

Geraldo Alves Damasceno-Junior
Arnildo Pott *Editors*

Flora and Vegetation of the Pantanal Wetland

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Geraldo Alves Damasceno-Junior • Arnildo Pott
Editors

Flora and Vegetation of the Pantanal Wetland

 Springer

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*I want to dedicate this book to the memory of
my mother, Eunice Silva Santos
(1936–2021), who was going along with me
during this book realization but did not
survive the pandemic to see the end.
(Geraldo A. Damasceno-Junior)*

Foreword

The Pantanal is one of the largest tropical floodplains in the world, with a total of circa 160,000 km² of which some 140,000 km² in Brazil. The rest is located in parts of Bolivia and Paraguay that are adjacent to the Brazilian Pantanal. The annual flooding in the Pantanal, during and following the rainy season, is mainly caused by the overflow of the rivers, and the inundation can last from about 20 to more than 270 days per year, depending on local topographic features and the amount of influx of water. Although the local differences in elevation may be rather small, they have strong impacts on the length of the period of inundation and the depth of flooding and they created strong contrasts in habitat conditions and vegetation types. Across rather short elevational gradients, strong differences in ecological conditions occur allowing “cacti to grow very near to aquatic plant species”, or more accurately: patches of tropical forest and wooded savanna vegetation (“cerrado” and “cerradão”) are superseded by herbaceous vegetation and still lower down by aquatic vegetation. During the dry season, fires are frequent and recurrent, favoured by low air humidity ratios and boosted by strong winds.

Though many local studies on a rather varied array of detailed inventories, and of biological and ecological features and aspects of land-use have been carried out, and the results have been published, mainly in Portuguese in specialized journals and reports, so far there was no integrated overall account of the plant growth and ecology of the Pantanal, certainly not in English. It was lucky therefore that the main editors of the present volume, Dr. Geraldo Alves Damasceno-Junior and Dr. Arnildo Pott, both of the Universidade Federal de Mato Grosso Do Sul in Campo Grande, MS, Brazil, offered to establish a large team of local specialists to create such an integrated overview of the presently existing floral and plant ecological knowledge of the Pantanal. In the following chapters the authors attend to patterns in the species composition, diversity and endemism in the flora and vegetation of the Pantanal, and discuss the biogeographical relations with the adjacent areas covered with tropical forests of the Amazon and the Atlantic coast of Brazil, with the “cerrado” and “cerradão” and the “chaco”. They also point out what is known of the inundation ecology and fire ecology of the species and vegetation types, of their phenology, reproduction and seed dispersal, and they pay attention to the practical

use of the various species and vegetation types. They created a stimulating work of reference for researchers and students, well-illustrated by photographs and informative maps.

This volume was written and completed in a very disturbing period of time, with the Corona-COVID-19 virus raging fiercely in Brazil, taking the lives of many, and also twice hitting one of the main editors (GAD-J), but luckily he recovered and proceeded with this book. I congratulate the main editors and all authors with the completion of this useful book. For me it was a pleasure to work with you on this book project, and I am very pleased to present it as a volume in the series Plant and Vegetation to the international readership.

Utrecht, The Netherlands

Marinus J. A. Werger

Preface

“Pantanal destroyed by flames”, “Pantanal in fire” were headlines in 2020. However, is it still considered a pristine and natural wetland? The book comes at a timely moment to help to understand all that. Being a wetland, should it not be flooded? Why, how, where, and when the Pantanal burns? And will it recover?

The book is intended to be of interest to researchers, lecturers, teachers, students, botanists, biologists, ecologists, wetland scientists, environmentalists, tourists, policy makers, land managers, conservationists, and other Nature lovers.

Probably we can explain why the Pantanal is so surprising, unpredictable, and unstable, although so resilient. Not long ago, there was very little information on flora and vegetation of the Pantanal. Nowadays, numerous reports are available, but still scattered. Therefore, we invited experts on various themes related to flora and vegetation of the Pantanal to bring together the existing knowledge and our field experience to fulfill the demand for this state-of-the-art book.

Campo Grande, Mato Grosso do Sul, Brazil

Geraldo Alves Damasceno-Junior
Arnildo Pott

Acknowledgments

This book received an effective collaboration from about 50 reviewers that dedicated time to help us improve the quality of what the authors have done. We are very grateful to these reviewers since, without them, this publication would be impossible. We are also grateful to the Federal University of Mato Grosso do Sul that sponsored our work and the colleagues who relieved us of some duties during this book accomplishment. We are also grateful to the Brazilian agencies who have been supporting the research that is placed here mainly to CNPq (Brazilian National Council for Scientific and Technological Development), CAPES (Brazilian Coordination for the Improvement of Higher Education Personnel), FUNDECT (State Foundation for Science and Technology of Mato Grosso do Sul), and FINEP (Studies and Projects Financing Agency).

We also wish to thank Marinus J.A. Werger, João Pildervasser, Luciana Christante de Mello, Meenahkumary Aravaj and all the Springer editorial team for the confidence in our work and for being patient with the process of this book production that was hindered by many personal problems and the COVID pandemic.

We want to thank our families who had to undergo the process of this book construction, especially our sons.

Geraldo Alves Damasceno-Junior
Arnildo Pott

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Chapter 1

General Features of the Pantanal Wetland



Geraldo Alves Damasceno-Junior and Arnildo Pott

1.1 General Information on the Pantanal and Book Contents

The Pantanal is the world's largest continuous tropical freshwater wetland, an inland floodplain (Nunes da Cunha and Junk 2014; Assine et al. 2015c). There is some controversy on the size of the Brazilian Pantanal, depending on the criteria to define its limits; most accepted is the delimitation of 138,183 km² (Silva and Abdon 1998), similar to a previous estimate of 137,000 km² (Hamilton et al. 1996). It extends into Paraguay (5,000 km²) and Bolivia (15,000 km²) (Junk and Nunes da Cunha 2012). The Pantanal is part of the High Paraguay River Basin. Together with the floodplain, the Upper Paraguay basin has 496,000 km², including 363,442 km² in Brazil and 132,558 km² in Bolivia and Paraguay (ANA 2003). In a general way, we consider the Pantanal restricted to only the floodplain; but in socio-economics and nature conservation, the discussion about the Pantanal also encompasses the residual hills located along the Brazilian western border of the plain. These hills are much older residual relief relicts, *i.e.*, inselbergs or tops of partially buried hills (*morros*), e.g., from North to South: Solteiro, Taiamã, Caracará, Campo, Amolar, Chané, Sargento, Azeite, Comprido, Grande, Coimbra, Fecho dos Morros and Pão de Açúcar; they are connected underneath the surface to the nearby mountain ranges. These hills are surrounded by seasonally floodable areas (Fig. 1.1). In this book, most chapters use the concept of the Pantanal as only the floodplain, but some, e.g., Lichens (Chap. 6) and Wild Food Plants (Chap. 19), include information on the hills.

The Pantanal kept the old name Pantanal Matogrossense, meaning from Mato Grosso (MT), although 2/3 of the area is in the State of Mato Grosso do Sul (MS), split in 1977. Therefore, the designation Pantanal of Mato Grosso do Sul or South Pantanal is sometimes used, but we prefer to call it all just Pantanal.

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Fig. 1.1 Hills surrounded by the floodplain of the western border of the Pantanal

The lowland genesis is associated with the Andes uplift and associated subsidence of part of the Upper Paraguay Basin (Del'Arco et al. 1982; Ab'Sáber 1988). The basin subsidence with the first sedimentation process has begun at an undetermined time between Paleocene and Miocene (Assine et al. 2015c). The subsidence process is still in progress, and most of the sediments that nowadays cover the surface of the floodplain are from the Quaternary (Assine et al. 2015b). There are many megafans, the greatest being the Taquari megafan with circa 50.000 km² and up to > 400 m deep sediments. There is a discussion about the origin of these sediments, especially of the Taquari megafan. Some authors (Tricart 1982) claim an aeolian origin of this extremely high amount of sand. Nevertheless, the alleged ancient dunes were not confirmed (Irion et al. 2011), though they existed previously on the highlands.

One of the first comprehensive surveys on the Pantanal was made by the Radambrasil Project, based on radar images (Alvarenga et al. 1982). The Pantanal as a floodplain is very flat with a slope of 30–50 cm/km in the east-west direction and 3–15 cm/km in the north-south direction (ANA 2003). That is the main reason of the inundations in the region. Even being very flat, there are many regional differences, and the Pantanal is subdivided into many subregions that can vary according to the author. One of the most accepted and used subdivisions is the one made by Adámoli (1982) and modified by Silva and Abdon (1998), where the Pantanal has 11 subregions (Fig. 1.2). Other subdivisions were also made (Hamilton et al.

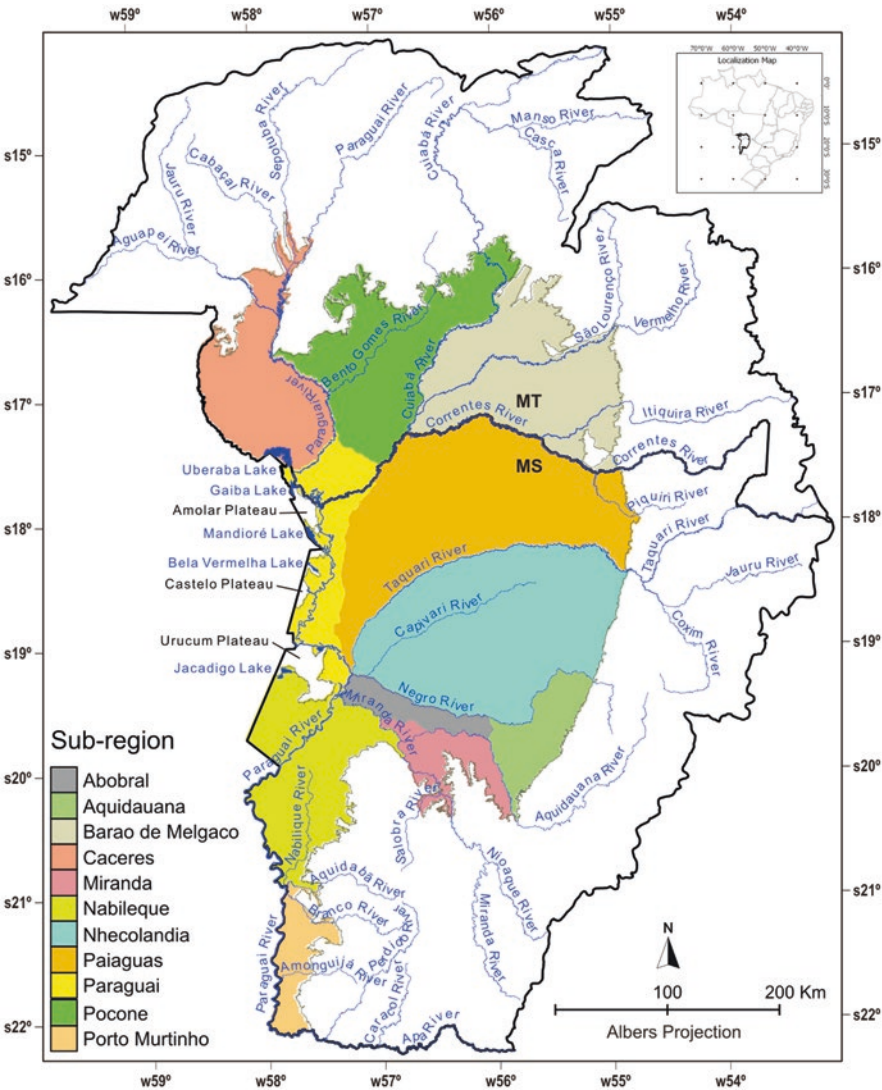


Fig. 1.2 The Brazilian Pantanal, showing its location in the map of Brazil, and its subdivision into 11 subregions and main rivers. Map by João dos Santos Vila da Silva (According to Silva and Abdon 1998)

1996; Padovani 2010). Although having many regional differences, one of the most characteristic geomorphological features of the Pantanal is the contrasts in the microreliefs on the floodplain. That is critical to the vegetation once these microreliefs can define what, where, and how long these environments can be flooded. Some important microrelief features are the paleodikes. These paleodikes receive regional names. When they have a circular or an elliptical form they are called



Fig. 1.3 Aerial photo showing the Pantanal of the Paiaguas landscape with *cordilheiras* (long-lined forested areas) and seasonally flooded grasslands. (Photo by Geraldo Alves Damasceno Junior)

capão (caa = forest and pon = rounded, in Tupy language). When the paleodikes are much longer than wide, then they are called *cordilheiras*. Curious is that *cordilheira* in Portuguese means mountain range or high hills, but here it is used to designate micro-mounds, which are mostly flood-free or flooded only in exceptional flooding (Fig. 1.3). The paleodikes were formed under paleoclimates in the Quaternary (Ab'Sáber 1988; Irion et al. 2011; Assine et al. 2015c); they originated from the lateral movement of the rivers that usually form a fluvial dike when the channel is active. These *cordilheiras*, *capões*, and riparian forests are mainly occupied by woody vegetation. A comprehensive overview of this vegetation can be found in the Chap. 9 on Woody and Palm Vegetation of the Pantanal. Information on the Flora of the whole Pantanal is given in the Checklist chapter (Chap. 3). Nevertheless, if the reader is interested in organized information on how this vegetation is distributed in the entire Pantanal; see the Chap. 2 on Vegetation and Maps. The differences in vegetation physiognomy are also most helpful to distinguish the main habitats in the Pantanal according to the flooding regime. In this book, we can find information on Macrohabitats of the Pantanal using vegetation as an indicator (Chap. 7).

The climate is seasonal Awa according to the Köppen classification (Soriano 1997). The mean annual temperature is 25°C with maxima of 40°C. The mean annual minimum is 21°C, and the absolute minimum is around zero (Soriano 1997). Occasional frosts can also occur. The annual rainfall at the western border of the Pantanal (Corumbá) is below 1100 mm and concentrated between November and March (250–300 mm). Toward the high parts of the Upper Paraguay Basin, there is

an increment in precipitation, reaching more than 1500 mm/year (Alfonsi and de Camargo 1986; Thielen et al. 2020). The Pantanal is located within the Intertropical Convergence Zone, and this generates a circumglobal belt of climatic instability, responsible for deserts and semiarid vegetation (Marsh and Kaufman 2013). The South Atlantic Convergence Zones are responsible for most rain in the Upper Paraguay Basin (Thielen et al. 2020). The pluriannual variation in rainfall is related to La Niña and El Niño-Southern Oscillation (ENSO) and other Sea Surface Temperature Systems (SST). The primary system related to severe droughts in the Pantanal is the warming of SSTs occurring in the North Atlantic and North Pacific oceans (Thielen et al. 2020). These climatic variations can be detected in dendro-chronological records (Fortes et al. 2018; Gris et al. 2020). Low rainfall means lesser flood, associated with more wildfires (see the Chap. 18 on Fire and Flood). These seasonal conditions have effects on the phenological behavior of Pantanal species and also on pollination and dispersal. Some information on species phenology can be found in the chapter on Phenology (Chap. 13) with complements on Pollination and Dispersal for *capão* vegetation (see Chap. 14 on temporal patterns of Pollination and Seed dispersal). The seasonality, sometimes dry, benefits some plant families such as Leguminosae which has the highest number of species in the Pantanal (see Chap. 5 on Leguminosae).

Rivers are avulsive in the Pantanal wetland (Assine et al. 2015a), with a monomodal flood pulse (Junk et al. 1989). The Pantanal has been considered an inland delta, as the rivers have defluents instead of affluents, i.e., inverted branching compared with a standard convergent tributary system. Thus, the main bed of rivers such as the Taquari enter the floodplain with a much larger volume than the discharge at their mouth, which is even more notorious in dry years in the Rio Negro, not flowing anymore near the Paraguay River; indeed, trees grew inside the riverbed during the very dry cycle in 1960–74. Another peculiar phenomenon is rivers running backwards when the delayed flood of the Paraguay River is higher than the water level of tributaries such as the Miranda and Negro in the dry season. The maximum area flooded was 110,000 km² and a minimum of 11,000 km² in rainy years (1979–1987) of higher floods (Hamilton et al. 1996), compared with a maximum of 52,900 km² and a minimum of 5,500 km² in 2000–2009 (Padovani 2010).

The Brazilian Navy has taken daily records of the Paraguay River level at Ladário since 1900, a valuable and much-used data set. In this database pluriannual cycles of floods and drought are noticeable (Fig. 1.4). There was a high variation in the river level from 1900 until 1960. From 1963 until 1973, the Pantanal underwent the driest recorded period. From 1974 until 2018, there was a consistent period of high inundation, and the dry spell in 2020 was consistent with the 1960s (Fig. 1.3). These variations have essential consequence in the vegetation cycles, once there are species that benefit from more inundated years, species that benefit from dry years and fire (see Chap. 18 on Fire, Flood and Vegetation), and species that need the combination of fire and flood to become monodominant (see the Chap. 8 on Monodominant Stands). These seasonal and pluriannual variations in flooding create conditions for the existence of many adaptive features in aquatic and terrestrial vegetation (see the Chap. 16 on Plant Morphoanatomical Adaptations) that can also be metabolic with

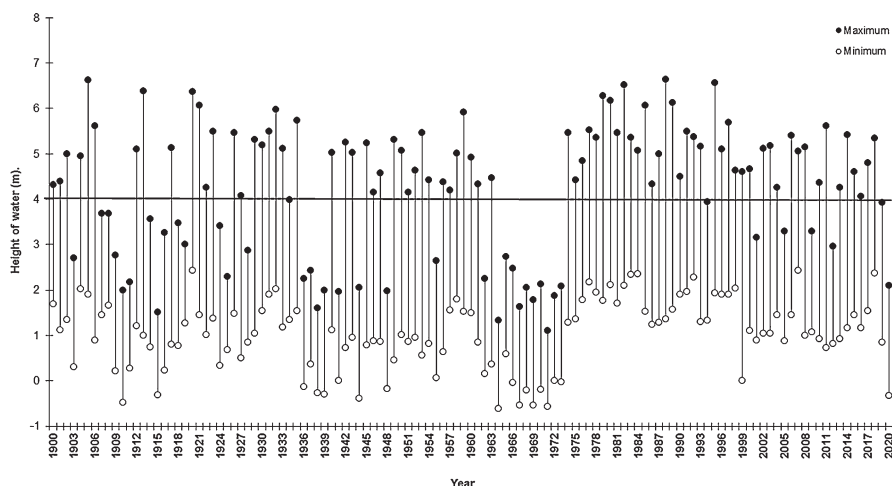


Fig. 1.4 Yearly maximum and minimum levels of the Paraguay River from 1900 to 2020 in Ladário. The 4 m line marks the upward limit for river overflow. (Data provided by the Brazilian Navy)

many compounds of secondary metabolism that can vary according to environmental features (see the Chap. 17 on Metabolomics). One striking feature of the Pantanal vegetation is that it has a flex seed bank where the dry phase activates the terrestrial species, and the aquatic seed bank is active mainly during flooding (see the Chap. 15 on Seed bank).

Most of the Pantanal is considered Aquatic Terrestrial Transition Zone (ATTZ), *i.e.*, under alternating aquatic and terrestrial phases (Junk et al. 1989), associated with various macrohabitats (Nunes da Cunha and Junk 2014) (see the Chap. 7 on Macrohabitats) and their respective vegetation types (see the chapters on Mapping (Chap. 2), Grasslands (Chap. 10), Monodominants (Chap. 8) both in the aquatic (see Aquatic Plants (Chap. 4)) and the terrestrial environments (see the Chap. 9 on Seasonal Forests).

Soils vary from oligotrophic sands on the upper parts of the alluvial fans tending to eutrophic alkaline and saline, heavy clays toward the deltas (Brasil 1982a; Brasil 1982b). Peculiar soil types are the shell-derived calcareous soil (Cunha et al. 1985), the pre-Columbian human-made earth mounds (*aterro*), and the organic histosol of floating mats (see the Chap. 4 on Aquatic Plants).

Ferns and allies were surveyed (Assis and Labiak 2009a; Assis and Labiak 2009b), though not throughout the plain. Bryophytes are not abundant in the Pantanal and yet insufficiently known (Câmara and Vital 2004; Camara and Vital 2006), and the typical wetland moss *Sphagnum* is missing (Heckman 1998). Surveys on fungi are scarce, except lichens, which became better known in the last decade (see the Chap. 6 on Lichenes).

The Pantanal plain is not very favorable to keep ancient records; in fact, it is geologically recent, except the older surrounding high terrain. However, lake

sediments have given evidence on the history of climate, fire, and vegetation (Power et al. 2016). In the limestone at Corumbá fossils of foraminifera have been found, e.g., *Corumbella wernerii*, named after Corumbá, and a little horse (*Equus vandonii*). For fossil pollen, see the Chap. 12 on Palynology.

The most ancient archeological site in the Pantanal was found in the Paraguay River in Ladário with nearly 8200 years. The inhabitants at this locality were dedicated to collecting molluscs, fishing, and there are no records of ceramic or the use of plants. People lived in this location from 150 to 200 years (Schmitz et al. 2014). After that, from 6000 to 4000 ybp, there was a climatic optimum, and archeological sites that show uses of plants extensively in the floodplain. These archeological sites are embankments built with mollusc shells to escape from inundation. They can be found along rivers such as the Paraguay and Miranda and spread over the floodplain in the Abobral subregion (Schmitz et al. 2009; Peixoto and de Arruda 2015) in forest islets (*capão*), on calcareous soils (Schmitz et al. 2009). There are lithographs on the lateritic foothills of the Serra do Urucum and on the rocks of the Paraguay River margin (Schmitz et al. 2014). The use of Pantanal plants by indigenous people is documented (Oliveira 1996), and detailed information is given in the Chap. 19 on Wild Native Food Plants of the Pantanal.

For over two centuries the primary land use is traditional cattle ranching (see the Chap. 10 on Natural Grasslands) on the 95% private land, followed by fishing and ecotourism. The human population is scattered, living on cattle ranches, in tourist resorts, and in a few riverside villages; towns are only peripheral, and there are few roads and schools are scarce. The Paraguay River is utilized for navigation to transport grain, iron ore, cement, cattle, tourists, and residents. Grasslands cover most Pantanal areas (see the Chap. 2 on Maps), and the primary use of the vegetation is as native pastures where the management is made with the use of fire on tough grasses (see the Chap. 18 on Fire). The pluriannual variation in the flooding regime can promote some bush encroachment that is a challenge for the sustainable management of many native pastures (see the Chap. 11 on Encroachment). Even with the main use as native pastures, the Pantanal has undergone deforestation and that is stronger near the borders (Guerra et al. 2020). That places an extra challenge to the management, treated in the Restoration chapter (Chap. 20).

The Pantanal was declared National Heritage by the Brazilian constitution, and Natural Humanity Heritage, and Biosphere Reserve by UNESCO; however, most still is private land, except official parks and indigenous land.

National and State Parks include: Parque Nacional do Pantanal (includes the old Biological Reserve Caracará) (MT), Ecological Station Taiamã (MT), Encontro das Águas State Park (MT), Pantanal do Rio Negro State Park (MS), Park Road (MS), Baía Negra Municipal Protected Area, and Ramsar Sites (MS, MT). The main Indian reserves are Reserva Indígena Kadiwéu (in part within the Pantanal, MS), Ilha Insua (MT), and Perigara (MT).

There are a growing number of RPPNs (a legal category of conservation unit, Private Reserves of the Natural Patrimony). In Mato Grosso: Estância Ecológica SESC Pantanal (the largest, 108,000 ha), Doroché, Fazenda São Francisco do Perigara. In Mato Grosso do Sul: Acurizal, Penha, Rumo ao Oeste, Arara Azul,

Caiman Ecological Refuge, Dona Aracy, Fazenda Alegria, Fazendinha, Neivo Pires/Portal do Pantanal Sul, Nhumirim, Paculândia, Pioneira do Rio Piquiri, Poleiro Grande, Rancho Seguro, Reserva Natural Eng. Eliezer Batista, Rio Negro, Santa Cecília, Santa Sofia, and Tupaciara (Nunes da Cunha and Junk 2014; IMASUL 2021).

Despite its main economic activity as cattle ranching, this high number of private conservation units represents the high potential of the Pantanal for other economic activities still poorly developed, such as tourism. The economics and other not easily valuable aspects are also evaluated in the Chap. 21 on Ecosystem services. More about non-vegetation themes can be found in other books on the Pantanal (Junk et al. 2011; Bergier and Assine 2016). We hope that the reader may benefit from our efforts to assemble this information in a single publication and that it can be helpful to stakeholders, researchers, students, decision-makers, and the general public interested in tropical wetland vegetation.

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Chapter 2

Classification and Mapping of the Vegetation of the Brazilian Pantanal



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2.1 Introduction

This chapter connects with most other chapters, such as Flora (Chap. 3), Aquatic Plants (Chap. 4), Monodominants (Chap. 8), Native Grasslands (Chap. 10), Phenology (Chap. 13), Fire and Encroachment (Chap. 18).

The Pantanal is a geologically young (Quaternary) sedimentary plain, which undergoes variable inter- and intra-annual flooding, caused by local rain or river overflow (Silva et al. 2003). Owing to its dimensions, the Pantanal is considered the largest continuous floodplain of inland waters (Silva and Abdon 1998). This plain is located in the Upper Paraguay River Basin (UPRB), in the Brazilian Central-West region, in the centre of South America, most of the area laying in Brazil, and smaller parts in Bolivia and Paraguay (Silva et al. 2003).

Several studies dealt with the delimitation of the Pantanal in Brazil, standing out Silva and Abdon (1998), who mapped the UPRB (361,666 km²) and the Pantanal floodplain (138,183 km²) considering the aspects of floods, relief, soils, and vegetation (Fig. 2.1). However, IBGE (2004) delimited the Pantanal as a biome (150,335 km²), a divergence arisen from different conceptual criteria, field observations, and the adopted scale. The term “biome” is considered by the governmental

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