

Plant diversity of the Pantanal wetland

Pott, A.^{a*}, Oliveira, AKM.^b, Damasceno-Junior, GA.^a and Silva, JSV.^c

^aDepartamento de Biologia, Universidade Federal de Mato Grosso do Sul – UFMS,
CP 549, CEP 79070-900, Campo Grande, MS, Brazil

^bPrograma de Pós-graduação em Meio Ambiente e Desenvolvimento Regional, Universidade Anhanguera – Uniderp,
Rua Alexandre Herculano, 1400, Jardim Veraneio, CEP 79037-280, Campo Grande, MS, Brazil

^cEmbrapa Informática na Agropecuária, CP 641, CEP 13083-886, Campinas, SP, Brazil

*e-mail: arnildo.pott@gmail.com

Received October 14, 2010 – Accepted December 13, 2010 – Distributed April 30, 2011

Abstract

This is a review of current studies in diversity of the flora and main vegetation types in the Brazilian Pantanal. The flora of this wetland, nearly 2,000 species, constitutes a pool of elements of wide distribution and from more or less adjacent phytogeographic provinces, such as *Cerrado*, dry seasonal forests, Chaco, Amazonia and Atlantic Forest. The most numerous group includes wide-distribution species, mainly herbs, while the second contingent comes from the *Cerrado*. Endemic plants are rare, numbering only seven. The vegetation of the sedimentary floodplain is a mosaic of aquatics, floodable grasslands, riparian forests, savannas (*cerrados*), *cerrado* woodlands, dry forests, and a large area of mono-dominant savannas, and pioneer woodlands. The main vegetation types are briefly described with their characteristic species, and their estimated areas are given according to the latest mapping.

Keywords: Cerrado, Chaco, flora, forest, savanna.

Diversidade de plantas do Pantanal

Resumo

Esta é uma revisão sobre o estado do conhecimento sobre a flora e os principais tipos de vegetação do Pantanal brasileiro. A flora da planície inundável, de aproximadamente 2.000 espécies, é um encontro de elementos de ampla distribuição e de províncias fitogeográficas mais ou menos vizinhas, tais como o Cerrado, florestas estacionais, Chaco, Amazônia e Mata Atlântica. O grupo mais numeroso é de espécies de ampla distribuição, enquanto o segundo contingente vem do Cerrado. Plantas endêmicas são raras, somente sete. A vegetação da planície sedimentar é um mosaico de aquáticas, campos inundáveis, florestas ripárias, savanas (*cerrados*), *cerradão*, floresta decidual, e uma grande parte de savanas e florestas pioneiras monodominantes. Os principais tipos de vegetação são brevemente descritos em termos de espécies características, e suas áreas estimadas são dadas conforme o recente mapeamento.

Palavras-chave: Cerrado, Chaco, flora, floresta, savana.

1. Introduction

The history of the botany of the Pantanal goes back to early European naturalists who visited the region, as reported by Sampaio (1916). Later on, Hoehne (1923), collecting beyond the confined areas along river routes, gave the first broader report on the vegetation and plant species of the old State of Mato Grosso, including the Pantanal. A few geographers gave some landscape descriptions, with scanty reports of the vegetation. Veloso (1947, 1972) and Prance and Schaller (1982) gave some details on vegetation types. With aerial photographs and the onset of satellite imaging, a general view of the physiography was shown and the first vegetation maps were produced

(Furtado et al., 1982; Loureiro et al., 1982; Abdon et al., 1998). The Brazilian botanist who most collected in Mato Grosso and Mato Grosso do Sul was Hatschbach (Museu Botânico Municipal, Cutitiba), as can be verified in Dubs (1988). Quite recently local botanists and collaborators have started to collect and to publish information on the flora (*e.g.*, Pott and Pott, 1994, 1999, 2000) and the vegetation (*e.g.*, Ratter et al., 1988; Nunes da Cunha and Junk, 2001; Damasceno-Junior et al., 2005; Nunes da Cunha et al., 2007).

A brief review will be given on the state of art concerning diversity of vegetation types and main plants in the Pantanal.

2. Results and Discussion

2.1. Flora

Considering only the Pantanal plain, 1,863 species of phanerogams were listed, legumes being the most numerous (240 spp.), followed by more than 200 grasses (Pott and Pott, 1999). The list could be updated to nearly 2,000 species (Pott and Pott, 2009). The most numerous families are Fabaceae (240), Poaceae (212), Malvaceae (98), Cyperaceae (92), Asteraceae (87), Rubiaceae (62), Myrtaceae (45), Convolvulaceae (41), and the best represented genera are *Paspalum* (35), *Cyperus* (29), *Ipomoea* (24), *Panicum* (22), *Eugenia* (20), *Ludwigia* (19), *Mimosa* (18) and *Rhynchospora* (18) (Pott and Pott, 1999), with a prominence of herbaceous species, around 1,000, due to their adaptation to floodable areas, largely occupied by amphibious and grassland habitats. Pott and Pott (2000) show 242 aquatic macrophytes, lately re-counted as 280 species. There are 10 species of palms (Pott and Pott, 1994), and two additional species of *Bactris* have been found, as yet unidentified.

2.2. Phytogeography

The central position of the Pantanal in South America has allowed the encounter among distinct phytogeographic provinces, which are Amazonia to the North, the Cerrados to the East, the Meridional Forests to the South, and the Bolivian and Paraguayan Chaco to the West, favouring a great variety of vegetation types, one of the reasons for the plural term “pantanal” (Adámoli, 1982; Alho, 2008a,b; Oliveira, 2008). Uetanabaro et al. (2007, p. 280) stated that the region lies within the “central portion of the large diagonal area of open vegetation forms of South America, which goes from the Caatinga in Northeast Brazil to the Chaco in Argentina, where areas of contact occur among Pantanal, Chaco and *Cerrado*”, qualifying it “of great biogeographic importance”. The Meridional Forests may be considered as the Paraná basin Forest (Spichiger et al., 2007).

Due to the floristic mix, with gallery forests, palmlands, floodable grasslands, *Tabebuia aurea* savannas, *cerrados*, *cerrado* grasslands, and flood-free ridges (paleodykes) covered with *cerrado* woodlands and forests, the vegetation used to be called “Pantanal Complex”, a concept dropped by Adámoli (1982), considering “mosaic” a more proper term.

The flora receives influence from some main neighbouring phytogeographic domains (Adámoli, 1982). The main influence is the group of wide distribution, mostly herbaceous species; around 160 of them are weedy. The second contingent is the *Cerrado* (with uppercase C when referring to a biogeographic province), connected to the sandy highlands where the woody savanna called *cerrados* (lowercase c to designate the vegetation form) are the main vegetation type. A great part of the areas inside the Pantanal with *Cerrado* have soils deposited by the Taquari River. The Taquari alluvial fan covers 50,000 km², about 30% of the Pantanal, but only a small part of it is actually occupied by *cerradão* type woodland, while most of it is

covered with grasslands and floodable vegetation, with some woody elements of *Cerrado*.

The other floristic province which influences the region is the Amazon forest, mainly on the Paraguay River floodplains. The headwaters of many affluents of this river begin near the transition with the Amazon basin and so work as corridors for some species to reach the Pantanal, especially those from floodable areas (*Igapó* or *Várzea*) such as *Nectandra amazonum* Nees, *Victoria amazonica* (Poepp.) J.C. Sowerby and *Alchornea castaneifolia* (Willd.) A. Juss., or occur in a similar wetland, the Araguaia floodplains, and Lhanos de Mochos, e.g. *Vochysia divergens* Pohl. The flooding regime of the Paraguay River has a few months lag after the rains fall on the upper watersheds, to reach the Pantanal. So, when inundation occurs the dry season has already begun in the lowland, and even without local rain the Amazon species can survive due to the floods.

The next phytogeographical influence is the Chaco, which occurs mainly in Paraguay, Bolivia and Argentina. According to Prado et al. (1992) the real Chaco areas inside the Pantanal can be found only in Porto Murtinho. Nevertheless, some Chaco species can be found in other sub-regions, and the most widespread is the palm *Copernicia alba* Morong, which forms mono-dominant types in extensive areas, mainly in the South Pantanal.

Other types of flora characterising the Pantanal are the seasonal deciduous and semideciduous forests (dry forests). Both occur on ancient levees (locally called “cordilheiras”), mainly in the São Lourenço and Taquari fans. These formations have in fact two distinct origins. The semi-deciduous forest has floristic elements present in the Brazilian Atlantic Forest, according to the official Brazilian classification (IBGE, 1992), such as *Albizia hassleri* (Chodat) Burkart. The deciduous forest contains floristic elements of the Pleistocene arch (Prado and Gibbs, 1993), found in the Chiquitania (Bolivia) and in Central Brazil in connection with the *Caatingas* of NE Brazil, contributing with species such as *Amburana cearensis* (Allemão) A.C. Sm., *Phyllostylon rhamnoides* (J. Poiss.) Taub., *Sebastiania brasiliensis* Spreng., *Seguiera aculeata* Jacq., etc. Damasceno-Junior et al. (2009) estimated about 1.5 % of the Pantanal was covered with deciduous forests. Dry forests are mainly found on the calcareous hills of Corumbá and on residual plateaus of Urucum-Amolar and Bodoquena, which are part of the Paraguay Upper Basin.

2.3. Main vegetation types

According to Silva et al. (2000), *Cerrado* occupies about 36 % of the region. There are various degrees of *Cerrado* cover: more than 70% in the sub-regions of Aquidauana, Barão de Melgaço and Paiaguás (central and Eastern part of Pantanal); between 40 and 50% in the sub-regions of Cáceres, Nhecolândia and Miranda; and 10% in the sub-region of Poconé), whereas *Cerrado* vegetation is absent in the sub-regions of Nabileque and Paraguay – with dominance of Chaco and Amazonian vegetation, respectively.

According to Prance and Schaller (1982), Pott and Pott (1994, 2000) and Silva et al. (2000), there are various vegetation types in the region, and mosaics of floodable grasslands, *cerrado* woodland (*cerradão*), *cerrado*, semideciduous forest, riparian forest, swamps and floating vegetation are particularly conspicuous, plus other physiognomies. A synthesis of vegetation types is given in Table 1.

The Savanna (*Cerrado*) predominates in 50% of the Pantanal. Flood dynamics causes rapid changes in vegetation cover and promotes great diversity in pioneer types, varying from herbaceous to woody formations. In general there is a continuum from semi-deciduous forests to dry and forested savanna (*cerradão*). The species listed for the vegetation types described below were recorded during field work on inspected remnants and are based on herbarium collection and the authors' experience.

- 1) Seasonal Deciduous Forest (Tropical Dry Forest), found on rich or calcareous soils, presenting a tree stratum average 20 m tall with deciduousness above 50%, with two very distinct seasons (one rainy and another dry); it can be subdivided into:
 - 1.1) Lowland Seasonal Deciduous Forest, commonly called dry forest, or calcareous forest, with more than 60% of trees dropping their leaves; species include *Anadenanthera colubrina* (Vell.) Brenan, *Aspidosperma pyrifolium* Mart., *Myracrodruon urundeuva* Allemão, *Phyllostylon rhamnoides*, *Tabebuia impetiginosa* (Mart. ex DC.) Standl., etc;
 - 1.2) Submontane Seasonal Deciduous Forest, amongst several species, *Acacia paniculata* Willd., *Albizia hassleri*, *Anadenanthera colubrina*, *Aspidosperma pyrifolium*, *M. urundeuva*, etc. can be cited, but some are rare on the plain, such as *Chorisia pubiflora* (A. St.-Hil.) Dawson, *Sterculia striata* A. St.-Hil. & Naudin, or were not found, e.g., *Acosmium cardenasii* H.S. Irwin & Arroyo, *Coutarea hexandra* (Jacq.) K. Schum.;
 - 2) Seasonal Semi-deciduous Forest, characterised by leaf loss in 20 to 50% of trees, average 20 m tall, reaching up to 30 m. It is subdivided into:
 - 2.1) Alluvial Seasonal Semi-deciduous Forest, also called riparian forest, found lining rivers of the basin and often periodically flooded, with denser formations found mainly along the Paraguay River, in the sub-regions of Paraguay and Poconé, and along the São Lourenço River in Barão do Melgaço, with trees such as: *Albizia inundata* (Mart.) Barneby & J.W. Grimes, *Cassia grandis* L.f., *Vitex cymosa* Bertero, etc;
 - 2.2) Lowland Seasonal Semi-deciduous Forest, occurring on flood-free ground (ridges or ancient levees), with species such as: *Anadenanthera colubrina*, *Astronium fraxinifolium* Schott, *Attalea phalerata* Mart. ex Spreng., *Copernicia alba*, *Protium heptaphyllum* (Aubl.) Marchand, *Pterogyne nitens* Tul., *Tabebuia impetiginosa*, *T. roseo-alba* (Ridl.) Sandw., etc;
 - 3) Savanna, regionally called *cerrado* and which is already internationally accepted, is found in areas with vegetation presenting xeromorphic features due to the dry season, usually on dystrophic soils, except for the forested type. *Cerrado* and *cerrado* woodland ("cerradão") on poor sands in the central and Eastern parts of the Pantanal show a lack of palms except for the small *Allagoptera leucocalyx* (Drude) Kuntze, many Fabaceae [*Acosmium dasycarpum* (Vog.) Yakol., *Andira cuyabensis* Benth., *Bowdichia virgilioides* Kunth, *Hymenaea stigonocarpa* (Mart.) Hayne, *Vatairea macrocarpa* (Benth.) Ducke], Myrtaceae [*Eugenia* spp., *Gomidesia palustris* (DC.) Kausel, *Myrcia* spp.], and Vochysiaceae [*Qualea* spp., *Salvertia convallariodora* A. St.-Hil., *Vochysia* spp.], *Kielmeyera rubriflora* Cambess. There are few hardwoods on poorer soils, used for fencing, usually legumes, e.g., *Dipteryx alata* Vog., *Diptychandra aurantiaca* (Mart.) Tul., *Plathymenia reticulata* Benth.; also *Lafoensia pacari* A. St.-Hil. Other common *Cerrado* trees: *Aspidosperma tomentosum* Mart., *Byrsonima coccolobifolia* Kunth and *Caryocar brasiliense* Cambess.
- During dry years some *cerrado* and other pioneering species "invade" grasslands, even occurring in dried-out pond beds: in sandy areas, *Annona dioica* A. St.-Hil., *Bowdichia virgilioides*, *Buchenavia tomentosa* Eichler, *Caryocar brasiliense*, *Curatella americana* L., *Hymenaea stigonocarpa*, *Luehea paniculata* Mart., *Simarouba versicolor* A. St.-Hil., etc.; on clay, other species increase, e.g. *Callisthene fasciculata* (Spreng.) Mart. and *Tabebuia aurea* (Manso) Benth. & Hook. f. ex S. Moore, etc.
- 3.1) Forested Savanna, called "Cerradão", is a denser woodland where tree canopies touch each other and part of the species are semi-deciduous, 8 to 15 m tall, occurring more in the East and centre of the plain, on sandy soils (sub-regions of Cáceres, Barão do Melgaço, Nhecolândia, Aquidauana and Miranda), on flood-free ground; some of the species are: *Byrsonima crassifolia* (L.) Kunth, *Caryocar brasiliense*, *Dimorphandra mollis* Benth., *Eriotheca gracilipes* (K. Schum.) Robyns, *Kielmeyera coriacea* Mart., *Qualea grandiflora* Mart., *Q. parviflora* Mart., *Xylopia aromatica* (Lam.) Mart., etc;
 - 3.2) Woody Savanna, also called *cerrado* grassland, *cerrado* or open *cerrado*, is a form of *cerrado stricto sensu*, well represented in the Pantanal, with shrubs and scattered trees up to 10 m tall, with thick bark and tortuous trunks, on a predominant grassy/herbaceous stratum, occurring more in the Eastern and central parts of the plain, on sandy soils

Table 1. Quantification (km²) of the vegetation cover of the Pantanal, mapping based on Landsat images of the year 2002. Vegetation names according to the official Brazilian nomenclature (IBGE, 1992), common terms in parentheses.

Phytoecological region, formation or subtype	Area (km ²)
I – Semi-deciduous Seasonal Forest	
Alluvial forest (riparian forest, gallery forest)	6,131.0
Submontane forest (dry forest)	92.3
II – Deciduous Seasonal Forest	
Alluvial forest (riparian forest, gallery forest)	9.6
Lowland forest (“Mata”, dry forest, calcareous forest)	519.0
Submontane forest (“Mata”, dry forest, calcareous forest)	910.0
III - Savanna (<i>Cerrado</i>)	
Forested (<i>Cerrado</i> woodland, <i>Cerradão</i>)	8,984.0
Wooded (<i>Cerrado</i> grassland, <i>Cerrado</i> , open <i>Cerrado</i>), with and without gallery forest	25,205.9
Grassy-Woody (Grassland, open grassland, bushy grassland, <i>Elyonurus</i> grassland, and flooded grassland), with and without gallery forest	8,880.7
Forested + Wooded and Wooded + Forested	80.3
Wooded + Grassy-Woody and Grassy-Woody + Wooded	734.5
IV – Steppic Savanna (Chaco)	
Wooded	213.3
Park (“Carandazal”)	6,590.7
Grassy-Woody (“campo”)	4,526.1
Wooded + Forested	80.3
Wooded + Grassy-Woody	244.2
Grassy-Woody + Grassy-Woody	490.3
V – Pioneer Formations: Vegetation with Fluvial and/or Lacustrine Influence: <i>Mauritia</i> palmland (“Buritizal”), Spiny scrub (“Espinheiral”), <i>Vochysia divergens</i> woodland (“Cambarazal”), Giant sedge (“Pirizal”), tussock grassland (“Macega”), <i>Couepia uti</i> woods (“Pateiral”), <i>Licania parvifolia</i> woods (“Pimenteiral”), Fireflag (“Caetezal”), Swamp, floating meadow and bushy grassland	5,216.2
VI – Areas of ecological tension or floristic contacts	
Ecotone	
Savanna/Deciduous Seasonal Forest (“Mata”)	315.9
Savanna/Semi-deciduous Seasonal Forest (“Mata”)	2,258.5
Deciduous Seasonal Forest/Pioneer Formations (“Mata”)	4,697.4
Savanna/Pioneer Formations (<i>Cerrado</i> , Bushy Grassland, “Cambarazal”)	16,429.5
Steppic Savanna/Deciduous Seasonal Forest (“Mata”)	803.9
Enclave	
Savanna/Deciduous Seasonal Forest (“Mata”)	904.9
Savanna/Deciduous Seasonal Forest (“Mata”)	53.3
Savanna/ Semi-deciduous Seasonal Forest (“Mata”)	298.5
VII – Vegetation refuges (remnant communities): Herbaceous submontane refuge (Grassland)	28.4
VIII – Anthropogenic areas	
Secondary vegetation (of Savanna, Forest, Forested and Park Steppic Savanna)	403.6
Agriculture	411.5
Sown pasture (in Seasonal Forest, Savanna and Steppic Savanna)	16,511.8
IX – Other Anthropogenic Areas: Urban Influence + Mining degraded areas	132.7
X – Others: Water bodies (rivers, streams, oxbows, channels, lakes, ponds, brackish ponds)	2,557.3
TOTAL	151,186.2

Source: Silva et al. (2007).

(sub-regions of Cáceres, Barão do Melgaço, Paiaguás, Nhecolândia, Aquidauana and Miranda), on lower areas, tending to grassland as the degree of inundation increases, or the opposite, to woodier when drier. The most common species found are: *Annona dioica*, *Buchenavia tomentosa*, *Curatella americana*, *Dimorphandra mollis*, *Luehea paniculata*, *Qualea parviflora*, *Simarouba versicolor* and *Stryphnodendron obovatum* Benth., among others;

3.3) Park Savanna (Park of *Cerrado*) occurs in floodable areas, normally with dominance of a single tree or shrub species over a grassy stratum:

3.3.1) *Byrsonima orbignyana* scrub (“canjiqueiral”) – homogeneous shrubby formation, 1-5 m tall, dominated by *B. orbignyana* A. Juss., on sandy or silty soils, floodable (ca. 50 cm deep), in the sub-regions of Paiaguás, Nhecolândia, Aquidauana, Abobral and Cáceres; as a pioneer woody element, it is considered a pasture weed, and in past decades it was the main controlled species. *Byrsonima orbignyana* savanna, on floodable sandy areas, also sometimes occurs on ancient silted drainage channels amongst *Tabebuia aurea* savanna and spread over most of the plain;

3.3.2) *Curatella americana* (“lixerial”) – a sort of park savanna dominated by this tree, which occurs in floodable areas; often it is associated with slightly higher ground, while it is a rather shrubby (multi-stem) dwarfed shrub on ill-drained land or a ca. 15 m tall tree in flood-free woodland (Pott and Pott, 2004, 2005); it is the most frequent woody species in the Pantanal, being very abundant on the dystrophic sands of the Eastern zone (Pott and Pott, 2004), and in the earth-mound savanna in the Northern part of the floodplain (Ponce and Nunes da Cunha, 1993); it is also considered a weed by ranchers, mainly during dry years (Pott and Pott, 2004);

3.3.3) *Tabebuia aurea* (“paratadal”) – floodable savanna with a single tree species stratum, mean density of 363 individuals/ha (Soares and Oliveira, 2009), 5-12 m tall, generally growing on a type of earth-mound or termite-like hummocks; other woody species (e.g. *Astronium fraxinifolium*) appear in drier years, but are kept back by wildfires or return of floods; occurs mainly in the South of the Pantanal between the rivers Nabileque and Miranda, associated with slightly alkaline waters and sediments (Pott, 1994); it used to be interpreted as *cerrado* (Furtado et al., 1982; Loureiro et al., 1982), but lately it has been considered to be linked to the Chaco flora (Silva et al., 2007), due to the associated species,

such as *Aposorella chacoensis* (Morong) Spegazz., *Camptosema paraguariense* Chodat & Hassl., *Dolichopsis paraguariensis* (Benth.) Hassl., *Prosopis rubriflora* Hassl., etc. (Pott, 1994), and because such vertic soils do not exist under *Cerrado*.

3.4) Grassy-woody Savanna, called *Campo* or flooded grassland, normally made up of grasses and herbs. It can be divided into flooded and dry grasslands, the proportions varying in function of local rainfall and/or river overflow, representing 31.1% of the vegetation of the region, being more associated with drainage factor than soil fertility. Higher predominance in some portions of the Pantanal (Abobral, Paiaguás, Nhecolândia and Nabileque), with dominance of grasses and sedges. Among coarse grasses [*Andropogon* spp., *Paspalum carinatum* Humb. & Bonpl., *P. lineare* Trin. and *Trachypogon spicatus* (L. f.) O. Kuntze], there are other species such as wild-rice *Oryza* spp., *Mesosetum* spp., *Reimarochloa* spp., *Paratheria prostrata* Griseb., plus *Paspalum* spp., *Digitaria* spp., *Panicum* spp. Some species are found more on poor soils, such as *Axonopus purpusii* (Mez) Chase, while *Paspalum alnum* Chase is associated with fertile soils. Grasslands, depending on cycle of flood or drought, can be taken over by woody vegetation of *cerrado*, or vice-versa.

4) Steppic Savanna, commonly called Chaco and linked to the floristic province of Chaco in Argentina, Paraguay and Bolivia; the only true Brazilian Chaco occurs at the SW end of Mato Grosso do Sul and belongs to the *Chaco Húmedo* (Prado et al., 1992). There is a predominance of spiny vegetation with features of semi-arid vegetation (presence of xeromorphic species, plus cacti), with physiognomy similar to the Brazilian *Caatinga*, although it also contains wet areas, mainly in the Eastern Chaco; it is present on salty clays in the sub-regions of Nabileque and Porto Murtinho, and can be subdivided into four vegetation forms:

4.1) Forested Steppic Savanna, commonly called Chaco, dry forest or Chaquénian forest, with dry forest appearance, deciduous, average 5-7 m tall; some typical species are *Aspidosperma quebracho-blanco* Schldtl., *Caesalpinia paraguariensis* (D. Parodi) Burkart, *Diplokeleba floribunda* N.E. Br., *Parkinsonia praecox* (Ruiz & Pav. ex Hook.) J. Hawkins, *Piptadenia viridiflora* (Kunth) Benth., *Prosopis rubriflora*, *P. ruscifolia* Griseb., *Schinopsis balansae* Engl., *Zizyphus oblongifolius* S. Moore, etc.; lately undergoing strong deforestation;

4.2) Steppic Scrub Savanna, also called Chaco, is similar to the previous one, but with shorter and

- spaced trees, interspersed in a stratum of spiny treelets which normally do not surpass 4 m, such as *Acacia farnesiana* Willd., *A. paniculata*, *Capparis retusa* Griseb., *C. speciosa* Griseb., *C. tweediana* Eichl., *Celtis pubescens* Kunth, *Zizyphus* spp., etc., and frequently a ground cover of *Selaginella sellowii* Hieron.;
- 4.3) Steppic Park Savanna (“Carandazal”, “Campina de Carandá”) – made up of a grassy sward and a woody stratum with predominance of the palm *Copernicia alba*, 8-20 m tall, occurring mainly in the Southern Pantanal, in large areas of the sub-regions Nabileque and Porto Murtinho, on black alkaline or saline clays, with sub-surface calcium carbonate concretions; it also occurs on sandy soils, if fertile or high pH, as around brackish ponds (Nhecolândia) or shell-derived hummocks (Abobral), in floodable areas, while on drier patches it becomes denser, as palm woodland, with associated species such as *Capparis speciosa*, *Cereus bicolor* Rizzini & Mattos, *Diplokeleba floribunda*, *Machaerium hirtum* (Vell.) Stellf., *Mimosa* spp., *Prosopis ruscifolia*, *Tabebuia nodosa* (Griseb.) Griseb., etc;
- 4.4) Steppic Woody-grassy Savanna, various types of grassland, such as open grassland, bushy grassland, flooded grassland or spiny grassland, made up of a grassy sward with spiny dwarf plants; common species: *Acacia farnesiana*, *Celtis spinosa* Spreng., *C. pubescens*, *Mimosa* spp., *Paspalum simplex* Morong, etc;
- 5) Pioneer formations or monodominant vegetation types – areas under fluvial and/or lacustrine influence (sedimentation habitats, periodically or permanently flooded), made up of unstable ground covered by vegetation in constant succession, such as *Vochysia divergens*, spiny scrub, giant sedge stands, plus others described below. This type of vegetation, a result of abiotic (soil and/or hydrological) factors, allows the presence of various types of association, few plant species dominating large areas, forming typical landscapes with their local names in brackets:
- 5.1) *Attalea phalerata* (“acurizal”) – homogeneous or mixed forest understory made up of this shady palm, occurring on flood-free ridges and grooves and on river banks, which are periodically flooded by flowing water; it often indicates anthropic action, as it can colonise cleared or frequently burned areas;
- 5.2) *Attalea speciosa* palmland (“babaçal”) – homogeneous dense forest predominantly of this palm, 10-22 m tall, occurring in the extreme North of Cáceres sub-region and central Nhecolândia (0.3% of the region); some dry forest trees grow inside, held back by periodical fires, such as *Astronium fraxinifolium*;
- 5.3) Floating mats (“camalote”) and floating islands (“baceiro”, “batume”) – both found in permanent water bodies such as ponds, lakes, canals, oxbows and rivers; floating mats are attached banks of floating macrophytes, or not anchored, which then float downriver or move by wind; the main species are the water hyacinths *Eichhornia crassipes* (Mart.) Solms and *E. azurea* (Sw.) Kunth, both rooted or free-floating, and other aquatic plants, water lettuce *Pistia stratiotes* L. and water fern *Salvinia auriculata* Aubl., free-floating; floating meadows have denser vegetation, made up of grasses and sedges, mainly *Oxycaryum cubense* (Poepp. & Kunth) Lye and *Eleocharis plicarhachis* (Griseb.) Svens., rooted on histosol (decomposing organic material) (Pivari et al., 2008) accumulated on the densely entangled roots, most frequent in the sub-regions of Abobral and Cáceres and along the rivers Paraguay, Cuiabá, Negro, Miranda and Nabileque;
- 5.4) Swamp (“brejo”) – permanently flooded or waterlogged areas, except in drier years, are confined to a few places, such as the Negro River (Aquadauana) and sub-regions of Abobral, Paraguay and Poconé; contains shrubby species, climbers, grasses and sedges, often forming dense thickets of spiny shrubs (*Byttneria filipes* Mart. ex K. Schum., *Mimosa weddelliana* Benth., etc.) and vines (*Cissus spinosa* Cambess., *Combretum* spp., *Ipomoea* spp.). Giant sedge *Cyperus giganteus* Vahl (“pirizal”) and fireflag *Thalia geniculata* L. (“caetetal”) is a sort of swamp or temporary pond dominated by these herbaceous species, mainly in the sub-regions of Abobral, Nabileque and Poconé, and increasing in the flooded Taquari delta; cat-tail *Typha domingensis* Pers. (“taboal”) is a similar tall aquatic herb which occurs in permanent or temporary ponds and increases in disturbed flooded areas;
- 5.5) *Vochysia divergens* woodland (“cambarazal”) – homogeneous formation of an Amazonian tree, 5-18 m tall, on clay or loamy soils, tolerates periodical flood well, but not permanently; found mainly in the sub-regions of Barão do Melgaço, Poconé and Paraguay, adding up to 3.2% of the Pantanal vegetation, in fact much more nowadays; it is a pioneer which forms dense pure stands, considered a natural grassland weed for shading out grasslands (Allem and Valls, 1987). Since 1980, large areas have been invaded on floodplains of the Cuiabá and Paraguay rivers, now also on the lower Taquari flooded delta (Pott and Pott, 2005), but it slowly dies back under permanent deep flood;

- 5.6) *Elyonurus muticus* grassland (“caronal”), on intermediate, and only occasionally flooded or flood-free sandy ground, lately being replaced to cultivate *Brachiaria humidicola* Rendle or other exotic grasses;
- 5.7) *Bromelia balansae* stands (“gravateiro”) – community of a pineapple-like plant, generally indicating flood limit; when in large amounts inside groves and woods, it may indicate selective logging with opening of gaps, which allow fast growth and spread, blocking passage of large animals, then the leaves have very spiny edges; it is not viable to map it yet;
- 5.8) *Couepia uti* scrub (“pateiral”) – native grassland area invaded by this tree species, considered a weed (pioneer), being abundant on sandy soils on floodplain and among riparian vegetation;
- 5.9) *Licania parvifolia* scrub (“pimenteiral”) – native grassland areas invaded by this pioneer tree, occurring over nearly the whole Pantanal floodplain;
- 5.10) *Tabebuia heptaphylla* woods (“piuval”), a deciduous tree occurring in savanna or woodland, in floodable areas, generally not far from rivers and seasonal streams, tending to riparian forest in the succession;
- 5.11) *Mauritia flexuosa* palmland (“buritizal”) – almost homogeneous formation of “buriti” palm, 5-15 m tall, with restricted distribution near the Eastern border of the plain, along the Aquidauana and Taquari Rivers, and in Barão de Melgaço;
- 5.12) *Erythrina fusca* woods (“abobral”) – one of the main trees, usually in groups, along the Paraguay River in the Cáceres sub-region, also spread along the margins of the Aquidauana river; the flowers are visited by psittacids;
- 5.13) *Xylopia aromatica* savanna (“pindaival”) – *Cerrado* tall shrub or tree community common in the NE of the plain.

2.4. Remarks upon vegetation types

- Dry forests – Dry forests, more abundant on the hills rather than on the plain (Hoehne, 1923; Prance and Schaller, 1982; Ratter et al., 1988), were recently described in more detail by Damasceno-Junior et al. (2009). This vegetation type covers c. 4% of the Pantanal, as few significant areas occur on the plain: Mata do Cedro and Fuzil in Paiaguás, Mata do Bebe in Barão de Melgaço, and other scattered patches in South Poconé, Abobral, Miranda, around brackish ponds in SE Nhecolândia, Soldado and Porto Murtinho (Damasceno-Junior et al., 2009). Typical species are: *Acrocomia aculeata* (Jacq.) Lodd. Ex Mart., *Astronium fraxinifolium*, *Casearia gossypiosperma* Briq., *Combretum*

leprosum Mart., *Cordia glabrata* (Mart.) A. DC., *Dipteryx alata*, *Myracrodruon urundeuva*, *Pisonia zapallo* Griseb., *Pouteria gardneri* (Mart. & Miq.) Baehni, *Pterogyne nitens*, *Rhamnidium elaeocarpum* Reiss., *Spondias mombin* L., *Sterculia apetala* Karst., *Tabebuia impetiginosa*, *Zanthoxylum caribaeum* Lam., etc. (Damasceno-Junior et al., 2009). The Chaco influence becomes stronger southwards, as in the areas of Soldado and Porto Murtinho. Some of the dry forest areas can be interpreted as a junction of many ancient levees, generally an alluvial fan built at the earlier encounter of a tributary with the calm flood waters of a larger river. For example, sediments of the Taquari River were deposited where they met the still flood waters of the Paraguay River, before the Paraguay was gradually pushed westwards.

- Riparian forests – Most information on gallery forests is given by Damasceno-Junior et al. (2005), for the Southern part of the Pantanal, and by Nunes da Cunha and Junk (2001), for the Northern sub-regions. Some riparian trees are sort of generalists, found along almost every water course, such as *Andira inermis* Kunth and *Inga vera* ssp. *affinis* (DC.) T.D. Penn., whereas others tend to be more frequent on heavily flooded clay, e.g., *Albizia inundata* and *Sapium obovatum* Klotzsch ex Müll. Arg. In the Northern section of the Paraguay River on the plain a few grow in nearly pure stands, such as *Erythrina fusca* Lourt. and *S. obovatum*, often like orchards, and some Amazonian species occur which have not been found much downstream, such as *Brosimum lactescens* (S. Moore) Berg and *Sloanea garckeana* K. Schum., plus an as yet unidentified red-fruited species of *Bactris*. Along some outgoing temporary streams (diffluents) of the Taquari River, there occur dense stands of *Tapirira guianensis* Aubl., hardly seen elsewhere in the Pantanal. It seems rather paradoxical that some trees share very distinct habitats, such as the riverside and dry forests; for example, *Albizia hassleri* and *Vitex cymosa*. Many species of gallery forests of upland streams do not grow on the plain, or only as far as the river is fast-flowing, such as *Hirtella gracilipes* (Hook. F.) Prance and *Licania humilis* Cham. & Schltld. on the Taquari River, still close to the Eastern border. A curious case is *Salix humboldtiana* Willd., which has restricted occurrence on sandy levees of the Aquidauana River at the very entrance to the plain; after a disjunction it reappears on heavy clay along the Paraguay River at the far end of the Pantanal. Below Corumbá the Paraguay River does not often exhibit a proper riparian forest, but pioneer stages of flexible shrubs, which withstand flood flow, such as *Alchornea castaneifolia*.

Due to the dynamics of the rivers, strips of “old” forest are eroded away and new ones start on the opposite bank,

where sediments accumulate and become first colonised by aquatic plants, often nearly mono-dominant, mainly grasses (*Panicum dichotomiflorum* Michx., *P. pernambucense* (Spreng.) Mez ex Pilg., *Paspalum fasciculatum* Willd.) and sedges (*Cyperus*, *Fuirena*, *Rhynchospora*), *Polygonum* spp., then subshrubs [*Aspilia latissima* Malme, *Ipomoea carnea* var. *fistulosa* (Mart. ex Choisy) D.F. Austin], shrubs (*Alchornea castaneifolia*), later trees, all entangled with a great mass of vines, such as *Combretum lanceolatum* Pohl, *Cissus spinosa*, *Mikania* spp. Some of the main species of riparian forests are: a) early stage of succession with *Cecropia pachystachya* Trécul, *Ruprechtia brachysepala* Meisn., *Inga vera*, *Sapium obovatum* and *Vochysia divergens*; b) late successional stage trees are, for example *Erythrina fusca*, *Ficus* spp., *Genipa americana* L., *Pouteria glomerata* (Miq.) Radlk. and *Triplaris americana* L. Succession stages frequently occur in progressive chronological zoning, but are also intermingled due to gaps caused by flood or fire. Along seasonal streams often grows a hedgerow of *Licania parvifolia* Hub., sometimes *Calophyllum brasiliense* Cambess. The sequence described here depends on the level of inundation that the considered river can reach, and on the region drained.

Riparian species may grow many kilometres from the river, such as *Combretum lanceolatum*, *Licania parvifolia* and *Vochysia divergens*, often in closed mono-dominant populations, therefore frequently considered undesirable invasive woody plants, as they may take over and even shade out useful grasslands.

- Grasslands – Allem and Valls (1987) produced the first comprehensive study, a benchmark on natural grasslands of the Pantanal. Grasslands are by far the biggest vegetation type of the Pantanal. Often the open landscape is mistaken for deforested area, instead of natural vegetation due to seasonal flood, even though there is some spotty shrub control done by ranchers. The effect of flood holding back woody vegetation can be observed during years without flood, when grasslands become shrubby, as during the last 15 years.

Grassland composition depends so much on flood level that a few centimetres difference is enough to determine change in species. Besides the main grasses, there is a great number of herbaceous plants, annuals or perennials, most of them growing in particular conditions of flood or soil, and these may be indicators, for example: therophytes or annual species propagated by seed (*Bacopa arenaria* (J.A. Smith) Edwall, *Heliotropium filiforme* Lehm., *Ludwigia octovalvis* (Jacq.) Raven, *Sacciolepis myuros* (Lam.) Chase); indicators of clay [annuals *Brachiaria adspersa* (Trin.) Parodi, *Eriochloa punctata* (L.) Desv., *Heliotropium procumbens* Mill., and perennials *Hemarthria altissima* (Poir.) Stapf & Hubb., *Paspalum millegrana* Schrad.]; indicators of salinity [annuals *Microchloa indica* (L.f.) Beauv., *Sporobolus pyramidatus* (Lam.) Hitchc., *Tripogon spicatus* (Nees) Ekm., and perennial *Paspalum vaginatum* Sw.]; and indicators of poor soils [*Gymnopogon spicatus* (Spreng.) O.Kuntze, *Leptocoryphium lanatum* (H.B.K.)

Nees, *Mesosetum cayennense* Steud., *Panicum stenodes* Griseb.] (Pott, 1988).

2.5. Endemic and rare species

As the Pantanal is a geologically-recent (Holocene) Quaternary floodplain, very few endemic species have been found, such as *Arachis diogoi* Hoehne, *A. hoehnei* Krapov. & W.C. Greg., or new and also endemic plant species, e.g. *Arachis vallsii* Krapov. & W.C. Greg., *Euplocca pottii* J.I.M. Melo, *Habranthus pantanensis* Ravenna, *Stilpnopappus pantanalensis* H. Rob., *Xanthosoma pottii* E.G. Gonçalves. Some are endemics in the broad sense, such as *Bergeronia sericea* Mich. and *Lonchocarpus nudiflorens* Burkart. There seem to be more endemic plants on surrounding hills than on the plain, such as *Aspilia grazielae* Santos, *Discocactus ferricola* Buining & Bradero, *Gomphrena centrota* Holz., *G. matogrossensis* Suessenguth, *Lonchocarpus variabilis* R.R. Rodrigues & Tozzi, *Mentzelia corumbaensis* Hoehne, *Mimosa ferricola* R.R. Silva & A.M.G.A. Tozzi, *Deuterocohnia meiziana* Kuntze ex Mez, etc.

- Rare species: *Cereus saddianus* Rizz. & Mattos, *Dieffenbachia aglaonematifolia* Engl., *Discolobium psoralifolium* Benth., *Eichhornia diversifolia* (Vahl) Urb., *Evolvulus pterygophyllus* Mart., *Eulophia alta* (L.) Fawc. & Rendl., *Habenaria nabucoi* Ruschi, *Ipomoea piresii* O'Donell, *Ludwigia affinis* (DC.) Hara, *Nymphaea belophylla* Trickett, *Utricularia trichophylla* Spruce ex Oliv., *Xanthosoma aristiguietae* (Bunting) M. Madison.

Acknowledgements – To Dr. J.A. Ratter for suggestions on the manuscript. The author A. Pott is grateful to CNPq and CAPES for the present research grants PQ2 and PVNS, and JSV. Silva thanks for the fund of the PROBIO-Pantanal Project (Ministério do Meio Ambiente/Embrapa/SEMACT-MS).

References

- ABDON, MM., SILVA, JSV., POTT, VJ., POTT, A. and SILVA, MP., 1998. Utilização de dados analógicos do Landsat-TM na discriminação da vegetação de parte da sub-região da Nhecolândia no Pantanal. *Pesquisa Agropecuária Brasileira*, vol. 33, no. especial, p. 1799-1813.
- ADÁMOLI, J., 1982. O pantanal e suas relações fitogeográficas com os cerrados. Discussão sobre o conceito de "Complexo do Pantanal". In *Anais do XXXII Congresso Nacional de Botânica*. Teresina. p. 109-119.
- ALHO, CJR., 2008a. The value of biodiversity. *Brazilian Journal of Biology*, vol. 68, no. 4, p. 1115-1118.
- , 2008b. Biodiversity of the Pantanal: response to seasonal flooding regime and to environmental degradation. *Brazilian Journal of Biology*, vol. 68, no. 4, p. 957-966.
- ALLEM, AC. and VALLS, JFM., 1987. *Recursos forrageiros nativos do Pantanal Mato-grossense*. Brasília: Embrapa. 339 p.
- DAMASCENO-JUNIOR, GA., POTT, A. and SILVA, JSV., 2009. Florestas estacionais do Pantanal, considerações florísticas e subsídios para conservação. *Geografia*, vol. 34, no. 143, p. 697-707.

- DAMASCENO-JUNIOR, GA., SEMIR, J., SANTOS, FAM. and LEITÃO-FILHO, HF., 2005. Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. *Flora*, vol. 200, no. 2, p. 119-135.
- DUBS, B., 1988. *Prodrômus Florae Matogrossensis*. Betrona Verlag: Küssnacht. 444 p.
- FURTADO, PP., GUIMARÃES, JG., FONZAR, BC. and PIRES, JM., 1982. Vegetação. In Ministério das Minas e Energia. *Projeto Radambrasil. Folha SF.21 Campo Grande*. Rio de Janeiro: Secretaria Geral. p. 281-333. Levantamento de Recursos Naturais, 28.
- HOEHNE, FC., 1923. *Phytophysionomia do Estado de Matto Grosso e ligeiras notas a respeito da composição e distribuição da sua flora*. São Paulo: Cia. Melhoramentos. 94 p.
- Instituto Brasileiro de Geografia e Estatística – IBGE, 1992. *Manual técnico da vegetação brasileira*. Rio de Janeiro: IBGE. 92 p. Séries Manuais Técnicos em Geociências, no. 1.
- LOUREIRO, RL., LIMA, JPS and FONZAR, BC., 1982. Vegetação. In Ministério das Minas e Energia. *Projeto Radambrasil. Folha SE.21 Corumbá e parte da Folha SE.20*. Rio de Janeiro: Secretaria Geral. p. 329-372. Levantamento de Recursos Naturais, no. 27.
- NUNES DA CUNHA, C. and JUNK, WJ., 2001. Distribution of woody plant communities along the floodplain gradient in the Pantanal of Poconé, Mato Grosso, Brazil. *International Journal of Ecology and Environmental Sciences*, vol. 27, no. 2, p. 63-70.
- NUNES DA CUNHA, C., JUNK, WJ. and LEITÃO-FILHO, HF., 2007. Woody vegetation in the Pantanal of Mato Grosso, Brazil: a preliminary typology. *Amazoniana*, vol. 19, no. 3/4, p. 159-184.
- OLIVEIRA, AKM., 2008. Pantanal – origens e características gerais. In OLIVEIRA, AKM., GARNÉS, SJA. and FAVERO, S., Ed. *Meio ambiente e produção interdisciplinar: sociedade, natureza e desenvolvimento*. Campo Grande: Uniderp. p. 11-25.
- PIVARI, MOD., POTT, VJ. and POTT, A., 2008. Macrófitas aquáticas de ilhas flutuantes (baceiros) nas sub-regiões do Abobral e Miranda, Pantanal, MS, Brasil. *Acta Botanica Brasílica*, vol. 22, no. 2, p. 563-571.
- PONCE, VM. and NUNES DA CUNHA, C., 1993. Vegetated earth mounds in tropical savannas of Central Brazil: a synthesis with special reference to the Pantanal do Mato Grosso. *Journal of Biogeography*, vol. 20, p. 219-225.
- POTT, A., 1988. *Pastagens no Pantanal*. Corumbá: EMBRAPA-CPAP. 58 p. Documentos, no. 7.
- , 1994. Ecosistema Pantanal. In: PUIGNAU, JP., Ed. *Utilización y manejo de pastizales*. Montevideo: IICA-PROCISUR. p. 31-44. IICA-PROCISUR Diálogo, no. 40.
- POTT, A. and POTT, VJ., 1994. *Plantas do Pantanal*. Brasília: Embrapa. 320 p.
- , 1999. Flora do Pantanal – listagem atual de fanerógamas. In *Anais do Simpósio sobre Recursos Naturais e Sócio-Econômicos do Pantanal, Manejo e Conservação*, 2, 1996. Corumbá: Embrapa Pantanal. p. 297-325.
- , 2004. Features and conservation of the Brazilian Pantanal. *Wetlands Ecology and Management*, vol. 12, no. 6, p. 547-552.
- , 2005. Alterações florísticas na Planície do Baixo Taquari. In GALDINO, S., VIEIRA, LM. and PELLEGRIN, LA., Ed. *Impactos ambientais e socio-econômicos na Bacia do Rio Taquari, Pantanal*. Corumbá: Embrapa Pantanal, p. 261-293.
- , 2009. Vegetação do Pantanal: fitogeografia e dinâmica. In *Anais do II Simpósio de Geotecnologias no Pantanal*. Corumbá: Embrapa Informática Agropec./INPE. p. 1065-1076.
- POTT, VJ. and POTT, A., 2000. *Plantas Aquáticas do Pantanal*. Brasília: Embrapa. 404 p.
- PRADO, PE. and GIBBS, PE., 1993. Patterns of species distribution in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden*, vol. 80, p. 902-927.
- PRADO, PE., GIBBS, PE., POTT, A. and POTT, VJ., 1992. The Chaco-Pantanal transition in southern Mato Grosso, Brazil. In FURLEY, PA., PROCTOR, J. and RATTER, JA., Ed. *Nature and Dynamics of Forest-Savanna Boundaries*. London: Chapman & Hall. p. 451-470.
- PRANCE, GT. and SCHALLER, G., 1982. Preliminary observations on vegetation types of the Pantanal, Mato Grosso, Brazil. *Brittonia*, vol. 34, no. 2, p. 228-251.
- RATTER, JA., POTT, A., POTT, VJ., CUNHA, CN. and HARIDASAN, M., 1988. Observations on woody vegetation types in the Pantanal and at Corumbá, Brazil. *Notes from the Royal Botanic Garden of Edinburgh*, vol. 45, no. 3, p. 503-525.
- SAMPAIO, AJ., 1916. A flora de Matto Grosso: memória em homenagem aos trabalhos da Comissão Rondon. *Archivos do Museu Nacional*, vol. 19, p. 1-125.
- SILVA, JSV., ABDON, MM. and POTT, A., 2007. Cobertura vegetal do Bioma Pantanal em 2002. In *Anais do XXIII Congresso Brasileiro de Cartografia*. Rio de Janeiro: Sociedade Brasileira de Cartografia. p. 1030-1038.
- SILVA, MP., MAURO, R., MOURÃO, G. and COUTINHO, M., 2000. Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. *Revista Brasileira de Botânica*, vol. 23, no. 2, p. 143-152.
- SOARES, JJ. and OLIVEIRA, AKM., 2009. O paratidal do Pantanal de Miranda, Corumbá, MS, Brasil. *Revista Árvore*, vol. 33, no. 2, p. 339-347.
- SPICHIGER, R., BISE, B., CALENGE, C. and CHATELAIN, C., 2007. Biogeography of the Forests of the Paraguay-Paraná Basin. In PENNINGTON, T., LEWIS, GP. and RATTER, JA., Ed. *Neotropical savannas and seasonally dry forests, plant diversity, biogeography and conservation*. Boca Raton: Francis & Taylor. p. 193-211.
- UETANABARO, M., SOUZA, FL., LANDGREF FILHO, P., BEDA, AF. and BRANDÃO, RA., 2007. Anfíbios e répteis do Parque Nacional da Serra da Bodoquena, Mato Grosso do Sul, Brasil. *Biota Neotropica*, vol. 7, no. 3, p. 279-289.
- VELOSO, HP., 1947. Considerações sobre a vegetação de Mato Grosso. II. Notas preliminares sobre o Pantanal e zonas de transição. *Memórias do Instituto Oswaldo Cruz*, vol. 45, p. 253-272.
- , 1972. *Aspectos fito-ecológicos da Bacia do Alto Paraguai*. São Paulo: USP. USP, Biogeografia, no. 7.