

What is the Flora of the Pantanal Wetland?

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ABSTRACT

The Brazilian Pantanal is a vast Neotropical wetland, in the upper Paraguay River basin. Rainfall and flooding are seasonal. The landscape is heterogeneous showing a mosaic of vegetation types. Overall, it is predominantly a savanna, with aquatic plants, riparian and dry forests, forest islets, woodlands, grasslands and many monodominant formations. The flora is composed of over 2,200 species of Angiosperms, and the species-richest families are Fabaceae (Pea Family) and Poaceae (Grass Family), each with over 300 species, followed by Asteraceae (Daisy Family) and Cyperaceae (Sedge Family), both with more than 100 species each. The species richest genera are *Paspalum*, *Ipomoea* (morning glories), *Mimosa* (sensitive plants), *Croton*, *Eugenia*, *Ludwigia* (primroses) and *Arachis* (wild peanuts). Very few are endemic species, as the region is geologically recent. The flora comes from surrounding domains, such as Cerrado, Chaco, Amazon, and Atlantic Forest, although most species have broad distribution. However, their arrangement and dynamics are unique in the Pantanal. Human population is quite low, except on the edges. Cattle ranching is the main economy for over 200 years. The conservation status of the Pantanal is still considered rather natural and pristine. Tourism is increasing, mainly for the abundant wildlife.

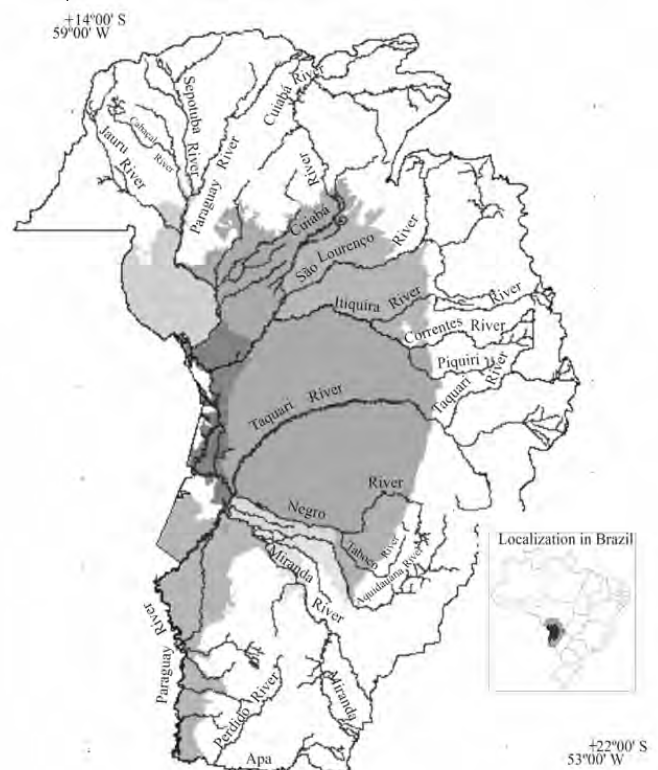
INTRODUCTION

The Pantanal is the largest continuous freshwater wetland in South America, located in the middle of the continent, with 140,000 km² in Brazil (Figure 1), and additional 15,000 km² in near Bolivia and 5,000 km² in Paraguay (Junk et al. 2011). It is situated in a vast intracontinental flat lowland, filled with Pliocene-Pleistocene sediments, forming a somewhat inland delta in the upper Paraguay River basin (Junk et al. 2011). It is a heterogeneous wetland for its complex hydrology (Junk et al. 2011), sediments and vegetation types, and for that reason it has been subdivided into 11 subregions. The term Pantanal, derived from *pântano* or swamp, can be misleading since most of the

region is not a swamp, but seasonally flooded land that also includes slightly higher flood-free ground.

The climate is typical of savanna, type Aw (tropical wet-and-dry), with annual rainfall around 800-1400 mm, most of which comes from variable summer rains (Arruda et al. 2016; Figure 2) creating an oscillating pluriannual flood cycle (Pott and Pott 2004), as shown in Figure 3. The irregular flood regime has been associated with oscillations of sea surface temperature such as ENSO (El Niño South Pacific Oscillation) (Thielen et al. 2020). The general flood pulse is monomodal (Junk et al. 2011), although the Paraguay River tributaries such as Aquidauana can show more than one yearly flood peak. Rainfall is higher in the upper watershed, wherefrom whatever surplus runs off to the plain. The asynchrony between local rainfall and delayed river flood creates a prolonged wet period for the riverine vegetation, allowing some Amazon rain forest species to grow there.

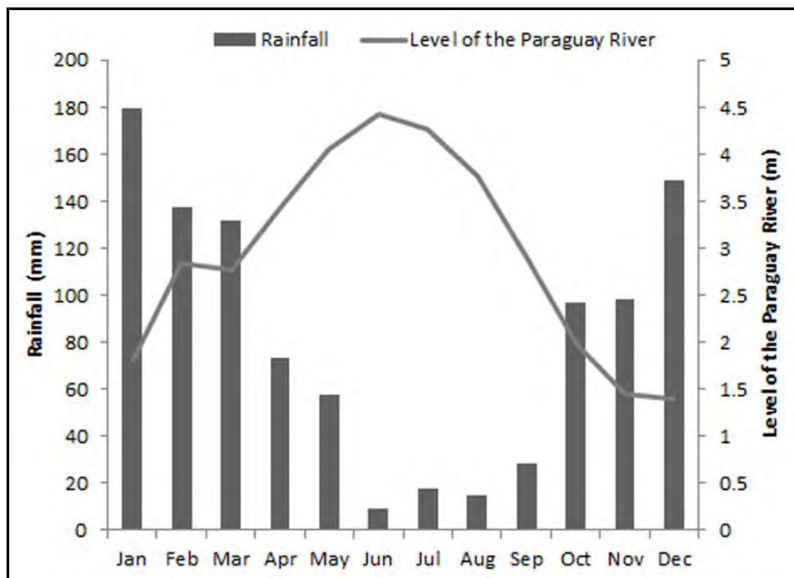
FIGURE 1. Map of the Brazilian Pantanal wetland (grey) and the upper watershed (white) with the tributaries of the Paraguay River. (Source: Arruda et al. 2016.)



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FIGURE 2. Mean monthly rainfall and Paraguay River level (Brazilian Navy fluviometric gauge at Ladário), showing the asynchrony of rains and flooding. (Source: Arruda et al. 2016.)



Research on the Pantanal in the last 30-40 years has been made mainly by local institutions such as Embrapa Pantanal, IPP (Research Institute for the Pantanal) and several universities (i.e., Federal University of Mato Grosso do Sul - UFMS, Federal University of Mato Grosso - UFMT, Catholic University Don Bosco - UCDB, University of the State of Mato Grosso – Unemat, and University for the Development of the State and the Pantanal Region – Uniderp), sometimes with collaboration of other Brazilian and international scientists.

PLANT LIFE IN THE PANTANAL

The flora of the Pantanal wetlands is represented by over 2,200 native species of Angiosperms, according to the updated checklist we compiled from reliably identified vouchers in herbaria, strictly considering the sedimentary floodplain. Nearly 800 species are illustrated in our two identification guides (Pott and Pott 1994, 2000). The most numerous families are Fabaceae (Pea Family) and Poaceae (Grass Family), each with over 300 species, followed by Asteraceae (Daisy Family) and Cyperaceae (Sedge Family), both with more than 100 species. Genera exceeding 20 species are *Paspalum*, *Ipomoea*, *Mimosa*, *Croton*, *Eugenia*, *Ludwigia* and *Arachis*. That follows the pattern of species of these genera being very abundant in Neotropical open vegetation types. Due to the recent geological age of the floodplain, very few species are endemic to the Pantanal, and five of them remarkably belong to the genus *Arachis* (wild peanuts).

The number of aquatic macrophytes is over 300 species. The species-richest families are Cyperaceae and Poa-

ceae, with the richest genera being *Bacopa* (water-hyssops), *Cyperus* (umbrella sedges), *Eleocharis* (spike rushes), *Ludwigia* (water primroses), *Rhynchospora* (beak rushes), and *Utricularia* (bladderworts). The Pantanal has a range of aquatic habitats and seasonally wet zones that favor a diversity of species. Most aquatic species are common to other vast South American wetlands, such as the Paraná River floodplain (extending from Brazil to the Esteros de Iberá in Argentina; Neiff et al. 2011), Amazonia (including Araguaia, Guaporé and Amapá in Brazil, and the Beni region in Bolivia; Haase and Beck 1989), and the Llanos and Orinoco basin in Colombia and Venezuela (Rial 2009).

Wherefrom does the flora come? The plants of the Pantanal wetlands are composed of species from the surrounding phytogeographical provinces: Cerrado, Chaco, Amazonia and Atlantic Forest, in addition to a major contingent considered of wide distribution (Pott and Pott 2004). Cerrado, the Bra-

zilian savanna, nearly surrounds the entire Pantanal. Chaco is a unique vegetation type in Brazil, located the southernmost subregion of the Pantanal - in Porto Murinho, on the Paraguayan border, belonging to the Humid Chaco (Prado et al. 1992). Amazonian species reach the riparian forests because the overflow of the Paraguay River has a three-month delay from the rainy season (i.e., it overflows three months after the local and upper watershed rainy season; Figure 2). That adds meteorological and edaphic wet periods with a similar effect of an Amazonian climate. The Atlantic Forest species include elements from the Seasonally Dry Forest. The wide-ranging group represents half of the species of the Pantanal plain (Pott and Ratter 2011; Pott and Silva 2015) and includes all plant habits, most of them grassland herbs. However, the plant diversity of the Pantanal is unique, despite the flora being made up of associations of species from various phytogeographical origins (Pott and Ratter 2011), tolerant of a harsh wet-and-dry environment.

The number of naturalized species is relatively high but mostly concentrated on less flooded ground. We can deduce that in a future scenario of a drier Pantanal, they will expand their distribution. Indeed, *Leucaena leucocephala* (leucaena or white lead tree, a fast-growing tree from Central America and Mexico) is already spreading on road embankments. So far, there are no massive exotic woody invaders that are common in other tropical wetlands, although some native shrubs (*Mimosa* spp. and *Vernonanthura brasiliensis*) and trees (e.g., *Curatella americana*) increase in dry years. There are many naturalized herbaceous plants, mainly on less floodable grasslands. The few exotic

weeds to invade permanently wet habitats are *Panicum repens* (torpedo grass) and the worst invader *Urochloa arrecta* (tanner grass) (Pott and Pott 2004).

Overall, most of the vegetation of the Pantanal is predominantly a seasonally flooded savanna (Pott and Pott 2004), with mosaics of aquatic plants (including floating mats, floating meadows and swamps) (Figure 3), riparian forest, dry forest, forest islets, woodlands, grasslands (Figure 4), and many monodominant formations. Plant species are arranged over a flooding gradient varying from lakes and permanent swamps to flood-free ancient levees, and floodable grassland in between (Figure 5). Soils vary in texture and fertility from 97% sandy to heavy clays, according to the sediment type. The largest alluvial fan in the Pantanal is the Taquari River, encompassing 50,000 km² of sand.

A striking feature of the Pantanal is the monodominant vegetation types, mainly floodable savannas or woodlands, with a single dominant tree, such as *Attalea phalerata* (urucuri palm or *acuri*), *A. speciosa* (babassu palm), *Byrsonima cydoniifolia* (*canjiqueira*), *Copernicia alba* (caranday palm or *carandá*) (Figure 6), *Erythrina fusca* (purple coral tree or *abobreira*), *Handroanthus heptaphyllus* (pink trumpet tree or *piúva*) (Figure 7) and its relative *Tabebuia aurea* (Caribbean trumpet tree or *paratudo*) (Figure 8). Some of the monodominant species cause encroachment on natural grasslands, e.g., the trees *Curatella americana* (sandpaper tree or *lixeira*) and *Vochysia divergens* (*cambará*) (Figure 9), and shrubs as *Combretum* spp. (*pombeiro*). Some herbaceous species are also monodominant such as *Cyperus giganteus* (giant sedge or *piri*, similar to the Nile papyrus), *Elyonurus muticus* (*carona*), *Oryza latifolia* (wild rice), *Thalia geniculata* (fireflag or *caeté*) (Figure 10) and *Typha domingensis* (cattail or *taboa*).

A very interesting vegetation type is the floating meadow (Figure 11). It is a floating islet that starts from a floating mat of free-floating plants such as *Salvinia auriculata* (water fern). On its top the sedge *Cyperus blepharoleptos* (formerly *Oxycaryum cubense*) germinates as an epiphyte and grows, forming a dense rhizomatous entangled meadow where debris and decaying plants accumulate. Within a few years a layer of floating organic soil (histosol) builds up. Caymans and birds nest on it. When that floating soil reaches 1 m deep, it is possible to walk on, and even shrubs and a few treelets grow on it. That sudd can clog old river beds and canals, or drift by winds or float downstream. When the lake dries out, the plants die, the organic soil decomposes or can be consumed by a wildfire, and the process restarts after the water returns.

Interestingly, alkaline ponds (pH 8-10) called “salinas” also occur; they are surrounded by a flood-free ridge covered with dry forest and so isolated from other waters.

FIGURE 3. Zonation of monodominant stands: anchored floating mats of water hyacinths (*Eichhornia azurea* + *E. crassipes*) and *Pontederia rotundifolia*, on the left, and emergent *Oryza latifolia* (wild rice), on the right, western border of the Pantanal wetland, Brazil. (Photo by A. Pott, June 2, 2009.)



FIGURE 4. Floodable grassland, at drawdown, Pantanal wetland, Brazil. (Photo by A. Pott, June 12, 2007.)



FIGURE 5. Typical landscape of the Pantanal wetland, with pond, floodable grassland and seasonal forest or woodland, over the topographic flooding gradient, at the end of flood in a wet year, Brazil. (Photo by A. Pott, May 9, 2009.)



FIGURE 6. Monodominant stand of *Copernicia alba* (caranday palm or *carandá*), Paraguay River, Pantanal wetland, Brazil. (Photo by A. Pott, July 9, 2013.)



FIGURE 8. Monodominant floodable savanna of *Tabebuia aurea* (Caribbean trumpet tree or *paratudo*), at flood, Pantanal wetland, Brazil. (Photo by P.R. Souza, May 22, 2007.)



FIGURE 10. Monodominant stand of *Thalia geniculata* (fireflag or *caetê*), Paraguay River floodplain, Pantanal wetland, Brazil. (Photo by A. Pott, June 3, 2009.)



FIGURE 7. Monodominant floodable savanna of *Handroanthus heptaphyllus* (pink trumpet tree or *piúva*, or *ipê-rosa*), in the dry season, Miranda River floodplain, Pantanal wetland, Brazil. (Photo by A. Pott, September 2000.)



FIGURE 9. Monodominant floodable forest of *Vochysia divergens* (*cambará*), at flower, along seasonal streams, in flooded grassland, at drawdown, Pantanal wetland, Brazil. (Photo by Fábio Edir Costa, July 29, 2008.)



FIGURE 11. Floating meadow with 1m deep histosol (8 persons walking on including the photographer): *Polygonum acuminatum* in the foreground, the red plant is *Rhynchanthera novemnervia*, and riparian forest in the back, in the lake Baía Vermelha, near the Paraguay River, Pantanal wetland, Brazil. (Photo by A. Pott, June 2, 2009.)



Scarce angiosperms grow inside, e.g., *Ceratophyllum* spp. (hornworts), besides Characeae (large algae); the water is a soup of algae, resulting in ponds of various colors. While there are no fish, amphibians, myriads of small crustaceans and water insects attract young caymans and migratory birds such as sandpipers.

FACTORS AFFECTING VEGETATION

We have analyzed soil seed banks from seasonal ponds, floodable grasslands, *Tabebuia aurea* (Caribbean trumpet tree) monodominant savanna, and riparian forest, and found that annual species predominate even under forest. The discrepant composition of the standing vegetation and the seed bank is a general finding. Under simulated flooding, aquatic plant seedlings emerged from the soil samples, while switching to terrestrial species after alternation to drained conditions. We called this a “flexible seed bank” – one that is ready to occupy gaps in either the dry or wet season quickly. Furthermore, the aquatic plants can hold the exotic grasses back (Bao et al. 2020).

As a seasonal savanna, the Pantanal undergoes wild-fires, often lit by lightning mainly on the surrounding hills, then fed by dry biomass of grasslands and accumulated histosol. The vegetation evolved under fire. Interestingly, even riparian forests regenerate after fires and exhibit a striking favorable interacting response to fire and flood (Arruda et al. 2016). The most fire-prone habitats are ungrazed deep-flooded grasslands along the Paraguay and Miranda Rivers, compared with less flooded savannas where cattle stay year-round. When cattle are excluded, the grasslands either in swamps or dryland change to tall tussock grasses that are fuel for inevitable wildfires. In 1988, we excluded the cows from a 680 ha preserve to see what would happen: within one year the short creeping grasses were replaced by tall bunch grasses, and wildfire has swept through many times, despite the presence of a 10 m wide firebreak. The same has occurred in other areas, e.g., the 108,000 ha private preserve SESC Pantanal, created in 1996, frustrating the expectation that the grasslands would turn into a forest after cattle exclusion. Prescribed burning can be a management tool for conservation.

Despite over 200 years of cattle ranching on native grasslands, the impact seems to be low because there is a surplus of available forage grass, amounts far above what can be consumed by the few species of native herbivorous mammals (Pott and Pott 2004). The most numerous of these herbivores are capybaras (*Hydrochoerus hydrochaeris*, the world’s largest rodent). Others are naturally more scattered, sometimes with vigorous populations despite being threatened elsewhere; they include the pampas deer (*Ozotocerus bezoartius*), a few related deer species (i.e., brockets, *Mazama* spp. and marsh deer, *Blastocerus*

dichotomus), plus the tapir (*Tapirus terrestris*). This surplus of forage is quite different from the situation in African savannas that are under high pressure from herds of herbivores. The worst impact in the Pantanal has been from tree clearing of ridges for cultivated pastures. However, lately, deforestation has lost financing and lessened this activity in the region. Instead, many areas of coarse grasses are being replaced by *Urochloa humidicola* (koronivia grass – an African tropical forage species, widely cultivated in South America) around the woody patches on hummocks, thereby maintaining the general landscape pattern and even reducing fire incidence. Besides, capybara and deer relish this evergreen introduced grass.

Buffaloes have a heavy impact, mainly in ponds, as we observed, reducing the species richness, in favor of a few benefiting from their dung, e.g., *Pistia stratiotes* (water lettuce). They are no longer raised in the Pantanal because they escape and become feral.

HAVENS FOR WILDLIFE

Like other sedimentary floodplains and alluvial fans, the Pantanal contains various types of water bodies, such as rivers, river branches, old river beds, oxbow lakes, lakes, permanent and temporary ponds, seasonal streams and flooded grasslands. All these water bodies are habitat for the abundant wildlife: fish, anaconda, bulldog bat, giant otter; birds such as anhinga, cormorant, ducks, herons, ibis, jabiru stork, kingfishers, limpkin, screamer, skimmer, spoonbill, terns, wattled jacana, wood stork, and many more. However, for the most part, there is no permanent water, only seasonal water bodies including excavated water holes or where underground water is pumped for cattle, and it is, of course, also utilized by the wild fauna. The harmonic coexistence of domestic and wild animals begins by sharing that provided water, as well as the salt.

Despite being floodable, the Pantanal is also rich in terrestrial fauna, such as agouti (rodents), armadillos, coati-mundi, crab-eating foxes, giant anteaters, howler monkeys, and peccaries. The big cats – jaguar and puma - are also frequent. Many species of birds, especially three species of macaws including the hyacinth macaw (elsewhere endangered), as well as parrots, parakeets, cardinals, the noisy speckled chachalaca, burrowing owl, flycatchers, hummingbirds, lapwing, red-legged roadrunner, rhea, toucans and woodpeckers.

HUMAN USE AND CONSERVATION

The Pantanal people do not hunt for meat, except the non-native feral pig, as they prefer beef. For over 200 years, people have raised cattle in the region. The human population is quite low on the plain, except in a few towns on the edges. Crop agriculture is not allowed on the plain,

however it is naturally limited by unfavorable soils. A subsistence shift cultivation used to be practiced by riverside inhabitants and is now legally restricted under protective environmental laws. Nonetheless, land mismanagement in the 1980s (e.g., land clearing *Cerrado* woodland of sandy slopes for cattle pastures, creating deep gully erosion and damaging small headwater wetlands called *veredas*) in the upper watershed is interfering with water and soil conservation, causing significant river silting downstream, mainly in the Taquari River that has lost its bed and gallery forest and became a swamp. Silt and overflow is spreading over a nearly permanently flooded delta. Compared with the Pantanal plain, the upper watershed has a higher richness of aquatic plants, as well as of endemic species, mainly in *vereda* wetlands in the *Cerrado* savanna. These wetlands are wet year-round, functioning as water storage for the creeks that feed the rivers. There are also springs on karstic limestone of the Serra da Bodoquena plateau that support a different aquatic flora (Pott 1999).

The official conservation areas are the National Park of Pantanal, the State Park Rio Negro, the State Park Encontro das Águas, and the Taiaman Biological Station (Ramsar site). Fishing is controlled, forbidden during the spawning period when river waters rise in the rainy season. Ecotourism is a growing economic activity in the region, for its abundance of wildlife and scenery, e.g. bird watching. There is also a potential for scientific tourism. In conclusion, as already stated (Heckman 1998; Junk et al. 2011), the overall conservation status of the Pantanal is still high, and it is considered a pristine, natural wetland. ■

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