity, support comparative studies, and offer a scientifically based framework in which further scientific information can be incorporated, such as edaphic parameters, the occurrence of animals, and management aspects.

Nevertheless, our typology is still preliminary because the Pantanal has not been studied sufficiently to allow the characterization of all its vegetation types. As already stated in the introduction, the names given to the units are informal and do not follow the strict international syntaxonomic rules described by BARKMAN et al. (1986). However, this allows terms to be used more flexibly without interfering with the international classification system. We have not considered herbaceous communities and aquatic habitats. Furthermore, classification in general is difficult, because: (1) there are no fixed boundaries separating the many vegetation types, (2) the flood pulse changes the habitat conditions in the aquatic-terrestrial transition zone throughout the year, and (3) multi-annual climate changes lead to large-scale changes in habitat conditions and related changes in vegetation cover. For instance, *carvoal* occurs in a dense formation with high trees, and this physiognomic feature was the basis for its classification as unit 3.1.4, i.e., "Deciduous forest with *Callisthene fasciculata* (*carvoal*)", corresponding to the forest-ecotone-grassland concept of the *cerrado* (COUTINHO 1978). However, according to RATTER et al. (1973, 1977), the floristic composition of *carvoal* suggests its assignment to the mesotrophic facies *cerradão*. In some areas of the Pantanal, the properties of the *carandazal* support its listing as unit 2.3 (seasonally flooded woodland savanna with *Copernicia alba*), but in others the soil may be permanently waterlogged. If this is ultimately found to occur over major areas, a new unit should be established (e.g., 2.6 Swampy woodland savanna with *Copernicia alba*).

The problem of typifying vegetation is also demonstrated by plant communities growing on levees. Along the main river channels and oxbow lakes there are levees of different height and extension that support different plant communities. A difference of a few decimeters in the height of the topography alters the flood and drought stresses as well as the sedimentation pattern and may therefore change the structure of the community.

Levees in the Pantanal show a longitudinal and a transversal height gradient (Fig. 4). The longitudinal gradient is detectable over long distances, from shallowly to deeply flooded parts of the Pantanal. Well-developed large levees are found, for instance, in the little flooded northern part of the Pantanal, whereas small levees at the beginning stages of development are frequent in the deeply flooded southern Pantanal. Transversal gradients are present anywhere along the levees. Moreover, in some areas, the rivers do not form levees. Instead, the shores are rather flat and flooded for long periods of time

at high water levels and covered by a species-poor forest (unit 3.2.5, *abobral*). In addition to changes in species composition according to flood intensity, there are changes in the floristic composition along the north-south gradient, e.g., due to the entrance of species from the southern humid Chaco.

In the Cassangue River, a medium-sized tributary of the Cuiabá River, NUNES DA CUNHA & JUNK (1999) differentiated eight communities and 50 woody species along the transversal transect of a levee, according to the flood gradient. Two sub-types were distinguished: forests growing on the highest part of the levee that is rarely flooded and forests growing in frequently flooded areas (Fig. 4). Units of the rarely flooded areas are semi-deciduous and deciduous while those of the periodically flooded areas are semi-evergreen. The transversal gradient shows differences in species composition between low-lying areas on the channel side, where there is running water, and on the campo side, where there is standing water. *Sloanea garckeana* K. SCHUM., *Coccolobas mollis* CASAR, *Crataeva tapia* L., and *Campomanesia eugenioides* (CAMB.) LEGR. are characteristic species of the channel side, whereas *Salacia elliptica* (MART) PEYR, *Byrsonima cydoniifolia* ADR. JUSS., *Guarea macrophila* VALL, *Eugenia tapacumensis* O. BERG., *Eugenia inundata* DC., *Rheedia brasilienses* (MART.) PI. & TR., and *Triplaris americana* L. show a preference for the campo side.

At the highest parts of the levees of the Paraguay River, DAMASCENO-JUNIOR et al. (2005) identified *Tabebuia heptaphylla* (VELL.) TOL., *Hymenaea courbaril* L. var. *stilbocarpa* (HAYNE) Y.T. LEE & LANGENH and *Guazuma tomentosa* H.B.K.; *Albizzia inundata* (MART.) BARNEBY & J.W. GRIMES. At the lower parts, flood-tolerant species, such as *Crataeva tapia* L., *Alchornea castaneifolia* (WILLD.) A. JUSS., *Inga vera* WILLD. ssp. *affinis* (DC.) PENNINGTON, *Zygia inaequalis* (H.B.K.) PITT., and *Mouriri guianensis* AUBL. were observed.

Low-lying parts of the levees that extend above the water level only during the low-water period are covered by dense monospecific stands of semi-aquatic grasses, e.g., *Panicum elephantipes*, and robust herbs, such as *Polygonum ferrugineum* WEDD. *Ludwigia* spp., and *Aspilia latissima* MALME (Fig. 4). Levees of intermediate height are covered by different successional stages of the forests on well-developed levees (Fig. 4). Succession begins with several species, including *Alchornea castaneifolia, Mimosa pellita* HUMB. & BONPL. ex WILLD., *Crataeva tapia* L., and *Bactris glaucescens* DRUDE. With increasing height of the levee, these species become denser and finally eliminate herbaceous species due to shading. Monospecific stands of *Inga vera, I. uruguensis, Sapium obovatum*, and *Alchornea castaneifolia* (HUMB. & BONPL. ex WILLD.) A. JUSS. may also be found. *Inga* spp. occur mostly in the northern part of the Pantanal and are replaced in the middle and southern part by *Sapium*. When the levee becomes more pronounced, all species of the semi-evergreen forest are present. Spatial zonation of the levees represents successional stages that change when sediment deposition has increased the height of the levee, which diminishes flood duration.

The phytogeographic analysis of the woody vegetation of the Pantanal has demonstrated the mosaic of species from different regions. No endemic species were found and the overwhelming majority of tree species has a wide distribution. Most species originate from the Cerrado Province or the Central-Western Province (BRIDGEWATER et al. 2004) but there are also many species of deciduous forests in the eastern Pantanal as well as the mesophytic deciduous forest of the Chiquitos hills (*morrarias*), which features rocky outcrops of limestone and quartz, and the subtropical deciduous and

mesophytic forests of western and central Brazil (SEIBERT 1996, KILLEEN et al. 1998).

PRADO (2000) postulated floristic links between the deciduous and semi-deciduous forests of Gran Chaco and Brazilian Caatingas and speculated as to the influence of earlier wet-dry climatic fluctuations on the present-day disjunctions of the seasonal forests on the continent. Some of the characteristic species of these biogeographic formations (PRADO & GIBBS 1993) are also common in the two types of deciduous forests on *cordilleiras, capoes*, and levees in the Pantanal. Although the participation of species from the Amazon Basin is less significant, several species that occur in Amazonia are frequently found in the Pantanal.

The absence of endemic species of arboreal plants is coherent with observations regarding other species groups, including butterflies, mammals, reptiles, amphibians, and birds (PRANCE & SCHALLER 1982; BROWN 1986; JUNK et al. 2006a; BROWN 1986). JUNK et al. (2006b) concluded that the Pantanal is not a center of endemic species, but instead absorbs species from flooded and non-flooded habitats of the borders. The same affirmation can be made for the arboreal vegetation of the Pantanal.

Conclusion

The Pantanal of Mato Grosso is a vast floodplain covered by different vegetation types, such as savanna, seasonal forest, scrubland, and grassland. The vegetation in this region is associated with different landscape units and influenced by different factors, such as length and depth of the flooding, climate, soil quality, fire, competition, animal grazing, and human impact. Annual and multi-annual wet and dry periods result in large-scale changes in the vegetation cover.

Ecologists, farmers, and policy-makers require a vegetation typology to serve as a framework for organizing the increasing amount of scientific information concerning the Pantanal, quantifying changes in its vegetation cover, and establishing management and protection measures. Woody vegetation is especially appropriate as the basis for a typology because it is a prominent feature of the landscape. Furthermore, woody species have long life spans and thus represent the environmental conditions of their habitats over decades or even centuries. For this reason, woody vegetation guided the typology constructed in this study. Three types were identified: savannas (5 units), forests, with two sub-types: seasonal forests on dry ground (5 units) and seasonally flooded semi-evergreen forests (5 units), and scrublands (4 units). The units are characterized by typical tree species previously identified in phytosociological studies, but our knowledge of the vegetation of the Pantanal is still insufficient to allow a comprehensive classification following strict international syntaxonomic rules. Many of the vegetation and landscape units are derived from the local population's perception of their environment. These names have been incorporated into the present study.

While the typology presented in this study is preliminary, it should nonetheless encourage scientists and people living in the Pantanal (*pantaneiros*) to propose and characterize further units, which can be incorporated into our framework. The results of our analysis can also contribute to the comprehensive classification system of wetland habitats that is required for the sustainable management and protection of the Pantanal.

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References

ABDON, M.M., SILVA, J. DOS S.V. DA, POTT, V.J., POTT, A. & M.P. SILVA (1998): Utilização de dados analógicos do LANDSAT-TM na discriminação da vegetação de parte da sub-região da Nhecolândia no Pantanal. - Pesquisa Agropecuária Brasileira **33**: 1799-1813.

ADAMOLI, J. (1982): O Pantanal e suas relações fitogeográficas com os cerrados. Discussão sobre o conceito "Complexo do Pantanal". - Cong. Nacional de Botânica, Terezina Soc. Bras. De Bot. **32**: 109-119.

AGUIRRE, A. (1945): A caça e a pesca no Pantanal de MT. - Serviços de Informaçao Agricola, Ministerio da Agricultura, Divisão de Caça e Pesca, Rio de Janeiro, Brasil.

ALLEM, A.C. & J.F.M. VALLS (1987): Recursos forrageiros nativos do Pantanal Mato-Grossense. - EMBRAPA-CENARGEM, Documento 8, Brasilia, Brazil.

ARIEIRA, J. & C. NUNES DA CUNHA (2006): Fitossociologia de uma floresta inundável monodominante de *Vochysia divergens* POHL (Vochysiaceae), no Pantanal Norte, Mato Grosso (Brasil). - Acta Botanica Basilica **20**(3): 569-580.

ASSINE, M.L. & P.C. SOARES (2004): Quaternary of the Pantanal, west-central Brazil. - Quaternary International **114**: 23-34.

BARKMAN, J., MORAVEC, J. & S. RAUSCHERT (1986): Code of phytosociological nomenclature. - Vegetatio **67**(3): 145-197.

BRASIL (1997): Plano de Conservação da Bacia do Alto Paraguai. Diagnóstico dos meios físico e biótico: Meio Biótico. - PCBAP/Projeto Pantanal, Programma Nacional do Meio Ambiente, Vol. II, Tomo III, PNMA, Brasília, Brasil.

BRASIL MINTER (1979): Estudo de desenvolvimento integrado da Bacia do Alto Paraguai. - Edibap Relatório da 1ª fase. Brasília, SUDECO, T. 2 e 3.

BRIDGEWATER, S., RATTER, J.A. & J.F. RIBEIRO (2004): Biogeographic patterns, biodiversity and dominance in the cerrado biome of Brazil. - Biodiversity and Conservation **13**: 2295-2318.

BROWN, K. Jr. (1986): Zoogeografia da região do Pantanal Matogrossense. - In: EMBRAPA (ed.): Anais I Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal: 137-178. EMBRAPA, Corumbá, Brasil.

CASTRO, A.A.J.F. (1994): Comparacao floristica de especies do Cerrado. - Silvicultura **14**: 16-18.

CASTRO, O.M. (1999): Caracterização floristica e estrutural de dois tipos de campos de murunduns na região do Pirizal - Pantanal de Poconé-MT. - Monografia, TCC curso de Ciencias Biologicas, IB/-UFMT, Cuiabá, MT, Brasil.

COLE, M.M. (1960): Cerrado, Caatinga and Pantanal: The distribution and origin of the Savanna vegetation of Brasil. - The Geographical Journal **126**(2): 162-179.

COSTA, S.C. (2002): Análise fitossociológica da transição floresta savana em uma cordilheira no Pantanal de Poconé (MT). - M.Sc.-thesis, Universidade Federal do Mato Grosso, Brasil.

COUTINHO, L.M. (1978): O conceito de Cerrado. - Revista Brasileira de Botânica **7**: 17-23.

COUTINHO, L.M. (1982): Ecological effect of fire in Brazilian Cerrado. - In: HUNTER, B.J. & B.H. WALTER (eds): Ecology of tropical Savannas: 273-291. Ecological Studies, Vol. 42. Springer Verlag, Berlin.

DAMASCENO-JUNIOR, G.A, SEMIR, J. & F.A.M. SANTOS (2004): Mortalidade de árvores em uma floresta ripária do rio Paraguai, Pantanal, Brasil, após uma cheia excepcional. - Acta Bot. Bras. **18**(4): 839-846.

DAMASCENO-JUNIOR, G.A, SEMIR, J., SANTOS, F.A. & M.H.F. LEITÃO-FILHO (2005): Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. - Flora **200**: 119-135.

DEL'ARCO, J.O., SILVA, R.H., TARAPANOFF, I., FREIRE, F.A., PEREIRA, L.G.M., LUZ, D.S., PALMEIRA, R.C.B. & C.C.G. TASSINARI (1982): Geologia. Levantamento de recursos naturais. - In: MINISTÉRIO DA MINAS E ENERGIA (ed.):Brasil. Projeto Radambrasil: 25-160. Folha SE-21, Corumbá e parte da Folha SE-20, Vol. 20, Rio de Janeiro, Brasil.

DITTUS, W.P.J. (1977): The ecology of semi-evergreen forest community in Sri Lanka. - Biotropica **9**(4): 268-286.

DUBS, B. (1994): Differentiation of woodland and wet savanna habitats in the Pantanal of Mato Grosso, Brazil. - Betrona-Verlag. Küsnacht, Switzerland.

EITEN, G. (1972): The cerrado vegetation of Brazil. - Botanical Review **38**: 201-341.

EITEN, G. (1978): Delimitation of the cerrado concept. - Vegetatio **36**(3): 169-178.

EITEN, G. (1983): Classificação da vegetação do Brasil. - CNPq, Brasília, Brasil.

EITEN, G. (1990): Brazilian "Savannas". - In: HUNTER, B.J. & B.H. WALTER (eds.): Ecology of tropical savannas: 25-47. Ecological Studies, Vol. 42, Springer Verlag, Berlin, Germany.

EITEN, G. (1994): Vegetação do Cerrado. - In: PINTO, M.N. (ed.): Cerrado: 17-73. Sematec/Editora UnB, Brasília, Brasil.

GOODLAND, R.J. & R. POLLARD (1973): The Brazilian cerrado vegetation: a fertility gradient. - Journal of Ecology **61**: 219-224.

GUARIM NETO, G. (1984): Plantas utilizadas na medicina popular cuiabana - um estrudo prelimina. - Revista da Universidade Federal de Mato Grosso **4**(1): 45-50.

GUARIM-NETO, G., GUARIM, V.L.M.S., MORAES, E.C.C. & L.A.D. FERREIRA (1996): Fitossociologia de matas ciliares no Pantanal Mato-Grossense. - Boletim do Museu Paraense Emílio Goeldi, série Botânica **12**(2): 251-263.

HAMILTON, S.K., SIPPEL, S.J. & J.M. MELACK (1996): Inundation patterns in the Pantanal wetland of South America determined by passive microwave remote sensing. - Arch. Hydrobiol. **137**: 1-23.

HAMILTON, S.K., SIPPEL, S.J., CALHEIROS, D. & J.M. MELACK (1999): Chemical characteristics of Pantanal waters. - In: EMPRAPA (ed.): Anais do II Simpósio sobre Recursos Naturais e Sócio--econômicos do Pantanal: 89-100. EMBRAPA, Corumbá, Brasil.

HOEHNE, F.C. (1936): O grande Pantanal de Mato Grosso. - Bol. Secret. Agricultura **37**: 443-470.

HUECK, K. & P. SEIBERT (1981): Vegetationskarte von Südamerika. - In: WALTER, H. (ed.): Vegetationsmonographien der einzelnen Grossräume: 14. Band II a, Gustav Fischer Verlag, Stuttgart, Germany.

HUECK, K. (1972): As florestas da América do Sul, ecologia, composição e importância econômica. - Editora da Universidade de Brasília, Editora Polígono, S.A., São Paulo, Brasil.

IBGE - FUNDAÇÃO INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA (1992): Manual técnico da vegetação Brasileira. - IBGE, Rio de Janeiro, Brasil.

IRIONDO, M.H. & N.O. GARCIA (1993): Climatic variations in the Argentine plains during the last 18,000 years. - Palaeogeography, Palaeoclimatology, Palaeoecology **101**: 209-220.

JUNK, W.J., BAYLEY, P.B. & R.E. SPARKS (1989): The flood pulse concept in river - floodplain systems. - Can. Spec. Publ. Fish. Aquat. Sci. **106**: 110-127.

JUNK, W.J., NUNES DA CUNHA, C., WANTZEN, K.M., PETERMANN, P., STRÜSSMANN, C., MARQUES, M.I. & J. ADIS (2006a): Biodiversity and its conservation in the Pantanal of Mato Grosso. - Aquatic Sciences **68**: 278-309.

JUNK, W.J., BROWN, M., CAMPBELL, I.C., FINLAYSON, M., GOPAL, B., RAMBERG, L. & B.G. WARNER (2006b): The comparative biodiversity of seven globally important wetlands: a synthesis. - Aquatic Sciences **68**: 400-414.

KILLEEN, T.J., JARDIM, A., MAMANI, F. & N. ROJAS (1998): Diversity, composition and structure of a tropical semideciduous forest in the Chiquitanyá region of Santa Cruz, Bolivia. - Journal of Tropical Ecology **14**: 803-827.

KUHLMAN, E. (1953): Os grande traços da fitogeografia do Brasil. - Bol. Geog. **11**(117): 618-628.

KUHLMAN, E. (1954): A vegetação de Mato Grosso e seus reflexos na economia do estado. - Rev. Bras. Geog. **16**(1): 77-122.

LEWIS, J.P. (1991): Three levels of floristical variation in the forest of Chaco. - Argentina Journal of Vegetation Science 2(1): 130.

LORENZZI, H. (1992): Árvores brasileira: manual de identificação e cultivo de plantas arbóreas natives do Brasil. - Plantarum, Nova Odessa, Brasil.

LOUREIRO, R.L., LIMA, J.P.S. & P.C. FONZAR (1982): Vegetação. As regiões fitoecológicas, sua natureza e seus recursos econômicos. - In: MINISTÉRIO DAS MINAS E ENERGIA (ed.): Brasil: Projeto Radambrasil: 329-372. Folha SE-21, Corumbá e parte da Folha SE-20, Rio de Janeiro, Brasil.

LUGO, A.E. (1990): Introduction. - In: LUGO, A.E., BRINSON, M. & S. BROWN (eds): Forested wetlands. Ecosystems of the world: 1-14. Vol. 15, Elsevier, Amsterdam, The Netherlands.

MARIMON, B.S. & E.S. LIMA (2001): Caracterização fitofisionomica e levantamento floristico preliminar no Pantanal dos Rios Mortes-Araguaia, Cocalinho, Mato Grosso, Brasil. - Acta Bot. Bras. 15(2): 213-229.

NASCIMENTO, M.T. & C. NUNES DA CUNHA (1989): Estrutura e composição florística de um cambarazal no Pantanal de Poconé-MT. - Acta Bot. Bras. 3(1): 3-23.

NAVID, D. (2002): The international law of migratory species. - The Ramsar Convention. Natural Research Journal 29: 1001-1016.

NUNES DA CUNHA, C. (1990): Estudos floristicos e fitofisionomicos das principais formações arboreas do Pantanal de Pocone-MT. - M.Sc.-thesis, Universidade Estadual de Campinas, São Paulo, Brasil.

NUNES DA CUNHA, C. (1998): As comunidades arbustivoarbóreas de capão e de diques marginais no Pantanal de Poconé-MT: Caracterização e análise de gradiente. - Ph.D.-thesis, Universidade Federal do Mato Grosso, Brasil.

NUNES DA CUNHA, C. & W.J. JUNK (1999): Composicao floristica de capoes e cordilheiras: Localizacao das especies lenhosas quanto ao gradiente de inundacao no Pantanal. - In: EMBRAPA (ed.): Anais II Simposio sobre Recursos Naturais e Socio-Economicos do Pantanal, Manejo e Conservacao: 387-405. EMBRAPA Pantanal, Corumbá, Brasil.

NUNES DA CUNHA, C. & W.J. JUNK (2001): Distribution of woody plant communities along the flood gradient in the Pantanal of Pocone, Mato Grosso, Brazil. - Int. J. Ecol. Environ. Sci. 27: 63-70.

NUNES DA CUNHA, C. & W.J. JUNK (2004): Year-to-year changes in water level drive the invasion of *Vochysia divergens* in Pantanal grasslands. - Applied Vegetation Science 7: 103-110.

NUNES DA CUNHA, C., PRADO, A.L. & P. RAWIEL (1996): Vegetation map: Pantanal of Mato Grosso, Brazil, Part North of Poconé, Programa Shift, Projeto Ecologia do Gran Pantanal, UFMT. - Fachhochschule Karlsruhe, Fachbereich Geoinformationswesen, Germany.

NUNES DA CUNHA, C., RAWIEL, P., WANTZEN, K.M., JUNK, W.J., & A. LEMES DO PRADO (2006): Mapping and characterization of vegetation units by means of Landsat imagery and management recommendations for the Pantanal of Mato Grosso (Brasil), north of Poconé. - Amazoniana 19(1/2): 1-33.

OLIVEIRA, A.K.M. (1993): Alguns aspectos de estrutura e comparação entre três Paratudais no Pantanal de Miranda-MS. - M.Sc.-thesis, Universidade of São Carlos, São Carlos, Brasil.

OLIVEIRA-FILHO, A.T. & J.A. RATTER (1995): A study of the origin of Central Brazilian forests by the analysis of plant species distribution patterns. - Edinb. J Bot. 52(2): 141-194.

OLIVEIRA-FILHO, A.T., SHEPHERD, G.J., MARTINS, F.R. & W.H. STUBBLEINE (1989): Environmental factors affecting physiognomic and floristic veriation in an area of cerrado in central Brazil. - J. Trop. Ecol. 5: 413-431.

PAFFEN, K.H. (1957): Caatinga, Campos und Urwald in Ostbrasilien. - Tagungsber. D. Dt. Geographentag Hamburg, Wiesbaden 1955: 214-226.

PONCE, V.M. & C. NUNES DA CUNHA (1993): Vegetated earthmounds in tropical savannas of Central Brasil: a synthesis. - Journal of Biogeography 20: 219-255.

POTT, A. & V.J. POTT (1994): Plantas do Pantanal. - EMBRAPA Empresa Brasileira de Pesquisa Agropecuaria, CPAP - Corumbá, Brasil.

POTT, V.J. & A. POTT (2000): Plantas aquáticas do Pantanal. - EMBRAPA, Brasília, Brasil.

POTT, A. & V.J. POTT (1996): Flora do Pantanal - listagem atual de fanerogamas. - In: EMBRAPA (ed.): Anais do II Simposio sobre Recursos Naturais e Socio-Economico do Pantanal. Manejo e Conservacao: 297-325. EMBRAPA Pantanal, Corumbá, MS, Brasil.

PRADO, D.E. (1993): What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of flora and vegetation of the Chaco. - Candollea **48**: 145-172.

PRADO, D.E. (2000): Seasonally dry forests of tropical south America: from forgotten ecosystems to a new phytogeographic unit. - Edinb. J. Bot. **57**(3): 437-461.

PRADO, D.E. & P.E. GIBBS (1993): Patterns of species distributions in the dry seasonal forests of South America. - Annals of the Missouri Botany Garden **80**: 902-927.

PRADO, A.L., HECKMAN, C.W. & F.R. MARTINS (1994): The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone: II. The aquatic macrophyte vegetaion in the Pantanal of Mato Grosso, Brazil. - Int. Revue Ges. Hydrobiol. **79**(4): 569-589.

PRANCE, G.T. (1989): A terminologia dos tipos de florestas amazonicas sujeitas a inundação. - Acta Amazonica **10**(3): 495-504.

PRANCE, G.T. & G.B. SCHALLER (1982): Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. - Brittonia **34**(2): 228-251.

RADAMBRASIL (1982): Levantamento de recursos naturais. - Volume 27, Folha SE.21, Corumbá, Ministério das Minas e Energia. Projeto Radambrasil, Rio de Janeiro, Brasil.

RATTER, J.A. (1987): Notes on the vegetation of the Parque Nacional do Araguaia (Brazil). - Notes from the Royal Botanic Garden **44**(2): 311-342.

RATTER, J.A. & T.C.D. DARGIE (1992): An analysis of the florisitic composition of 26 cerrado areas in Brazil. - Edinb. J. Bot. **49**: 235-250.

RATTER, J.A., RIBEIRO, J.F. & S. BRIDGEWATER (1997): The Brazilian cerrado vegetation and threats to its biodiversity. - Annals of Botany **80**: 223-230.

RATTER, J.A., ASKEW, G.P., MONTGOMERY, R.F. & D.R. GIFFORD (1977): Observações adicionais sobre o cerradão de solos mesotróficos no Brasil Central. - In: FERRI, M.G. (ed.): IV Simpósio sobre o Cerrado: 303-316. Universidade de São Paulo, Brasil.

RATTER, J.A., BRIDGEWATER, S., ATKINSON, R. & J.F. RIBEIRO (1996): Analysis of the florisitc composition of the Brazilian cerrado vegetation. II. Comparison of the woody vegetation of 98 areas. - Edinb. J. Bot. **53**: 153-180.

RATTER, J.A., RICHARDS, P.W., ARGENT, G. & D.R. GIFFORD (1973): Observations on the vegetation of northeastern Mato Grosso. 1. The woody vegetation types of the Xavantina-Cachimbo Expedition area. - Phil. Trans. Roy. Soc. B **266**: 449-492.

RATTER, J.A., POTT, A., POTT, V.J., CUNHA, C.N. & M. HARIDASAM (1988): Observations on woody vegetation types in the Pantanal and at Corumbá, Brasil. - Notes RBG, Edinb. **45**(3): 503-525.

RICHARDS, P.W. (1996): The tropical rain forest: An ecological study. - 2nd ed, Cambridge University Press, Cambridge, UK.

RIZZINI, C.T. (1963): Nota previa sobre a divisão fitogeografia do Brasil. - Rev. Brasil. Geogr. **25**: 3-64.

RIZZINI, C.T. (1979): Tratado de fitogeografia do Brasil. - Vol. 2, HUCITEX, São Paulo, Brasil.

SALIS, S. (2000): Fitossociologia da vegetação arbórea no entorno de uma lagoa no Pantanal matogrossense, Brasil. - Naturalia **25**: 225-241.

SALIS, S. (2004): Distribuição das espécies arbóreas e estimativa da biomassa aérea em savanas florestadas, Pantanal da Nhecolândia, Estado de Mato Grosso do Sul. UNESP/IB, Brasília, Brasil.

SCHESSL, M. (1999): Floristic composition and structure of floodplain vegetation in the northern Pantanal of Mato Grosso, Brazil. - Phyton **39**: 303-336.

SEIBERT, P. (1996): Farbatlas Südamerika Landschaften und Vegetation. - Ulmer Verlag, Stuttgart, Germany.

SILVA, J.S.V., ABDON, M.M., BOOCK, A. & M.P. SILVA (1998): Fitofisionomias dominantes em parte das sub-regioes do Nabileque e Miranda, Sul do Pantanal. - Pesq. Agrop. bras. Brasilia **33**(1): 703-1711.

SILVA, M.P., MAURO, R.Y. & G. MOURAO (2000): Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. - Rev. bras. Bot. **23**(2): 143-152.

STEVAUX, J.C. (2000): Climatic events during the late Pleistocene and Holocene in the upper Parana River: Correlation with NE Argentina and South-Central Brazil. - Quaternary International **72**: 73-85.

TROLL, C. (1936): Termiten-Savannen. - In: LOUIS, H. & W. PANZER (eds.): Länderkundliche Forschung: 275-312. Festschrift zur Vollendung des sechzigsten Lebenjahres von Norbert Krebs, Engelhorn, Stuttgart, Germany.

VELOSO, H.P., RANGEL FILHO, A.L.R. & J.C.A. LIMA (1991): Classificação da vegetação brasileira, adaptada a um sistema universal. - IBGE, Rio de Janeiro, Brazil.

WALTER, H. (1971): Ecology of tropical and subtropical vegetation. - Oliver and Boid, Edinburgh, UK.

WILHELMY, H. (1958): Das grosse Pantanal. - Die Weltumschau **18**: 555-559.

ZEILHOFER, P. (1996): Geoökologische Charakterisierung des nördlichen Pantanal von Mato Grosso, Brasilien, anhand multitemporaler Landsat Thematic Mapper-Daten. - Ph.D.-thesis, Universität München, Germany.

ZEILHOFER, P. & M. SCHESSL (1999): Relationship between vegetation and environmental conditions in the northern Pantanal of Mato Grosso, Brazil. - J. Biogeogr. **27**: 159-168.

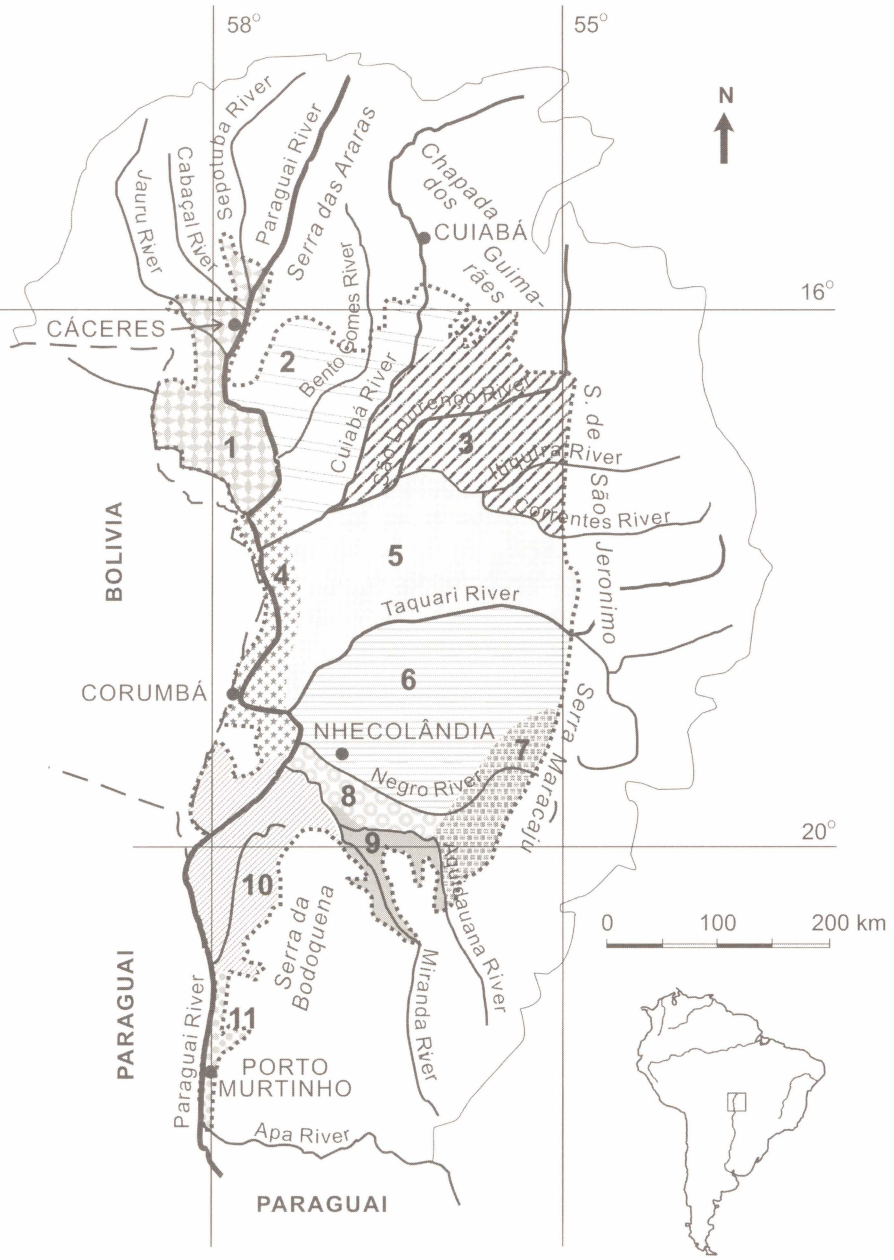

Fig. 1:
Map of the Brazilian part of the Pantanal, with subdivisions according to ADAMOLI (1982). **1** = Cáceres; **2** = Poconé; **3** = Barão de Melgaço; **4** = Paraguai; **5** = Paiaguás; **6** = Nhecolândia; **7** = Aquidauana; **8** = Abobral; **9** = Miranda; **10** = Nabileque; **11** = Porto Murtinho.

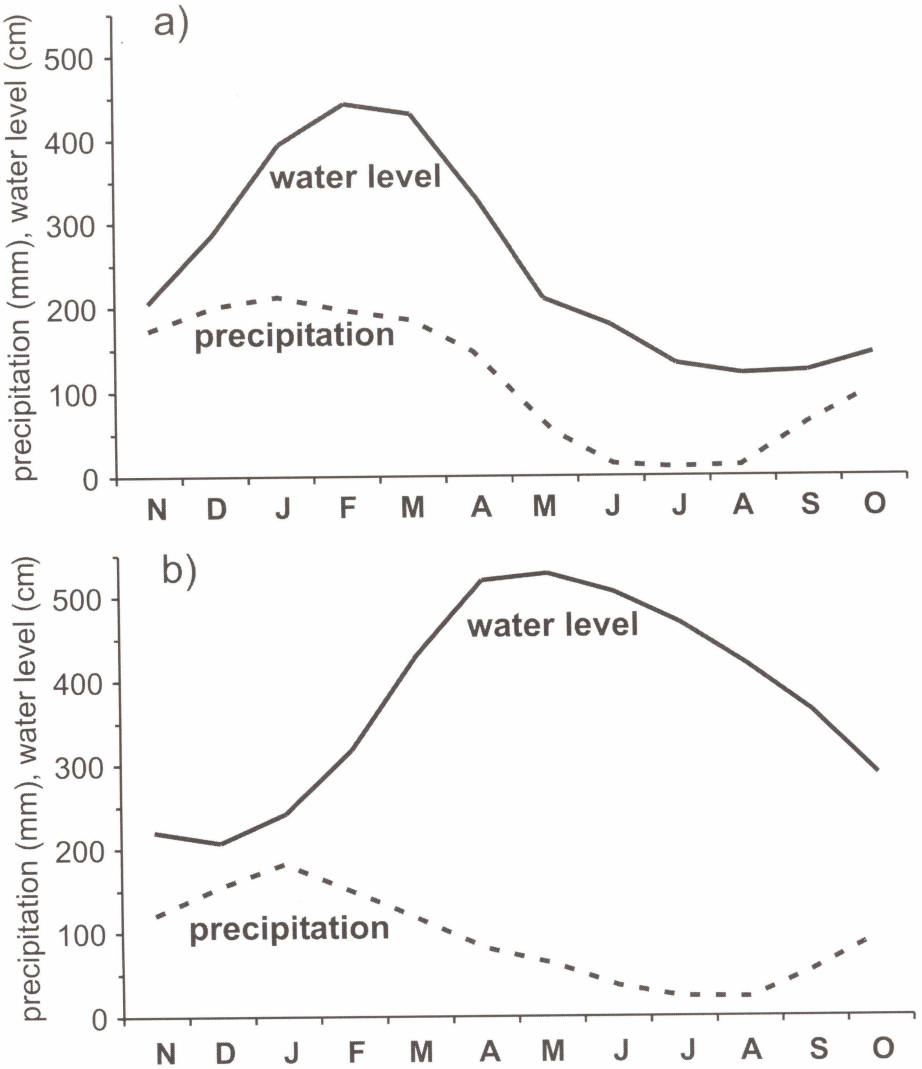

Fig. 2:
a: Mean monthly precipitation near Cuiabá (1933-1993) and mean water level of the Cuiabá River at Cuiabá (1971-1988), northern Pantanal, (data according to ZEILHOFER 1996); **b**: mean monthly precipitation near Corumbá (1912-1971) and mean water level of the Paraguay River at Ladário (1979-1987), southern Pantanal (data according to HAMILTON et al. 1999).

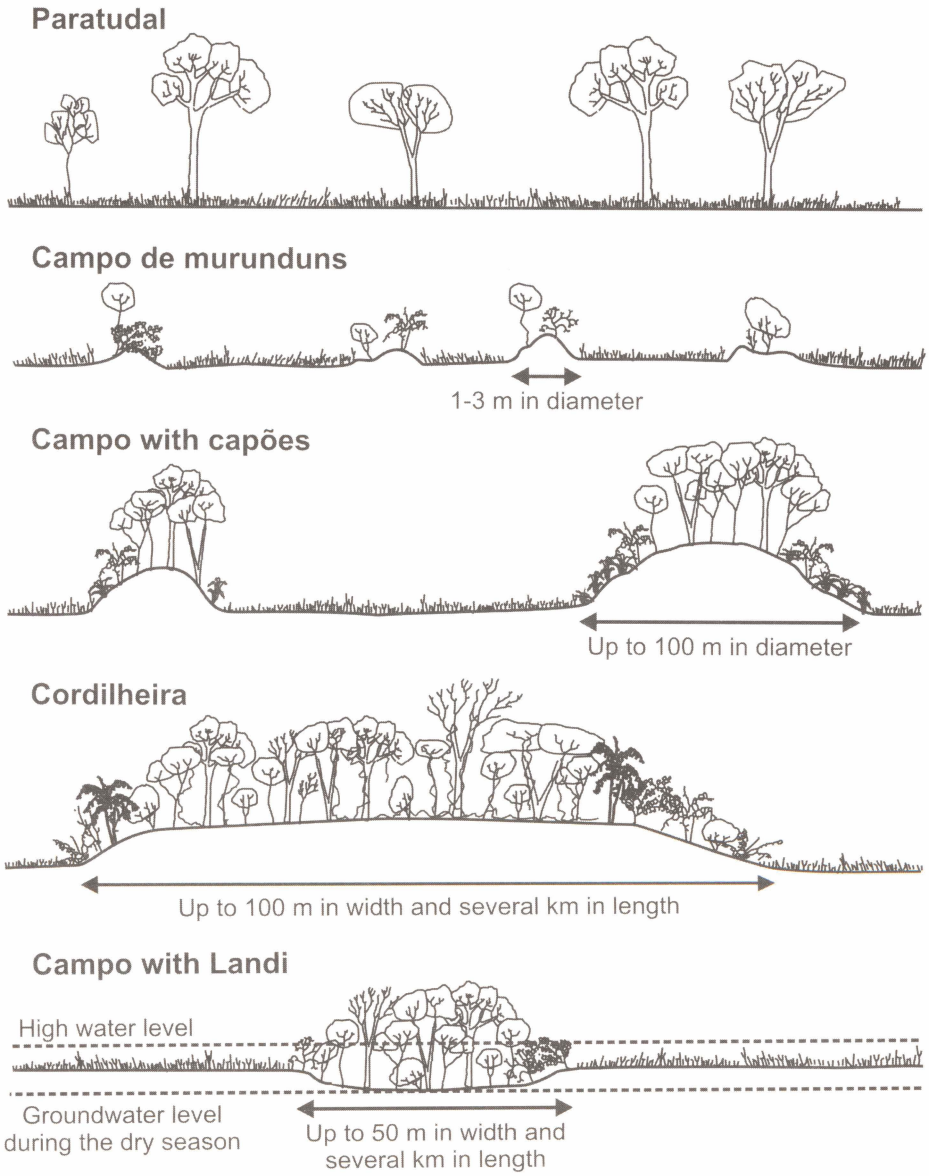

Fig. 3:
Forested landscape units of the Pantanal.

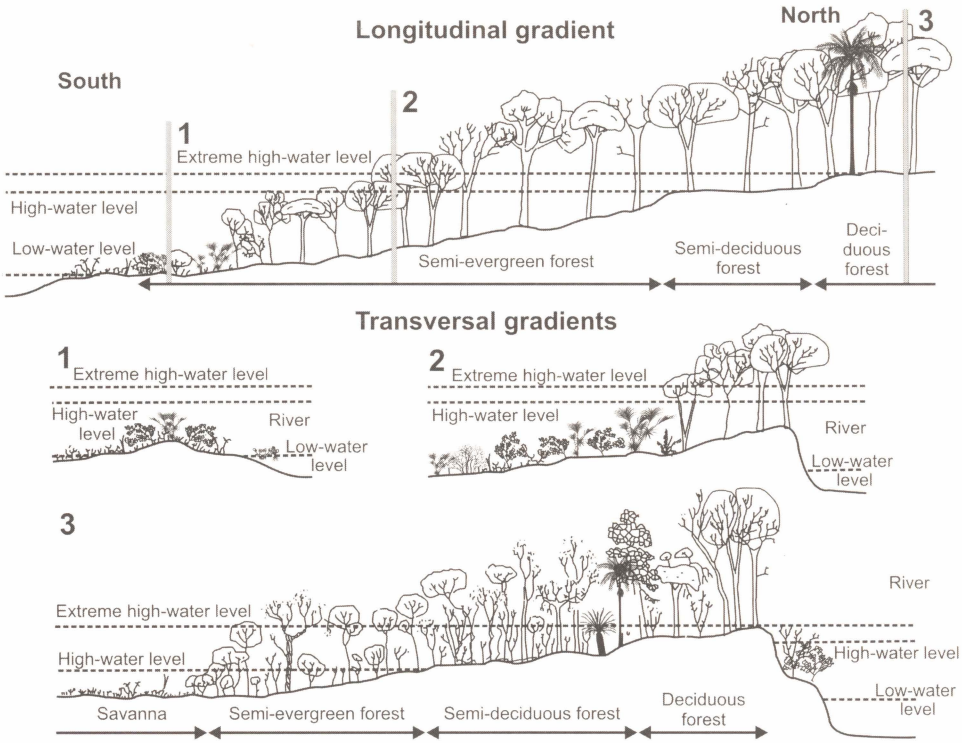

Fig. 4:
Distribution of woody vegetation along a schematic longitudinal gradient and three transversal gradients on a levee. Different forest types occur according to the length of the inundation period. The longitudinal gradient can extend over hundreds of kilometers, from higher lying to lower lying parts of the Pantanal. Transversal gradients cover distances of tens of meters in weakly developed parts (**1**), and up to 500 m in well-developed parts (**3**) of the levee.